Coupling of seasonal variations in the zooplankton community within the limnetic and littoral zones of a shallow pond

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Abstract – Seasonal dynamics of zooplankton were investigated in three different habitats of the shallow and temperate Kačležský pond (Czech Republic) during 2003–2004. The studied habitats included the limnetic zone and two littoral zones, each dominated by a different type of emergent macrophyte, reed grass (*Glyceria maxima*) and common reed (*Phragmites australis*). Species richness (calculated as number of taxa) was higher in both littoral zones than in the limnetic zone. The seasonal development of limnetic and littoral zooplankton communities differed. In contrast to the two littoral zones, close correlation with chlorophyll-*a* concentration was found for rotifers and cladocerans in the limnetic zone. Moreover, cladocerans inhabiting littoral areas (mainly *Bosmina longirostris*) reached annual maxima during spring when chlorophyll-*a* concentrations were low.

Key words: Limnetic zone / littoral zone / seasonal succession / shallow lake / zooplankton

Introduction

There are only a few lakes of natural origin in the Czech Republic, but the landscape is rich in man-made aquatic habitats (*e.g.*, reservoirs or carp ponds). Among these artificial systems, the several centuries long tradition of carp breeding has led to the establishment of many man-made carp ponds, which are still widely used for fish production. The majority of the carp ponds are shallow and exhibit characteristics highly similar to those of shallow lakes. The maximum depth of the shallow ponds is usually a few metres and, generally, the sediment of the extensive near-shore area is located in the photic zone (Padisák and Reynolds, 2003). Although there is no "true" pelagial area in the centre of such a pond, a limnetic zone differing from littoral areas occurs. Littoral zones are characterized by the presence of beds of submerged and emergent macrophyte vegetation forming complex microhabitats inhabited by benthic and planktonic assemblages discrepant from those occurring in the limnetic zone (Gliwicz and Rybak, 1976). The seasonal succession of macrophyte vegetation influences both biotic (*e.g.*, Jeppesen *et al.*, 1997; Castro *et al.*, 2005) and abiotic

(*e.g.*, Horppila and Nurminen, 2001; Joniak *et al.*, 2007) conditions in littoral zones.

The role of zooplankton in ponds is of great importance. The current state of the zooplankton community can help us to assess the ecological quality of shallow lakes. Large-bodied zooplankton could be more efficient in grazing on phytoplankton. Their presence in the lake can indicate the trophic structure (notably presence and/or absence of zooplanktivorous fish) (Hrbáček, 1962). Reduction of phytoplankton through the filtration activity of zooplankton grazers enhances water quality, thus helping to restore the often eutrophic shallow lakes (Beklioğlu, 1999; Moss, 2007).

The spatio-temporal distribution of zooplankton in shallow lakes has been widely studied in recent decades (*e.g.*, Cryer and Townsend, 1988; Lauridsen *et al.*, 1996; Smiley and Tessier, 1998; Nurminen and Horppila, 2002; Rybak and Węgleńska, 2003; Romare *et al.*, 2003). According to its predominant incidence, zooplankton species may be divided into littoral or limnetic specialists (Smiley and Tessier, 1998) or species occurring in both environments, but with a preference for either the littoral or limnetic zone (Cryer and Townsend, 1988). Diel horizontal migration, described in some shallow lakes (Van de Meutter *et al.*, 2005), implies that the density of many zooplankton species varies between limnetic and

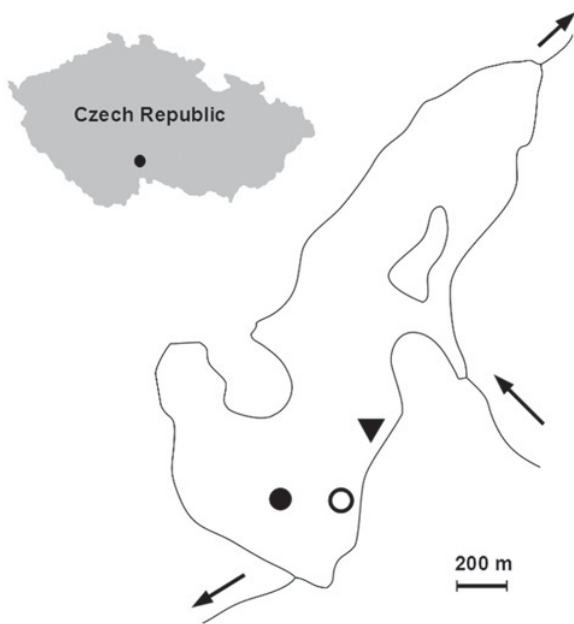---

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Fig. 1. Schematic map of the study site, Kačležský pond, and three sampled habitats – the limnetic zone (full circle), the reed grass-dominated littoral zone (blank circle) and the common reed-dominated littoral zone (full triangles). An inflow and outflows are represented with an arrow.

littoral zones during the day. The central role of macrophytes is crucial for the horizontal migration hypothesis since they may provide daytime refuge for large-bodied zooplankton from fish predation (Burks *et al.*, 2001). Horizontal migration has been recorded even when macrophytes are absent in the littoral zone (Węgleńska *et al.*, 1997). Knowledge of the reasons for the changing distribution along the horizontal gradient remains scarce (as reviewed in Burks *et al.*, 2002).

