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RESEARCH PAPER — OPEN ACCESS

Habitat factors differentiating the occurrence of Ostracoda (Crustacea) in the floodplain of a small lowland River Krąpiel (N-W Poland)

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Abstract – We analysed the occurrence of ostracods in a small river, taking into account all the types of water bodies in the floodplain – these included helocrenes, oxbow lakes, and ponds, as well as the main river channel. The objective of the study was to investigate the variation in ostracod communities and identify those factors determining species distribution. The environmental factors considered were the type of water body, responsible for 17% of the variance, the physical and chemical water properties (29%), and the biotic and abiotic factors associated with the substrate type (23%). Among the factors associated with the substrate, sediment sorting, plant coverage and insolation were the most important. The ostracod fauna of the helocrenes differed from that of the other water bodies in the floodplain. In the water bodies of the Krąpiel valley and in the main river channel, 33 ostracod species were recorded, of which 26 were found in the main river channel. Refugia in the floodplain were the main source of the diversity and abundance of ostracods in the main river channel. The mean density in the main river channel was very low, at 330 indiv. m^{-2}, while in the water bodies of the floodplain it was the greatest, reaching up to 5568 indiv. m^{-2}.

Keywords: Benthos / environmental conditions / substrate / species distribution

Résumé – Facteurs d'habitat différenciant la présence des Ostracodes (Crustacea) dans la plaine d'inondation de la petite rivière de plaine Krąpiel (N-O Pologne). Nous avons analysé la présence des ostracodes dans une petite rivière, en tenant compte de tous les types de plans d'eau dans la plaine d'inondation; ceux-ci comprenaient des sources hélocrènes, des bras morts et des étangs, ainsi que le chenal principal de la rivière. L'objectif de l'étude était d'étudier la variation des communautés d'ostracodes et d'identifier les facteurs déterminant la distribution des espèces. Les facteurs environnementaux considérés étaient le type de masse d'eau, responsable de 17% de la variance, les propriétés physiques et chimiques de l'eau (29%), et les facteurs biotiques et abiotiques associés au type de substrat (23%). Parmi les facteurs associés au substrat, le tri des sédiments, la couverture végétale et l'ensoleillement étaient les plus importants. La faune ostracodienne des sources hélocrènes différait de celle des autres masses d'eau de la plaine d'inondation. Dans les masses d'eau de la vallée de la Krąpiel et dans le chenal principal de la rivière, 33 espèces d'ostracodes ont été enregistrées, dont 26 dans le chenal principal de la rivière. Les refuges dans la plaine d'inondation étaient la principale source de la diversité et de l'abondance des ostracodes dans le canal fluvial principal. La densité moyenne dans le canal fluvial principal était très faible, 330 indiv. m^{-2}, tandis que dans les masses d'eau de la plaine d'inondation, elle était la plus élevée, atteignant jusqu'à 5568 indiv. m^{-2}.

Mots-clés : benthos / conditions environnementales / substrat / répartition des espèces

1 Introduction

Freshwater ostracods are small, bivalved, benthic crustaceans, generally 0.3–5 mm long (Meisch, 2000). They are present in almost all aquatic habitats, including lakes, canals, oxbow lakes, ponds, ditches, and rivers, but in mountain brooks they are restricted to calm areas and interstitial habitats. They usually live on the surface of the bottom sediments or burrow in them, but species with long natatory setae on their antennae can also swim (Meisch, 2000). In rivers, their densities are much greater in habitats with a slow current and

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more organic matter in the sediments than in typical lotic habitats (e.g. Szlauer-Łukaszewska, 2013, 2015a, 2015b). There have been very few studies on the distribution of ostracods along the whole length of a river valley, from the headwaters to the mouth of the river. Those studies known from the literature are limited to selected stretches of a particular river or valley (Scharf, 1988; Marmonier and Creuzé des Châtelliers, 1992; Creuzé des Châtelliers and Marmonier, 1993; Mezquita *et al.*, 1999a, 1999b; Nagorskaya and de Jonge, 2002; Nagorskaya and Keyser, 2005; Kiss, 2006; Kiss and Schöll, 2009; Higuti *et al.*, 2009, 2010; Scharf and Brunke, 2013; Szlauer-Łukaszewska, 2013, 2015a, 2015b). A very few studies have considered the other habitats of the river valley outside the main river channel: these include oxbow lakes (Scharf, 1988) or oxbow lakes and backwater canals (Kiss, 2006; Kiss and Schöll, 2009; Nagorskaya and de Jonge, 2002; Higuti *et al.*, 2009, 2010). Studies on rivers have generally not taken into account springs situated in the valley, but these have been studied separately, without associating them with the river system (Roca and Baltanás, 1993; Mezquita *et al.*, 1999c; Rosati *et al.*, 2014; Zhai *et al.*, 2015).

