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PHYTOPLANKTON

Functional groups of phytoplankton shaping diversity of shallow lake ecosystems

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Abstract Phytoplankton of eutrophic shallow lakes are frequently dominated by one species or species of the same functional group, resulting in species-pure algal assemblages. Knowledge of the structure of these assemblages is essential to understand their functioning; therefore, species and functional diversity were investigated in five sub-types of eutrophic shallow lake. Among the sub-types, astatic saline lakes and hypertrophic ponds had type-specific assemblages dominated by S_N and W0, W1 codons. The diversity of the phytoplankton in the sub-types was quite similar, except for the astatic saline lakes, which were characterised by lower values of both functional and species diversity. We found that both functional and species diversity were low when bloom-forming cyanobacteria (H1, S_N functional groups) became dominant. Dominance of other groups (J, Y, L_O and W1) did not coincide with decrease in species diversity. Analysis of the biovolume versus diversity relationships revealed that decrease in diversity might be expected at biovolume >20 mm^3 l^{-1} for shallow lakes.

Keywords Shallow lakes · Algal assemblages · Species diversity · Functional diversity

Introduction

Due to geomorphology and climatic conditions, there are no oligotrophic deep lakes in the lowland area of the Carpathian Basin. In this region, eutrophic shallow lakes are typical. As a result of scientific achievements in recent years, much has been learned about the operation of these systems (Scheffer, 1998). A key result in shallow lake ecology is that such ecosystems have two alternative stable equilibria, e.g. macrophyte-dominated versus turbid state (Scheffer et al., 1993). This helps to understand the operation of the systems and provides theoretical background for lake restoration (Drenner & Hambright, 2002). It is now recognised that various alternative regimes might exist depending on lake depth and size, climate or nutrients (Scheffer & Carpenter, 2003; Scheffer & Van Nes, 2007). Krasznai et al. (2010) demonstrated that macrophyte dominance in shallow oxbow lakes does not necessarily result in clear water state, because dense

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algal populations can develop in the small pools among the macrophytes.

The phytoplankton diversity of eutrophic lakes is usually lower than that of oligotrophic lakes (Moss, 1973). Nevertheless it was shown that those shallow lakes which have high habitat diversity have exceptionally rich algal flora (Borics et al., 2003). Experimental studies demonstrated that functional diversity may be a stronger determinant of ecosystem processes than species diversity (Hooper & Vitousek, 1997; Huston, 1997; Tilman et al., 1997; Wardle, 1999); therefore, investigation of the functional diversity of phytoplankton of shallow lakes is important to understand the operation of these systems. There are several ways of measuring functional diversity (Petchey & Gaston, 2006). One of these approaches is to gather species into functional groups, for which diversity metrics are calculated (Hadar et al., 1999). In phytoplankton ecology, use of functional groups can be traced back to the early 1980s. Reynolds (1980) identified 14 algal groups from analysis of the seasonal periodicity of lake phytoplankton. This system was upgraded and supplemented with other groups that share similar morphological and physiological features (Reynolds et al., 2002; Borics et al., 2007; Várbíró et al., 2007; Padisák et al., 2009); more than 30 functional groups were proposed in these studies, and their ecological traits were also outlined. The functional group concept became an increasingly popular approach in phytoplankton ecology, being used both in theoretical studies (Padisák et al., 2003, Salmaso & Padisák, 2007; Várbíró et al., 2007) and in applied hydrobiology, such as for water quality assessment (Padisák et al., 2006; Borics et al., 2007). Nevertheless, the diversity of functional groups has never been studied in shallow lake ecosystems.

Several papers have been published on the composition and species diversity of phytoplankton of eutrophic shallow lakes in the Carpathian Basin, but these studies usually report diversity in a single lake. Eutrophic shallow lakes include various types of water body that differ from each other in terms of alkalinity, macrophyte coverage, hydrology etc. These differences should also appear in the composition and diversity of phytoplankton.

