

## Spatial and temporal diversity of small shallow waters in river Lužnice floodplain

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**Abstract** To propose a concept of their mutual diversity, twenty-nine permanent shallow floodplain pools and oxbows in the river Lužnice floodplain were analysed for area, depth, shape, flooding, and shading by terrestrial vegetation, and sampled in all seasons for their water chemistry, phytoplankton composition and biomass, and zooplankton composition. The sites are

regularly flooded, eutrophic, and often shaded by surrounding vegetation. Cryptophyceae, Chryso-phyceae and Euglenophyceae dominated the phytoplankton, while Cyanophytes were rare. Within the rich zooplankton assemblage (63 species), cladocerans and rotifers dominated. Correlation matrices and multivariate analyses indicated that shaded and relatively deeper sites had lower oxygen saturation and higher concentrations of  $\text{PO}_4\text{-P}$  and  $\text{NH}_4\text{-N}$ . Shade and relative depth correlated negatively with phytoplankton biomass and number of phytoplankton taxa, and positively with Cryptophytes and large cladocerans—thus indicating poor mixing, poor light availability and low fish pressure on herbivores. Decomposition of leaf litter increased oxygen consumption, while shade from terrestrial vegetation restricted photosynthesis and decreased oxygen production. Larger sites were more species-rich in phytoplankton and supported Euglenophyceae, green algae and rotifers.

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Guest editors: R. D. Gulati, E. Lammens, N. De Pauw & E. Van Donk  
Shallow lakes in a changing world

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**Keywords** Floodplain · Terrestrial–aquatic interactions · Phytoplankton · Zooplankton · Shading · Flooding

### Introduction

In a floodplain with a natural hydrological regime, aquatic ecosystems are characterised by their

transience between being either marshy, lotic or lentic in character. Their mutual connectivity remains relatively high because water flowing through the underlying sediments influences the lotic subsystems biogeochemically and ecologically from the adjacent river, and from the soil and bedrock sediments (Jones & Mulholland, 2000). Moreover, flood events enhance the connectivity, accelerating the exchange of plankton communities, plant seeds and fish among the various pools and oxbows. After each flood event, a process of diversification begins again as the water level declines, the water current diminishes, and finally the floodplain lakes and oxbows become disconnected (Pithart, 1999).

Water level fluctuations and the transient character of the many aquatic parts of the floodplain intensify the interactions between the floodplain's terrestrial and aquatic environments (Prach, 1996). As the volume of each water body decreases, the ratio between its surface and volume increases, enhancing the intensity of exchange between the sediment and water column. Similarly, the relative impact of terrestrial vegetation—with its effect of shading and leaf litter—increases with decreasing area. The small, shallow lakes and pools can be relatively deep, with a tendency towards intense stratification and oxygen deficits, influencing the whole aquatic community, and in particular the fish (Pithart & Pechar, 1995; Pechar et al., 1996).

The aim of this study is to describe and explain the spatial and temporal diversity of the permanent lotic ecosystems of the hydrologically well-preserved Lužnice river floodplain. We focus on the environmental factors specific to these pools and oxbows, and try to maintain a multi-dimensional viewpoint that incorporates both spatial as well as temporal changes (Ward, 1989). We use the term diversity *sensu lato* as the overall heterogeneity of our studied subsystems; one that includes environmental variables as well as species occurrence, composition and biomass.

Long-term limnological monitoring of two floodplain pools has been carried out for about 20 years, resulting in several papers being published: about the plankton of the Lužnice floodplain, describing the plankton dynamics (Hrbáček et al., 1994; Pechar et al., 1996); flagellate vertical

migrations (Pithart, 1997) or and phytoplankton composition (Kylbergerová et al., 2002). This more synthetic paper is based on repeated synoptical samplings of a larger set of different localities.