The aim of the study was to investigate the variation in ostracod communities and identify the factors determining species distribution along the entire valley of a small lowland river in the temperate zone, from the headwaters to the mouth of the river. On a spatial scale, we analysed the upstream–downstream gradient of environmental variability and the variability of all the water bodies of the floodplain as integral components of the river valley and the processes taking place in it. The analysis took into account all the types of water bodies situated in the floodplain: the main river channel, helocrenes, oxbow lakes, and ponds.

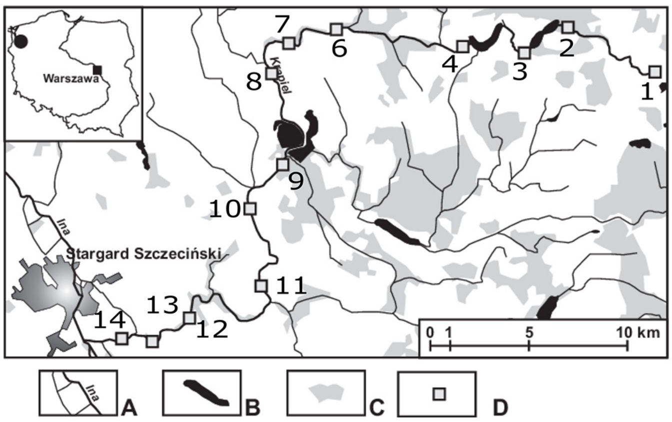

Fig. 1. Map of the River Krąpiel with sampling sites. A – rivers, B – lakes, C – forests, D – sampling sites (1–14).

2 Material and methods

2.1 Methods of sampling and processing

Samples were collected from the small lowland River Krąpiel (in northwest Poland), which is 65 km in length, and has a catchment area of 596 km^2. Its source is located at 96 m above sea level and the mouth at 21 m above sea level The width of the river valley ranges from 10 m to 400 m. Most of the river flows in a postglacial channel. From Pęzino, it carries water through a moraine plateau area in a deep gorge valley. The initial stretch of the river has the character of a lowland loess or loamy stream, while in the lower reaches it is classified as a lowland gravel river. The river flows through agricultural areas for nearly its entire length. The valley is covered by deciduous forest (Stępień *et al.*, 2015).

The fieldwork was conducted in May, August and October 2010. The research covered the entire length of the river, where 13 sampling sites were established (Fig. 1), distributed in such a way as to cover all habitat types, where possible. The following types of habitats were distinguished:

– the main river channel – including lotic habitats (riv lo) and lentic habitats (riv le)
– water bodies in the floodplain – oxbow lakes, ponds, backwaters (flo le) and springs (helocrenes – hel)

Table 1 shows the number of samples taken in each habitat type along the Krąpiel valley. Helocrenes were the least common habitats in the river valley; only 7 were found that were large enough not to be destroyed by sampling (these were Sites 2, 3, 4, 7 and 12). We found 12 standing water bodies in the floodplain (flo le), at Sites 1, 4, 6, 7, 8, 9, 10, 12 and 14. Habitats from the main river channel were represented at each site.

Each sampling consisted of 10 energetic sweeps and covered an area of about 0.5 m^2, so the samples can be considered semi-quantitative. In some months, due to a lack of water or very high water, no samples were collected from certain habitats. A total of 111 samples were collected in which the presence of ostracods was detected.

The following environmental parameters were determined for each sample: the physical and chemical parameters of the water, the sludge particle size, and the vegetation cover. The following water variables were determined: temperature, pH, electrolytic conductivity, and dissolved oxygen content, which was examined using an Elmetron CX-401 multiparametric

Table 1. Number of samples, ostracod density, SD in particular habitat types in the Krąpiel valley in different seasons. The abbreviations; riv lo- lotic habitats of the main river channel, riv le- lotic habitats of the main river channel, flo le- lentic habitas of the floodplain, hel- helocrenes.