In temperate eutrophic systems, transition of functional groups is expected during the phytoplankton succession C-G-M-P (Reynolds et al., 2002). Nevertheless, it is reasonable to suppose that other groups can also be dominant in the various sub-types of shallow lake. In Hungary, 17 sub-types of shallow lake exist, based on depth, size, macrophyte coverage, lakebed material and alkalinity (Szilágyi et al., 2008). This system can be considered as a mechanistic typology and not an operational one. Some types are represented by single lakes (Balaton, Neusiedler See, Lake Velence), whereas some of the other types are quite similar to each other. Validation of these sub-types based on biological elements demonstrated that several sub-types can be merged; therefore, the number of sub-types is <17, being 5–8 depending on the biological elements considered (Borics et al., 2009). According to these findings, five lake sub-types were defined based on hydrology, water depth, conductivity and macrophyte coverage (Table 1). These criteria have substantial influence on the composition of phytoplankton assemblages. Sub-type 1 includes the relatively deep oxbow lakes; these

Table 1 Sub-types of lakes with the hydrological, morphological, physical and biological criteria used for typological assignment

Code	1	2	3	4	5
Name of the types	Oxbows	Macrophyte-dominated lakes	Hypertrophic lakes	Open water lakes	Alkaline saline lakes
Hydrology	Perennial	Perennial	Perennial	Perennial	Astatic
Average depth (m)	<3	<3	<3	<3	<1
Max. depth (m)	10	3	3	3	1.5
Conductivity (μS cm^{-1})	400–800	400–800	400–900	400–900	>2,000
Macrophyte coverage (%)	5–20	>50	<5	5–20	0–10
Number of lakes	11	12	3	16	3
Number of samples	92	125	45	179	9

lakes can be stratified by growing season. Lakes in sub-types 2, 3 and 4 are identical in terms of hydromorphology, but differ in macrophyte coverage and fishing activity. In sub-type 5, very high-alkalinity astatic saline lakes, which are specific to the Carpathian Basin, are grouped (Felföldi et al., 2009). It seems reasonable to suppose that differences in the characteristics of the proposed sub-types will manifest themselves in the phytoplankton composition and diversity.

Comparative analysis of phytoplankton regarding composition and diversity has not been carried out for the possible sub-types of shallow lake in the Carpathian Basin. After compiling a large phytoplankton database for eutrophic shallow lakes, the dominance of the functional groups of algae in the various sub-types of lakes and the characteristics of the dominance–diversity relationships were studied.

To address these issues, we tested the following hypotheses:

- Despite their similar trophic state, sub-types of eutrophic lakes can be characterised by different dominant algal assemblages;
- Functional and species diversity of the phytoplankton depend on the lake sub-type;
- Besides the characteristic bloom-forming algae, other groups can also dominate the phytoplankton;
- Functional groups shape the diversity of the algal assemblages in a different way;
- Decreasing diversity is related to increasing algal biovolume.

Materials and methods

Database

Phytoplankton data were provided by the Hungarian National Monitoring System. Data for 26 lakes (294 samples, taken between 1993 and 2010) were inputted into a database. Monthly samples were taken by tube sampler from the trophic layer of the lakes in the growing season. In case of shallow lakes with maximum depth ($D_{\max}$) less than 2 m, the whole water column was sampled. For algal counting, the Utermöhl (1958) technique was used. Phytoplankton biovolumes were calculated according to Hillebrand et al. (1999).

Diversity

Both species and functional diversity were calculated by the Shannon index of diversity (Shannon, 1948). Assignment of a species to a functional group was based on Reynolds et al. (2002), Borics et al. (2007) and Padisák et al. (2009). Functional diversity was defined as the biovolume-based diversity (H) of the functional groups in the sample. Functional groups making at least 80% contribution to total biovolume were considered as dominant.

Statistical analyses

One-way analysis of variance (ANOVA) was used to compare diversity among the five sub-types. During exploratory data analyses, line plots, scatterplots, LOWESS curves (Cleveland, 1979) and principal component biplot (PCA) were used to extract the functional groups associated with the lake sub-types.

Functional group–functional diversity relationships

The relationships between the diversity of the functional groups and the relative abundance of a given functional group were also investigated using a simple model (Fig. 1). This model can be applied to functional group/functional diversity and functional group/species diversity investigations. The grey field indicates the possible range within which diversity values may vary. The maximum diversity occurs in that state where all the elements are equal; i.e. $H_{\max}$ is at $p_a = p_b = \cdots = p_z = 1/Z$, where p_i is the relative abundance of the ith functional group (or species) and Z is the number of functional groups (or species). The upper boundary of the grey area indicates the actual maxima ($H_{\max}$) of the diversity at a given abundance of the investigated functional group. The lower arch of the graph indicates the $Z = 2$ situation ($H_{\min}$) at different relative abundance of the elements.

