



## Zooplankton Diversity and Correlations with Biotic and Abiotic Factors in Water Bodies in the Middle Danube River Basin, Hungary

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**Abstract:** Species composition and seasonal and spatial distribution of the crustacean zooplankton groups Cladocera and Copepoda were studied in two lake-type wetlands, the Mocskos–Danube and the Riha, and the Danube River at Mohács, located in the protected side of the Béda-Karapanca National Park in the Middle Danube River, Hungary. The investigations were carried out from April to October in 2014. A total of 23 crustacean species were found, 17 Cladocera and six Copepoda. The species richness was the lowest in the river and the highest in the isolated Riha Lake. The total abundance, especially of some cladoceran species, was the highest in the connected Mocskos–Danube Lake in the spring during the high waters. Positive correlations of zooplankton with the organic carbon, temperature and total phosphorus were found. The correlation with chlorophyll-a was negative, indicating strong grazing pressure on the phytoplankton. The bacterioplankton, which had the highest abundance in the spring, during the flood in May, had a weak negative correlation with Copepoda and positive one with the attached bacteria, and with the alien species *Eurytemora velox*. Cladocera negatively affected only the medium-sized free-living bacteria. The macrophyte species *Ceratophyllum demersum*, better developed in Riha Lake, probably as a better competitor led to N- and P- limitations for the phytoplankton and bacterioplankton, and due to the isolation from the river these plankton communities had less development in Riha Lake compared to the Mocskos–Danube and Mohács sites.

**Key words:** Zooplankton, *Eurytemora velox*, bacterioplankton, chlorophyll-a, relations, lakes in the Middle Danube River.

### Introduction

Riverine floodplains host exceptionally high biodiversity attributed to the high spatial and temporal heterogeneity (TOCKNER & STANFORD 2002, CHAPPARO et al. 2018). Crustacean zooplankton is a key community in the grazer and microbial food webs (HAVENS 1998, JÜRGENS & MATZ 2002, ZÖLLNER et al. 2003, ZSUGA 2015). Higher abundance of zooplankton in wetlands exists during the transitional phase between the flooding and the

stabilisation periods (JONIAK & KUCZYNSKA-KIPPEN 2016). Trophic interactions appear to play a minor role in the regulation of zooplankton, while water level fluctuation is the main driving force in shaping the zooplankton succession during the extraordinary hydrological cycles in shallow eutrophic floodplain lakes (CHAPPARO et al. 2011). Zooplankton should be more abundant and diverse in the floodplain lakes connected with a river (transitional lakes) than in the isolated ones (NAPIÓRKOWSKI et al. 2019). Species richness, diversity and population

density of zooplankton assemblages increase during the receding period in all types of water bodies except in the river eupotamal in the Danube Hungarian floodplains (SCHÖLL et al. 2012). The degree of wetland connectivity (isolation) to the main river and the macrophyte development are among the main and common factors explaining the spatial variations of physical and chemical variables, including the nutrients (N- and P- forms) of wetlands in the Middle and Lower Danube River (KALCHEV et al. 2014).

Between 2002 and 2013 (except 2005–2006 and 2010–2011) detailed investigations were carried out in the Gemenc-Béda-Karapanca floodplains of the Danube River (rkm 1497–1440), part of the Danube-Drava National Park (Hungary). The studies focused on the zooplankton assemblages (KAZAKOV et al. 2014, KISS et al. 2014, 2015), but also on other aquatic communities (TARJÁNYI & BERCZIK 2014) and hydrochemical factors (KALCHEV et al. 2014) in the water bodies with various connectivity to the main river. KISS et al. (2015) published on the presence and distribution of rare and alien microcrustacean species and on the species composition of different water bodies in the floodplain for that period (2002–2013). The zooplankton was not studied in the years characterised with extreme floods (high waters) along the Danube River (2005, 2006 and 2010) (MIKHAILOVA 2017), except during the flood in 2002. The heavy rainfalls and a flood in May 2014 enabled a comparison of the zooplankton diversity during the low and high waters at some sites in the Béda-Karapanca floodplain.

Bacterioplankton plays an important role in the microbial food web as a food source, in the utilisation of dissolved organic carbon, as well as in the decomposition of the dead organic matter, the remineralisation of nutrients and the self-purification in the aquatic ecosystems (COLE 1999, JÜRGENS & MATZ 2002, VADSTEIN et al. 2003, FREESE et al. 2007). Detailed information about the bacterioplankton in the Béda-Karapanca floodplain studied in 2014 was published by KALCHEVA et al. (2016).

With the present study we aimed to compare the species diversity and the density of crustacean zooplankton groups Cladocera and Copepoda in two wetlands, the Mocskos-Danube and the Riha, in the Béda-Karapanca floodplain, Hungary, with different connectivity to the Danube River, as well as in the river near Mohács, and to evaluate their possible correlations with the water physical and chemical factors, macrophytes and the other main plankton communities, bacterioplankton and phytoplankton.

