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Spatial and temporal distribution patterns of zooplankton assemblages (Rotifera, Cladocera, Copepoda) in the water bodies of the Gemenc Floodplain (Duna-Dráva National Park, Hungary)

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Abstract. The Gemenc Floodplain, situated between the 1498th and 1470th river-kilometres of the River Danube, is part of the Danube–Dráva National Park in Hungary. The floodplain is one of the largest in Europe with an area of 18,000 hectares, and within its territory various typical side arms and backwaters can be found. The area needs hydrological revitalization because of the sinking river bed, caused by the regulation of the main arm at the end of the 19th century. In order to assess the conditions of the intervention, an exhaustive knowledge about the hydrobiological relations of the different water bodies will be necessary. The aim of our study was to explore connections between the hydrological events, the physical–chemical parameters of the water-bodies, and the abundance of the planktonic crustacean and rotifer assemblages.

INTRODUCTION

Compared to the extent informations about limnology of stagnant waters, our knowledge about the ecological and hydrobiological functions of rivers and floodplains is scant. The definitions of conservation and restoration possibilities of river-floodplain systems are inadequate. Therefore the research of rivers and still remaining floodplains is a pressing need, especially under the current conditions of growing human interference, with mostly adverse effects (e.g. regulation, water-use, pollution)(Tockner *et al.,* 2000).

The importance of retentive inshore habitats and adjacent floodplain water-bodies for the growth and abundance of lotic zooplankton is well established (Baranyi *et al.,* 2002, Reckendorfer *et al.,* 1999, Zimmermann-Timm *et al.,* 2007). The quantitative influence of the floodplain on the zooplankton community depends on the abiotic (flow velocity, physical and chemical parameters) and biotic characteristics (competition, predation, presence of macrophytes) of each tributary. Most of these parameters is defined by the overall discharge of the main arm and is therefore temporally variable (Lair, 2005). Before the necessary conservation work can start, it is important both to understand how the affected floodplain ecosystems function and to increase our knowledge about the relation between local hydrological and ecological parameters (Berczik & Buzetzky, 2006).

The Danube is the second largest river in Europe with a length of 2860 km and a catchment area of about 817,000 km^2. As a consequence of the 19th century regulation of the Middle-Danube the length of the river bed decreased, its shape stabilized, causing most of the adjacent floodplains to become uninundated areas outside the dams. The increased flow velocity at the shortened reach of the river caused significant erosion in the river bed, what led to the drying out of the floodplains and to the weakening of the lateral interactions (Guti, 2001). The floodplain of Gemenc covers 18,000 hectares (180 km^2), leaving it the only notable floodplain of the Middle-Danube today. It is also one of the largest in Europe, with a unique natural value (Zinke, 1996). As it lies entirely within the dam-system, the characteristic hydrological processes of the river-floodplain system can go on unperturbed. We can observe in the area every characteristic “functional unit” (eu-, para-, plesio- and paleopotamal) of an ecological succession, providing a great opportunity to compare them simultaneously (Roux *et al.,* 1982; Guti, 2001).

To understand the ecological and hydrobiological functions of the floodplains, the Hungarian

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Danube Research Station has started the Gemenc Research Project, which covers the investigation of zooplankton assemblies, too (Berczik, 2003; Schöll, 2006; Dinka & Berczik, 2005; Kiss, 2006). Besides the faunistical characterisation of the Gemenc foodplain, the aims of our study include the comparison of the zooplankton assemblies in the main riverbed and the floodplain water bodies (spatial-temporal fluctuations, differences in diversity and abundance), the investigation of the dynamic connections between assemblages of the river and affluent arms (connectivity, colonisation, constancy), and uncovering the effects of floods on the floodplain zooplankton populations.

In this paper we present our results on the abundance patterns of zooplankton assemblages collected from the different water body types of the Gemenc floodplain between 2002–2004.

MATERIALS AND METHODS

The investigated area

The Gemenc floodplain is situated on the right bank of the Danube, between the 1503rd and 1469th river kilometres. It is 30 km long and 5-10 km wide (Tamás & Kalocsa, 2003a). In this reach of the Danube the mean annual discharge is 2400 m^3s^{-1}, with a minimum of 618 m^3s^{-1} and a maximum of 7940 m^3s^{-1} (Marosi & Somogyi, 1990). Total amplitude of water level fluctuation reaches 9 m. The stream gradient is about 5 cm km^{-1} in the main arm, with a 0.8–1.2 m s^{-1} flow velocity at MQ. In 2002 the river started to cover the floodplain after it reached a 500 cm water level in the main riverbank (Tamás & Kalocsa, 2003b).