In this study, seasonal succession of zooplankton species was observed in Kačležský pond during a two-year cycle of fish production (2003–2004). The carps are seeded in the spring and harvested in the autumn of the following year. The objectives of this study were (1) to explore the variation of zooplankton in the limnetic as well as the littoral zones of a water body dominated by different emergent macrophytes and (2) to explain the causes of these inter-habitat differences through multivariate analysis.

Material and methods

Study site

The study was conducted in the man-made Kačležský pond, which was established in 1544 and is located at an altitude of 539 m a.s.l. 120 km south from Prague, Czech Republic, Central Europe (49°5′38.74″ N, 15°5′34.93″ E) (Fig. 1). With an area of 176 ha and a maximum depth of 4 m, the pond belongs to the smaller shallow water bodies.

Kačležský pond is surrounded by a mosaic of spruce forests and meadows. However, an agricultural farm situated on the north-west shore could potentially enhance nutrient loading. Three sampling points were established – one in a limnetic zone and two in the littoral zone featuring different types of dominant emergent macrophytes: reed grass (*G. maxima*) and common reed (*P. australis*), respectively. The *Phragmites* zone represents a typical emergent macrophyte vegetation with compact plant cover, while the *Glyceria* zone is formed by reed grass beds with small water pools around.

This study encompassed a two-year cycle of fish production (2003–2004). The fish biomass at the end of 2004 reached 437 kg.ha^{-1}. Common carp (*Cyprinus carpio*) constituted the major part (94.9%) of the fish production. The remaining 5% consisted of pike (*Esox lucius*) and pike perch (*Sander lucioperca*). In addition, we observed a shoal of *Pseudorasbora parva*.

Sampling and laboratory analysis

Sampling was conducted monthly from March to November 2003 and from April to November 2004 except in summer of the first year (June–August) when fortnightly intervals were used. Temperature, dissolved oxygen concentrations, pH and conductivity were measured with a WTW Multi 340i probe (WTW, Germany) near the water surface. Total phosphorus (TP), ammonium, nitrate, nitrite and organic nitrogen were analysed three times in 2003. TP and ammonium were measured along the water column profile (each 0.5 m starting at the surface) and transparency was determined using a Secchi disc on the shady side of a boat. From each sampling site, a 1-L water sample was taken for laboratory extraction of chlorophyll-*a* according to Lorenzen (1967). Emergent littoral macrophytes were described as above water vegetation cover. Zooplankton was sampled approximately at the same time of day during morning hours. Limnetic crustaceans were sampled by vertical hauls with a 200 μm Apstein net on 2–3 occasions depending on the quantity of zooplankton in the sample. Rotifers were collected by integration of samples from 0, 1, 2 and 3 m depth using a van Dorn sampler tube (with a volume of 6.25 L) and concentrated through a 40 μm mesh size plankton net into a 100 mL polyethylene bottle. To avoid difficulties with sampling using the plankton net among emergent macrophytes, both crustaceans and rotifers were sampled by the van Dorn sampler. Three volumes of the sampler tube were taken in the littoral zones. In all samples, zooplankton specimens were narcotized by adding carbon dioxide (soda water) to prevent contraction of soft-bodied organisms. The samples were preserved in 4% formaldehyde solution. Occasionally, qualitative samples were collected for detailed determination of zooplankton species. In the laboratory, subsamples were examined and counted in an open Sedgwick–Rafter cell using a light microscope (Edmonson, 1971).

Table 1. Phosphorus and nitrogen availability in Kačležský pond during 2003. All concentrations are in mg.L^{-1}.

Date	NH$_4$-N	NO$_3$-N	NO$_2$-N	N$_{org.}$	TP
28.5.2003	1.352	0.221	0.048	2.600	1.322
15.7.2003	0.078	< 0.113	< 0.003	2.100	0.165
18.8.2003	0.069	0.104	< 0.003	1.900	0.193

Statistics

Data on zooplankton densities were transformed by log $(x + 1)$ for further analysis (ANOVA, regressions) to avoid problems concerning assumptions of ANOVA and absence of species (*e.g.*, absence of adult copepods in littoral zones). One-way ANOVA with *post hoc* Fisher LSD tests allowed us to determine habitat preferences of zooplankton species. Assumptions of ANOVA (normality, homogeneity of variances) were also tested. In each of the three studied habitats, relationships between abiotic factors and zooplankton were determined by linear regressions. The percentage of explained variation was based on R^2.