## Materials and Methods

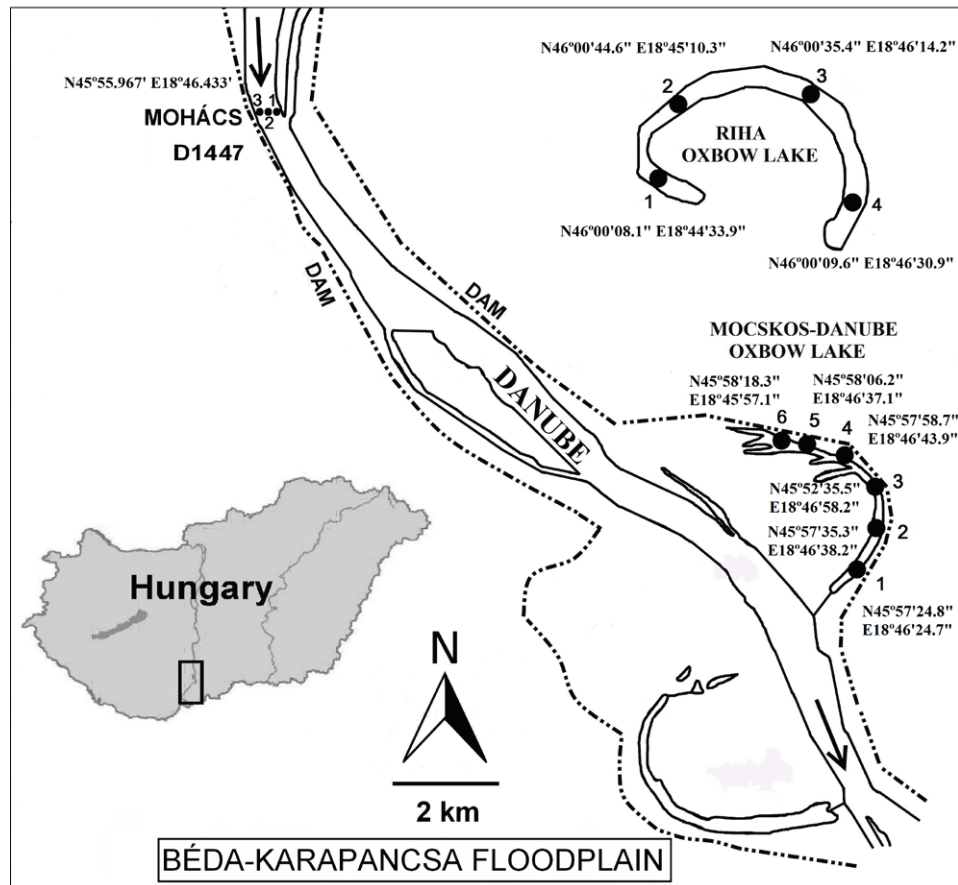
### Study area and sampling

Two lake-type wetlands, the Mocskos–Danube (MDU) and the Riha (RIH) were studied, both located in the protected side of the Béda-Karapanca National Park in the Middle Danube River, Hungary (Fig. 1). The investigations were carried out from April to October covering the spring, summer and autumn seasons in 2014. Parallel samples were taken from the main channel of the Danube River at Mohács (rkm 1447). This site was chosen to observe the differences in the biodiversity and the environmental factors in comparison to the adjacent wetlands. The dates of sampling at the three sampling sites, including 13 different points, were as follows: 7 April, 7 May, 8 July, 12 August, 9 September and 7 October 2014.

The Mocskos-Danube (MDU) (rkm 1442–1440) is situated in the active floodplain of the Béda-Karapanca area and is dominated by the native aquatic plant *Trapa natans*. The area is approximately 3.4 km long, 60 m wide, with shallow water (average depth of 1.5 m) and dense macrovegetation. It has a temporary connection with the Danube River, the water flowing at 700 cm (gauge of Mohács, rkm 1447) at the upper end, and at 550 cm at the lower end of the oxbow. The water of MDU flows rarely (1–5 times per year), and only for short periods of time. The sampling points were six, from MDU1 to MDU6 (Fig. 1). The samples at MDU3 were taken only in April and in May, when the flood happened and the side arm had the highest water level (points MDU1, 2, 4 and 5 were under the water). From July to October the points MDU1, 2, 4 and 5 were sampled, while the point MDU6 was sampled during all months.

The Riha Oxbow Lake (RIH) is located in the protected side of the floodplain and has no connection with the main channel. It is 4.5 km long and 80 m wide. The average water depth is approximately 1–1.5 m. It is a strictly protected nature reserve area covered by dense macrovegetation with dominance of the invasive alien species *Ceratophyllum demersum*. The sampling points were four: from RIH1 to RIH4 (Fig. 1). The point RIH1 was sampled only once, in May, while the other points RIH2, 3 and 4 were examined during all months.

The Mohács (MOH) is a lotic site from the main channel of the Danube River at Mohács (rkm 1447) (Fig. 1). Three points were sampled near the ferry harbour: MOH1, MOH2 and MOH3, respectively, to the left bank, middle part and right bank of the river (lateral profile).



**Fig. 1.** Study area in Béda-Karapanca floodplain, Hungary, and location of the sampling points at Mocskos-Danube (MDU: 1, 2, 3, 4, 5 and 6), Riha (RIH: 1, 2, 3 and 4) and Mohács (MOH: 1, 2 and 3), with the geographic coordinates.

The samples taken for the whole studied period were 61 in total (8 in April, 9 in May and 11 monthly in July – October) for each of the observed parameters, except for the zooplankton. The crustacean zooplankton samples, 48 in total, did not include the following points: MDU1 in July, August and September, MDU5 in July and August, MDU6 in May and August, RIH2 and RIH3 in May, RIH2, RIH3 and RIH4 in September and RIH2 in October.