In order to compare the different planktonic assemblies, our sampling covered a wide range of water bodies, with different properties: the main arm (D1489), two parapotamal type side arms, the 15 km long Rezéti-Holt-Duna (RDU) and 5 km long Vén-Duna (VDU), the plesiopotamal Grébeci-Holt-Duna (GDU) and the paleopotamal oxbow Nyéki-Holt-Duna (NYHD) (Fig. 1).

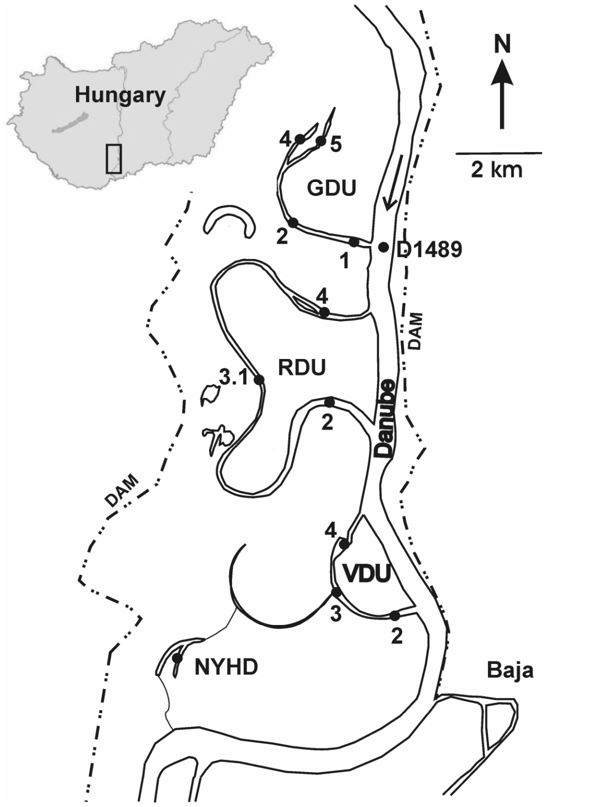

Figure 1. The investigated area and sampling sites

Sampling and data analysis

Zooplakton samples were collected by filtering 20 L (Rotifera) and 50 L (Crustacea) of water through of a 40 µm (rotifers) or 70 µm (Crustacea) mesh size net from the surface of the water. Samples were immediately preserved in 4% formalin solution. Rotifers were identified according to Koste (1978), and then counted in Sedgewick-Rafter chambers at 40–100× magnification using a light-microscope. Microcrustaceans were enumerated by using inverted microscopy and the adult individuals were identified at species level according to Dussart (1967, 1969), Gulyás & Forró (1999), Gulyás & Forró (2001). Juvenile stages of copepods were also counted and incorporated in total density.

The hydrophysical and hydrochemical parameters as well as hydrological conditions of the water bodies were monitored simultaneously. Water temperature (ºC), conductivity (µS cm^{-1}), pH, dissolved oxygen (mg l^{-1}) and oxygen saturation (%) were measured in the field (in situ) by WTW Multi 340i .

Spearman's rank correlation with Bonferroni correction was used to test the relationship between the main physical and chemical parameters and biological variables. All statistical analysis was performed by the Statistica 7.0 software package (Statsoft, 2005). The multivariate analysis was calculated using the PAST software-package (Hammer *et al.,* 2001).

RESULTS

The water level fluctuation of the main arm was 827 cm during the investigated period (Fig. 5–7). In the course of our observations, the water regime varied significantly from year to year, what could have had an important impact on zooplankton assemblages.

During our observations at Gemenc, 38 Cladocera, 23 Copepoda and 75 Rotifera taxa were found (Kiss, 2006; Schöll, 2006). The range of the zooplankton density was 0-455,750 ind.*100 L^{-1} in the case of rotifers, 0-1,366 ind.*100 L^{-1} in the case of cladocerans, and 0-6,436 ind.*100 L^{-1} in the case of copepods (Figs. 2–4, Table 1). There were significant differences between the zooplankton abundance and the spatial and temporal patterns of assemblages in the various water bodies. The minimum of the density and the biomass was generally recorded during late fall, while the maximum every year was in July.