Functional group–species diversity relationships

Functional groups contain different numbers of species. There are only two species in the S_N functional

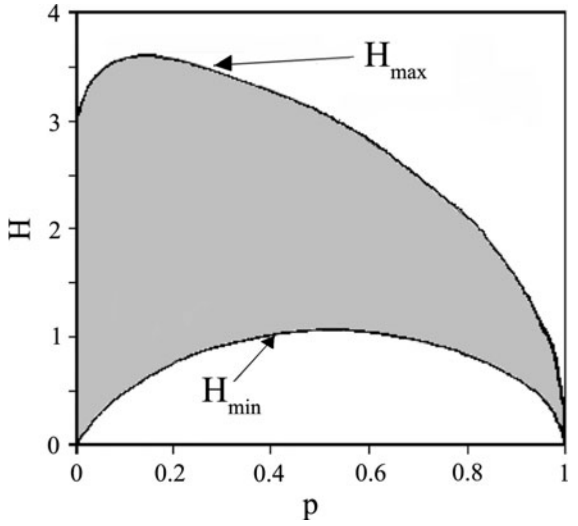


Fig. 1 Relationship between the relative abundance of a functional group and the diversity (*H*) of the assemblage. The *grey area* indicates the range in which diversity values may vary depending on the relative abundance of a functional group

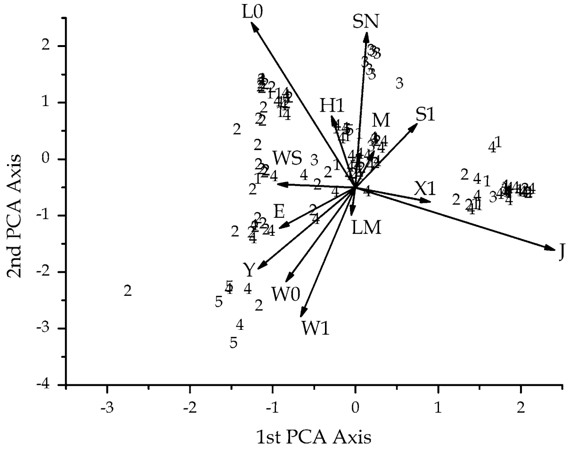


Fig. 2 PCA biplots of the lake sub-types and the functional groups of algae. Numbers encode the lake sub-types (Table 1)

group, while there are more than 100 species in the J functional group. Therefore, when the impact of a given functional group on species diversity was analysed, those species that belong to this functional group were deleted from the database and diversity was calculated for the rest of the species. This procedure was repeated as many times as there were functional groups. Species diversity calculated in this way is called "residual species diversity" (RSD) herein. When the relationships between functional groups and species diversity were analysed, the relative biomass abundance of the given functional group was considered as independent and the RSD values as dependent variables. The analyses were performed at sample level.

Results

Characteristic functional groups of the lake sub-types

The oxbows (1) and macrophyte-dominated lakes (2) were mostly characterised by the motile species groups (Lo, WS, Y and E) (Fig. 2). The hypertrophic lakes (3) were clearly separated by the principal component analysis. These lakes were frequently dominated by *Cylindrospermopsis raciborskii* (S_N). The open water lakes (4) could not be characterised by a certain group of algae. In this sub-type, phytoplankton was occasionally dominated by J, Lo, Y, S1 and E functional groups. The astatic saline lakes (5) were dominated by the elements of the W0 and W1 (euglenophytes) functional groups.

Phytoplankton diversity in the lake sub-types

One-way ANOVA indicated significant difference in both species ($F[4; 636] = 4.81$; $P < 0.005$) and functional diversity ($F[4; 635] = 3.07$; $P < 0.005$) among the lake sub-types (Fig. 3). In sub-types 1–4 both the median and range of the data were almost identical. The median values ranged from $H = 1.8$ to 2.1 for species and from 1.3 to 1.4 for functional diversity. The exception was the sub-type of astatic saline lakes, in which the lake phytoplankton was characterised by lower species and functional diversity.

Dominant functional groups

Based on the relative frequency of functional groups, 16 groups proved to be dominant (Fig. 4). In terms of absolute biovolume, there was five orders of magnitude difference among the dominant groups. Dominance of D (centric diatoms), U (*Uroglena* spp.), E (*Dinobryon* spp.), W1 (*Euglena* spp.) and X1, X2 (small-celled flagellates) was exceptionally rare. Nevertheless, in the higher biovolume range (biovolume $> \sim 20$ mm^3 l^{-1}) only bloom-forming cyanobacteria