	May 2010				August 2010				October 2010				Sum
	riv lo	riv le	flo le	hel	riv lo	riv le	flo le	hel	riv lo	riv le	flo le	hel	
number of samples density indiv m^{-2}	17	8	9	7	17	12	6	1	17	10	6	1	**111**
	229	537	99	193	13	159	1006	696	34	214	152	1303	
SD	536	832	211	114	9	240	2043	0	46	210	241	0	

sampling probe; BOD_5 was determined by Winkler's method; water flow (velocity) was identified using a SonTek acoustic FlowTracker flowmeter; NH_4^+, NO_3^-, PO_4^{3-}, Fe^{2+}/Fe^{3+}, and carbonate hardness [mg l^{-1}] with a Slandi LF300 photometer; turbidity with a Slandi LF 205 photometer; and insolation with a CEM DT-1309 light meter. The analysis of the bottom sediment included its granulometric composition and the content of organic and mineral matter. Calculations for granulometric analysis were made using the Krumbein phi scale, in which grain size (d) in mm is expressed in phi (ϕ) units, where:

$$\phi = -\log_2 d \text{ [mm]}.$$

Mean grain size (the graphic arithmetic mean) was calculated, *i.e.* the mean diameter, $M = (\phi\ 16 + \phi\ 50 + \phi\ 84)/3$, as well as grain-size sorting (through graphic standard deviation), and a measure of the dispersion of grain diameter values:

$$W = [(\phi\ 84 - \phi\ 16)\ /\ 4] + [(\phi\ 95 - \phi\ 5)\ /\ 6.6].$$

Individual sediment samples were freeze-dried in a Christ Alpha 1-2 LD plus freeze dryer, and then the organic matter was removed from each sample by heating the sample in a Nabertherm furnace at 550°C to obtain a solid mass. In this manner, the percentages of mineral and organic matter were determined.

The degree of vegetation cover was specified on a scale of 0 to 5.

2.2 Data analysis

For the statistical tests and data analysis we used STATISTICA ver. 10 INC StatSoft, according to the methods applied by Sokal and Rohlf (1995), and PAST ver. 2.17c (Hammer *et al.*, 2001).

NPManova (Non-Parametric MANOVA) was performed between groups of ostracod samples from different types of river habitats in the main river channel and from the water bodies in the floodplain.

Diversity indices, *i.e.* the number of taxa (S), the density, the dominance (D), the Shannon index (H), and the Buzas and Gibson's evenness index (e^H/s), were calculated for different habitat types: lotic rivers (riv lo), lentic rivers (riv le), the lentic floodplain (flo le) and the helocrenes (hel). The dominance (D) corresponds to 1-Simpson index, and ranges from 0 to 1:

$$D = \sum_i \left(\frac{n_i}{n}\right)^2$$

where n_i is a number of individuals of taxon i. The Kruskal-Wallis test was also performed between them for these diversity indices.

The relationship between Ostracoda species composition and habitat variables was analysed using the CANOCO v. 4.5 software package (ter Braak and Šmilauer, 2002). We used CCA (Canonical Correspondence Analysis) (ter Braak, 1986) to analyse the patterns of species distribution in relation to the environmental variables, having previously obtained the results of indirect DCA (Detrended Correspondence Analysis), which defined the structure of the data (Jongman *et al.*, 1987). The species and environmental data were not transformed; species recorded fewer than 4 times were removed before analysis. The significance of the effect of each environmental variable on the diversity of species composition was determined using stepwise variable selection ($p \leq 0.05$). The Monte Carlo test was conducted with 499 permutations to identify the most significant variables. Variation in Ostracoda composition, explained by habitat type, substrate, and the physical and chemical variables included in the analysis, was expressed as a percentage – the ratio of the sum of all the canonical eigenvalues to the value of the total variance (total inertia). Variation in ostracod composition explained by individual variables was calculated from the ratio of Lambda A to the total variance (total inertia), expressed as a percentage. Spearman's rank correlation coefficient was used to identify correlations between densities of ostracod taxa and habitat type; chemical water variables and habitat type; and substrate variables and habitat type.

Cluster analysis was performed to determine the relationships between segments of the river on the basis of ostracod species composition in the river channel (via the Unweighted Pair Group Method with Arithmetic Mean – UPGMA, using correlation similarity).

Table 2. Diversity indices for individual habitats of the Krąpiel valley.

	riv lo	riv le	flo le	hel
Average number of taxa S	3.47	5.37	3.40	6.56
Total number of taxa	27	27	18	20
Total number of species	21	22	14	16
Density (indiv. m^{-2})	92	278	387	372
Dominance D	0.58	0.55	0.57	0.46
Shannon H	0.76	0.90	0.78	1.07
Evenness e^H/S	0.77	0.58	0.81	0.46

3 Results

The NPManova performed for groups of samples from different river habitat types showed that the samples collected from lotic habitats in the river and from helocrenes differed significantly from the other groups of samples ($p < 0.05$). Significant differences were also found between the samples from lentic habitats in the main river channel and from ponds. Thus the samples were grouped as follows for further analysis: lotic river (riv lo), lentic river (riv le), lentic floodplain (flo le), and helocrenes (hel).