The minimum density was usually recorded in the main arm and the Vén-Duna. At the VDU4 site, which is the border on the main arm, for all three examined planktonic groups minimal densities were observed. The maximum density was usually recorded in the Grébeci-Holt-Duna and the Rezéti-Holt-Duna. The density peak was in the GDU4 site (the farthest from the Danube) for crustaceans, and the RDU3.1 site, situated in the middle of the side arm, for rotifers (Figs. 2–4.). The ratio of copepods was larger than the ratio of cladocerans in each sampling site except the main arm. The observed higher ratio of cladocerans in the main arm was due to the high density of the small-sized *Bosmina longirostris*, a species typical for the Danube. The average density of the two planktonic microcrustacean groups gradually increased in the Grébeci-Holt-Duna diverging from the main arm. Similarly, the average density of copepods in the Rezéti-Holt-Duna gradually decreased distally from the main arm.

The average abundance of all three zooplankton groups was higher in 2003 than in 2002 and 2004, in a significant proportion of the sampling sites (Table 1). The ratio of predator or omnivorous species (*Thermocyclops*, *Mesocyclops*, *Cyclops*) in the Copepoda assemblages was high in all sampling sites, but there was no relationship between the fluctuation of Rotifera and Copepoda density.

The main arm

Rotifera

The density of rotifer assemblages in the main arm was between 500 és 139,000 ind.*100 L^{-1} but usually was below 10,000 ind.*100 L^{-1}. The average density was 5725 ind.*100 L^{-1} in 2002, 43,685 ind.*100 L^{-1} in 2003 and 22,900 ind.*100 L^{-1} in 2004 (Table 1). The maximum values were recorded usually in May and June; the minima were always in autumn. The highest density (07. 05. 03. – 139,000 ind.*100 L^{-1}, 07. 01. 04. – 94,250 ind.*100 L^{-1}) was measured at middle water. Two weeks prior to the higher abundance values the water level was medium (300–350 cm). The minimum abundance values were recorded in cold water or at low water levels.

Crustacea

The abundance of Crustacean assemblages was between 1 and 470 ind.*100 L^{-1} (Cladocera: 1–422 ind.*100 L^{-1}, Copepoda: 0–86 ind.*100 L^{-1}) in the main arm. Here assemblages with low density were typical and the dominance of *Bosmina longirostris* (Cladocera) was observed. The temporal density dynamics of the two examined Crustacean groups were considerable different.

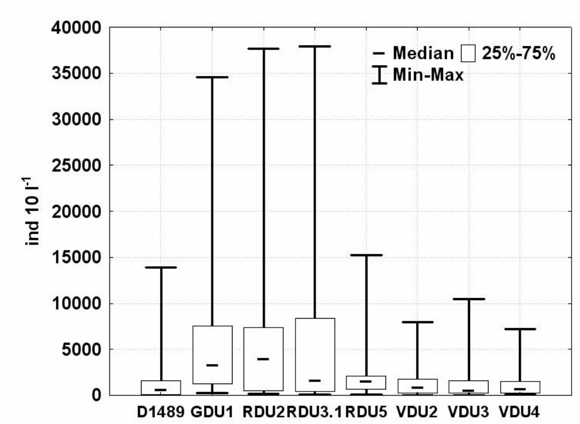

Figure 2. The average density of rotifer species at the sampling sites (for the abbreviations of sampling sites see the Methods section)

