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Small-scale patchiness of the phytoplankton in a lentic oxbow

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Horizontal sampling within a lentic oxbow demonstrated the uneven distribution of algae at both large and small scales. An index of heterogeneity is proposed to characterize the fine-scale horizontal patchiness, which is defined as the ratio of the coefficient of variation among samples and the error in counting the algae. Applying a vertical grid sampling strategy, a distinct patchy distribution of several algal species was observed. Most of the patches were formed by those species that have good buoyancy-regulating mechanisms (blue–green algae, dinoflagellates). Atelomixis caused by surface cooling may be the explanation of the heterogeneity. We have shown that the anisotropic horizontal distribution of the phytoplankton could cause high uncertainty in lake quality assessment. Therefore, to improve accuracy composite sampling is needed.

KEYWORDS: algae; stratification; horizontal and vertical distribution; quality assessment

INTRODUCTION

New techniques such as detection of *in vivo* fluorescence of chlorophyll *a* using submersible fluorometers or the analysis of data from satellite-borne optical sensors have provided strong evidence that horizontal distribution of phytoplankton is not homogeneous in aquatic systems. This heterogeneity exists at a scale from a few centimetres to hundreds of kilometres. Lateral stirring with mixing events (Abbott *et al.*, 1980), local upwellings (Salonen *et al.*, 1999) or surface drifts (Wu *et al.*, 2010) can also be responsible for patch generation in large lakes and in estuaries (Lucas *et al.*, 1999). Irish and Clarke (Irish and Clarke, 1984) showed that in small water bodies, differences in the horizontal distribution of larger, buoyancy-regulating algae can be expected. Besides the field observations modelling approaches like the KISS theory (Kierstead and Slobodkin, 1953), 3-D computational fluid dynamics models (Hedger *et al.*, 1999) and flow field modelling (Schernewski *et al.*, 2005) help us understand the role of physical processes in the development of the uneven distribution of planktonic organisms.

Measurement of photosynthetic pigments is an easy and quick way to estimate phytoplankton biomass, but does not yield any information on the local dispersal of the different groups of algae. The study of the horizontal distribution of the various algal groups requires the microscopic investigation of large numbers of plankton samples. The other problem is that the accuracy of the traditional counting methods in most investigations is not sufficient to reveal differences in distribution of planktonic groups. Counting of 400 units with 10%

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accuracy can be achieved (Lund *et al.*, 1958), but this accuracy refers to the total number of algae. The counting error of the less abundant taxa is much higher. Thus, the differences observed for the rare taxa may not be realistic, just sampling artefacts produced by the investigator. Therefore, there is a high uncertainty as to whether, and to what extent uneven distributions of planktonic algae occur. Knowledge of the properties of the small-scale patchiness of algae can be important both from theoretical and practical points of view.

Most of the oxbows in the Carpathian Basin are well sheltered and can be stratified stably in the growing season (Grigorszky *et al.*, 2000, 2003; Teszárné Nagy *et al.*, 2003). Therefore, oxbows are good subjects for investigations which focus on the small-scale spatial distribution of planktonic algae, especially in calm and hot midsummer weather conditions which favour the development of small convection cells in the water and patch formation generated by algal mobility.

The primary purpose of this paper is to characterize the horizontal distribution of algae in a lentic oxbow, in a period of the year when stable weather conditions maximize heterogeneity in the phytoplankton. Additionally, we aimed to explain the observed pattern.

We hypothesized that horizontal differences in the phytoplankton distribution (i) develop between the macrophyte dominated and open water sites, (ii) do not exist among the open water sites and (iii) do not exist at the fine scale (less than 1 m).

These hypotheses were tested by detailed investigation of the horizontal and vertical distribution of algae. In particular, we seek to answer the following questions:

- Are there any differences in the horizontal distribution of algae along the longitudinal axis of the oxbow?
- How can the heterogeneity be characterized numerically?
- Which taxa, and to what extent are responsible for the heterogeneity?
- Do the differences exist at fine scale (1 m)?
- Which mechanisms are responsible for the development of algal patches?
- To what extent can the horizontal patchiness influence the results of quality assessment?