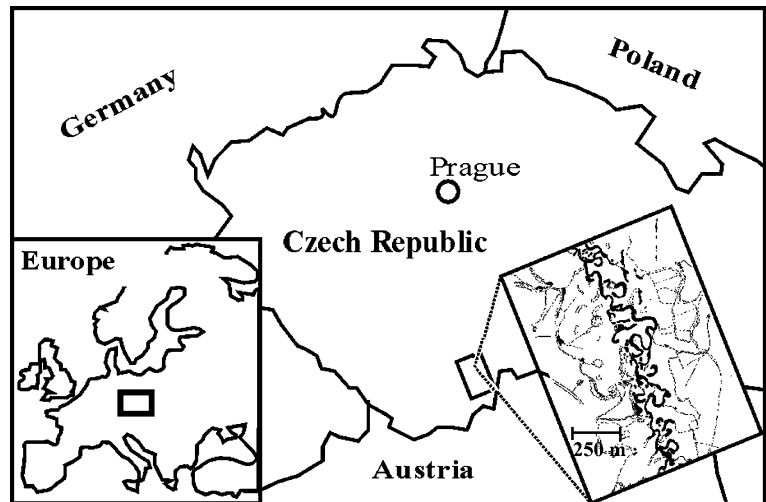
### Sampling sites

The Lužnice floodplain within the study area remains one of the last floodplains in the Czech Republic whose natural hydrological regime has not been altered substantially by any massive river regulation. The river channel is still meandering and changing its course after every major flood event, including the cutting of new meanders. The studied area is flooded for several weeks every year, mostly in March and April, with occasional floods in winter or summer. The area, about 25 km long and 1–2 km wide, lies to the south of the Czech Republic between the Austrian border and the town of Suchdol nad Lužnicí (Fig. 1). The average (50 years) river discharge is  $5.8 \text{ m}^3 \text{ s}^{-1}$ . The floodplain area consists of: the main stream and standing water bodies (15% of area, about 200 permanent pools and oxbows); meadows, both maintained and abandoned (the latter prevailing, mainly overgrown by *Phalaris arundinacea* and *Urtica dioica*); pastures; and floodplain softwood forest (15% dominated by willow and white poplar with an admixture of oak and alder). In winter, the pools regularly freeze over, the ice being mostly covered by snow. Water levels fluctuate within a range of 1.5 m.

The 29 permanent oxbows and pools chosen for this study represent a range of parameters typical of the studied area in terms of their surface area, depth, shape, level of shading by shore vegetation, distance from the river, and macrophyte vegetation.

In this paper, we use the term “oxbow lake” for water bodies with a length many times exceeding their width; they originate in former meanders that have been cut off from the active river channel. The term “pools” we use for circular or oval-shaped water bodies that originated from oxbows but were reshaped by heterogeneous silting-up and erosion caused by floods.

**Fig. 1** Location of studied sites and landscape character of the river Lužnice floodplain



## Methods

Sampling was carried out five times to cover different parts of the seasonal development: September 6–7 1994, October 25–26 1994, January 24–25 1995, May 2–3 1995, and August 19–20 1997.

During each of these samplings, water temperature, dissolved oxygen concentration, pH and conductivity were measured *in situ* by WTW field probes and Multi-line P4 measuring set.

Total alkalinity (TA) was determined by endpoint (pH = 4.5) titration with 0.1 M HCl. For nutrient and phytoplankton analysis, an integrated water sample (3 l) was taken with a Plexiglas tube from the first 1–1.5 m of the water column. Concentrations of  $\text{NH}_4\text{-N}$ ,  $\text{NO}_3\text{-N}$ , and  $\text{PO}_4\text{-P}$  were determined using a Tecator flow injection analyser (FIA Star 5010, Tecator, Sweden; Ruzicka & Hansen, 1981) in samples filtered through Whatman GF/C filters. Total nitrogen (TN) and total phosphorus (TP) were determined in samples filtered through 100  $\mu\text{m}$  mesh after mineralisation by persulphate as  $\text{NO}_3\text{-N}$  and  $\text{PO}_4\text{-P}$  (for details, see Pithart & Pechar, 1995). Chlorophyll-*a* concentration was estimated spectrophotometrically or fluorometrically after extraction in an acetone–methanol mixture (Pechar, 1987).

For enumeration, 100 ml of the sample was preserved by Lugol solution, sedimented in chambers and analysed under the inverted microscope. Algal species were counted in random

fields at a magnification of 200 $\times$  or 400 $\times$  up to the number of 300 individuals for each dominant species; cell volume was calculated as the volume of corresponding geometrical body (Javornický, 1978). Macrophytes in the pools were determined to species, and their coverage was estimated.

Zooplankton was sampled in a qualitative way. One or two mixed samples were taken from each of the pools, two samples in the case of a separate free-water area and nearshore macrophyte area. From free-water areas (without macrophytes), several bottom-up tows by a conical plankton net (mesh size 100  $\mu\text{m}$ ) were taken and mixed together. Zooplankton from macrophyte beds was sampled from throughout the water column using a plastic vessel, and filtering through a plankton net (mesh size 100  $\mu\text{m}$ ). All samples were preserved by formalin. Later, 300–400 individuals were determined and counted. Zooplankton was not sampled in August 1997. In zooplankton samples, cladocerans and rotifers were determined mostly to species, or at least to genus level. Copepods were determined only to groups: nauplii, copepodids, diaptomids and harpacticids (Straškraba, 1964).