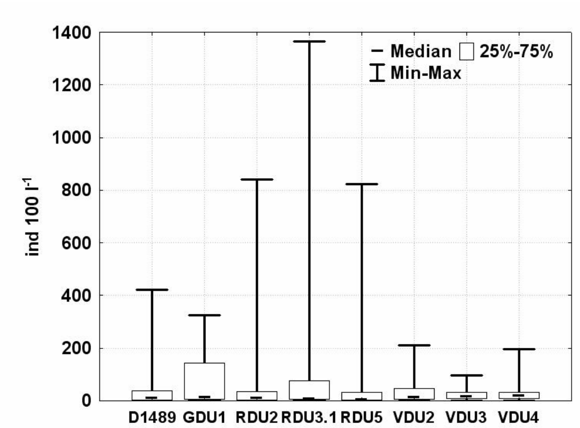

Figure 3. The average density of Cladocera species at the sampling sites

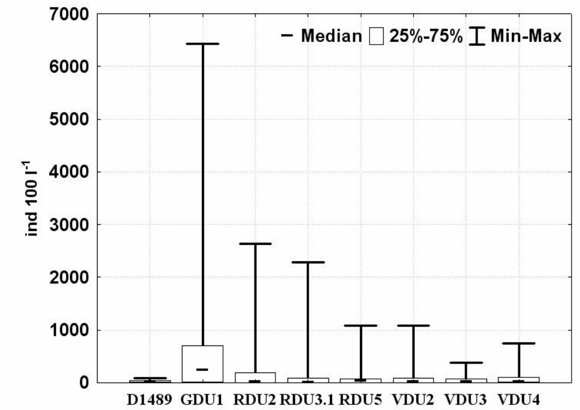

Figure 4. The average density of Copepoda species at the sampling sites

In case of Cladocera, the density peak was in the warmer period, in cold water (<15 Cº) period the density was generally low. The density of copepods fluctuated less and the density maxima were observed in spring. The average density of cladocerans was considerable higher in 2004 than in 2002 and 2003, but in case of copepods there were no differences among the sampling years.

Grébeci-Holt-Duna

The connection of this plesiopotamal type side arm with the main arm depends on the water level of the Danube. The highest densities of zooplankton assemblages were recorded in periods following higher water levels in the main arm. The influx of water during such periods was followed by the fall of water levels, and as a result the influent water from the main arm gradually became stagnant water in the side arm. It is noteworthy that when the water levels of the river fall below 200 cm (measured on the water-gauge of Baja), only the GDU1 sampling site was accessible.

Rotifera

The pooled density fluctuated between 3000 and 455,750 ind.*100 L^{-1}. The highest densities were recorded in the Grébeci-Danube. There were notably differences between the sampling years. Generally, during the whole sampling period, the abundance decreased passing on the river mouth (Table 2). In the Grébeci-Danube the pooled density increased with rising temperature (N: 36, R: 0.49, t: 3.30, p: 0.013)

Crustacea

The density of crustacean assemblages fluctuated between 9 and 6762 ind.*100 L^{-1} (Cladocera: 1-5268 ind.*100 L^{-1}, Copepoda: 7-5800 ind.*100 L^{-1}). Similarly to rotifer assemblages, the highest densities for these taxa were recorded in this Danube-section. However, the temporal variation of the two crustacean groups was different.

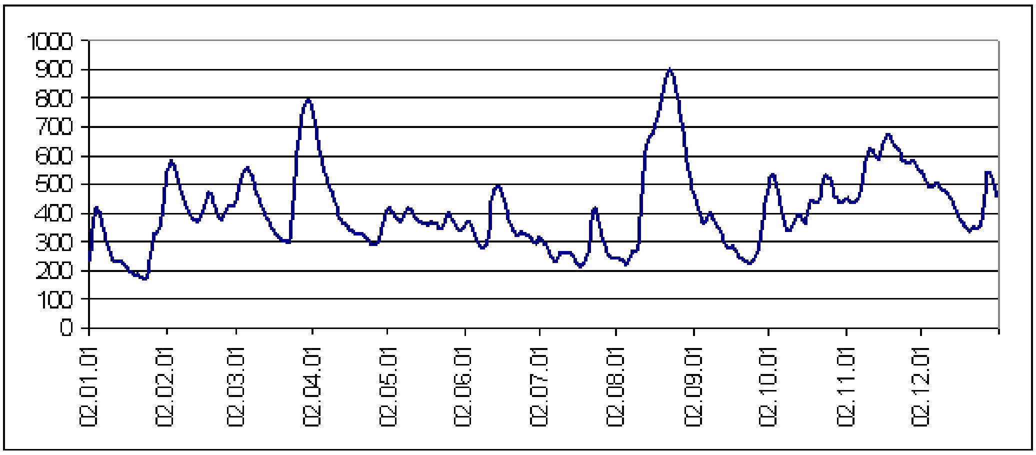

Figure 5. Water level fluctuation (cm) in 2002 (Gauge Baja, rkm 1478)