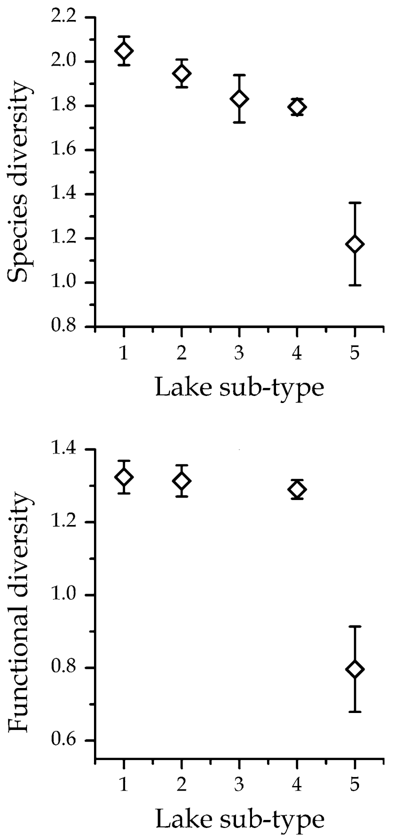


Fig. 3 Distribution of species and functional diversity values in the five investigated lake sub-types

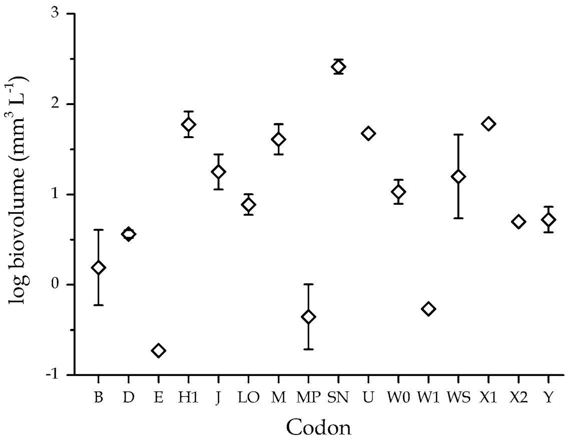


Fig. 4 Characteristic ranges of biovolume where the different functional groups occurred as dominant (relative biovolume abundance >80%)

(H1, S_N and M groups), *Synura* spp. (WS), chlorococcaleans (J) and dinoflagellates (Lo) were capable of developing dominant assemblages.

Functional group–functional diversity relationships

First, relationships between functional groups and functional diversity were investigated (Fig. 5). Scatterplots of the functional groups were similar. In most of the cases (D, J, Y, Lo, MP), the scatterplots of the data were identical to that of the theoretical model; that is, the maximum values of diversity occurred at about 0.1 relative abundance. Different distribution characterised the S_N, M and H1 functional groups, the most frequently occurring cyanobacteria. The maximum diversity values occurred when the abundance of these groups was zero. Minimal occurrence of these groups resulted in a steep decrease in the functional diversity. At higher abundance ranges, all the functional group–functional diversity relationships were characterised by a similar distribution pattern.

Functional group–species diversity relationships

In most cases, the impact of functional groups on the RSD was negligible (Fig. 6). High RSD values could be observed even in case of high relative abundance (>0.9) of the functional groups. A different pattern characterised the H1 and especially the S_N groups. At higher relative abundance of these groups, the RSD showed a decreasing tendency. The Lo and S_N functional groups showed the most characteristic type of functional group versus RSD relationship (e.g. no relationship and decreasing tendency). Fitting a LOWESS curve to the plots of these groups (Fig. 7), it seems clear that the RSD is independent of the relative abundance of the Lo group, but in case of the S_N group, a pronounced decline started from relative abundance of 0.5.

Biovolume–diversity relationships

Both functional and species diversity values showed hump-shaped, right-skewed curves on a logarithmic biovolume scale (plots not shown). Diversity values were highly scattered, even in the high ($>50\ \mathrm{mm}^3\ \mathrm{l}^{-1}$) biovolume range. The LOWESS curves indicated that, for biovolume $>20\ \mathrm{mm}^3\ \mathrm{l}^{-1}$, a sharp decline in diversity might be expected in terms of both functional and species diversity.