The impact of environmental variables on species abundances was investigated by direct gradient analysis using Canoco 4.5. Species datasets expressed as absolute densities in ind.L^{-1} were transformed by log $(x + 1)$ and centred by species. Considering the length of the gradient determined by detrended canonical correspondence analysis (DCCA), corresponding to the linear method, redundancy analysis (RDA) was used to determine correlations between species abundances and environmental characteristics (Lepš and Šmilauer, 2003). Significances of explanatory variables and canonical axes were tested by the Monte Carlo permutation test ($\alpha = 0.05$). Permutations were done under the full model with 999 permutations and considering the temporal structure of the dataset. Moreover, to eliminate the influence of time, sampling dates were set as co-variables. Environmental variables included in the model were selected using forward selection. An affiliation to each of three selected sampling points was expressed by coding habitats as dummy variables. For better orientation in the final ordination, the species fit range was set from 10% to 100%. More details about multivariate analysis are given in Lepš and Šmilauer (2003).

Results

Abiotic factors and chlorophyll-*a* concentration

TP concentrations exceeded 1 mg.L^{-1} in May 2003, while balancing around 0.2 mg.L^{-1} for the rest of the year (*cf.* Table 1). Three peaks in chlorophyll-*a* concentrations occurred in the limnetic zone in 2003 followed by a gradual increase in 2004 (excepting a decrease in May). The highest concentration of chlorophyll-*a*, corresponding to a considerable reduction in Secchi depth, was observed in July 2003 (Fig. 2). The summer of 2003, especially July, was very dry, with temperatures ranging above the long-term average. The annual mean chlorophyll-*a* concentration was 80.4 µg.L^{-1} in 2003 and 39.3 µg.L^{-1} in 2004. In both years, minimum chlorophyll-*a* concentrations were observed in spring. According to the Secchi disc maxima, this corresponds to the clear water period.

The physico-chemical characteristics measured did not vary between the studied habitats (Table 2). Temperature stratification did not establish in either 2003 or 2004. In the limnetic zone, the temperature was 3.7 °C at the end of October 2003 and 25.3 °C in June 2003. In spring, both littorals were warmer than the limnetic zone during limited periods exhibiting a temperature increase, but the increase was not significant over the season. Temperatures in the reed grass and common reed beds were 1.98 and 1.63 °C higher, respectively, than in the limnetic zone during the first year. Due to the limited number of sampling dates, 2004 cannot be divided into seasons. Summer and autumnal temperatures were similar in the surveyed habitats.

The seasonal pattern of dissolved oxygen showed an anoxic layer with a maximum thickness of 80 cm from June until the end of the season in 2003. A similar anoxic layer was observed in 2004, but only during June–July. Conductivity fluctuated between 132 and 145 µS.cm^{-1} in the limnetic zone and did not change considerably in the two littoral zones either (133–148 µS.cm^{-1} among common reed and 132–147 µS.cm^{-1} among reed grass). pH rose with photosynthetic activity in summer, the maximum value of all sampling sites being 9.8 in the open water zone in July 2003.

Species diversity

A total of 69 zooplankton species were identified at the study site. A checklist distinguishing between the limnetic and the two littoral zones is given in online supporting material at http://www.limnology-journal.org. Some of the taxa listed in the table (*Lecane bulla*, *Scaridium longicaudum*, *Camptocercus rectirostris* and *Macrocyclops albidus*) occurred in the pond, but outside our surveyed sampling sites, and were therefore omitted from the statistical analysis.