METHOD

Oxbow studied

The Tiszadob oxbow (longitude: 21.1974, latitude: 48.0163) is one of the largest oxbows of the Tisza valley (Carpathian basin), situated in the middle section of the river. The 11 km long oxbow is separated by embankments into five sections (Fig. 1). The longest section is called Malom-Tisza (length: 4.6 km, mean depth: 3 m, max. depth: 12 m). A considerable part of this oxbow is a typical pelagic ecosystem, but at the eastern, shallow part of the oxbow the littoral macrovegetation extends over almost the entire basin. Floating islands of different shape are formed by emergent plants (*Typha latipholia* L.) and the marsh fern (*Thelypteris palustris* L.). Among the islands, various growth forms of submerged and floating-leaved macrophytes cover the basin with small pools of open water. As for most of the other oxbows along the Tisza-valley, the Malom-Tisza is a well sheltered, eutrophic oxbow (Krasznai *et al.*, 2010), and characteristic physical and chemical variables are shown in Table I.

Sampling design

To reduce the wind-induced mixing, the sampling was in the middle of a consistent time period of a stable high pressure on 23 July 2007.

For mapping the horizontal distribution of the phytoplankton, 11 sample sites were selected along the longitudinal axis of the oxbow (Fig. 1). Using a tube sampler (length 2.5 m, diameter 0.06 m), three independent column samples were collected from the euphotic layer at each sample site in the vertices of a triangle with 1 m side length. The resulting 33 samples were preserved in acid Lugol's solution.

To investigate the distribution of algae at smaller scale, a vertical grid sampling scheme was also implemented. Samples were collected along a transect in the middle part of the oxbow at site no. 8 perpendicular to the shoreline (Fig. 1). The length of the transect was 90 m, and the samples were taken at 15 m intervals. The sampling device was a hard plastic tube-sampler (length: 5 m, built from two 2.5 m long sections; diameter: 0.03 ms). The sampler has a bottom stopper and equipped with side valves at 0.25 ms intervals. To obtain the water samples from the different layers, the tube (with open bottom stopper and with closed side ports) was lowered vertically into water. After reaching the required depth the bottom stopper was closed, and the tube was slowly removed. When a side valve came above the water surface, it was opened and the sample (0.25 m water column) was poured into 250 mL glass bottles. Altogether, 69 samples were collected from the vertical grid. Phytoplankton samples were kept in these bottles and preserved immediately after sampling. This technique enabled us to sample algae on a fine vertical scale. In this case, the whole

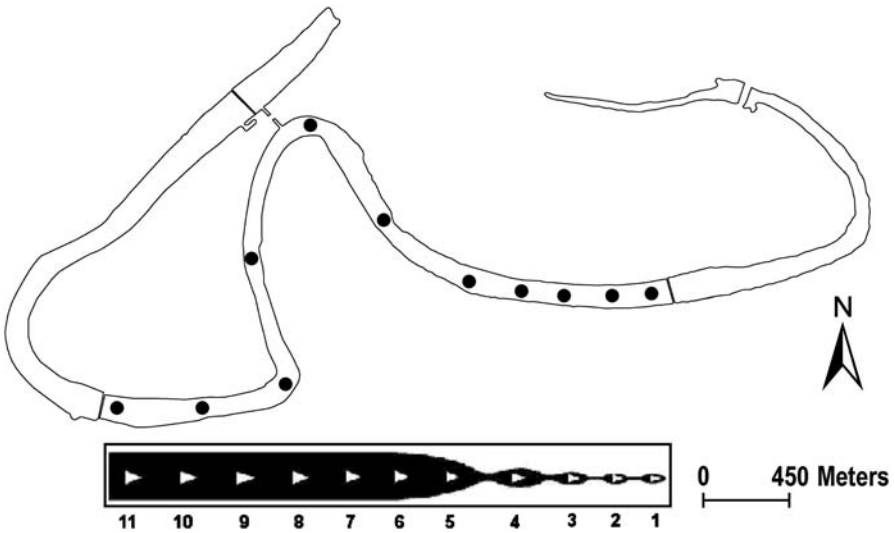

Fig. 1. Oxbow area map with the sampling sites (above) and the schematic view of the oxbow, illustrating the ratio of the open water (black) and the macrophyte covered regions (white).