Fig. 5 Impact of the functional groups of algae on functional diversity

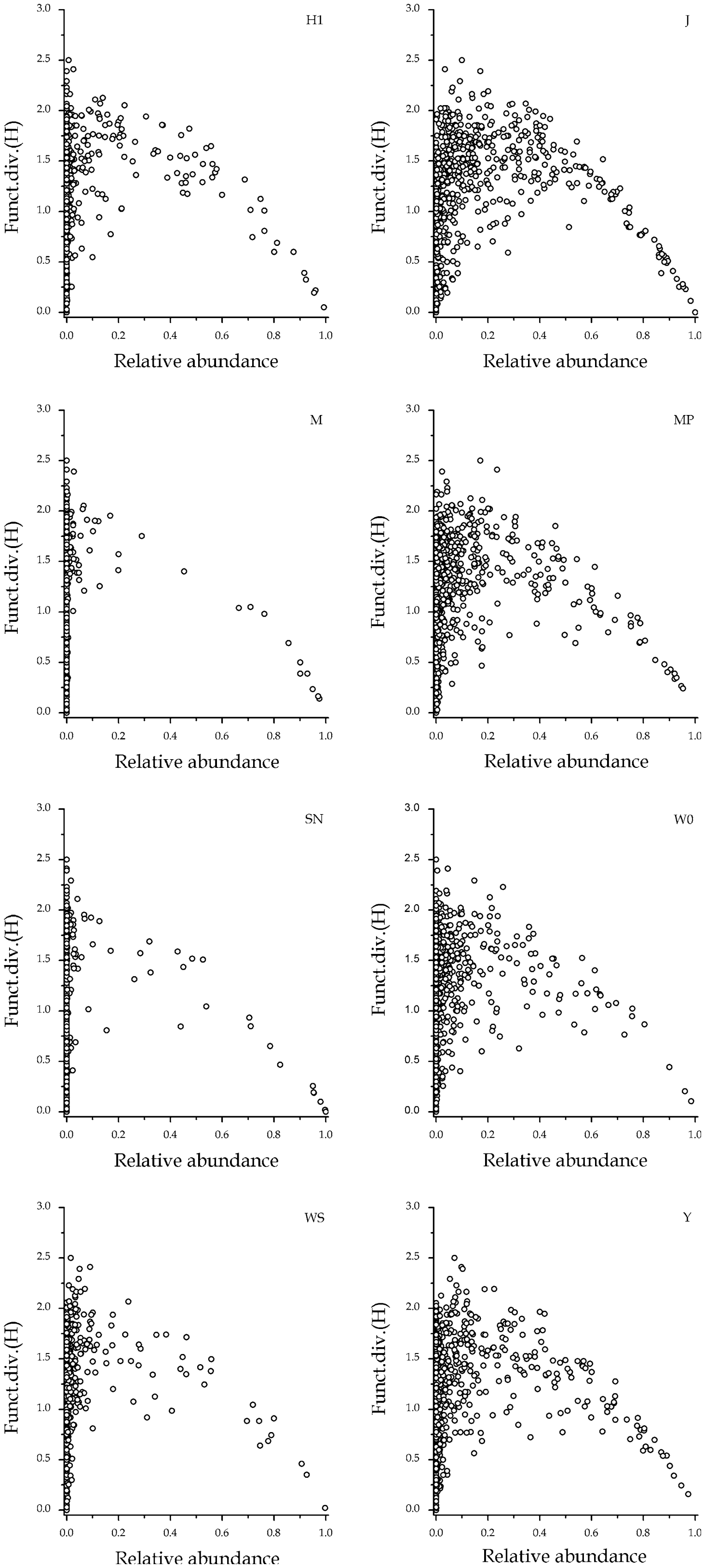
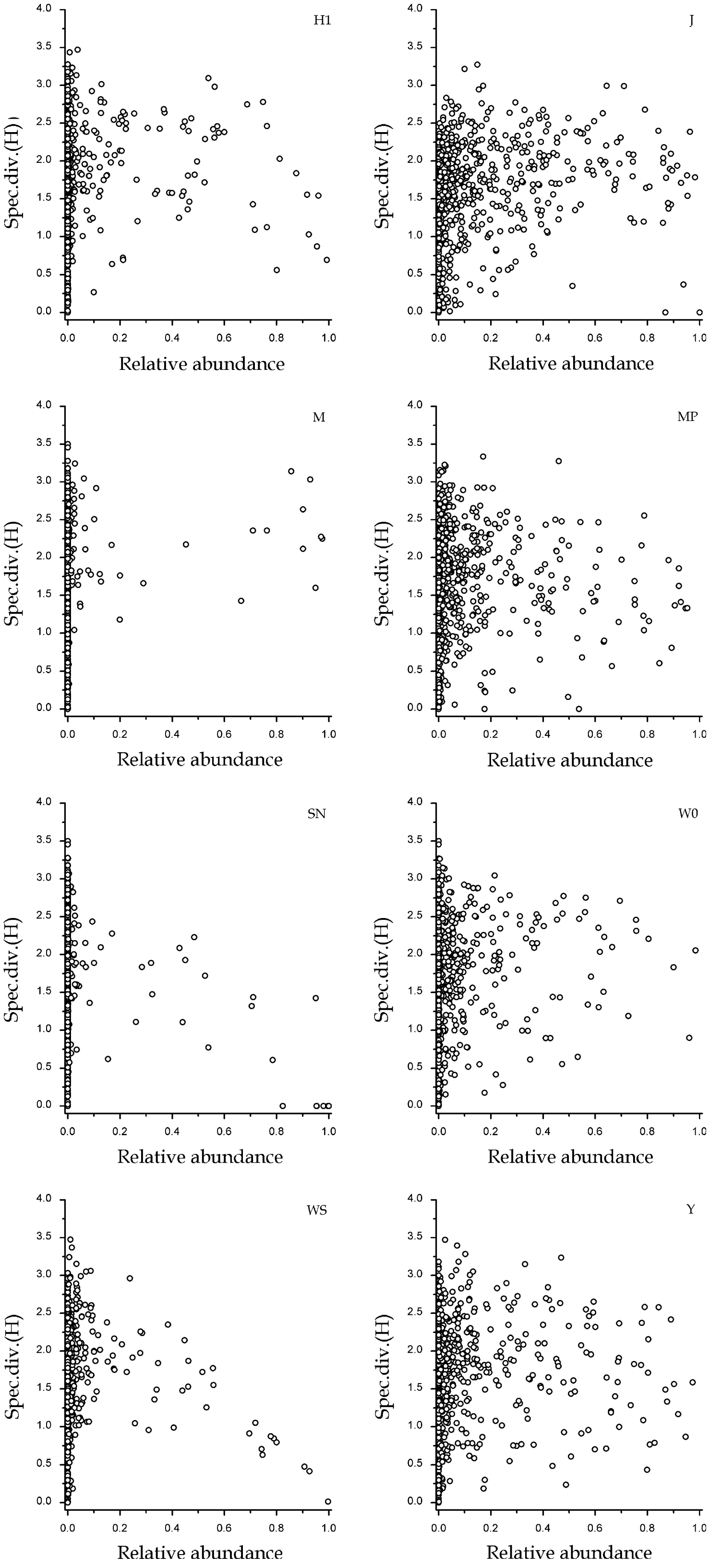


