The variation of phytoplankton in different types of floodplain pools: a case study from the River Morava floodplain (the Czech Republic)

Variabilita fytoplanktonu v různých typech tůní: studie z povodí řeky Moravy (Česká Republika)

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Abstract

The composition and dynamics of phytoplankton communities in different types of floodplain pools (the River Morava floodplain, the Czech Republic) were studied in relation to selected physical and chemical parameters. Significant differences in phytoplankton were found between meadow and forest types of pools. On the contrary, no significant differences were found between periodical and permanent types of pools and between natural and artificial pools. Seasonal dynamics of phytoplankton is significant and is influenced by temperature course during the year.

Introduction

Plankton studies in river systems are usually focused on the main channels. Surprisingly little attention has been paid to plankton communities in the floodplain pools along these rivers, despite the fact that their production may reach higher values in backwaters and very slowly flowing side channels than in the main channels (ERTL 1985, WISSMAR et al. 1981).

The alluvial pools are one of the most influenceable freshwater habitats. The composition and dynamics of phytoplankton can be influenced by strong variation in hydrological and geomorphological conditions of the pools and by the surrounding terrestrial ecosystems (PRACH 1996). This highly dynamic nature of pool environment should be studied from both spatial and temporal points of view. Nevertheless, studies concerning phytoplankton structure and
dynamics are very sparse and usually based on a single sampling (Van Den Brink et al. 1994).

The presented paper is focused on the study of the composition and dynamics of phytoplankton communities in different types of floodplain pools in relation to selected physical and chemical parameters. We used repeated sampling during the investigated period in pools with different origin (natural vs. artificial), contrasting habitats (meadow vs. forest) and contrasting variation of water table level during the season (periodical vs. permanent). Our study addresses the following questions: (i) Is there any effect of the studied environmental factors on the species composition of phytoplankton in pools ignoring variation in time?, (ii) Do studied environmental factors influence variation in species composition in time ignoring different types of pools?

Materials and methods

In total, 22 floodplain pools were studied at three regions of the Litovelské Pomoraví Protected Landscape Area (Central Moravia, the Czech Republic, Fig. 1). Nevertheless, most of periodical pools exhibited extreme dynamic of water level and thus were dried-up during most of the period under study. Finally, we selected 14 floodplain pools for statistical analysis (Table 1):

1. the village of Střeň environs: one forest periodical pool (No. 10)
2. the village of Černovír environs: a total of 4 forest permanent pools (No. 11-14)
3. the Plané Loučky natural reserve: from 9 meadow pools were 2 periodical and 7 permanent, some of them were artificially created by excavation four years before sampling (see Table 1).

Samples were taken four times during the study in 1996-1997: X.1996, II.1997, IV.1997, XI.1997. We were unable to take summer samples due to extreme flood in 1997.

Free water samples were collected as mixed samples through the whole water column using 1m long sampling tube (Hindák ed. 1978). Samplings were provided carefully without any sediment disturbance during sampling at the deepest site free of macrophytes. The majority of parameters under study (dissolved oxygen, conductivity, pH, water temperature and ice thickness) were measured in situ using mobile instruments (oximeter OXI 96, pH 90 WTW, conductometer WTW; caliper). Cover of Lemna sp. was estimated visually as a percentage of the overgrown pool surface. Alkalinity was estimated in the laboratory by standard methods (Hrbáček ed. 1972). The abundance of algae as whole was counted in Bürker chamber as the numbers of cells per 1 ml, the proportions of individual species (groups) were evaluated by the 6-order scale according to Hindák ed. (1978).

The investigated pools are small and shallow. The size of pools varied from 7 to 300 m²; the observed depths ranged from 10 cm to 160 cm. Maximal
seasonal change of the water table was about 1 m. Pools are not regularly flooded, except the extreme floods (e.g. in 1997) and their water can be held as infiltrate river water. At the relatively small territory of the Morava River floodplain we can found meadows and fluvial forests due to the different management in the past several decades. The meadows are protected (Plané loučky natural reserve) and kept by mowing. Extinct pools are experimentally restored by excavation. The trophic state of this part of the Morava River can be characterized as mesotrophic - eutrophic (Rulík et al. 1994, 1995).

The character of pools was classified from three points of view (nominal variables; 0/1):
(i) origin of pool – natural vs. artificial;
(ii) habitat type – meadow vs. forest;
(iii) variation of water table during a season – periodical vs. permanent.