Table I: Relevant physical and chemical variables of the oxbow.

Variables	Mean	Minimum	Maximum
pH	7.93	7.85	8.04
Conductivity ($\mu S\ cm^{-1}$)	332	323	345
DO (mM)	2523	2518.68	2528.62
BOD (mM)	2513.5	2511.56	2516.56
SRP (μM)	0.74	0.50	1.12
DIN (μM)	18.51	11.57	27.78
NH4-N (μM)	8.43	4.07	15
NO2-N (μM)	0.60	0.57	0.64
NO3-N (μM)	9.48	6.92	12.14
Chl *a* ($\mu g\ L^{-1}$)	15	4	25

Monthly samples from the photic layer were taken at site 7, from May to October in 2007. Data were provided by the Hungarian National Monitoring System.

water column was sampled. To avoid disturbing the bottom sediment, depth of the water was measured by a fish sonar (Humminbird 350tx) at each sample site. Samples taken with a 2-L Ruttner sampler were used to describe the vertical temperature and oxygen profile at site 8. Samples were collected from surface to bottom at intervals of 1 m.

Sample preparation

Phytoplankton samples were left to settle in 5 mL settling chambers for 48 h, and examined with a Leica DMIL inverted bright-field microscope. To estimate the number of the larger forms (>40 μm), the whole area of the chamber was investigated at a magnification of 10×20. To estimate the relative abundance of the smaller algae, a minimum of 400 settled units (cells, filaments or colonies) were counted in each sample at a magnification of 10×63. Using this magnification, three transects of the counting chamber were investigated to give the total number of smaller species.

Counting uncertainty was estimated by five repeated investigation of a randomly selected sample. The variability was expressed by the coefficient of variation (CV) for each species.

Statistical methods

The ESRI ArcMap Spatial Analyst program was used to illustrate the distribution of the selected algal taxa in the vertical profile of the oxbow. Data were smoothed by regularized spline interpolation with the parameters of weight = 1 and points = 8. Similarity of the samples was displayed by hierarchical cluster analysis using the MSSQ fusion algorithm based on Bray–Curtis dissimilarity (Legendre and Legendre, 1998). The R environment for statistical computing and graphics (R Development Core Team, 2010) was used for the calculations.

Numerical characterization of heterogeneity

A simple graphical display of the taxon numbers or biomass values is an illustrative approach, but can be misleading, especially in case of species with low relative abundance. Therefore, an index of heterogeneity (IH) was adopted for each taxon as follows: IH = CVs/CVe,

where CVs is the coefficient of variation of the algal counts among the column samples and CVe is the algal counting error. CVe was estimated by repeated counting on five counting chambers of 5 mL which were filled with one of the phytoplankton samples. The whole area of the chambers was screened during the counting; to minimize the counting error, only the large-size taxa were counted. Usually, we counted ~500 specimens in the chambers. Based on the five repeated counts, the CV and means of the relative frequency of the enumerated taxa were calculated. The CV values of the taxa were plotted against the means of relative frequencies and a regression equation was fitted. For the small-sized taxa, we estimated the CVe using this regression equation. We used the following equation: $CVe = 43.221\ x^{-0.5102}$, where x is the relative frequency of the taxon ($R^2 = 0.9683$). Both the large-sized and the small-sized taxa are randomly distributed in the counting chamber, thus their CVe can be estimated by this regression equation. This relationship between CVe and the mean relative frequency is an analogue of Taylor's power law (Taylor and Taylor, 1977).