Fig. 6 Impact of the functional groups of algae on the residual species diversity (RSD) (where species belonging to the functional group used as the independent variable were not considered in the diversity calculation)



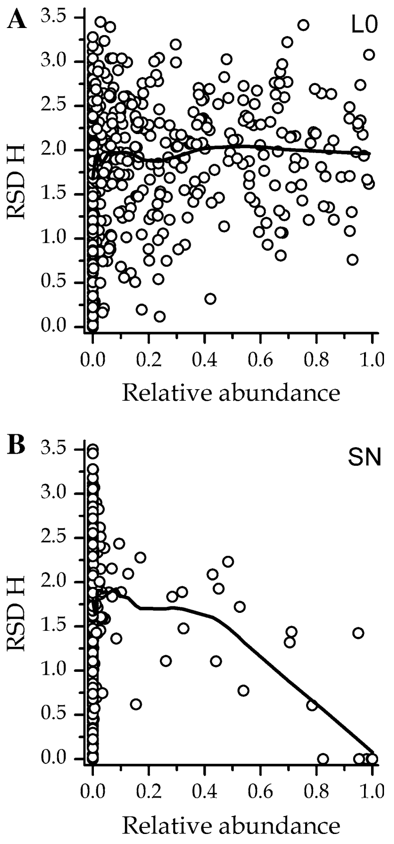


Fig. 7 LOWESS curves fitted to the plots of L_O—residual species diversity (**A**) and S_N—residual species diversity (**B**) relationships. These two functional groups showed the most characteristic type of functional group–RSD relationship (i.e. no impact and strong negative impact)