The previous investigations in that area were carried out as follows: in 2012–2013 in Riha; in 2009, 2012–2013 in the Mocskos-Danube; and in 2007–2009, 2012–2013 in Mohács (Kiss et al. 2015).

#### Abiotic and biotic variables and methods

The zooplankton samples were collected by filtering 10–50 L of water from the surface through a 70  $\mu\text{m}$  mesh size net. The samples were immediately preserved in 4% formalin solution. Cladocera and Copepoda were enumerated by using inverted microscopy and the adult individuals were identified at species level according to DUSSART (1967, 1969)

and GULYÁS & FORRÓ (1999, 2001). The abundance was calculated in  $\text{ind. m}^{-3}$ .

The bacterioplankton samples were taken at 0.3 m under the surface layer, preserved in 2% formalin and stored in dark at 4°C. Bacteria were filtered through 0.2  $\mu\text{m}$  pore sized membrane filters and enumerated at 1600 $\times$  magnification with a phase contrast microscope after staining with erythrosine by the method of direct count (KALCHEVA et al. 2014, 2016). The bacterioplankton was counted separately for cells (cocci and rods) freely dispersed on the filter (free-living bacteria) and for cells that were associated with detritus particles (attached bacteria). The mean cell volume, the biomass and the cell size classes were calculated.

The chlorophyll-a (chl-a) by ISO Standard method (ISO 10260:1992) was measured, giving quantitative assessment of phytoplankton biomass (SANDU et al. 2003). The macrophyte cover (in %) was assessed using special sampling techniques (TARJÁNYI & BERCZIK 2014).

Thirteen water physical and chemical parameters were monitored simultaneously. The

water temperature, conductivity, pH, dissolved oxygen and oxygen saturation were measured in situ by WTW Multi 340i. In the laboratory the total organic carbon (TOC), the dissolved organic carbon (DOC) and the total nitrogen (TN) were determined by a TOC analyser (Elemetar-liqui-TOC). Standard analytical methods (GOLTERMAN et al. 1978) were used to determine the suspended solids, the nitrate and ammonium nitrogen ( $\text{NO}_3\text{-N}$ ,  $\text{NH}_4\text{-N}$ ), and the total and phosphate phosphorus (TP and  $\text{PO}_4\text{-P}$ ).

The statistical analyses ANOVA, Pearson's (r) and Spearman's ( $R_s$ ) correlations were performed by the Statistica 7.0 software package (STATSOFT INC. 2004). The triplot multivariate analysis (Redundancy analysis, RDA) was performed to find the relations between the response (zooplankton and bacterioplankton) and the environmental (abiotic and chl-a) variables at the three sampling sites, using the CANOCO for Windows 4.5 (TER BRAAK & SMILAUER 2002).

## Results

All physical, chemical and hydrobiological variables are presented in Table 1. There were significant differences between the wetlands when the environmental factors were compared. In the isolated Riha Lake the conductivity, TN, DOC and TOC were in higher concentrations, while the pH, oxygen content, concentration of  $\text{NO}_3\text{-N}$ ,  $\text{NH}_4\text{-N}$ ,  $\text{PO}_4\text{-P}$  (N- and P- forms) and the suspended solids had the lowest values compared to the connected wetland and the river. Chl-a concentrations were the lowest in the Riha and the highest in the Mocskos-Danube. The macrophyte cover (in %) included mainly the two species: the water chestnut (*Trapa natans*), and the hornwort (*Ceratophyllum demersum*). After the flood in May, *T. natans* was better presented (90%) only in MDU at points 1 and 2 in July. In MDU, *C. demersum* had patches at point 6 in April; it was absent in May, due to the high water level, and with 90% cover at points 5 and 6 in July. In Riha, *C. demersum* was present in July – September (Table 1). The macrophyte cover was related positively to the temperature ( $R_s=0.48$ ) and negatively to TN ( $R_s=-0.55$ ), indicating the need of the nitrogen-containing nutrients.

### Zooplankton abundance and species richness

The zooplankton abundance reached the maximum of 62,800 ind.  $\text{m}^{-3}$  with a mean value of 3,797 ind.  $\text{m}^{-3}$  ( $\pm 3,875$  ind.  $\text{m}^{-3}$  standard deviation (StDev)), differing between the sites (Table 1). Its lowest abundance was registered in MOH.

A total of 23 crustacean species were found, 17 Cladocera and six Copepoda. The species richness was the lowest in the river (MOH) – only four species of low numbers, while in MDU and RIH it was 16 and 19, respectively (Table 2). The most frequently occurring species in the wetlands were *Bosmina longirostris*, *Chydorus sphaericus* and *Simocephalus vetulus* among cladocerans and the cyclopoid *Eucyclops serrulatus*. The dominant species were different in RIH and MDU. The most abundant cladocerans were *Bosmina longirostris* in RIH, and *Chydorus sphaericus* and *Simocephalus vetulus* in MDU. The dominant Copepoda species were *Thermocyclops crassus* in RIH, *Eucyclops serrulatus* and *Acanthocyclops robustus* in MDU. *Macrocyclops albidus* was found only in MDU with relatively high abundance.