The dimensions of pools were measured during a period of average water level to calculate their area and shape. Maximum depth was measured from the ice cover. Relative depth was calculated according to the equation  $z_r = 50 \cdot z_{\text{max}} \cdot \sqrt{\pi/\sqrt{A}}$  (without dimension, usually  $<2$  for shallow lakes; Hutchinson, 1957) and Landscape Shape Index

(equalling 1 for a circle) according to the formula  $LSI = p/(2\sqrt{\pi} \cdot A)$  (McGarigal & Marks, 1995); where  $A$ —area,  $z_{\max}$ —maximum depth,  $z_r$ —relative depth, and  $p$ —perimeter. Position along the longitudinal river course (river km) and distance from river was estimated from aerial photographs.

Shading was measured during clear-sky days by simultaneous measurement of relative PhAR by Li-Cor 150 with SA 190—sensors at an unshaded site outside the locality, and on the water surface of the water body, at each point of a virtual network consisting of  $2 \times 2$ ,  $3 \times 3$  or  $5 \times 5$  m squares (according to pool area; total number of points per water body ranged from 20 to 40). Average values from all points of the network and two measurements (morning and afternoon) were used.

An index of flooding was developed as an estimate of probability of flooding for each of the pools, i.e., direct surface contact of a pool with main stream water. We had observed that pools underwent more flooding depending on their proximity to the river, and the more they were upstream. Also, we found that  $\text{NO}_3\text{-N}$  concentration strongly correlated linearly in the same way, i.e., negatively with distance from river and positively with river kilometre. Thus, we used  $\text{NO}_3\text{-N}$  concentration as an indicator of flooding. Using our dataset (distance from river, river kilometre and average  $\text{NO}_3\text{-N}$  concentration) we developed a linear function for calculating the flood index:

$$FI (\sim \text{NO}_3 - \text{N}) = -3610.65 + 32.67 * \text{river km} + (-5.06 * \text{river distance})$$

Correlation between the measured and predicted  $\text{NO}_3\text{-N}$  concentration was 0.30,  $P = 0.009$ . From this analysis 6 pools were excluded, as these pools clearly obtained most of their water supply from terrace runoff and hence their  $\text{NO}_3\text{-N}$  values were very high.

For data analyses, correlation matrices were calculated for all parameters for each pool using all sampling data (total), from the average value of parameters, and finally for particular seasonal samplings separately. For multivariate statistics we used CANOCO software; DCA method was tried first and finally RDA or CCA. Only the most relevant environmental factors were used for models. For phytoplankton, only relative contributions of selected important groups to the total biovolume were used; for zooplankton, only relative contributions of large pelagial cladocerans and pelagial rotifers to total zooplankton biomass. To make the biplots more understandable, the environmental factors were divided into two groups: (1) morphology, flooding, shading and distance to the river; and (2) water chemistry parameters.

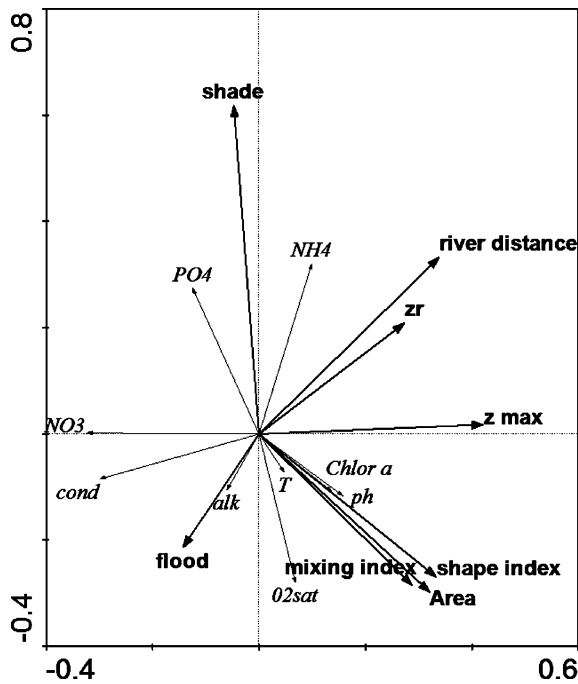
## Results

### Morphology, distance to the river, flooding and shading

The studied set of water bodies are small, shallow lakes (Table 1) of different shapes, from almost circular pools to elongated oxbows ( $LSI = 3.7$ ). Some of them were permanently connected to the river (parapotamon-type side arms). Despite most pools maximum or average depth being rather shallow, relative depths can reach rather extreme values (maximum 17). Due to their small area and bankside woody vegetation, pools can be substantially shaded (up to 79%). Some morphological parameters were correlated (see Fig. 2); shape index was correlated significantly with area because the elongated oxbows were also the largest water bodies. All oxbows were also close to the river, therefore their relative depth correlated with distance from river.