Discussion

We demonstrated that the composition of phytoplankton in the sub-types differ from each other. The taxonomic composition of the astatic saline lakes was remarkably different from the others. In these lakes, elements of the W0 (*Euglena* spp., which prefer polysaprobic conditions) and W1 (*Phacus* and *Lepocinclis* spp.) groups were dominant. Due to high concentration of organic compounds, these waters favour development of euglenophytes blooms. It is also known that these lakes are frequently dominated by photoautotrophic picoplankton as a result of serious light limitation (Felföldi et al., 2009). Phytoplankton of hypertrophic lakes was also remarkably different from the others. S_N dominance in this sub-type is not unusual (Borics et al., 2000) and causes serious blooms in other lakes in this region (Padisák & Reynolds, 1998). Success of this species is attributed to tolerance of self-shading and production of large numbers of akinetes. In the shallow hypertrophic lakes, the reactive phosphorus concentration is high and the temperature fluctuation in the early autumn period can be significant. These characteristics contribute to the development of the highest akinete concentration in case of *C. raciborskii* (Moore et al., 2005). The phytoplankton of the oxbows had much in common with that of the macrophyte-dominated lakes, partly because of different reasons, although motile taxa prevailed in both habitats. The oxbows are a specific type of water body which is wind sheltered, therefore being characterised by stable stratification. Investigating the temperature and oxygen profile of a sheltered oxbow, Borics et al. (2011) demonstrated that in summer period the mixing layer depth is only 2 m. In these lakes, non-motile organisms easily sink down from the photic layer; therefore, motility is one of the most important functional traits of species inhabiting oxbows (Krasznai et al., 2009). There are several mechanisms by which macrophytes exert impact on the planktonic food web. Macrophytes reduce light penetration, can produce allelopathic substances (Hasler and Jones, 1949; Körner and Nicklisch, 2002), increase the sedimentation rate (Van den Berg et al., 1997) and provide habitat for grazers (Jeppesen et al., 1997). Due to these mechanisms, macrophytes have a clear effect on the structure of phytoplankton communities (Jasser, 1995; Søndergaard & Moss, 1998; Van Donk & Van de Bund, 2002). In the presence of macrophytes, dominance of flagellated algae, e.g. *Chalmydomonas* spp., *Cryptomonas* spp. euglenophytes and dinoflagellates, is expected (Borics et al., 2003; Krasznai et al., 2010; Schriver et al., 1995; Van den Berg et al., 1997). In the well-mixed open water lakes, the chlorococcalean green algae (J) were the most characteristic phytoplankton elements. These algae frequently dominate the phytoplankton of shallow enriched ponds (Reynolds et al., 2002).

The phytoplankton diversity (*H*) of the lakes varies between 0 and 4.5 bits, but typically is in the range of 2.4–2.6 (Harris, 1986). The value of the biomass-based diversity (*H*) ranged between 1 and 2.5 bits in case of eutrophic Danish lakes (Jeppesen et al., 2000), but higher values characterise oligotrophic systems (Margalef, 1980). Weithoff (2003) showed that, in the oligotrophic Lake Constance, the average phytoplankton diversity is approximately 3 bits and occasionally can be higher than 4. Besides the trophic state, diversity is influenced by other factors such as lake size, lake depth (Jeppesen et al., 2000), fish stock (Romo & Villena, 2005) or macrophytes (Declerck et al., 2007); therefore, we supposed that diversity is significantly different among the sub-types of shallow lakes. An unexpected result of this study is that, despite differences in the taxonomic composition and functioning of the lake sub-types, the diversity values were surprisingly similar. The lakes had high-diversity phytoplankton even in hypertrophic conditions (median values of H were within the range of 1.8–2.2). This can be explained by the high number of species with similar habitat template in naturally eutrophic water bodies (Reynolds, 1998). A common characteristic of these taxa is that they are evolutionarily adapted to elevated nutrient concentration. In case of the astatic saline lakes, low diversity can be explained by the astatic character and the extremely high salt concentration. These factors select the most tolerant euryhaline taxa such as euglenophytes (Caljon, 1987) and unique prokaryotic picocyanobacteria (Felföldi et al., 2009).

The fact that differences in diversity could not be found among the sub-types means that diversity is not a suitable metric for quality estimation in case of shallow eutrophic lakes.

The high number of functional groups that occurred as dominants was really surprising. It is known that lakes are frequently dominated by a few species or a certain functional group of algae in the late successional state, being called equilibrium (Sommer et al., 1993) or steady-state assemblages (Naselli-Flores et al., 2003). In shallow eutrophic systems, temperature and light availability are the most important factors driving development of phytoplankton assemblages. Usually, C, J, G, S1, H1, H2 and S_N assemblages are expected to be dominant in the growing season. Besides these, ten other groups proved to be dominant in the investigated lakes. There are several biotic and abiotic mechanisms that might result in steady-state assemblages (Rojo & Álvarez-Cobelas, 2003), among which competitive exclusion (Hardin, 1960) is the most important. Nevertheless, the overwhelming dominance of a few species does not necessarily mean that phytoplankton is in an equilibrium state. Short-term dominance can especially apply for those functional groups that dominate the first stage of phytoplankton succession (B, D, E) (Padisák et al., 2003), or for the mostly metaphytic W0, W1 groups, which can be protagonists in macrophyte-dominated lakes. In these habitats, benthic grazers could select small-celled taxa and help the dominance of large-sized species. In this case "the dominant species are not the best, but rather the remainder" (Rojo & Álvarez-Cobelas, 2003).