Two alien species were recorded, the chydorid cladoceran *Pleuroxus denticulatus* and the calanoid *Eurytemora velox* (Table 2). The former was found only in the Riha Lake with low abundance (in July and October), while the latter occurred in both lakes, with 23% on average of the total Copepoda abundance, with similar and relatively high values (mean and StDev: 111 $\pm$ 328 ind.  $\text{m}^{-3}$ ), which differ seasonally (ANOVA:  $p=0.02$ ), with maximum values in the spring (700 ind.  $\text{m}^{-3}$  in April in RIH and 1,900 ind.  $\text{m}^{-3}$  in May in MDU).

Seasonally the Copepoda abundance in MDU decreased from spring to autumn (ANOVA;  $p=0.02$ ), because of the spring maximum of *Eucyclops serrulatus*. In RIH the higher fluctuations were in the summer, however, to the opposite of MDU, the mean values increased from the spring to the autumn ( $p=0.03$ ). In the case of Cladocera, significant seasonal differences ( $p=0.0457$ ) were recorded only in MDU, with a spring maximum by *Simocephalus vetulus* and *Chydorus sphaericus*. In RIH, a summer maximum with dominance of *Bosmina longirostris* was found in August. In MOH, there were no significant differences in both the cladocerans and copepods. In addition to the seasonal distribution of the dominant Cladocera species mentioned above, *Daphnia cucullata* had its maximum in the spring, *Ceriodaphnia pulchella* and *Diaphanosoma brachyurum* reached their maximum in the summer, while *Moina brachiata* had its maximum in the autumn. In general, the Cladocera abundance had its maximum in the spring, decreasing till the autumn, while the Copepoda abundance had its maximum in the summer and higher values in the autumn. Only the abundance of Copepoda was statistically significant, increasing from MOH to RIH, while

**Table 1.** Physical, chemical and hydrobiological variables at the three studied sites (n – number of the samples) and significant correlation coefficients of zooplankton with the abiotic factors, chl-a and bacteria (Pearson's – r, with probability p: \*p<0.05, \*\*p<0.01, \*\*\*p<0.001; Spearman's – R<sub>s</sub>, p<0.05).

Sites	Riha Lake (n=19)	Mocskos–Danube Lake (n=24)	Mohács, the Danube River (n=18)	Correlations with the zooplankton
<b>Physical and chemical variables – mean (min–max)</b>				
Temperature (°C)	21.7 (16.2–30.1)	27.1 (21–32.7)	18.9 (16–26.3)	R <sub>s</sub> =0.51 (Copepoda)
pH	8.2 (8.1–8.7)	8.9 (7.7–9.85)	8.5 (8–8.73)	
Conductivity (µS cm <sup>-1</sup> )	788 (463–868)	284 (215–354)	426 (358–463)	
Dissolved oxygen (mg L <sup>-1</sup> )	9.06 (7.2–11.7)	11.5 (7.6–16.7)	10.46 (7.1–11.9)	
Oxygen saturation (%)	103 (88–120)	144 (100–188)	113 (100–120)	
TOC (mg L <sup>-1</sup> )	24.42 (22–25.4)	15.62 (11.6–25)	8.77 (8–9.5)	R <sub>s</sub> =0.82
DOC (mg L <sup>-1</sup> )	22.26 (19.6–25.7)	14.6 (12.7–17.9)	7.58 (6.5–9.3)	R <sub>s</sub> =0.75
Suspended solids (mg L <sup>-1</sup> )	5.7 (0.8–10)	13.85 (3.2–35.2)	18.6 (5.7–33.6)	
TN (mg L <sup>-1</sup> )	2.35 (2.1–2.75)	1.8 (1.54–2.25)	2.5 (2.15–2.93)	
TP (mg L <sup>-1</sup> )	0.057 (0.04–0.09)	0.08 (0.05–0.17)	0.066 (0.04–0.11)	r=0.54*; r=0.58** (Cladocera)
PO <sub>4</sub> -P (mg L <sup>-1</sup> )	0.024 (0–0.043)	0.05 (0.02–0.11)	0.036 (0.01–0.06)	r=0.44* (Cladocera)
NO <sub>3</sub> -N (mg L <sup>-1</sup> )	0.008 (0.004–0.014)	0.013 (0.011–0.015)	0.56 (0.005–1.65)	
NH <sub>4</sub> -N (mg L <sup>-1</sup> )	0.018 (0.014–0.02)	0.02 (0.01–0.03)	0.009 (0.001–0.024)	
<b>Hydrobiological variables – mean (min–max) or %</b>				
Phytoplankton biomass by chl-a (µg L <sup>-1</sup> )	10.9 (4.4–24)	22.7 (1.8–97.7)	31.3 (4.4–51.5)	R <sub>s</sub> = -0.47
Macrophyte cover (%)	<i>Ceratophyllum demersum</i> –70–90% July – September	<i>Trapa natans</i> – 90 % in July, points 1, 2; <i>C. demersum</i> – 90% in July, p. 5, 6	–	
Total zooplankton abundance (ind. m <sup>-3</sup> )	7,848 (480–16,400)	4,709 (20–62,800)	11 (0–75)	
- Cladocera (ind. m <sup>-3</sup> )	1,585 (100–9,960)	3,781 (0–55,300)	3 (0–25)	
- Copepoda (ind. m <sup>-3</sup> )	6,263 (380–14,940)	928 (0–7,500)	8 (0–50)	
Bacterioplankton (cells mL <sup>-1</sup> )	178,504 (81,187–405,987)	315,594 (100,627–692,951)	297,115 (92,622–426,520)	r=0.33* ( <i>E. velox</i> )

that of Cladocera, although with a maximum value in MDU, did not differ by sites in the river and the two lakes (Fig. 2).