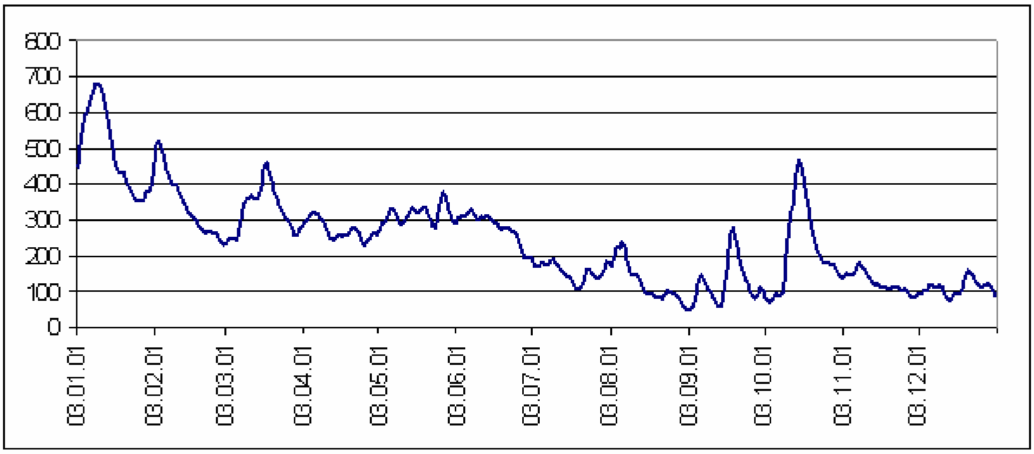

Figure 6. Water level fluctuation (cm) in 2003 (Gauge Baja, rkm 1478)

Figure 7. Water level fluctuation (cm) in 2004 (Gauge Baja, rkm 1478)

The density peak of cladocerans was when the temperature of the water was relatively warm, while high densities of copepods were observed both in cold and warm water periods. In general, during the three sampling years the average densities decreased passing on the river mouth for both cladocerans and copepods, but there were differences between the three sampling years (Table 2).

Rezéti-Holt-Duna

Rotifera

The pooled density for rotifers was between 0 and 379,500 ind.*100 L^{-1} in this parapotamal type side arm. The average density increased downstream, and the highest densited were recorded on the RDU2 sampling site locating close to the river mouth (Table 3). When water levels were low, the flow velocity of the water in the side arm decreased and matched the stagnant water conditions on certain sections of the side arm. In such situations the abundance of the evolving Rotifer assemblages was significantly higher than in the case of higher water levels in the main arm, such as during intensive flow periods (Schöll & Dinka, 2005; Schöll, 2006). We observed an inverse relationship between the water-level of the main arm and the abundance of the rotifer assemblages in the Rezéti-Holt-Duna (N: 36, R: -0.81, t: 8.14, $p<10^{-8}$), and a positive correlation between the temperature and the density of assemblages (N: 36, R: 0.47, t: 3.10, p: 0.018). This correlation was even more significant in downstream areas of the side arm and was highest on the RDU2 site (Dinka *et al.,* 2006).

Crustacea

The density of the microcrustacean assemblages was between 3–3650 ind.*100 L^{-1} (Cladocera: 0–1366 ind.*100 L^{-1}, Copepoda 0–2636 ind.*100 L^{-1}). For copepods, the average pooled density decreased passing on the river mouth, however this tendency was not consistent through all sampling years. In the case of the Cladoceran assemblages there was no relationship between density fluctuations and the distance from the river mouth.

Vén-Duna

Rotifera

In this relatively short (5 km) side arm with permanent flow the density of rotifer assemblages was low (2650–48,333 ind.*100 L^{-1}), similar to the main arm. There were no significant differences between the different sampling sites of the side arm. During the three sampling years we observed similar abundance values in 2002 and 2004, while a density peaks was obvious in 2003, when the water level was low in the main arm (Table 4).

Positive correlation (N: 41, R: 0.57, t: 4.37, $p< 0.0005$) was shown between pooled densities and water temperatures.