The data were subjected to canonical correspondence analysis, using program CANOCO 4 (Ter Braak & Šmilauer 1998). Prior to analyses, the species and environmental data were log-transformed ($y = \log [ax + b]$, where $a = 1$ and $b = 1$ [environmental factors] or $a = 10$ and $b = 1$ [species]). The effect of environmental variables on the species composition of phytoplankton was analyzed using Monte Carlo permutation test. Since pools were visited repeatedly during the investigated period, samples are not independent under a null hypothesis. The survey used a nested sampling design (split-plot design) – a hierarchical design with two levels of units: whole-plots (= pools) which contained split-plots (= the samples within pools). Whole-plots should be of equal size (Ter Braak & Šmilauer 1998). Missing samples from some pools (total of 3 cases) were replaced in raw data matrix by the data from previous sampling times.

The following null hypotheses (models) were tested:

1. There is no effect of the studied pool characters on the species composition of phytoplankton in pools ignoring variation in time.

The effects of a total set of environmental variables and each environmental variable that varies among whole-plots were tested by permuting whole-plots completely at random while keeping the split-plots of each whole-plot together. Time was used as a covariable. Other environmental variables were used as supplementary variables. Monte-Carlo test with 999 permutations under reduced model was used. In order to build an ordination model with a minimum set of environmental variables, forward selection of variables was applied to the analysis and selected variables were tested for their additional contribution to direct ordination. Monte Carlo test with the same options was used (Ter Braak & Šmilauer 1998).

2. There is no effect of the studied environmental factors on the species composition of phytoplankton in time ignoring variation among pools.

The effects of a total set of environmental variables and each environmental variable that varies within whole-plots were tested by permuting
split-plots without permuting whole-plots. To eliminate differences in “mean composition” of phytoplankton among pools, pools were used as covariables. Monte Carlo test with 499 permutations was used. Since the split-plots form a time-series, the split-plot permutations were restricted to account for autocorrelation among split-plots. Because pools (whole-plots) were repeatedly sampled in the same time over the season, the samples of different whole-plots could be dependent across the whole-plots. Thus the option ”Dependent across whole plots” was selected (TER BRAAK & ŠMILAUER, 1998).

Results

A total of 200 species belonging to the following groups were identified in studied pools: Cyanophyta (12 species), Dinophyta (8), Cryptophyta (16), Chrysophyceae (7), Bacillariophyceae (67), Xanthophyceae (6), Euglenophyta (36) and Chlorophyta (42). The list of species was published elsewhere (KOČÁRKOVÁ & POULÍČKOVÁ 2001). The number of species in respective samplings ranged from 5 to 28. Shannon index of diversity varied from 1.67 to 4.3 (Table 1). The average values of studied environmental parameters are summarized in Table 1.

Variation among pools

We rejected hypothesis 1. A significant influence of environmental factors on the species composition of phytoplankton was found in the studied pools ignoring variation in time (CCA; Monte-Carlo permutation test of the first axis: F = 2.088, P = 0.025; test of all canonical axes: F = 1.286, P = 0.06). The first canonical axis separated the meadow pools with lower water conductivity and alkalinity, lower cover of Lemna sp., lower temperatures and higher amount of oxygen from the forest pools. The second canonical axis separated natural pools from the artificial ones (Fig. 2).

The CCA clearly distinguished three groups of species. The first group in the right part of the ordination diagram (Fig. 2) is dominated by species with occurrence in forest pools, mainly flagellate forms and algae tolerating shade (Euglena viridis EHREN., Phacus platyaulax POCHM., Cryptomonas marssonii SKUJA, Chlamydomonas sp. and Oscillatoria sp., Fragilaria tenera, Achnanthes hungarica (GRUN.) GRUN., Eunotia bilunaris (EHREN.) MILLS, Cocconeis placentula EHREN., Nitzschia sp.). The second group in the left part of the ordination space is formed by “meadow” species. Except for blue-green algae, all groups of freshwater planktic algae are represented (Melosira varians AG., Cymatopleura librilis (EHREN.) PANT, Aulacoseira italica (EHREN.) SIMON, Stauroneis phoenicenteron (NITZSCH.) EHRENB., Navicula cryptocephala KÜTZ., Gomphonema acuminatum EHRENB., Tribonema sp., Pinnularia gibba (EHREN.) EHRENB.,
Chloromonas sp., Navicula sp., Synura spinosa KORŠ., Trachelomonas sp., Achnanthes sp., Dinobryon divergens IHM., Cryptomonas reflexa SKUJA, Gymnodinium cf. wawrikei SCHILLER). The small third group in the centre of the diagram includes only three species (Cryptomonas curvata EHRENB., Euglena sp. and Trachelomonas volvocina EHRENB.) common in all pools.