The seasonal dynamics of rotifers, cladocerans and copepods (which were divided into two subgroups – adults and developmental stages) indicated differences between the limnetic and littoral zones (Fig. 2). The limnetic zone was dominated by rotifers (*Anuraeopsis fissa*, *Brachionus angularis*, *Collotheca* sp., *Keratella cochlearis*, *Polyarthra dolichoptera* and *Pompholyx sulcata*) and cladocerans (*Bosmina longirostris*, *Daphnia galeata*, *Eubosmina coregoni* and *Chydorus sphaericus*). Dominant copepods
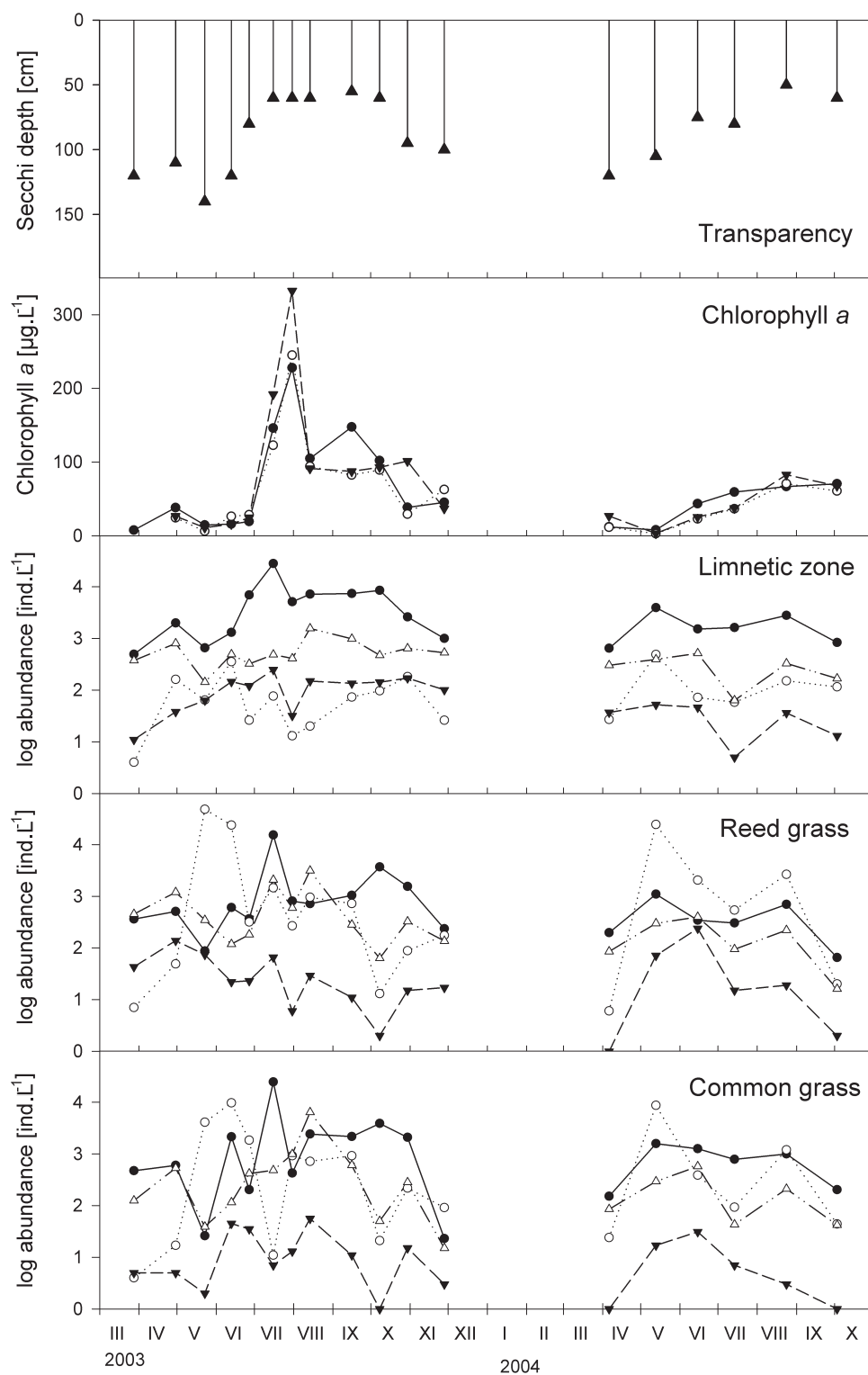
Fig. 2. Seasonal dynamics of rotifers (full circles), cladocerans (blank circles) and copepods (adults – full triangles, developmental stages – blank triangles) in three different sampling sites of Kačležský pond during the years 2003 and 2004. Two upper graphs represent changes in Secchi depth and chlorophyll-*a* concentrations (full circle – limnetic zone, blank circle – littoral zone dominated by reed grass, triangle – littoral zone dominated by common reed).

were *Cyclops vicinus*, *Eudiaptomus gracilis* and two summer species, *Acanthocyclops einslei* and *Thermocyclops crassus*. *K. cochlearis* was a dominant rotifer in both

littoral zones, while *Polyarthra dolichoptera* occurred mainly in the common reed littoral. The cladocerans *B. longirostris*, *Ceriodaphnia quadrangula* and *C. sphaericus*

Table 2. Physico-chemical parameters of Kačležský pond in 2003 and 2004. Year-long mean value ± standard error (N). Limnetic zone is represented by data measured near the water surface. Fractionation of chlorophyll-a was performed only in the open water zone.

	2003			2004		
	Limnetic zone	Reed grass	Common reed	Limnetic zone	Reed grass	Common reed
Total chlorophyll-a (µg.L^{-1})	75.6 ± 69.9 (12)	73.64 ± 67.74 (11)	91.99 ± 96.02 (11)	43.29 ± 27.52 (6)	34.14 ± 27.1 (6)	40.51 ± 29.53 (6)
Chlorophyll-a <40 µm (µg.L^{-1})	59.83 ± 44.85 (11)			33.45 ± 21.96 (6)		
Dissolved oxygen (mg.L^{-1})	10.66 ± 3.26 (10)	9.31 ± 2.61 (10)	9.72 ± 3.59 (10)	7.03 ± 2.85 (7)	5.39 ± 3.69 (5)	5.23 ± 3.08 (4)
Conductivity (µS.cm^{-1})	136.18 ± 2.14 (11)	135.55 ± 2.25 (11)	137 ± 3.32 (11)	140.33 ± 2.8 (7)	141.83 ± 2.99 (6)	141.33 ± 3.78 (6)
pH	8.03 ± 1.11 (11)	7.9 ± 1.17 (11)	8.05 ± 1.21 (11)	6.9 ± 0.34 (7)	6.88 ± 0.28 (6)	7.14 ± 0.36 (6)
Temperature (°C)	15.53 ± 7.34 (11)	16.12 ± 7.5 (11)	16.04 ± 7.48 (11)	15.25 ± 4.68 (7)	15.07 ± 4.72 (6)	15.43 ± 4.74 (6)
Secchi depth (cm)	88.33 ± 29.72 (12)			81.67 ± 26.58 (7)		

were found in both the common reed and reed grass areas of the littoral zone. Dominant copepod species could only be determined in the limnetic zone, because they were not found in sufficient numbers in the littoral zones.