Crustacea

The density of the planktonic microcrustaceans was between 2–1298 ind.*100 L^{-1} (Cladocera: 0-212 ind.*100 L^{-1}, Copepoda: 2–1086 ind.*100 L^{-1}). The amount of the Copepods in the Crustacean assemblages was significantly higher than Cladocerans. The density peaks were observed at the end of the summer and in the fall for both examined groups. The density of the assemblages was notably higher in 2003 than in 2002 and 2004 (Table 4). There was no relationship between the average density of assemblages and the distance from the Danube.

Nyéki-Holt-Duna

Rotifera

The sampling in the Nyéki-Holt-Duna was started only in 2003. Significant difference was shown between the density values during the two years of observation (Table 5).

There was no significant correlation between the abundance of the assemblages and the measured physico-chemical parameters of the water.

Crustacea

The density of the microcrustaceans has varied between 260 and 320 ind.*100 L^{-1} (Cladocera: 6-300 ind.*100 L^{-1}, Copepoda: 40-4026 ind.*100 L^{-1}). Similarly to rotifers, the average density values of the two sampling years were different because of the higher abundance of copepod assemblages in 2003 (Table 5).

Comparison of the examined water bodies with multidimensional statistical methods on the basis of the abundance values

Rotifera

In the cluster constructed based on density values of the Rotifera assemblages we could distinguish two main groups. The sampling sites of the Vén-Duna (VDU2, VDU3, VDU4) and the RDU5 site of the Rezéti-Holt-Duna situated in the proximity of the main arm were clustered as one group computing the mostly similar sites. The D1489 observation site, situated in the main arm also grouped with the aforementioned sites.

The further two down-stream sites of the Rezéti-Holt-Duna (RDU3.1, RDU2) were different from the first group, and from the GDU1 site in the Grébeci-Holt-Duna, which also differed from all other examined water bodies (Fig. 8).

Crustacea

The similarity between the sampling sites was higher for crustaceans than for rotifers (Fig. 9). However, similarly to the Rotifers, the most distinct sites were GDU1 and RDU2. Clustering of the other sites was not as obvious as for rotifers.

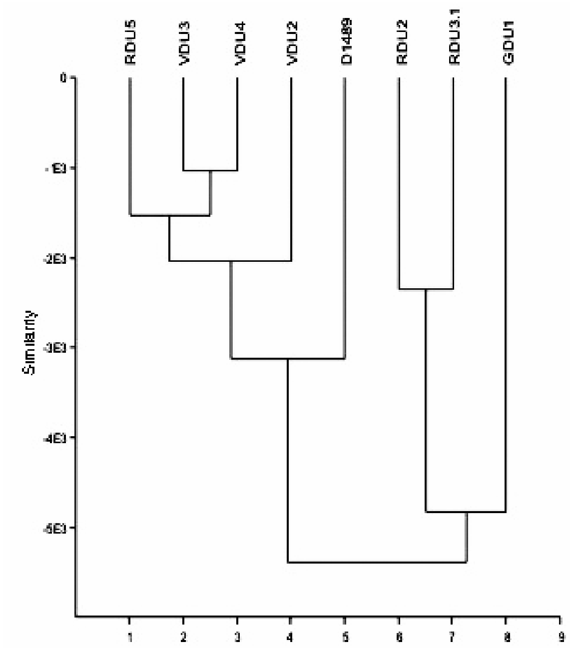

Figure 8. The similarity of the sampling sites on the basis of Rotifera densities (UPGMA, Euclidean distance)

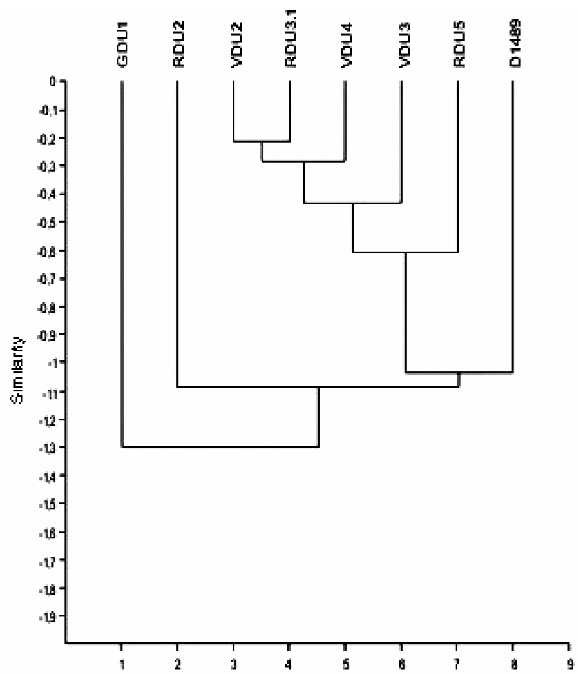

Figure 9. The similarity of the sampling sites on the basis of microcrustacean densities (UPGMA, Euclidean distance)