Table 2 presents marginal effects of environmental variables, i.e. significance of the effect of each variable as the only environmental variable. When taken separately, two variables showed significant effects on species variation among pools: habitat type (meadow vs. forest) and character (permanent vs. periodic). Forward selection of environmental variables selected one environmental variable (habitat type) according to its significant conditional effect (Table 2), which suffice to explain the variation in species composition.

To obtain a deeper insight into the species/environment relationships, meadow and forest pools were separately analyzed. In the analysis of forest pools, significant effect of the temporal character (permanent vs. periodical) on species composition of pools was identified (Monte-Carlo test of the first axis: F = 1.938, P = 0.002). Since we studied only one forest periodical pool, the interpretation of this result is limited.

In the analysis of meadow pools, no significant effect of environmental variables on the species composition of phytoplankton was found (Monte-Carlo test of the first axis: F = 1.498, P = 0.42; all canonical axes: F = 1.828, P = 0.38).

We did not find significant differences in species richness and diversity between forest and meadow pools (Repeated measures GLM ANOVA; species richness: F = 0.84, DF = 1, P = 0.38; species diversity: F = 2.02, DF = 1, P = 0.18). In spite of this fact we found differences in phytoplankton structure between these two habitats. Meadow pools had higher proportions of Bacillariophyceae and Dinophyta and lower proportions of Cyanophyta and Euglenophyta than the forest pools (Fig. 3).

Variation in time

We rejected hypothesis 2. There was found a significant effect of the total set of environmental variables that vary within the whole-plots on the species composition of phytoplankton (Monte-Carlo permutation test of the first axis: F = 1.239, P = 0.042; all canonical axes: F = 1.712, P = 0.014). The first canonical axis was related to a decreasing cover of Lemna sp. and to an increasing pH and ice thickness. The second canonical axis was related to a decreasing temperature and an increasing ice. When tested singly, only two variables – temperature and ice - showed a significant effect on species variation in pools in time (Table 3). The following variables were selected in the forward selection: temperature, conductivity and cover of Lemna sp. (Fig. 4, Table 3).
The CCA (Fig. 4) separated “winter” samples (II.1997, XI.1997) with higher abundance of diatom species (*Navicula lanceolata* (AG.) EHRENB., *N. cryptocephala*, *Synedra* sp., *Stauroneis phoenicenteron*, *Cocconeis placentula*) from the “spring and autumn” samples (X.1996, IV.1997) with high abundance of Cryptophyta and green algae (*Cryptomonas obovata* SKUJA, *C. curvata*, *C. marssonii* and *Pediastrum duplex* MEYEN, *Chlamydomonas* sp.). The position of the group of samples dominated by Euglenophyta was probably influenced by the increasing cover of *Lemna* sp. (*Euglena* sp., *Phacus platyaulax*).

**Discussion**


Our analysis proved mainly the difference between forest and meadow pools. Conductivity was the most important of the studied “passive” parameters. It was higher in forest pools due to the accumulation and decomposition of the leaves fallen from the surrounding vegetation. Due to shading and an abundance of organic matter, forest pools abound especially in flagellate species (Fig. 2) that tend to be mixotrophic, namely Euglenophyta (STARMACH 1983, PRINGSHEIM 1963). Marked dominance of Euglenophyta was observed by KOČÁRKOVÁ & STAŇKOVÁ (2000) in forest pools of Odra river floodplain (the Czech Republic), where it represented in average for 31% of phytoplankton abundance. PITHART (1999) also reports that bank vegetation prevents illumination, slows down the warming of pools, and the decomposition of fallen leaves consumes oxygen. According to him, shaded pools contain significantly less abundance of phytoplankton and lower number of species with the dominance of flagellata. On the contrary, unshaded pools show higher species abundance and diversity with coccal algae as well (PITHART 1999). Although our results concerning environmental differences between meadow and forest pools are in accordance with PITHART (1999), we did not find significant differences in species richness and diversity between these two habitats as reported by the mentioned author. These discrepancies can be partly explained by the various types of contact between pools and the main channel in the respective study areas. VAN DEN BRING et al. (1994) mention that the length of a pool’s connection with a river can influence the pool communities most. In contrast to pools of Lužnice river floodplain (PITHART 1999), pools under our
study are not regularly flooded, except the extreme floods (e.g. in 1997). Only one meadow pool (No. 1) is in direct contact with the river during the whole year which is reflected by high species richness but the lowest species diversity among studied pools (Table 1). In this case, species richness was increased by the species typical of running waters, especially by rheophile pennate Bacillariophyceae.