Species diversity, presented as the number of taxa inhabiting a particular habitat, decreased in the order rotifers – cladocerans – copepods (Fig. 3). Both littoral zones housed more species than the limnetic zone. A slightly higher number of species were found in 2004.

Seasonal dynamics

In spring 2003, we observed a maximum of net zooplankton followed by a decrease in cladocerans and rotifers in the limnetic zone. In contrast, copepod densities increased up to 247 adults per litre in July 2003. However, this pattern was triggered by variations in the copepod species composition, namely the occurrence of two summer genera, *Acanthocyclops* and *Thermocyclops*. After a decline at the end of July 2003, copepod densities remained around 140 ind.L^{-1} until the end of the year. The results of linear regression analysis indicated a strong positive relationship between limnetic adult copepods and rotifers ($R^2 = 0.31$; $F_{1,16} = 8.65$; $P < 0.01$), as well as between adult copepods and their own developmental stages ($R^2 = 0.42$; $F_{1,16} = 13.15$; $P < 0.01$). These relationships constitute, however, the only two significant regressions found in the limnetic zone. The chlorophyll-a maximum of July 2003 was well correlated with rotifers, which were entirely dominated by *K. cochlearis* (Table 3). The consecutive decrease in zooplankton in late July 2003 comprised all zooplankton groups. Limnetic rotifers were positively correlated with chlorophyll-a concentrations, but this relation was not confirmed for the littoral rotifer community (Table 3). A third annual peak in rotifers during the first year was observed in autumn, while the density of other groups decreased. The following year was characterized by spring and autumn maxima of zooplankton and a summer minimum, occurring at the same time of year as in the previous year. In contrast to 2003, there was no extreme peak in chlorophyll-a (as an available food) in summer 2004 (*cf.* Fig. 1).

The seasonal dynamics in littoral zones did not show as a harmonious trend as in the limnetic zone. The greatest difference was recorded in the annual maxima of cladocerans occurring in May and June in both littoral zones in both years. The small cladoceran *B. longirostris* constituted the main proportion of these peaks. Cladoceran abundance in the limnetic as well as the littoral zones increased utilizing a spring maxima of phytoplankton at the end of April. After *Bosmina* abundance peaked (up to 48 000 ind.L^{-1} in 2003), a decline to densities two orders lower occurred. These peaks appeared when chlorophyll-a concentrations were low and when all zooplankton in the open water reached minimum values. The increase in *B. longirostris* was well correlated with increasing cover of reed grass ($R^2 = 0.83$; $F_{1,5} = 31.03$; $P < 0.01$) and common reed ($R^2 = 0.76$; $F_{1,5} = 20.45$; $P < 0.01$). Another small
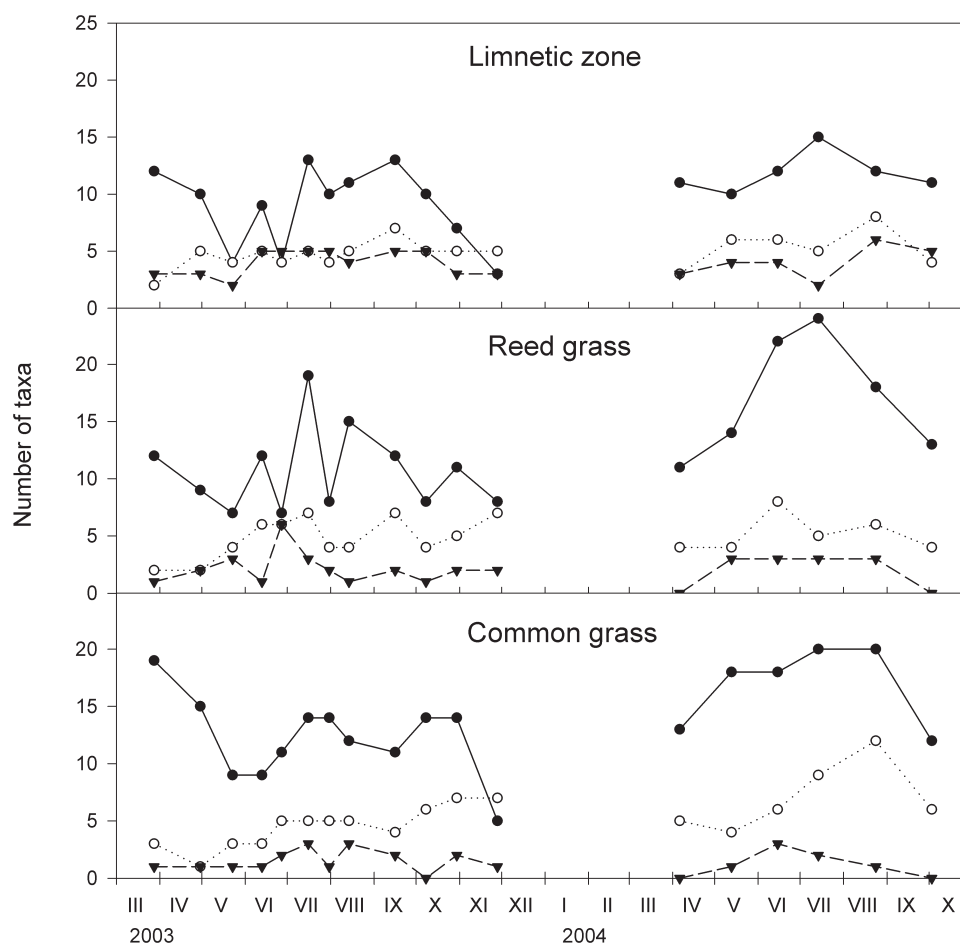
Fig. 3. Number of taxa of rotifers (full circles), cladocerans (blank circles) and copepods (adults – full triangles) in three different sampling sites of Kačležský pond during the years 2003 and 2004.