DISCUSSION

It is assumed that due to the limiting effect of the water flow the density of crustacean and rotifer assemblages is higher in river side arms and water bodies with slower flow, than in the main arms and faster-flowing segments of the side arms (Baranyi *et al.,* 2002). If the residence time of the water in the side arms increases, the density of the forming planktonic assemblages can be higher (Ruttner-Kolisko, 1972). As the generation time of the zooplankton is notably longer than that of the phytoplankton, the slower flowing or stagnant water segments in the river system should be especially important for the ecology of the zooplankton. In contrast, some earlier investigations did not find any relationship between the residence time of the water, the depth of light penetration and the biomass of the phytoplankton, which is the most important food-source for the zooplankton (Chételat & Pick, 2006).

As the Danube's water streams down into the side arms, its speed and the amount of suspended matter decreases, while the depth of light penetration increases. As a consequence, the biomass of the phytoplankton increases, providing better food-supply for the local zooplankton assemblages. We hypothesise, that the density of assemblages forming in the longer side arms with more varied habitats and slower flow is higher than in the shorter, fast-flowing water bodies, more similar to the main arm.

Our results show a significant deviation in the pooled densities for all three examined zooplankton groups (rotifers, copepods and cladocerans). The highest values were observed usually in summer, while the minima were in late autumn, in the cold water period. There were notable differences between the sampling years. The densities were usually low in the faster flowing water bodies (in the main arm and the Vén-Duna), and high in the Rezéti-Holt-Duna, with slower water flow, and the periodically stagnant Grébeci-Holt-Duna (due to the considerable deviation of the data, these differences were not significant). Compared to water bodies with permanent connection to the Danube, the density of rotifers was lower, while the density of crustaceans was higher in the usually stagnant Nyéki-Holt-Duna.

These observations can be partially explained by the fact, that the ability of rotifers to reproduce in waters with flow velocities above 0.4 m/s is very low, or indeed nil. In other words, the hydrological conditions of the water bodies can affect both directly and indirectly the structure of the assemblages (Ruttner-Kolisko, 1972; Rzoska, 1978). In water bodies with long water residence times, like the Nyéki-Holt-Duna, the importance of the biotic interactions increases and crustaceans with longer generation time constitute a significant part of the zooplankton assemblages (Baranyi *et al.,* 2002, Kiss 2006). For all these reasons, high density rotifer assemblages could develop in water bodies where the intensity of the flow and the frequency of the flow events are not inhibited, but at the same time the residence time of the water is not long enough to favour planktonic crustaceans. Although the generation time of this group is slower than the one of the rotifers, they are better suited to resist biotic interactions (exploitative and interference competition). The occurrence of crustacean assemblages with diverse composition in the paleopotamal-type Nyéki-Holt-Duna is also caused by the lack of constant fish populations. Yearly desiccation events also affected significantly the structure of the zooplankton.

We found a very strong negative correlation between the water levels of the main arm and the density of the assemblages in the Rezéti-Holt-Duna. This could be due to the gradually slowing flow in this 15 km long side arm during the low water period. The slower flow provides better conditions for rotifers to reproduce, the water is warmer, and the depth of light penetration also increases, therefore the chances for reproduction of phytoplankton is also better. The effect of the turbidity on biotic factors influencing rotifer assemblages was shown for other large rivers too (Lair, 2005; Pollard *et al.,* 1998). Decreasing turbidity also favours planktonic crustaceans, which therefore compete with rotifers for resources;

however rotifers are better equipped to tolerate the unfavourable influences of the flow.

Inside in the individual side arms we found no obvious trends; the lowest density and the lowest biomass were usually observed near the junction from the main arm, indicating similar physico-chemical characteristics to the Danube.