The Kruskal-Wallis test for diversity indices between habitat types showed significant differences for the number of taxa, mean density, and evenness index only between habitats: the lotic river, the lentic river and the helocrenes and between the helocrenes and the floodplain. No significant differences were found for the other indices tested.

The diversity index values for the habitats of the Krąpiel valley are presented in Table 2. The habitats of the floodplain (fol le) and helocrenes (hel) had the greatest ostracod density, and the helocrenes also had the highest mean Shannon index and the lowest evenness index. Spearman's rank correlation revealed the occurrence of significant negative correlations between the lotic river (riv lo) and all other habitats; and

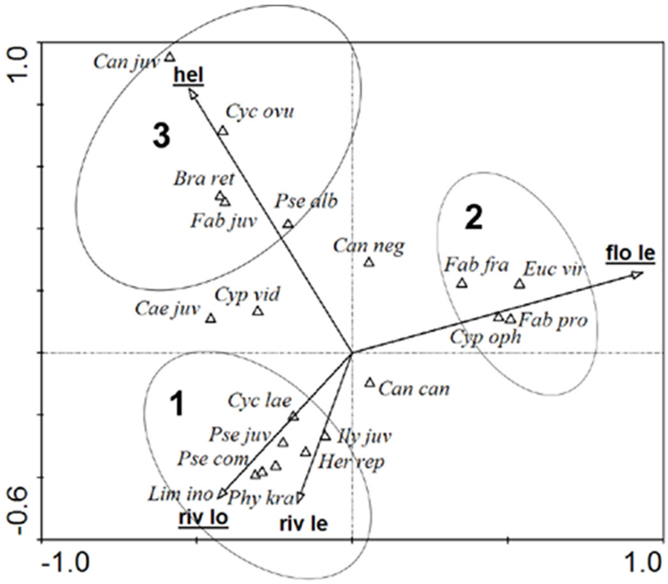

Fig. 2. The ordination diagram for ostracod species and habitat types on the first two CCA axes for samples from the Krąpiel valley. For explanations of species abbreviations see Table 3. Statistically significant habitat variables are underlined.

otherwise between the floodplain (flo le) and all river habitats ($p < 0.05$; k {–0.27; −0.56}).

The DCA analysis for ostracod samples from the River Krąpiel revealed that the length of the gradient represented by the first ordination axis was 3.3 SD, so we conducted a direct ordination analysis of the CCA type to determine the relationships between species occurrence and substrate variables. The CCA showed that habitat types were responsible for 17% of the total variance in ostracod assemblages in the valley of the Krąpiel. The stepwise selection of environmental variables in the multiple canonical analyses showed that flo le were responsible for 7.93% of the variance in ostracod assemblages, hel for 6.99%, and riv lo for 2.15%, while riv le did not significantly influence ostracod assemblages. The CCA diagram shows that only *Candona candida*, *Neglecandona neglecta* and *Cypridopsis vidua*, as eurytopic species, were not strongly related to any of the environmental vectors. Area 1 on the graph indicates species that are strongly related to lotic river habitats, area 2 indicates relationships with lentic habitats outside the river, and area 3 shows relationships with helocrenes (Fig. 2).

Spearman's rank correlation revealed numerous significant correlations between individual ostracod species and habitat types (Tab. 3). No species was found to be positively correlated with riv lo, but many positive correlations were found with the lentic habitats of the river valley: riv le, flo le and hel ($p < 0.05$; k {0.19; −0.74}). Particularly clear preferences of individual species were found for hel, where the correlation coefficients were relatively high. Most species showed a significant correlation with helocrenes (Tab. 3). In terms of ecological preferences, the species listed in the table can be classified as those characteristic of springs; those preferring small, boggy, often temporary water bodies; and eurytopic species. Species that were significantly positively correlated with standing water bodies in the floodplain were mainly represented by fauna characteristic of small, temporary or permanent water bodies and by eurytopic species (Tab. 3).

When the water level was very high in May, the densities were greater in the habitats of the river channel than they were in the water bodies of the floodplain. The reverse was observed in August, when the water was very low, and in October, when the water level had risen somewhat (Tab. 1). The percentage of individual species in different habitat types can be seen in Table 3.