RESULTS

Heterogeneity at the oxbow scale

The oxbow was characterized by a hypertrophic phytoplankton assemblage dominated by filamentous blue greens (*Limnothrix redekei*, *Pseudanabaena limnetica*, *Romeria leopoliensis*) and dinoflagellates (*Peridinium gatunense*, *Peridiniopsis elpatiewskyi*). There were considerable changes in the phytoplankton composition in the littoral region of the oxbow [sites 1–3 (4)] (Fig. 2), where the proportion of the chlorococcalean green algae (*Oocystis solitaria*, *Kirchneriella rostellata*, *Scenedesmus* spp.) was higher. An increase in the algal biomass was observed from the littoral to the pelagial zone (Fig. 3), indicating significant horizontal differences even in the pelagial part of the oxbow (5–11 sites), although this region has been considered previously as a homogenous environment.

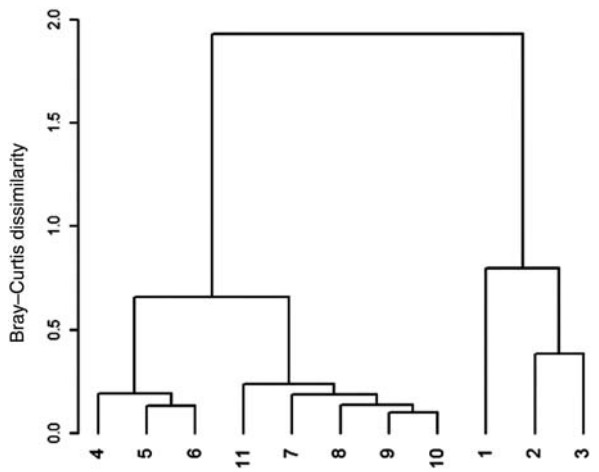

Fig. 2. Tree diagram of the sampling sites based on the MSSQ fusion algorithm and Bray–Curtis dissimilarity. Numeric codes of sample sites correspond to those in Fig. 1.

Small-scale heterogeneity

IH was calculated for each taxa, for all the 11 sites. Most of the values were in the range of 1–4, but several taxa had values higher than 4 (Table II). At site 1 where the macrophyte cover was the largest, the data indicated extreme differences in the horizontal distribution of the planktonic *Ceratium hirundinella*, *Peridinium gatunense* and the metaphytic *Pannus* sp. Patchy distribution of some chlorococcalean green algae was observed at the littoral (1–3) sites. In case of site 4, where intrusion of eutrophic pelagial phytoplankton was observed, the flagellated algae showed heterogeneous horizontal distribution, among which the otherwise subdominant *Peridiniopsis elpatiewskyi* showed the most pronounced patchiness. In the pelagial regions (5–11), the uneven distribution of the common cyanobacteria was observed at most of the sample sites, but occasionally flagellated algae were also characterized by high IH values.

Visualization of the vertical distribution of algae

Although the experienced horizontal differences might develop in a well-mixed water column, the stratified layers provide better background for the patch formation. The temperature measurements showed (Fig. 4) that despite its absolute shallowness, the oxbow was stably stratified. Sharp decrease in the temperature of

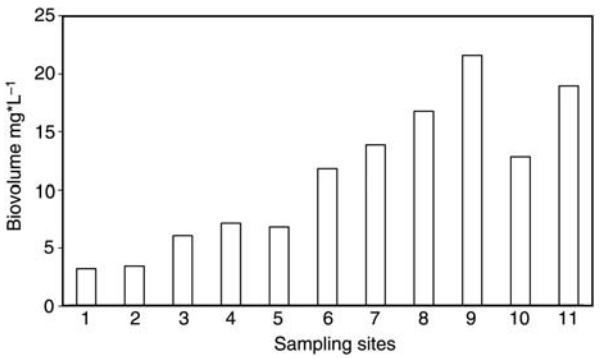

Fig. 3. Average biomass of algae (ind. mL^{-1}) at the 11 sample sites.

Table II: Taxa with high IH values (IH > 4) from the sample sites.