Another possible explanation is based on morphology of pools. According to Pithart (1999), differences between shallow and deep pools can be considerable. Unlike the very shallow pools that are strongly influenced by the chemical processes in sediments, the relatively deeper pools are not mixed by wind and therefore tend to have a stratified water column (Pithart et al. 2000). Pithart et al. (2000) tries to compare the proportions of flagellate species and coccal algae (blue-green algae, chlorella algae and Bacillariophyceae) in pools of the rivers Lužnice, Morava and Labe. The pools in the Morava river floodplain and in particular the Labe river floodplain are according to their study characterized by a higher proportion of coccal forms. Pithart et al. (2000) suppose that low proportion of coccal forms in the floodplain pools of the Lužnice river is caused by their greater relative depth and the absence of mixing by wind. They confirmed this hypothesis by an ecosystem experiment. The proportion of coccal forms significantly increased in the part of the pool where mixing was carried out (Pithart, personal communication).

Unfortunately, our study did not provide an opportunity to determine nutrients, even though they are undoubtedly, together with light and temperature, the most important factor for algae population growth (Reynolds 1984). A relationship between Cyanobacteria and Chlorophyta dominance over Bacillariophyceae on the one hand, and nutrient ratios on the other, has been frequently reported in studies concerning eutrophication processes in lentic water bodies (Sommer 1986). There are several sources of nutrients in pools, mainly a river with its flooding and infiltration, and actual pool sediments with organic matter of both pelagic and allochthonous origin. The influence of sediments on lake water chemistry generally increases with a decreasing water depth. In shallow floodplain lakes, regeneration of nutrients (Si, P) from sediments was found to be more important than in deep lakes (Van den Brink et al. 1993). Van den Brink et al. (1994) found a negative correlation between water depth and the levels of Si and P in water as well as a positive correlation between the annual flood duration and the levels of nutrients (N, P). Cyanobacteria, Chlorophyta and Euglenophyta were most frequently found in water bodies with low Si/N and Si/P ratios and a relatively long annual flood duration, whereas taxa which belong to Bacillariophyceae and Chromophyta were most frequently found in water bodies with high Si/N and Si/P ratios and a short annual flood duration (Van den Brink et al. 1994). Consequently, an increase in the concentration of N and P in floodplain lakes from the main channels during floods may change Si/N and Si/P ratios in favor of
Cyanobacteria and Chlorophyta. According to our results, meadow pools had higher proportions of Bacillariophyceae and Dinophyta and lower proportions of Cyanophyta and Euglenophyta than the forest pools.

Significant differences of our meadow and forest pools may be determined by a whole complex of environmental factors discussed above. The variability of phytoplankton structure inside of each group was influenced by different factors. Differences in phytoplankton composition among forest pools can be also related to composition and density of surrounding forest vegetation which is the main source of materials for decomposition processes in pools (Dvořák & Pechar 2000). Floristic differentiation among meadow pools is probably caused by the variable abundance of phytoplankton and submersed macrophytes (Kočárková, unpublished data) that is though their photosynthetic activity correlated with the concentration of oxygen in the water (Reynolds 1984).

Surprisingly, any significant differences between natural and artificial pools have not been found. This fact can be influenced by low number of analyzed artificial pools.

The differences in species composition between natural and artificial pools can be considerable especially soon after their excavation but during time they slowly disappear. Comparative study of zoobenthos of natural and artificial pools (Šmaková & Rulík 2000) showed that the species richness in newly established pools was lower than in natural ones only at the beginning of succession. After eight to nine months the number of species increases rapidly and in the second year the species richness in newly established pools was even higher than in natural pools. This is in accordance with our results concerning phytoplankton, since artificial pools under our study were established four years before sampling and any differences in species composition probably disappeared during time.

Testing hypothesis 2, we verified the well known importance of time. Seasonal dynamics of phytoplankton is mainly influenced by temperature course during the year. Analysis differentiated between spring & middle autumn phytoplankton compositions and late autumn & winter ones. The increasing occurrence of diatoms in winter and late autumn samples and spring dominance of Cryptophyta are in good agreement with the present knowledge about the seasonal dynamics of shallow stagnant waters of the temperate zone (Hutchinson 1967, Patrick 1977).