**Table 1** Mean, minimum and maximum values of morphometric characteristics and shading of studied localities

	Maximum depth (m)	Relative depth (%)	Area (m <sup>2</sup> )	LSI	Shade (%)	Distance to main stream (m)
Mean	1.1	8.6	753	1.6	36	44
Min–Max	0.2–3.3	1.5–17.0	58–5,800	1.03–3.74	3–79	0–135



**Fig. 2** RDA analysis of morphometry, shading, flooding and distance from river (explaining variables, thick vectors) and water chemistry as explained parameters. First axis explains 10.3% of variability, second 0.2%. Monte Carlo permutation test for first axis:  $F$ -ratio = 16.03,  $P = 0.058$

### Water chemistry

According to total nitrogen (TN, mean value  $3.7 \text{ mg l}^{-1}$ ), total phosphorus (TP,  $130 \text{ } \mu\text{g l}^{-1}$ ), and chlorophyll *a* ( $67 \text{ } \mu\text{g l}^{-1}$ ) concentrations, the studied sites would be classified as eutrophic or hypertrophic. Ranges between minimum and maximum values showed extreme variations in most parameters regardless of sampling date and site. Conductivity fluctuated mostly between 200 and  $300 \text{ } \mu\text{S cm}^{-1}$ . Alkalinity below  $1 \text{ meq l}^{-1}$  was found in 70% of cases; values higher than  $2.00 \text{ meq l}^{-1}$  were recorded in less than 5% of measurements. Values of pH ranged mostly from 6.5 to 7.

Some chemical parameters were associated with shading (Fig. 2), which was positively and significantly correlated with  $\text{PO}_4$  and  $\text{NH}_4$  and negatively with oxygen saturation. Area was correlated with chlorophyll *a* concentration, pH, temperature and shape index and associated with

oxygen. Flooding was associated with  $\text{NO}_3\text{-N}$ , alkalinity and conductivity.

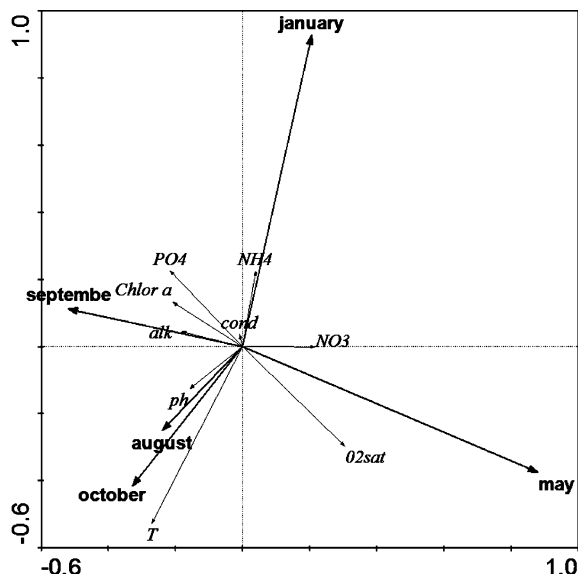
$\text{NO}_3\text{-N}$  was the prevailing component in the nitrogen budget for most sites: on average nitrate represented about 60% of TN. No significant correlations between  $\text{NO}_3\text{-N}$  and  $\text{PO}_4\text{-P}$  or  $\text{NH}_4\text{-N}$  were found. Also ratios of dissolved inorganic nitrogen to phosphate (DIN/ $\text{PO}_4\text{-P}$ ) and TN/TP were determined mainly by the nitrate concentrations (not shown).

At some sites,  $\text{NO}_3\text{-N}$  concentration exceeded the six-year river maximum (monitored monthly). These pools (6 in all) were considered to have an important source of water from some origin other than the river. The highest values of conductivity, sulphates and high alkalinity as well as lower temperatures in summer in these 6 pools indicate an intensive throughflow of underground water. The remaining 23 water bodies were assumed to be sourced by infiltrating river water. The flood index of these 23 pools correlated with biomass of diatoms ( $0.58$ ,  $P = 0.004$ ) abundant in the main stream plankton, and lotic species of diatoms (*Achnanthes lanceolata*, *Navicula lanceolata*, and *Navicula gregaria*; Poulíčková, 1997) were found there.

Some parameters also showed seasonal aspects (Fig. 3). High  $\text{NO}_3\text{-N}$  and oxygen were associated with spring (time of flooding), whereas high  $\text{NH}_4\text{-N}$  concentrations were associated with winter. Summer was characterised by higher chlorophyll *a*,  $\text{PO}_4\text{-P}$  and alkalinity.