	Sample sites										
	1	2	3	4	5	6	7	8	9	10	11
Aphanizomenon issatchenkoi								4.7			
Cyanogranis ferruginea			5.2						4.9		
Limnothrix redekei								5.4	4.7		
Pannus sp.	16.9										
Romeria leopoliensis							7.2	7.2			4.7
Kirchneriella lunaris			4.7								
Kirchneriella rostellata	6.1										
Monoraphidium contortum			4.7								
Monoraphidium minutum	5.4										
Quadrigula closterioides		4.6									
Cyclotella pseudostelligera				4.3							
Ceratium hirundinella	20.0										
Peridiniopsis elpatiewskyi				14.1	5.4	7.6					
Peridinium gatunense	11.8		6.8	4.5					15.0		
Peridiinium umbonatum				5.5							
Peridinium volzii		5.6		4.6							
Phacus glaber		5.0									
Phacus suecicus				5.7							
Phacus undulatus				4.6							
Cryptomonas reflexa										4.8	
Gonyostomum latum				6.3	7.1						

Higher values indicate that in case of the given taxa there were large differences in the biomass among the repeated samples taken from the given site.

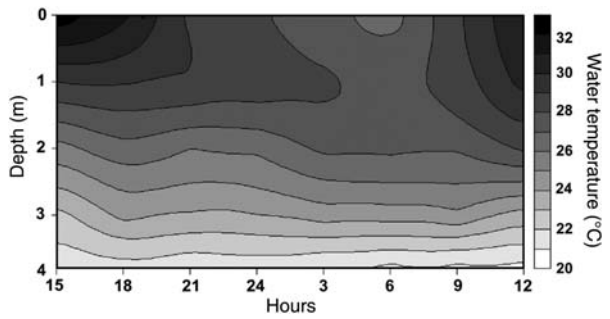

Fig. 4. Changes of the water temperature in the layers of the oxbow (site 8; 23rd of July 2007, 14:00–15:00 hrs).

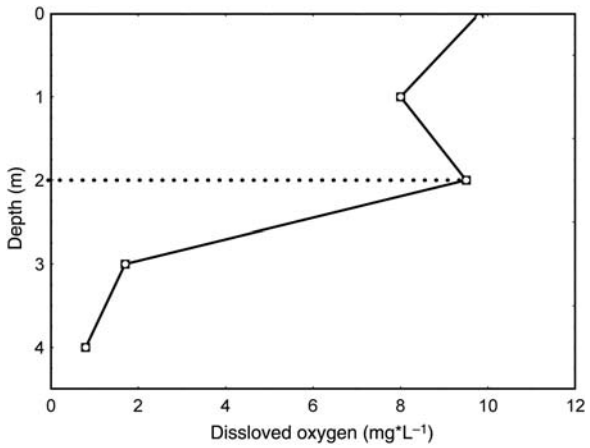

Fig. 5. Oxygen profile of the oxbow (site 8; 23rd of July 2007, 14:00–15:00 hrs). Dotted line indicates the depth of the euphotic zone (2.5 × Secchi depth).

the deeper layers was observed in the day of sampling. Depletion of oxygen was also observed, indicating the development of the upper euphotic and the lower aphotic layers (Fig. 5). These two layers were separated by the distribution of a blue–green alga, *Cylindrospermopsis raciborskii* (Fig. 6a), and the purple sulphur bacteria *Thiopedia rosea* (Fig. 6b).

We found that despite their similar ecological character, there were great differences in the horizontal distribution of species, like *Cylindrospermopsis raciborskii* and *Aphanizomenon ovalisporum* (Fig. 6c), or *Peridiniopsis elpatiewskyi* (Fig. 6d) and *Peridinium gatunense* (Fig. 6e). While the *C. raciborskii* was more or less evenly distributed in the photic zone, the *A. ovalisporum* showed distinct horizontal heterogeneities. The distribution of *Peridiniopsis elpatiewskyi* was also different from that of the *Peridinium gatunense*.