Nevertheless, variation in species composition explained by the mentioned factors reached only low values which point to quite complicated seasonal dynamic of the phytoplankton and environmental factors. This problem must be seen as a result of dynamic processes of growth factors – nutrients, light, temperature (Rhee & Gotham 1981) and losses – sedimentation, grazing, parasitism (Reynolds et al. 1982). The higher sampling frequency is necessary for this type of research.
Acknowledgement

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References


Table 2: Environmental variables ranked by their marginal (left) and conditional (right) effects on the phytoplankton of the studied data set, as obtained by forward selection (Hypothesis 1). $\lambda_1 = \text{fit} = \text{eigenvalue with respective variable only}; \lambda_A = \text{additional fit} = \text{additional variance each variable explains at the time it was included}; \ P = \text{significance level of the effect, as obtained with a Monte Carlo permutation test under the null model with 499 random permutations.}
Table 3: Environmental variables ranked by their marginal (left) and conditional (right) effects on the phytoplankton of the studied data set, as obtained by forward selection (Hypothesis 2). $\lambda_1 = \text{fit} = \text{eigenvalue with respective variable only}$; $\lambda_A = \text{additional fit} = \text{additional variance each variable explains at the time it was included}$; $P = \text{significance level of the effect}$, as obtained with a Monte Carlo permutation test under the null model with 499 random permutations (see Methods).

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<tr>
<th>Variable</th>
<th>$\lambda_1$</th>
<th>P</th>
<th>Variable</th>
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<td>Temperature</td>
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Fig. 3: Proportion of phytoplankton groups in meadow and forest pools (data from samplings within each pool were merged before analysis; means of proportion of each phytoplankton groups within respective pools were averaged separately for the forest and the meadow pools).
Fig. 1: A sketch of the Litovelské Pomoraví Protected Landscape Area; circles indicate the study sites.
Fig. 2: Joint ordination diagram of CCA (hypothesis 1, split-plot design, permuted whole-plots while keeping the split-plots of each whole-plot together). Whole-plots (= pools) are represented by circles (○), species by filled squares (■), passive environmental variables by arrows (quantitative variables), independent environmental variables by crosses (+) at the centroids of the pools of the corresponding types (nominal variables). Only species with both the highest weight and fit in the analysis are showed.

Species: 1 - Melosira varians AG.; 2 - Cymatopleura librilis (EHRENB.) PANT.; 3 - Aulacoseira italica (EHRENB.) SIMON.; 4 - Stauroneis phoenicenteron (NITZSCH) EHRENB.; 5 - Navicula cryptocephala KÜTZ.; 6 - Gomphonema acuminatum EHRENB.; 7 - Tribonema sp.; 8 - Pinnularia gibba (EHRENB.) EHRENB.; 9 - Chloromonas sp.; 10 - Navicula sp.; 11 - Synura spinosa KORŠ.; 12 - Trachelomonas sp.; 13 - Achnanthes sp.; 14 - Dinobryon divergens IHM.; 15 - Cryptomonas reflexa SKUJA; 16 - Gymnodinium cf. wawrikiae SCHILLER; 17 - Cryptomonas curvata EHRENB.; 18 - Euglena sp.; 19 - Trachelomonas volvocina EHRENB.; 20 - Euglena viridis EHRENB.; 21 - Achnanthes hungarica (GRUH.) GRUN.; 22 - Cryptomonas marssonii SKUJA; 23 - Planktosphaeria gelatinosa G.M.SMITH; 24 - Chlamydomonas sp.; 25 - Oscillatoria sp.; 26 - Fragilaria tenera; 27 - Phacus platyaulax POCHM.; 28 - Eunotia bilunaris (EHRENB.) MILLS; 29 - Cocconeis placentula EHRENB.; 30 - Nitzschia sp.; 31 - Scenedesmus quadricauda (TURP.) BRÉB.; 32 - Hormidium tribonematoideum SKUJA; 33 – Navicula lanceolata (AG.) EHRENB.; 34 – Synedra sp.; 35 – Pediastrum duplex MEYEN.; 36 – Phormidium sp.; 37 – Cryptomonas sp.; 38 – Pinnularia sp.; 39 – Nitzschia acicularis (KÜTZ.) W. SM.
Fig. 4: Joint ordination diagram of partial CCA (hypothesis 2, split-plot design, forward selection procedure, permuted split-plots within whole-plots without permuting whole-plots. Since the split-plots form parallel time series and time is an autocorrelated error component affecting all series, the same shift was applied to all time series, i.e. dependent split-plot permutations across whole-plots). Individual samples of the respective sampling date are represented by open circles (X.1996; ○), open squares (IV.1997; □), filled squares (II.1997; ■) and filled diamond (XI.1997; ◆), species by filled circles (●), environmental variables selected by the forward procedure by arrows. Only species with both the highest weight and fit in the analysis are showed.
Table 1. Selected parameters of the studied pools (mean ± standard deviation; n = 4 for all cases). Habitat: 1 – meadow, 2 – forest; Character: 1 – permanent, 2 – periodical; Origin: 1 – artificial, 2 – natural.

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<th>Alkalinity [mmol.l⁻¹]</th>
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