### Plankton composition

Phytoplankton composition was very different compared to that of other types of shallow or deep lakes (Kylbergerová et al., 2002). Typical was the year-round prevalence of Cryptophyceae, (70% of algal biomass in the whole set of localities in September, 67% in January), namely species such as: *Cryptomonas curvata*, *C. marssonii*, *C. reflexa* and *Rhodomonas minuta*; abundance of Euglenophyceae (*Trachelomonas volvocina*, *T. volvocinopsis* and a variety of species of *Euglena* and *Phacus*); Dinophyceae; and Chrysophyceae (namely *Synura* spp., *Mallomonas* spp. and *Chrysococcus* spp.) In contrast, except for diatoms, the phytoplankton groups



**Fig. 3** RDA analysis of season as explaining variable (thick lines) and water chemistry as explained variable. First axis explains 4.5% of variability, second 0.1%. Monte Carlo permutation test for first axis:  $F$ -ratio = 13.144,  $P = 0.004$

typical of eutrophic shallow lakes were either quite rare (Cyanophyceae contributed up to 2%) or were remarkably less abundant (green chlorococcal algae contributed up to 10%). The species richness for the whole set of water bodies was high, especially for green algae (66 species) and the flagellate groups—Euglenophytes (34 species) and Chrysophytes (16 species). Species richness per particular locality varied considerably from 4 to 42 species.

Zooplankton was collected in four sets of samples; 33 taxa of cladocerans and 30 taxa of rotifers were determined (copepods were not identified to species level). For the purpose of this analysis, the species were grouped in several distinguishable categories to simplify the dataset. In general the most relatively abundant were pelagial rotifers: species of genera *Anureopsis*, *Brachionus*, *Conochilus*, *Filinia*, *Gastropus*, *Hexarthra*, *Keratella*, *Notholca*, *Polyarthra*, *Pompholyx*, *Asplanchna*, *Synchaeta*, nauplii and copepodids, contributing together 75–90% to total individuals in zooplankton. Rotifers dominated in late summer (September, 39% of total count of zooplankton) and autumn (October 32%), whereas copepods including

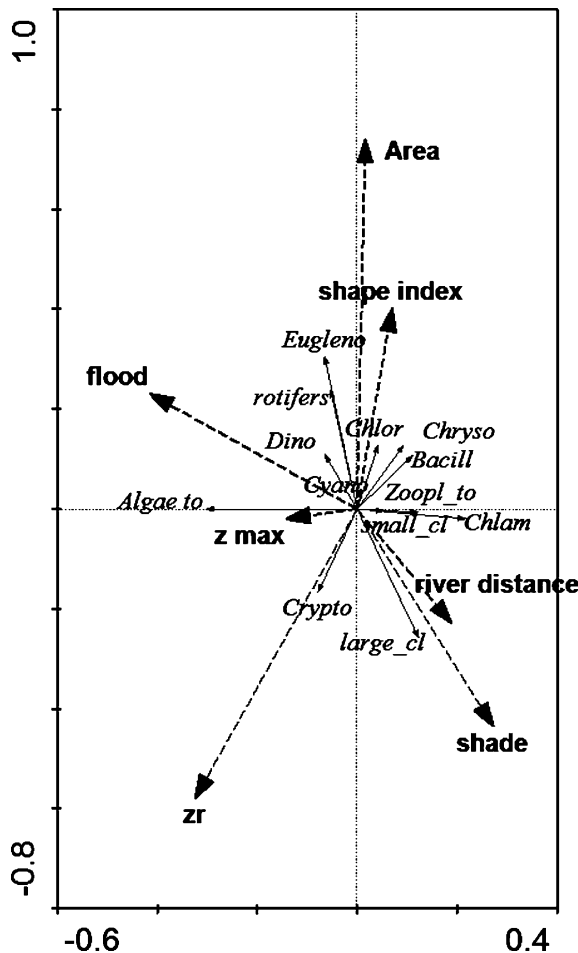
nauplii were most numerous in winter and spring (about 40%). Large pelagial cladocerans (*Daphnia longispina*, *Daphnia pulicaria*, and *Daphnia pulex*), littoral and surface cladocerans (*Sida* sp., *Simocephalus* sp., *Ceriodaphnia megops*, *C. reticulata*, *C. rotunda*, *Megafenestra* sp., and Chydoridae) were virtually absent in January, whereas small pelagic cladocerans (*Bosmina* sp., *Ceriodaphnia affinis*, *C. pulchella*, *Daphnia cucullata*, *Daphnia parvula*, *Diaphanosoma* sp. and *Moina* sp.) were at least present in May and otherwise held a stable share in the zooplankton assemblage.