Effects on the quality assessment

Knowing the perplexing variety of distribution patterns and the rate of differences, it is reasonable to assume that these might influence the results of lake quality assessments. For estimating the possible impact of the horizontal differences on the final result

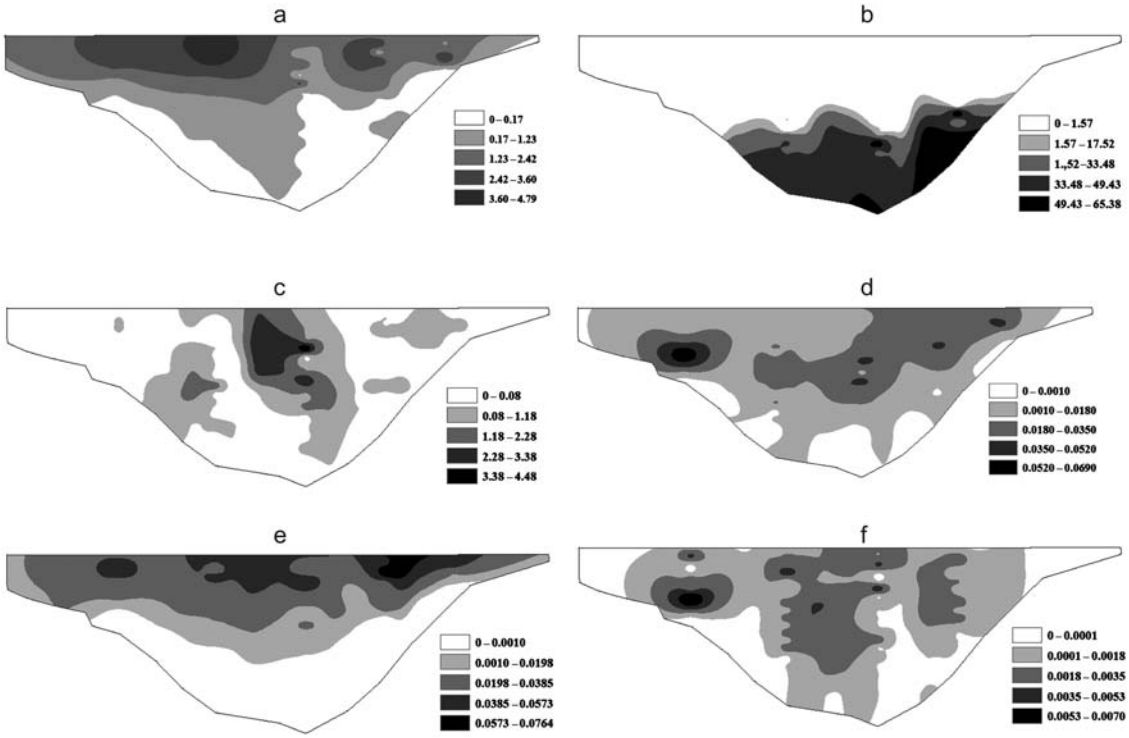

Fig. 6. Vertical distribution of algae and purple sulphur bacteria in the cross-section of the oxbow (23. July 2007, from 14:00 to 15:00 hrs). (**a**) *Cylindrospermopsis raciborskii*, (**b**) *Thiopedia rosea*, (**c**) *Aphanizomenon ovalisporum*, (**d**) *Peridinium gatunense*, (**e**) *Peridiniopsis elpatiewskyi*, (**f**) *Ceratium hirundinella*.

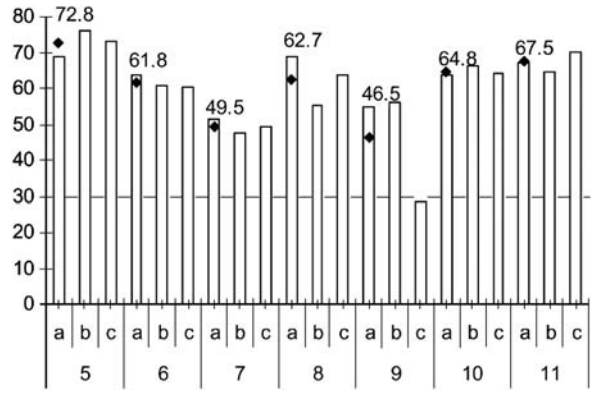

Fig. 7. Relative abundance (% of total algal biomass) of Cyanobacteria in the 5–11 (open water) sites. Columns indicate individual samples; the values are site averages.

of a phytoplankton-based quality assessment, a Cyanobacteria Index (% of total biovolume) was calculated for all the samples taken in the pelagial part of the oxbow (Fig. 7). The width of the range of values covered almost 50%, which indicates high uncertainty in the quality assessment. Eliminating the small-scale heterogeneity by averaging the values belonging to the same sites (Fig. 7), the range can be halved (26%) but still remained high.