Significant differences in the mean values of the total zooplankton (p=0.43) between the 13 sampling points of the three sites were not found (Fig. 3). However, the differences in the Copepoda (p=0.001) were significant, indicating the different conditions (habitats) for the copepods between the wetlands, as well as within the same wetland. Despite the lowest zooplankton abundance in MOH, often without zooplankton in the samples, a trend to an increase in the abundance of both groups was found (mainly in April) in the samples from the left side (MOH1) of the Danube River (Fig. 3).

### Zooplankton interactions with the environmental factors and chl-a

The Crustacean total abundance was correlated (by Spearman's tests) positively with the TOC and DOC (R<sub>s</sub>>0.7) and the T°C (R<sub>s</sub>>0.5) (Table 1). The total zooplankton and each of the two groups were negatively correlated with chl-a (R<sub>s</sub>>-0.45). The testing by Pearson's parametric tests showed positive relations of Cladocera with TP (r=0.58\*\*) and PO<sub>4</sub>-P (r=0.44\*), and of total zooplankton with TP (r=0.54\*) (Table 1).

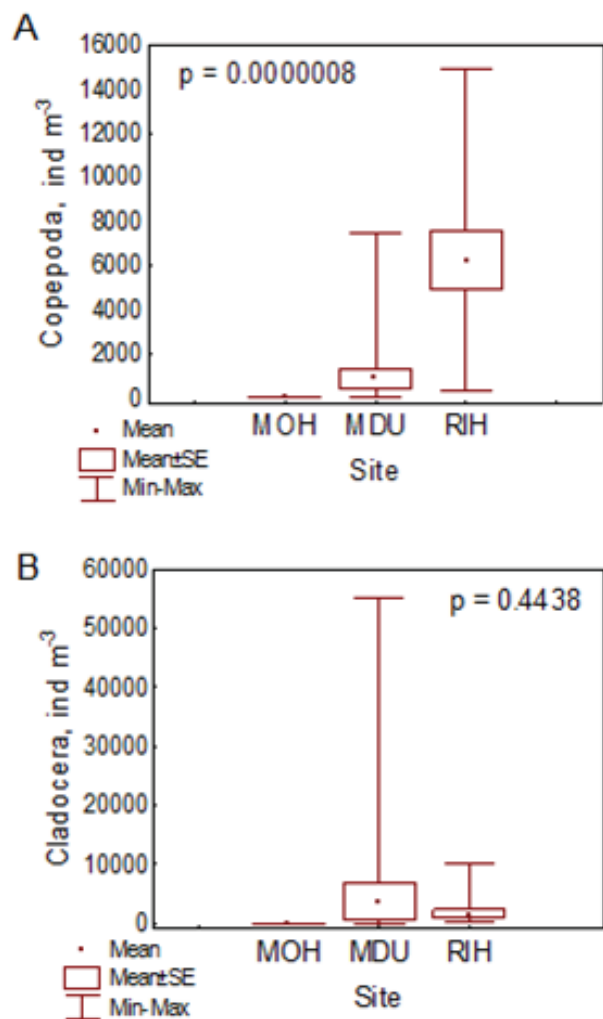
### Bacterioplankton and interactions with the environmental factors and chl-a

The bacterioplankton total number ranged from 8.12×10<sup>4</sup> to 6.93×10<sup>5</sup> (mean±StDev: 2.67±1.39×10<sup>5</sup>) cells.mL<sup>-1</sup> (Table 1, Fig. 3). The mean cell

**Table 2.** Species composition of crustacean zooplankton (Cladocera and Copepoda) in the studied lakes Riha (RIH) and Mocskos-Danube (MDU), and in the Danube River near Mohács (MOH) in 2014. Max – dominant species with the highest abundance; in bold – alien species.

Species	RIH	MDU	MOH
Cladocera			
<i>Acroperus harpae</i> (Baird, 1834)		+	
<i>Bosmina longirostris</i> (O. F. Müller, 1776)	max	+	
<i>Ceriodaphnia megops</i> Sars, 1862	+		
<i>Ceriodaphnia pulchella</i> Sars, 1862	+	+	
<i>Ceriodaphnia quadrangula</i> (O. F. Müller, 1785)	+		
<i>Chydorus sphaericus</i> (O. F. Müller, 1776)	+	max	+
<i>Daphnia cucullata</i> Sars, 1862	+	+	
<i>Daphnia longispina</i> (O. F. Müller, 1776)	+		
<i>Diaphanosoma brachyurum</i> (Liévin, 1848)	+	+	
<i>Disparalona rostrata</i> (Koch, 1841)			+
<i>Graptoleberis testudinaria</i> (Fischer, 1851)	+	+	
<i>Moina brachiata</i> (Jurine, 1820)	+		
<i>Pleuroxus aduncus</i> (Jurine, 1820)	+	+	
<b><i>Pleuroxus denticulatus</i></b> Birge, 1879	+		
<i>Pleuroxus truncatus</i> (O. F. Müller, 1785)	+		
<i>Scapholeberis mucronata</i> (O. F. Müller, 1776)		+	
<i>Simocephalus vetulus</i> (O. F. Müller, 1776)	+	max	
Copepoda			
<i>Acanthocyclops robustus</i> (Sars, 1863)	+	+	+
<i>Cyclops vicinus</i> Ulianine, 1875	+	+	
<i>Eucyclops serrulatus</i> (Fischer, 1851)	+	max	
<b><i>Eurytemora velox</i></b> (Lilljeborg, 1853)	+	+	
<i>Macrocyclus albidus</i> (Jurine, 1820)		+	
<i>Thermocyclops crassus</i> (Fischer, 1853)	+	+	+
Total	19	16	4