In parallel with the increasing dominance of any element of the assemblage, decreased diversity is expected. This tendency was quite obvious in case of the functional diversity, but was not observed in case of the RSD. In most functional groups, higher relative biovolume abundance did not coincide with lower RSD. This means that the dominant groups did not necessarily outcompete the other elements of the phytoplankton. In these cases, dominance of these groups (L_O, Y, W0, J, W_S) can be traced back to other biotic and abiotic reasons (Rojo & Álvarez-Cobelas, 2003). Dominance of motile taxa (L_O, Y, W0) is expected for stable stratification, or when nutrients are spatially segregated (Reynolds et al., 2002).

A characteristic decrease in RSD occurred exclusively in case of the dominance of S1 and especially S_N groups. Species in both groups are elongated, and this morphological adaptation makes them better photoadaptable light antennae (Reynolds, 1998); therefore, they are strong light competitors (Reynolds, 2006). It seems that only these strong light competitors exert impact on the diversity of the phytoplankton. When reasons other than light competition are responsible for the dominance of a certain functional group [species-specific abilities, e.g. mixotrophy or buoyancy regulation (Naselli-Flores et al., 2003)], the RSD of the other elements does not decrease. Although *Microcystis* spp. are also bloom-forming taxa and can dominate in late summer, these are not good light competitors, being instead rather sensitive to low light availability. Therefore, during the dominance of M functional group there was no reduction in RSD.

We found that minimal occurrence of the H1, M and S_N functional groups indicated loss of functional diversity. This means that, when functional diversity reaches its maximum, the system does not contain bloom-forming cyanobacteria at all. The presence of strong light competitors (H1 and S_N) indicates that light limitation drives the phytoplankton succession (Reynolds, 2006) and, if disturbances do not occur, results in low-diversity assemblages.

A unimodal relationship between productivity and diversity is quite common in both aquatic (Dodson et al., 2000) and terrestrial systems (Grime, 1973). The fact that increasing productivity coincides with an increase in diversity in the low and medium productivity range is well known (Abrams, 1995; Jeppesen et al., 2000). The descending arm of the curve in the higher productivity range has been explained by competition (Richman & Dodson, 1983), predation (Leibold, 1999) or abiotic factors (Jones et al., 1983). The hump-shaped distribution of the data in case of both species and functional diversity is in accordance with the previous findings. The unexpected result of this investigation is that the decreasing tendency revealed by the LOWESS curve appeared in a very high biovolume range ($20\ \mathrm{mm}^3\ \mathrm{l}^{-1}$). This concentration range corresponds to poor ecological quality based on the boundaries set for very shallow German hardwater lakes (Mischke et al., 2002), which are quite similar to the Hungarian lakes. Despite the decline of the curve, biovolume seems to be a poor predictor of diversity, meaning that the productivity–diversity relationship cannot be interpreted as indicating that productivity drives diversity (Gross & Cardinale, 2007). This kind of relationship can be observed exclusively in the extremely high biovolume range (Borics et al., 2000). These findings also support the view that diversity metrics do not work well in ecological state assessment.

Conclusions

1. Among shallow lakes, only hypertrophic lakes (sub-type 3) and astatic saline lakes (sub-type 5) had distinctive phytoplankton assemblage (Fig. 2).
2. Neither the functional nor species diversity showed differences among the lake sub-types (Fig. 3). Only alkaline saline lakes were less diverse than the others.
3. Besides the well-known bloom-forming groups (H1, S1, S_N, M, J), several other functional groups appeared as dominant (Fig. 4). The dominance of the functional groups developed in the extremely high range of biovolume (0.005–$500\ \mathrm{mm}^3\ \mathrm{l}^{-1}$).
4. The functional groups shaped the diversity in various ways (Fig. 5). Dominance of bloom-forming cyanobacteria reduced both functional and species diversity. When other groups dominated, the phytoplankton species diversity did not necessarily decrease (Fig. 6). The presence of bloom-forming cyanobacteria (even at low abundance) indicated loss in functional diversity.
5. Several groups can be dominant and produce high-biovolume assemblages, but they exert impact on the diversity only in the high biovolume range.

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