#### Multivariate analysis of environmental parameters and plankton

RDA (Fig. 4) showed that shaded and relatively deep sites were associated with abundant Cryptophytes, significantly in the total dataset, January and May ( $r = 0.49$ ;  $P = 0.01$ ) and large cladocerans, whereas large sites were associated with chlorophyll *a*. Area significantly correlated with chlorophyll *a* in August and September ( $r = 0.44$ ;  $P = 0.008$ ), with euglenophytes (August,  $r = 0.67$ ;  $P = 0.00$ ), and was positively associated with green algae and Cyanophytes (significantly in total dataset,  $r = 0.79$ ;  $P = 0.00$ ), and rotifers.

CCA (not shown) tested the impact of season on phytoplankton groups and showed that Euglenophytes, diatoms and green algae were typical for summer, whereas Cryptophyceae and large cladocera were more typical in autumn.

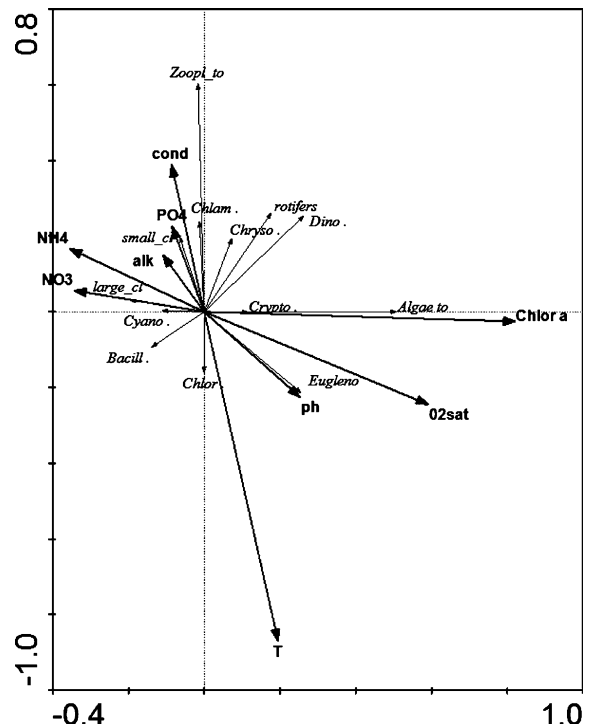
RDA used to model the relations of water chemistry parameters and plankton is shown in Fig. 5. A more detailed seasonal analysis (not shown) showed that surface oxygen saturation correlated in May with chlorophyll *a* ( $r = 0.43$ ;  $P = 0.02$ ) and with pH ( $r = 0.58$ ;  $P = 0.001$ ) but not with shade (at the beginning of May most leaves had not yet developed), indicating that the rapid growth of the algal spring bloom was the main source of oxygen in the water bodies. The correlation between the biomass of Chrysophytes (0.44;  $P = 0.02$ ) and Cryptophytes ( $r = 0.62$ ;  $P = 0.017$ ) as they reached their spring peak, supports this explanation. On the other hand, in summer, oxygen saturation correlated significantly with pH, chlorophyll *a* and negatively



**Fig. 4** RDA analysis of morphometry, shading, flooding and distance from river (explaining variables, dashed vectors) and plankton variables (relative contribution of groups to total biomass (phytoplankton) or count (zooplankton) as explained parameters. First axis explains 12% of variability, second 5%. Monte Carlo permutation test for first axis:  $F$ -ratio = 13.821,  $P$  = 0.102

with shade, whereas in October it correlated only with shade ( $r = -0.66$ ;  $P = 0.00$ ), indicating the reduction of photosynthesis as the day shortened and enhancing the role of sediment decomposition in the oxygen dynamics.

Concentrations of  $\text{NH}_4\text{-N}$  and  $\text{PO}_4\text{-P}$  (mostly mutually correlated, Fig. 2) were apparently bound to the oxygen regime as well. These variables were also associated with shade, a stronger correlation for  $\text{PO}_4\text{-P}$  (significantly correlated in September, January and October, and also for all seasons) than that for  $\text{NH}_4\text{-N}$  (significant only in September).



**Fig. 5** RDA analysis of water chemistry and temperature (explaining variables, thick lines) and plankton variables—relative contribution of groups to total biomass (phytoplankton) or count (zooplankton)—as explained variables. First axis explains 25% of variability, second 0.4%. Monte Carlo permutation test for first axis:  $F$ -ratio = 45.5,  $P$  = 0.002

Also a correlation between large pelagic daphniids and shade was repeatedly significant (in September  $r = 0.66$ ,  $P = 0.02$ ), indicating weak fish predation at these sites.