Significant positive correlation was shown between the temperature and the pooled density in the side arms (Grébeci-Holt-Duna, Rezéti-Holt-Duna, Vén-Duna) with permanent connection to the main arm. This correlation could be explained, if higher temperatures would increase the reproduction of the rotifers (Galkovskaya, 1987).

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Table 1. Average density of the three examined zooplankton groups in the examined side arms and the main arm

	site	2002	2003	2004	mean
ROTIFERA Ind* 100L^{-1}	***D 1489***	5725	43685	22900	24103
	GDU	68177	153792	185299	135756
	RDU	13946	59687	32025	35219
	VDU	6986	35986	7817	16929
	NYHD	-	68563	15161	41862
CLADOCERA ind.*100L^{-1}	***D 1489***	*4.0	37.3	94.6	57.3
	GDU	35.4	214.0	950.7	416.5
	RDU	3.0	314.2	114.4	118.7
	VDU	11.6	49.7	26.3	31.0
	NYHD	-	106.7	195.0	142.0
COPEPODA ind.*100L^{-1}	***D1489***	*18.0	34.5	31.6	30.2
	GDU	502.0	566.0	2724.2	1311.6
	RDU	9.7	582.5	288.3	251.8
	VDU	23.0	183.8	39.9	99.0
	NYHD	-	1578.0	365.0	1092.8

Table 2. Abundance values in the Grébeci-Holt-Duna

	site	2002	2003	2004	mean
ROTIFERA ind.*100L^{-1}	***GDU1***	38187	15625	88900	47571
	GDU2	52812	230500	163167	148826
	GDU4	113531	215250	303830	210870
	mean	68177	153792	185299	
CLADOCERA Ind.*100L^{-1}	***GDU1***	7.8	196.0	160.0	100.5
	GDU2	66.0	396.0	668.7	371.4
	GDU4	40.0	68.0	2023.3	787.3
	mean	35.4	220.0	950.6	
COPEPODA ind.*100L^{-1}	***GDU1***	747.3	467.0	2449.3	1089.1
	GDU2	26.0	1206.0	2454.7	1235.4
	GDU4	613.8	124.0	3268.7	1548.1
	mean	462.4	599.0	2724.2	

Table 3. Abundance values in the Rezéti-Holt-Duna

	site	2002	2003	2004	mean
ROTIFERA ind.*100L^{-1}	***RDU5***	9000	42750	12500	21417
	RDU3.1	8775	74375	41125	41425
	RDU2	24062	61937	42450	42816
	mean	13946	59687	32025	
CLADOCERA ind.*100L^{-1}	***RDU5***	2.6	34.0	214.5	81.1
	RDU3.1	4.8	465.5	40.5	170.3
	RDU2	2.0	232.5	93.4	100.5
	mean	3.1	244.0	116.1	
COPEPODA ind.*100L^{-1}	***RDU5***	15.0	563.0	44.0	161.7
	RDU3.1	9.8	899.3	52.5	246.4
	RDU2	4.4	497.5	672.4	383.9
	mean	9.7	653.3	256.3	

Table 4. Abundance values in the Vén-Duna

	site	2002	2003	2004	mean
ROTIFERA ind.*100L^{-1}	***VDU4***	8854	24875	5500	13076
	VDU3	7250	48333	2650	19411
	VDU2	4854	34750	15300	18301
	mean	6986	35986	7817	
CLADOCERA ind.*100L^{-1}	***VDU4***	10.8	77.0	17.2	32.0
	VDU3	8.0	38.7	33.2	26.2
	VDU2	12.4	70.5	28.6	34.8
	mean	10.4	20.7	26.4	
COPEPODA ind.*100L^{-1}	***VDU4***	33.6	303.5	37.2	112.0
	VDU3	19.5	196.0	35.2	70.2
	VDU2	15.2	324.0	47.2	114.9
	mean	22.8	274.5	13.3	

Table 5. Abundance values in the Nyéki-Holt-Duna

	Site	2003	2004	mean
ROTIFERA (ind.*100L^{-1})	***NYHD3***	68563	15161	41862
CLADOCERA (ind.*100L^{-1})	***NYHD3***	106.7	195.0	142.0
COPEPODA (ind.*100L^{-1})	***NYHD3***	1578.0	365.0	1092.8