littoral cladoceran, *C. quadrangula*, constituted the exception from the above-mentioned decrease by having a July peak among reed grass in 2003. The same pattern (but in lower densities) was observed in the subsequent year. *C. quadrangula* densities were lower in common reed than in reed grass.

Crustaceans had additional maxima in the littoral areas in August of both 2003 and 2004. Subsequently, and opposite to the pattern observed in the limnetic zone, crustaceans decreased until an October minimum. A remarkable increase in *D. galeata* abundance occurred – reflected by a gradual increase from March (1 ind.L^{-1}) to the first half of June 2003 (301 ind.L^{-1}) in the limnetic zone followed by a sudden decrease in the second half of June (9 ind.L^{-1}). A different trend was noticed in both littoral regions for *D. galeata*. Densities exceeded 630 ind.L^{-1} in May (the corresponding figure being 58 ind.L^{-1} in the limnetic zone) and declined to values around 20 ind.L^{-1} by the end of June.

In 2003, the annual maximum of rotifers occurred in July in both littoral zones. Rotifers peaked in June 2003, density being highest in common reed where *Polyarthra dolichoptera* was dominant. In contrast to littoral crustaceans, littoral rotifers did not exhibit a decline in densities

in November 2003, but reached a similar autumn maximum as in the limnetic zone. This pattern was also observed in November 2004, but further progress was interrupted by pond fishing. Adult copepods were found in much lower abundances in the littoral than in the limnetic regions. In contrast to the limnetic zone, where rotifers were always predominant, crustaceans were notably represented in the littoral assemblages. The relationship between adult copepods and rotifers observed offshore was substituted by a positive correlation in the littoral zones between adult copepods and cladocerans ($R^2 = 0.27$; $F_{1,15} = 6.77$; $p = 0.02$ for reed grass; $R^2 = 0.24$; $F_{1,15} = 6.11$; $p = 0.03$ for common reed). Developmental stages of copepods were also closely correlated with adults ($R^2 = 0.46$; $F_{1,15} = 14.71$; $p < 0.01$ for reed grass; $R^2 = 0.33$; $F_{1,15} = 8.93$; $p < 0.01$ for common reed). Although sampling was less intensive in the second study year, seasonal dynamics were highly similar to 2003.

The ordination plot of the redundancy analysis of zooplankton species and environmental factors (dissolved oxygen level, pH, temperature, conductivity and chlorophyll-*a* concentration) is presented in Figure 4. The separation among the limnetic zone and both littoral zones is clearly shown in the biplot. The whole RDA model

Table 3. Linear regression analyses between abiotic factors and densities of rotifers, cladocerans, adult copepods and developmental stages of copepods in all studied habitats (columns are expressed as R^2). Significant correlations are indicated as **$P < 0.01$; *$P < 0.05$.