Cryptophyceae was the only algal group positively correlated with shade (significantly in September,  $r = 0.58$ ;  $P = 0.008$ , and in the total and average dataset); the other algal groups, both in terms of biomass and proportion, showed a tendency to correlate negatively with shade (mostly not significantly). Not surprisingly, shade restricted algal species number ( $r = -0.53$ ;  $P = 0.015$  in September).

## Discussion

### Concept of spatial and temporal heterogeneity

The data analysis indicated the mutual interplay of the different mechanisms that result in the

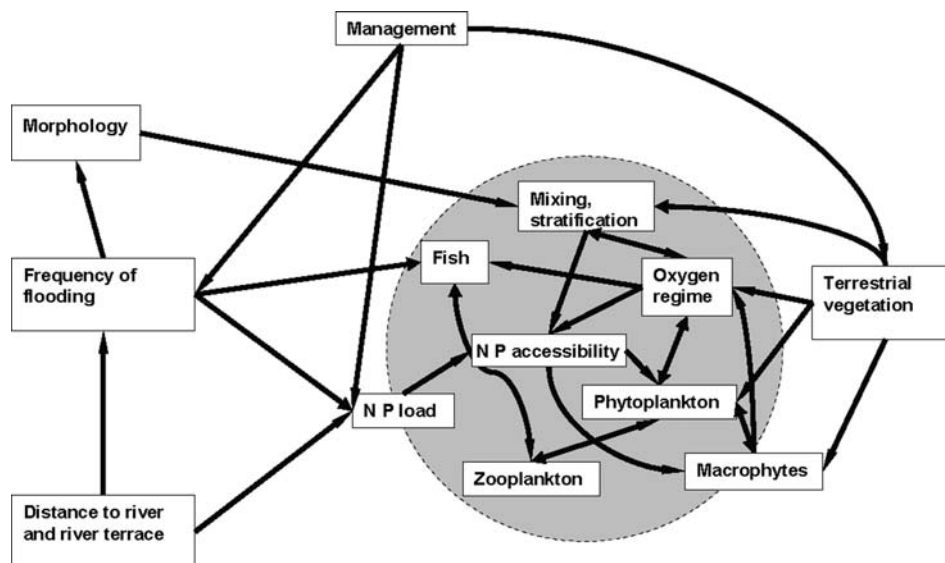
ecosystem diversity of the studied water bodies. Even if it is possible to explain the observed phenomena through the action of only one mechanism, it is more likely that other different mechanisms share a contribution to every phenomena, in different proportions from case to case or from time to time. To explain such a network of relations, we divide the factors driving the diversity among the studied localities into three groups (Fig. 6): (i) source of water: infiltration and flooding; (ii) morphology: area, shape and depth; and (iii) terrestrial vegetation: shading and leaf litter.

#### Source of water: infiltration and flooding

Ground water seeping to the floodplain water bodies through the permeable sandy alluvial sediments may flow in from either the main river stream or laterally from the elevated river terrace. The nutrient load of these two water sources is markedly different and thus their relative proportion in each case influences the alluvial water bodies substantially. Due to the adjoining intensive agriculture, the water seeping laterally has a much higher conductivity and concentration of  $\text{HCO}_3^-$ ,  $\text{NO}_3^-$ , and a relatively lower concentration of  $\text{PO}_4\text{-P}$ .

Perhaps somewhat surprisingly the river water is not the most important source of N and P for the studied sites. Correlation between water chemistry in the pools and the river is low most of the year, which indicates the prevalence of some other autonomous processes (Pechar et al., 1996). The high level of nutrients (N, P) in the pools can be considered the result of natural input and accumulation of allochthonous, mainly organic, matter from terrestrial vegetation.

An increasing discharge results in surface flow from the river channel to the adjacent ditches, oxbows and pools; later, the flooding of the whole floodplain connects the subsystems into one water body. The flood events influence the basic chemistry of floodplain waters, especially the concentrations of major ions. During a high discharge, their concentrations are usually diluted—with the exception of nitrates. With decreasing discharge and water levels, and even before the surface separation of water subsystems, a horizontal heterogeneity of water chemistry and plankton already appears, being accelerated by the subsequent surface separation of water bodies. Thus, the different spatial and temporal course of each flood causes a time shift in water chemistry and plankton development in different parts of the floodplain (Pithart, 1999).