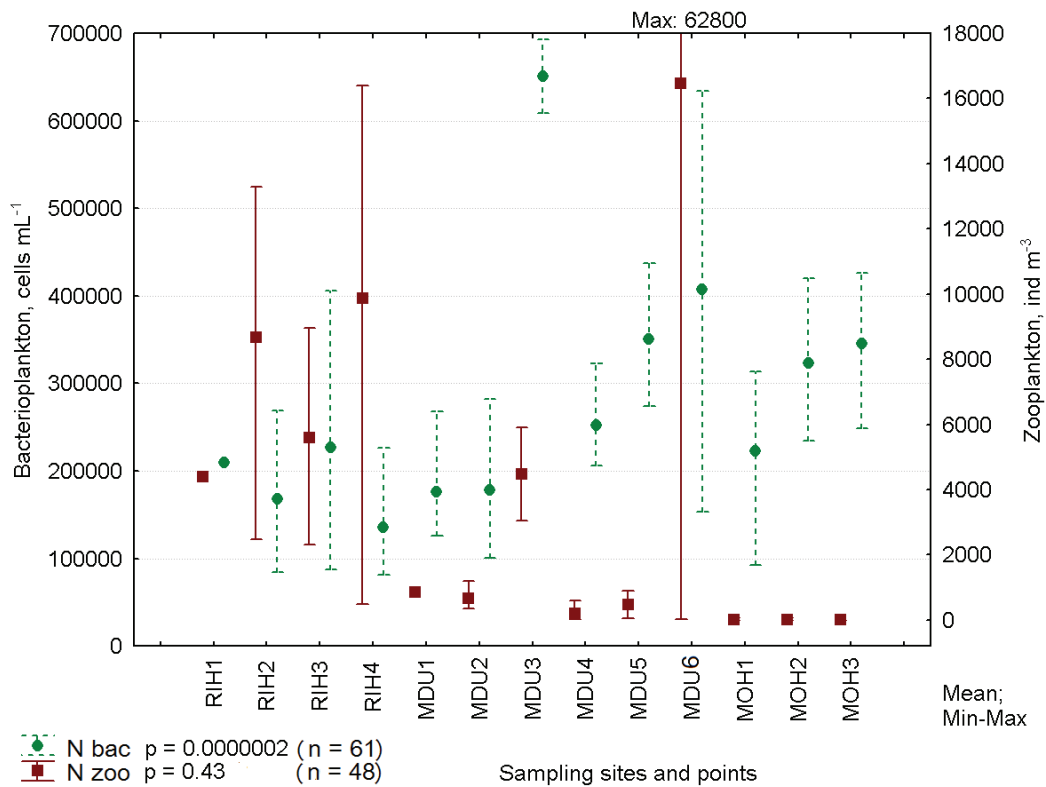
volume ranged from 0.033 to 0.080  $\mu\text{m}^3$ , which was a relatively small biovolume because of the prevalence of bacteria from the smallest size class, which was 0.2–0.5  $\mu\text{m}$ . The highest abundance was observed in the Mocskos-Danube (Table 1), due to the maximum in MDU3 during the flood (Fig. 3), increasing from point 1 to point 6, meaning that decreased with moving away from the river inflow



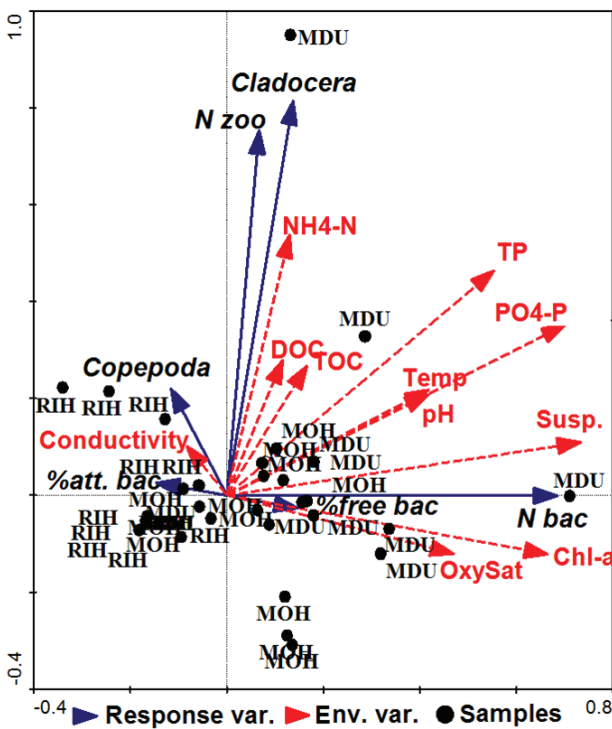
**Fig. 2.** Spatial development of Copepoda (A) and Cladocera (B) in Riha Lake (RIH), Mocskos-Danube Lake (MDU) and the Danube River at Mohács (MOH) in 2014. ANOVA test with p-values (significant for Copepoda).