|	Total chlorophyll-a	Chlorophyll-a < 40 μm	Dissolved oxygen	Conductivity	pH	Temperature	Secchi depth
Limnetic zone							
Rotifera	**0.40****	**0.40****	0.01	0.14	**0.30***	0.16	**0.45****
Cladocera	0.04	**0.25****	0.15	0.12	0.14	0.02	0.00
Cop. – adults	0.03	0.01	0.06	0.38	**0.30***	0.01	0.01
Cop. – dev. st.	0.06	0.05	0.10	0.03	**0.26***	0.01	0.04
Reed grass							
Rotifera	0.15		0.06	0.02	0.17	0.01	
Cladocera	0.03		0.19	0.02	0.05	**0.31***	
Cop. – adults	0.08		0.01	0.01	0.06	0.18	
Cop. – dev. st.	0.05		0.17	0.16	0.22	0.11	
Common reed							
Rotifera	0.09		0.07	0.08	0.15	0.05	
Cladocera	0.03		**0.34***	0.05	0.02	0.21	
Cop. – adults	0.01		0.06	0.01	**0.25***	**0.28***	
Cop. – dev. st.	0.18		0.03	0.11	**0.38****	0.19	
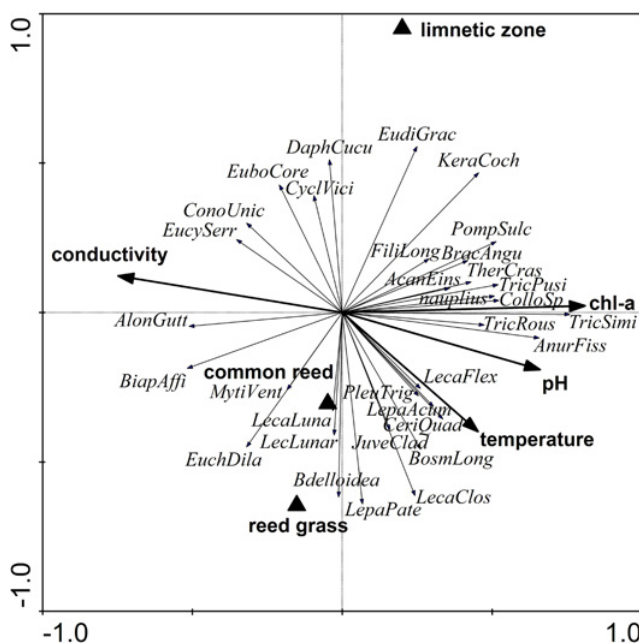
Fig. 4. Redundancy analysis (RDA) of abiotic factors (explaining variables, thick arrows) and zooplankton species as explained parameters. Sampling points were specified as nominal variables and are represented by centroids. The whole model explains 40.2% of variability (first axis explains 13.7%, second axis 8.7%). Monte Carlo permutation test: $F = 4.50$, $P = 0.01$. Species code are given in online supporting material at http://www.limnology-journal.org (JuveClad = juveniles of cladocerans, mostly daphnids; nauplius = copepod nauplii).

explained 40.2% of total variability ($F = 4.50$; $P = 0.01$), the first canonical axis 13.7% and the second axis 8.7%. All environmental variables, except dissolved oxygen, explained a significant ($P \leq 0.05$) part of the species data variation. Even though conductivity did not change

through seasons and ranged around 138 μS.cm^{-1} at all three sampling sites, it remained significant. Dissolved oxygen, on the other hand, changed strongly through the day. The calanoid copepod *E. gracilis* and the cladoceran *Daphnia cucullata* exhibited close relation to the limnetic zone and their position in the biplot is in contrast to littoral species. Increasing chlorophyll-*a* concentration in summer, together with increasing pH (and temperature), enhanced the abundance of species like *A. fissa*, *B. angularis*, *P. sulcata*, *Trichocerca* spp., *A. einslei*, *T. crassus* and the naupliar stages of copepods. The arrow representing the concentration of chlorophyll-*a* is situated between the limnetic and littoral zones, indicating relatively similar phytoplankton abundances in all habitats. Species typically living among or attached to aquatic plants, such as bdelloid rotifers, *Euchlanis dilatata*, *Lecane* spp., *Lepadella patella*, *Alona* spp., *C. quadrangula* or *Pleuroxus trigonellus*, are grouped around the triangles of "*Phragmites*" (common reed littoral zone) and "*Glyceria*" (reed grass littoral zone).

Discussion

Abiotic factors and chlorophyll-a concentration

The nutrient values and chlorophyll-*a* concentrations together with the low transparency classify Kačležský pond as a typical eutrophic water body. Generally, aquatic ecosystems, such as shallow carp ponds, are widely affected by eutrophication induced by enhanced nutrient input (Beklioğlu, 1999). In the case of Kačležský pond, the sources of eutrophication are derived from both the close surroundings (agriculture) and carp breeding. The chlorophyll-*a* maximum recorded in July 2003 was probably caused by the uncommonly high summer

temperatures in 2003 combined with lower flows and higher water retention time, allowing massive phytoplankton expansion. Kačležský pond did not show strong variation in either abiotic factors or water level fluctuation. The levels of physico-chemical parameters were similar between the limnetic and both littoral zones. The water surface is widely exposed to mixing by wind, which may have a strong effect on temperature stratification and zooplankton distribution within the pond. Thus, wind action may be the reason for the sporadic occurrence of some littoral zooplankton species in the limnetic zone (Lacroix and Lescher-Moutoué, 1995).

Species diversity

Rotifers were the most diverse zooplankton group in Kačležský pond (Fig. 3). Both littoral zones were inhabited by significantly more species than the limnetic zone. This is most probably due to the more structured microhabitats within macrophytes (Pejler, 1995; Radwan et al., 2003). The majority of the rotifer taxa identified in Kačležský pond belong to commonly occurring species in eutrophic water bodies (Bērziņš and Pejler, 1989). Small loricate Brachionids such as K. cochlearis or A. fissa often dominate the rotifer community (Vijverberg et al., 1993; Ejsmont-Karabin, 1995). Besides the regular occurrence of B. angularis, only two other Brachionus species were occasionally observed. More species of this genus generally occur in eutrophic shallow lakes (Beaver and Havens, 1996; Schöll, 2002). Lecane, Lepadella, Mytilina and Trichotria are genera whose species richness typically increases in littoral zones due to the habitat complexity provided by macrophyte vegetation (Castro et al., 2005).