**Fig. 6** Scheme of terrestrial–aquatic interactions in floodplain ecosystem complex. Grey circle indicates water bodies, dashed circle symbolizes the open character of the aquatic system



### Morphometry: area, shape and relative depth

The morphometry of any water body has a crucial impact on the mixing of the water column. Mixing was generally supposed to be poor throughout the entire set of studied localities. Even the relatively large oxbows have an elongated shape, curved character and elevated banks, preventing wind action. Larger and/or relatively shallower water bodies were better mixed -enhancing the growth of a wider spectrum of algal species.

Cryptophyceae, being well adapted to poor light conditions, also prospered well in the very stabilized water column, there occurring no water mixing to move the phytoplankton upwards to the light (Reynolds, 1984). As efficient swimmers among flagellates, they are able to locate themselves according to light conditions and nutrient gradients (Jones, 1988). Cryptophyceae dominate throughout most of the year in waters whose trophic status are very different, but which have a poorly mixed (and often shaded) water column (e.g., in Finish forest lakes: Smolander & Arvola, 1988; Lužnice river floodplain: Pithart, 1997; karstic lakes in Catalonia: Pedrós-Alió & Guerrero, 1993; and lakes covered with macrophytes: Blinn & Green, 1986, Izaguirre et al., 2004).

Planktic cyanobacteria frequently predominate in shallow eutrophic lakes all over the world (Scheffer, 1998), just as in the Třeboň basin (Pechar et al., 2002). They are well adapted to low light conditions and, similarly as with *Cryptophyceae*, they are able to regulate their position in the water column. However, unlike *Cryptophyceae* and other phytoplankton groups, *Cyanophyceae* were much less abundant in the alluvial pools, a fact that can be explained by the low pH of the alluvial waters. A similar disappearance of blue-greens as a result of a decrease in pH has been described by Shapiro (1984). Moreover, the decomposition of different plant materials, as for example barley straw (Barret et al., 1999), can restrict the development of *Cyanophyceae* and may favour the mixotrophic flagellates (Jones, 1988).

The impact of fish should also differ substantially between larger and smaller water bodies. Oxygen in large oxbows is never depleted throughout the whole water column; a better

oxygen saturation in winter and more frequent flooding (long oxbows have a closer connectivity with the river) can enhance the fish population. The distinctive zooplankton structure in large pools may serve as indirect evidence of the impact of fish: large pelagic cladocerans are virtually absent in the pelagial and small cladocerans contribute very little. In the littoral zone, however, small pelagial cladocerans significantly correlate positively with area, indicating the growing fish impact that results in the change of spatial distribution of zooplankton, as they seek refuge among macrophytes (Timms & Moss, 1984).

Pelagic rotifers most contribute to the zooplankton in large pools, correlating significantly and consistently with chlorophyll *a* (for the whole set of localities). This phenomenon seems to be the effect of both a release from competition, when large filtrators are not present (Lampert & Rothhaupt, 1991, Urabe, 1992) and simultaneously the elevated concentration of suitable food (Merriman & Kirk, 2000).

Similarly, the absence of any significant correlation between those nutrients occurring in high concentrations and phytoplankton biomass may also indicate the frequent light limitation (Scheffer, 1998) and therefore the importance of such mechanisms as mixing.

### Terrestrial vegetation: shading and leaf litter

Terrestrial vegetation has a crucial impact on the chemistry and life in these water bodies. Permanent shading and nutrient-rich leaf litter affect the oxygen regime and water chemistry as a whole, macrophyte development, fish survival, and consequently the whole structure of the plankton community (Fig. 6). Height and density of terrestrial vegetation on the banks and a pool's total area, determine the relative proportion of shaded area.

Shade restricts algal photosynthesis, resulting in lower oxygen production. At the same time, oxygen is consumed by decomposition: the amount of organic-rich leaf litter in the sediment would be expected to enhance this process. These two mechanisms have not been experimentally separated, but analysis of the seasonal aspects can help towards understanding which one is more

important in which situation for determining the final oxygen concentration.

Oxygen tends to be depleted under the ice cover in shaded small pools; therefore fish cannot survive in these localities and large filtrators are not consumed. On the other hand, larger pools with a longer, more twisted shoreline may support more fish, which would relieve the pressure of food competition for smaller cladocerans as fish graze on larger species. Poor mixing, shade, and humic substances leaching from the leaf litter, are all different mechanisms that again result in poor light conditions in the water column, to which most algal species are unable to adapt.

**Acknowledgements** This study was financially supported by Research Projects AV0Z60870520 and MSM 6007665806 of the Ministry of Education, Youth and Sport and projects of the Czech Grant agency GAČR 206/01/1113 and Ministry of Environment VaV - SL/1/6/04. We are obliged to Martina Kylbergerova for help with phytoplankton counting and Steve Ridgill for language corrections.

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