(the upper end), except MDU3. The abundance in Mohács was higher than in Riha (Table 1, Fig. 3) and distinguished by many detritus particles with attached bacteria, more abundant near the right river bank (MOH3). The minimum was in Riha where the macrophyte cover, mainly by *C. demersum*, was significant. The abundance was the highest in the spring and the biomass was at its maximum in the summer ( $p=0.02$ ). The morphotypes and cell sizes differed significantly by seasons and sites ( $p=0.002$ ), with prevalence of the free-living cocci.

Direct (positive) correlations existed between the bacterioplankton (total abundance and free-living bacteria) and the temperature, as well as the suspended solids, the oxygen content, pH,  $\text{PO}_4\text{-P}$  and chl-a (Fig. 4). Attached bacteria, with the highest values in MOH, correlated positively



**Fig. 3.** Total zooplankton abundance (N zoo) and bacterioplankton abundance (N bac) at each of the studied 13 points in the three sites (see Fig. 1) in 2014. ANOVA test with given p-values (significant for N bac).



**Fig. 4.** RDA triplot of correlations between zooplankton and bacterioplankton variables (response variables) and abiotic factors and chl-a (environmental variables) by sites (samples) in 2014. Monte Carlo test: AllEV=1.000, CanEV=0.469, F-ratio=3.935, p-value=0.002.

with the nutrients  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  and with the conductivity. Macrophyte cover was related very weakly negatively only to the quantity of the attached bacteria ( $r=-0.18$ ,  $p=0.17$ , not significant).

**Zooplankton-bacterioplankton relations**

The bacterioplankton had a weak negative correlation with Copepoda, while the fraction of the attached bacteria had a positive relation, probably because of the higher quantities of detritus from the copepods excretions (Fig. 4). Cladocera affected only the medium-sized (2–3  $\mu\text{m}$ ) free-living bacteria ( $R_s=-0.31$ ). *Eurytemora velox* and the bacterioplankton were positively correlated ( $r=0.33$ ) (Table 1), especially in the spring.

**Discussion**

Our findings about the total number of crustacean species in these wetlands, 23 in total, were similar to those of the other researchers, suggested 6–28 crustacean species as typical for the wetlands (HUDEC & ILLYOVÁ 1998, SHURIN et al. 2000). Nevertheless, KISS et al. (2015) reported higher species diversity, between 35 and 42 Cladocera and Copepoda species, regarding the same three sites in the previous years, representing 2–5 year-periods, mainly with low water

levels of the Danube River, with the highest species' richness in the plesiopotamon sites (including MDU). Our results showed that after the high waters (and the heavy rainfalls) in spring and with the approach of the summer the species' richness increased in the isolated Riha Lake (Table 2), but the abundance of some species, and especially of the Cladocera, was the highest in the connected Mocskos-Danube wetland (Table 1, Figs. 2 and 3). This was in agreement with the results of NAPIÓRKOWSKI et al. (2019) who found out that the zooplankton is more abundant in the floodplain lakes connected with a river (transitional lakes) than in the isolated ones. On the contrary, the species richness during our study was lower than that reported by NAPIÓRKOWSKI et al. (2019).

BLĘDZKI & RYBAK (2016) described *Pleuroxus denticulatus* (in p. 281) and *Eurytemora velox* (in pp. 525–526) as alien species in the freshwater ecosystems. Kiss et al. (2015) confirmed the expansion of the two alien species *P. denticulatus* and the adapted to euryhaline waters *E. velox* in the floodplain. This study also confirmed the low abundance of *P. denticulatus* and the higher abundance of *Eurytemora velox* (Table 2) in the same studied wetlands.

Higher crustacean abundance was observed at the left bank of the river near Mohács in our study (Fig. 3). During the Joint Danube Survey 3 in 2013 ZSUGA (2015) found that the crustacean density is elevated in the left side and this was explained with the different hydromorphological conditions in the lateral profile of the river (different water movement, different turbulence, etc).

As the chl-a content is an evaluation of the phytoplankton biomass (SANDU et al. 2003, HUOT et al. 2007), the negative relation between the zooplankton and the chl-a (Table 1) was an indicator of relatively strong zooplankton grazing pressure on the phytoplankton, and top-down effect (SINISTRO et al. 2007). Significant positive correlation of Copepoda with the temperature was found by other researchers as well (ILLYOVÁ et al. 2008, PAIDERE 2009). The higher positive correlation of Cladocera with TP and PO<sub>4</sub>-P than Copepoda (Table 1) could be explained with their different needs of phosphorus. Copepods have lower mass-specific P content, while the cladocerans tend to have higher P and RNA contents, with higher specific growth rates and frequently experience P-limited growth, likely due to a shortage of P for ribosome synthesis (HESSEN et al. 2008).