DISCUSSION

Differences at horizontal scale

The observed differences of the phytoplankton biomass at the whole oxbow scale were in accordance with the findings of other, similar investigations (Van den Berg *et al.*, 1997; Pełechaty and Owsianny, 2003). Increasing abundance of aquatic macrophytes creates inhospitable milieu for the truly planktonic algae, and results in changes in the species composition and decrease in the algae biomass by reducing the light penetration, increasing the sedimentation rate (Van den Berg *et al.*, 1997), providing habitat for grazers (Jeppesen *et al.*, 1997), producing allelopathic substances (Hasler and Jones, 1949; Körner and Nicklisch, 2002). Consequently, the phytoplankton of the macrophyte-dominated sites is not simply the low biomass version of the pelagial plankton, but it is a different assemblage from phytocoenotic point of view (Pełechaty and Owsianny, 2003). Although the role of biotic interactions like allelopathy or prey selective grazing (Urabe, 1990; Barker *et al.*, 2010) cannot be excluded especially at the macrophyte-dominated sites, the role of physical processes in shaping the spatial distribution of algae seem more probable explanation. Due to the reduced mixing in

regions of dense macrophyte cover, species with high-specific gravity (like diatoms) settle out from the photic layer. The centric diatom *Cyclotella pseudostelligera* that occurred in the pelagial sites of the oxbow in relatively large cell numbers was completely absent in the 1–4 sites. Similar pattern was observed in case of all those species that do not have the capability of active locomotion. Nevertheless, as it was found in bog lakes (Borics *et al.*, 2003), some euplanktic taxa (*Kirchneriella* sp., *Pannus* sp.) flourished in the metaphytic environment (site 1).

Besides the littoral versus pelagial differences, uneven distribution of algae was also characteristic for the open water (5–11) sites. Although these sites had larger similarity in overall species composition, the phytoplankton biomass appeared to be different and showed increasing tendency towards the western part of the oxbow (Fig. 3).

Numerical characterization of the heterogeneity

Knauer *et al*. (Knauer *et al.*, 2000) proposed a formula for the heterogeneity of chemical substances in water bodies; it was used to characterize the horizontal differences of several variables in the Lago Maggiore (Bertoni *et al.*, 2004). We tried to adapt this method for algae. Because of the differences between the measurement of chemical substances and estimation of the algal number by microscopy, this formula was not especially useful for algae. The error of the algae counting is density dependent, i.e. the uncertainty of the cell counts' estimation increases towards the rarely occurring specimens. This has to be considered during the elaboration of a proper formula. In the formula proposed in our study, the ratio of horizontal variability (CVs) and counting variability (CVe) was used (CVs/CVe). The index was useful in the quantitative characterization of the horizontal differences.

Fine-scale heterogeneity

The IH values showed clearly that in case of some taxa (e.g. dinoflagellates, cyanobacteria and clorococcalean green algae), there were considerable differences in the biomass among the three neighbouring water columns, despite that the distance between them was only 1 m. The distribution maps (Fig. 6) depicting spatial variability of algae provided valuable clues about the different behaviour of the planktonic species. The well-known surface avoidance of dinoflagellates (Heaney, 1976; Anderson and Stolzenbach, 1985; Gálvez *et al.*, 1988; Grigorszky *et al.*, 2003) was not observed (Fig. 6d–f). It may be explained by the fact that the occurring species (*Peridinium gatunense, Peridiniopsis elpatiewskyi*) were capable of tolerating higher temperature and illumination. These taxa are characteristic members of the phytoplankton in warm, well-illuminated tropical waters (Borics *et al.*, 2005). Due to lack of light and oxygen the dinoflagellates avoided the deeper layers, where both heterotrophic and autotrophic nutrition is impeded (Fig. 5).