Large-bodied crustaceans were restricted to D. galeata and copepods (C. vicinus and E. gracilis), apparently due to fish feeding (Okun et al., 2005). Macrophyte-associated taxa, mainly Chydoridae and species such as Diaphanosoma brachyurum and Sida crystallina, constituted a considerable part of the species richness. C. rectirostris and P. trigonellus were the only two chydorid species found in Kačležský pond whose occurrence did not exceed 20% in 66 European lakes in a study conducted by de Eyto et al. (2003).

Seasonal dynamics

In general, the seasonal dynamics of zooplankton in shallow Kačležský pond are in agreement with the PEG model of seasonal succession in eutrophic lakes, which proposed two phytoplankton peaks followed by zooplankton maxima (Sommer et al., 1986). While the PEG model was designed for deep water lakes, it describes general principles that are applicable for a wide range of permanent water bodies. In the second year of investigation, some exceptions from the model occurred, for instance the absence of spring zooplankton minima. These differences are probably due to the scarce sampling

events carried out in 2004. The second year of the two-year cycle of fish production was characterized by a decrease in total densities and species richness. One of the reasons may be a high fish stock and limited food availability for the cultured fish.

Our study showed that the coupling of seasonal dynamics between littoral and limnetic zooplankton communities was not as close as expected. The development of zooplankton in the limnetic and littoral zones exhibited different patterns despite seeming similarities. The abundance in the limnetic zone did not reflect abundances in the littoral zones and the transition from the limnetic to the littoral zone. An explicitly positive correlation exists between algal populations (chlorophyll-a concentration) and the densities of rotifers and cladocerans (Sommer et al., 1986). We confirmed this relation for the limnetic zone, but no such correlation was found for the two littoral zones. Horizontal gradients of habitats are also influenced by available food resources (Smiley and Tessier, 1998). Littoral zooplankton species can utilize limnetic seston as an equal food source, but limnetic taxa inhabiting littoral regions may experience difficulties in feeding on littoral seston (Smiley and Tessier, 1998). Although data are available on food availability in littoral zones (Rautio and Vincent, 2006), a comparison of food quality has not been recognized yet (Burks et al., 2002). One of the main dietary sources for littoral zooplankton is detritus (García et al., 2003). Next to detritus, planktonic organisms are able to feed on periphyton or benthic particles as an alternative source of food besides phytoplankton (Jeppesen et al., 2002). As a result, zooplankton may flourish even at low phytoplankton abundance. This could be one of the reasons why the small littoral cladocerans C. quadrangula and B. longirostris dominated the zooplankton community in the reed grass littoral. The reed grass littoral structure is not as uniform as in the common reed littoral and may therefore contain various alternative sources of food. Increasing macrophyte cover can form a space structure allowing the development of periphyton which may have induced the spring peaks in littoral cladocerans (cf. Fig. 2). There is a need to support this hypothesis by more detailed study aimed at possible food resources (particularly phytoplankton). Gliwicz and Rybak (1976) also recorded increasing B. longirostris and C. quadrangula densities among macrophyte stands. During our study, we observed B. longirostris densities of around 48 000 ind.L^{-1}. Straškraba (1967) recorded as many as 23 000 individuals in 150 mL, corresponding to 153 333 ind.L^{-1}. Bosmina, as well as some other cladocerans, probably tends to aggregate at food-rich places (Cerbin et al., 2003). Alternatively, a decrease in littoral chlorophyll-a concentration in spring can be driven directly by grazing of B. longirostris. Increased water clarity during the clear water state can enhance fish predation on large-bodied cladocerans and strengthen the dominance of Bosmina.

Littoral macrophyte vegetation may be used by zooplankton as a shelter against predation from zooplanktivorous fish (Burks et al., 2001). The littoral

zone can also serve as a refuge for planktivorous fish against predation by piscivores (Burks *et al.*, 2002; Okun *et al.*, 2005). Moreover, many piscivorous fish species feed planktivorously during their larval ontogenetic stages (Post *et al.*, 1997). During the day, larval fish tend to aggregate in the edge of the limnetic and littoral zones (Romare *et al.*, 2003). Perrow *et al.* (1999) have shown that also cladocerans use the edge or space among beds of macrophyte vegetation. Therefore, fish are responsible for a decrease in the grazing pressure upon primary production by reducing cladoceran densities to very low levels (Okun *et al.*, 2005).

The development of zooplankton communities in a shallow eutrophic pond differed between the limnetic and two littoral zones dominated by different species of emergent macrophytes. The results demonstrated that the presence and character of the littoral zone influence the composition and seasonal development of zooplankton. Although both systems are logically interconnected with a continuous transition zone, they reflect their own dynamics in terms of having a characteristic species pool as well as abundances of ecological groups.

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