The macrophyte cover in MDU in 2014 during the high water level of the Danube River (Table 1) was less represented than in the previous years. In MDU, in 2012, without flooding, *T. natans* was found from April till August, while in September it was only

rotten; in 2013, *T. natans* had weak development only in September and during the other months was replaced by *C. demersum* (TARJÁNYI & BERCZIK 2014). *Trapa natans* restricts the light availability, reduces the oxygen content, and displaces other emergent and floating vegetation. High water temperatures and continuous inflow of nutrients reported in the recent years most likely would induce the propagation of this species, potentially leading to further eutrophication (MARKOVIĆ et al. 2015). *Ceratophyllum demersum*, a submerged aquatic plant, native to North America, can spread rapidly and form beds, excluding other plant species and causing problems to their recreational activities (GISD 2006). The macrophyte development and the wetland connectivity to (or isolation from) the main river are the main factors, which explain the spatial variation in the physical and chemical variables, including the nutrients (N- and P- forms) in the wetlands of the Middle and Lower Danube River (KALCHEV et al. 2014).

PALIJAN et al. (2007) in Kopački Rit, Croatia, and KALCHEVA et al. (2014) in the Danube wetlands on Belene Island, Bulgaria, found a spring maximum of the bacterial abundance during the high water period of the Danube River, which was also observed in this study (Fig. 3). Prevalence of bacteria from the smallest size class, 0.2–0.5 µm, as in our study, has been found in freshwater ecosystems with different trophic state (COLE 1999, ZÖLLNER et al. 2003, PERNTHALER 2005). This is a normal phenomenon owing to abiotic factors outside of the optimum (temperature, pH, etc.), nutrient limitation (mainly of organic C or inorganic P), increased number of bacterivores (including crustacean zooplankton) or inactive state of the bacterial cells (KALCHEVA et al. 2014). The Mohács Town situated at the right bank of the river might have anthropogenic impact (wastewaters), leading to higher bacterial abundance, as shown by our results. ZSUGA (2015) suggested that the reason for this may be the higher turbulence, bringing bacteria from the deeper layers.

P-limitation very often is the reason for weak utilisation of DOC by the bacterioplankton because of C:N:P ratio out of the optimum, according to VADSTEIN et al. (2003). *Ceratophyllum demersum* increases the dissolved oxygen and decreases COD and the pollution in the water and can be an effective biosorbent for phosphorus, ammonium and nitrate (FOROUGH 2011). Such processes might have happened in Riha, where with its dominance this macrophyte species provoked lower bacterioplankton abundance and lower phytoplankton biomass, expressed by the lowest chl-a values (Table 1). The increased macrophyte cover is associated with a lower

fraction of particulate phosphorus in the epilimnia; the phytoplankton biomass (chl-a) is also lower in the macrophyte dominated lakes (ROONEY & KALFF 2003). During the high-water period neither N- nor P-limited bacterial growth is recorded, whereas during the low-water period, bacterial growth is P-limited and suppressed by competition with the phytoplankton rather than stimulated through the production of dissolved organic matter by the phytoplankton (REJAS et al. 2005). These findings once again suggest that the higher DOC content in the isolated Riha Lake (Table 1) could not be utilised by the bacterioplankton because of the P-limitation.

The negative correlation between Cladocera and the medium-sized free-living bacteria has been confirmed in other reports (COLE 1999, JÜRGENS & MATZ 2002, ZÖLLNER et al. 2003, PERNTHALER 2005). The positive relation of the attached bacteria with Copepoda (Fig. 4) and with the alien species *Eurytemora velox* (Table 1) could be explained with the different copepod diets that can have significant impact on the quantity and quality of their excretion compounds and can subsequently generate shifts in the active bacterial composition (VALDÉS et al. 2017).

## Conclusions

The species' composition of crustacean zooplankton recorded in the lakes Mocskos-Danube and Riha, 16 species and 19 species, respectively, during 2014 in the Béda-Karapanca floodplain, was lower than in the previous years, but similar to other research results concerning the wetlands. The Danube River at Mohács had the lowest diversity of the three studied sites, confirming that the wetlands are characterised with higher species richness than the river. Two alien crustacean species were recorded, the chydorid cladoceran *Pleuroxus denticulatus* of low abundance only in the Riha Lake, and the calanoid *Eurytemora velox* in both wetlands.

Seasonal differences in the zooplankton abundance were observed in the two lakes, i.e. a spring maximum abundance owing mostly to Cladocera in the Mocskos-Danube in the active floodplain, and a summer-autumn maximum in the isolated Riha Lake. We presume that those differences are due to the influence of the flood pulse in spring in the Mocskos-Danube. This reveals the importance of the river connectivity for the wetland biodiversity.

Positive correlations were found between Copepoda and the temperature, Cladocera and  $PO_4\text{-P}$ , between *Eurytemora velox* and the bacterioplankton, and between both crustacean groups with the carbon content (DOC and TOC) and TP. A negative

correlation was found between the zooplankton and the phytoplankton biomass (expressed by chlorophyll-a).

The invasive submerged *Ceratophyllum demersum*, better developed in the isolated Riha Lake, as good competitor for nutrients has created the necessary oxygen conditions and feeding for the zooplankton. We assume that at the same time it has caused N- and P-limitations for the phytoplankton and bacterioplankton, and, due to the isolation from the river, in Riha these communities had the lowest abundance.

**Acknowledgements:** The study was supported by the Programme for Collaboration and Visit Exchange of the Hungarian and the Bulgarian Academy of Sciences, between the Danube Research Institute, Budapest, and IBER-BAS, Sofia (2013–2018). The authors would like to thank especially to the ESENIAS network for the dedicated projects and events.

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