Our results also revealed that the similar buoyant properties do not necessarily result in similar spatial distribution. The cells of the dinoflagellate *Peridiniopsis elpatiewskyi* were present mainly in the immediate surface layer, while the *Peridinium gatunense* and *Ceratium hirundinella* showed contagious distribution. Investigating the spatial distribution of *Ceratium hirundinella* in Lake Balaton, Padisák (Padisák, 1985) assumed an active coastal avoidance of the species. Being one of the largest freshwater algae with active locomotion, *Ceratium* species are typical long distance movers in the world of algae. This species produced the largest IH value (20), i.e. showed the most striking horizontal difference at the first sampling site, in the still water of a small pool. *Pannus* sp. that do not have the capability of active locomotion also showed distinct horizontal patchiness (IH: 16.9) at the same site. Therefore, it is reasonable to suppose that other processes might also be responsible for the development of horizontal heterogeneities. Richerson *et al.* (Richerson *et al.*, 1970) indicated that if the rate of mixing was slow enough relative to the reproductive rate of algae, many different niches can develop and result in patchiness. In case of *Pannus* sp., a higher rate of cell proliferation can be hypothesized that may lead to patch formation in the lentic pool.

Mechanisms responsible for patch formation

Model results demonstrate (Webster, 1990; Verhagen, 1994) that both horizontal and vertical patchiness increase with the flotation velocity of the algae, and decrease if the strength of the horizontal currents is stronger than the strength of the circulation in the vertical plane. Investigating the role of Langmuir circulation in the spatial distribution of microscopic organisms, Smayda (Smayda, 1970) and George and Edwards (George and Edwards, 1973) called the attention to the importance of the individual buoyant properties of the particles. Irish and Clarke (Irish and Clarke, 1984) and Kuosa (Kuosa, 1988) also proved that the actively moving and passively drifting species show different horizontal distribution in lakes or coastal waters. Nevertheless, it should be noted that at calm, windless

weather the wind forced mechanisms are of lesser importance. The patchiness described in this paper developed under particular set of environmental conditions, i.e. small size of water body, irregular/elongated shape, wind shelter and stable stratification.

Horsch and Stefan (Horsch and Stefan, 1988) showed by laboratory experiments that surface cooling creates currents in both horizontal and vertical directions and results in the exchange of water parcels under calm conditions. The temperature profile of the oxbow (Fig. 4) suggests that surface cooling is a possible explanation for the observed patchiness. At the scale of the whole water column, the stratification was stable and it is demonstrated by the spatial segregation of the *Thiopedia rosea* (Fig. 6b) (purple sulphur bacteria) cells of which were missing from the upper layers. The temperature of the immediate surface layer cooled down to that of the layer at 2 m by 6 o'clock a.m. (Fig. 4) and this temperature decrease must have been large enough to generate convective currents, and to cause mixing in the upper 2 m of the water column. This atelomixis (Barbosa and Padisák, 2003) might result in patchy distribution of several phytoplankton taxa.

Effects on quality assessment

The EU and the member states initiated new legislative measures focusing on the ecological state of waters (WFD, 2000) and increasing attention has been paid to the monitoring of surface waters, including smaller bodies that were not in the focus of the water managers previously. Phytoplankton-based assessment methods are the most popular tools to evaluate the ecological status of lakes (Padisák *et al.*, 2006). The composition metrics are sensitive to the ratio of algal groups. Therefore, the high level of patchiness should be kept in mind during lake monitoring and assessment. The frequently used one sample/lake strategy may not be satisfactory even in the case of a small water body like an oxbow, because of the high uncertainty of the state assessment. Although the number of samples cannot be increased during a simple monitoring due to the increased work involved, the confidence of quality assessment can be achieved by reducing the inherent variability of the samples. This can be attained by improving the basic sampling methodology, for example taking a larger volume of sample. This can be accomplished by using a larger sampler or collecting more samples and mixing them. Using this technique, the uncertainty caused by the small-scale horizontal heterogeneity can be minimized. When large-scale heterogeneity is demonstrated by exploratory investigations, additional sampling sites are required.

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