The waters of riv lo were characterized by high values for oxygen, pH and BOD_5, and low values for phosphates and iron, while the reverse pattern was noted for flo le and hel (Tab. 4). In addition, the hel waters were low in nitrates and the flo le waters had high turbidity levels. Temperature, conductivity, hardness, and ammonia content were not significantly correlated with any habitat types. The riv le habitats were also not found to be significantly correlated with any of the chemical variables.

CCA showed that the chemical and physical variables of the water were responsible for 28.7% of the total variance in the ostracod assemblages in the Krąpiel valley. The stepwise selection of environmental variables in multiple canonical analyses showed that NO_3 was responsible for 6.8% of the variance in the ostracod assemblages, PO_3 for 4.3%, conductivity for 3.5%, and the remaining statistically significant environmental variables, *i.e.* O_2, NH_4, hardness and pH, for about 2% each. Area 1 in the CCA diagram (Fig. 3) indicates the species related to a low NO_3 value in the water, area 2 the species related to high values of hardness and conductivity, area 3 the species related to high values of NH_4 and NO_3 content, and area 4 those species related to high values of O_2 content and pH.

The water of riv lo had the highest flow velocity and the greatest proportion of mineral matter in the sediments, while flo le and hel had the lowest flow velocity and the greatest proportion of organic matter in the sediments (Tab. 5). The mean grain size in the various habitat types is indicative of medium-grained sand (M) and poorly sorted sediments (W). The riv le and flo le habitats had the greatest degree of plant cover.

CCA showed that the biotic and abiotic environmental factors associated with substrate type were responsible for 23% of the total variance in the ostracod assemblages in the valley of the Krąpiel. The stepwise selection of environmental variables in multiple canonical analyses showed that the W coefficient (sediment sorting) was responsible for 6.8% of the variance in the ostracod assemblages, plants for 4.2%, insolation for 5.2%, the M index (mean grain size) for 2.7%, and the proportion of mineral matter for 1.7%. Area 1 in the CCA diagram (Fig. 4) indicates species strongly related to the high proportion of organic matter in the substrate and with insolation, area 2 highlights species strongly related to the high value of the M index, area 3 shows species strongly related to the presence of plants, and area 4 indicates species strongly related to the high value of the W coefficient.

Based on the ostracod species composition at individual sampling sites in the main channel of the Krąpiel, 5 stretches of the river were distinguished (Fig. 5), within which the sites had certain common features. Group 1 consists of sites where the river is wide and deep, with a slow current and fine-grained sediments, and often with accumulated mud. Group 2 covers

Table 3. Comparison of density, SD, frequency, percentage and correlation coefficient (K) of ostracods in different habitat types. In the case of eudominants and dominants, euconstants and constants, and significant values for K, values are in bold. Abbreviations for habitat preferences: t – temporary, t/p – temporary and permanent, sp – springs, e – eurytopic, l- lakes, lp – profundal zone of lakes, ll – littoral zone of lakes, p – ponds, sw – swamps, v – vegetation (Meisch 2000).

		average density				SD				percentage %				frequency %				correlation coef. ($p < 0.05$)				habitat
		riv lo	riv le	flo le	hel	riv lo	riv le	flo le	hel	riv lo	riv le	flo le	hel	riv lo	riv le	flo le	hel	riv lo	riv le	flo le	hel	preferences
Bradleystrandesia fuscata (Jurine 1820)	Bra fus			0,55				1,05				0,14				5,00				**0,20**		t
Bradleystrandesia reticulata (Zaddach, 1844)	Bra ret	0,37	0,97	0,30	10,50	0,67	1,74	0,57	16,56	0,40	0,35	0,08	2,82	9,80	10,00	5,00	33,33	-0,11	-0,03	-0,06	**0,33**	t, sp
Candona candida (O.F. Müller, 1776)	Can can	3,51	61,55	45,60	20,13	5,28	93,15	73,68	34,49	3,81	**22,10**	**11,79**	5,41	37,25	**73,33**	**55,00**	44,44	**-0,22**	**0,20**	0,08	-0,02	e
Candona juv.	Can juv	0,12		0,20	125,26	0,23		0,38	97,33	0,13		0,05	**33,69**	1,96		5,00	**77,78**	**-0,20**		-0,10	**0,74**	–
Candona weltneri Hartwig, 1899	Can wel		0,03				0,06				0,01				3,33				0,16			sp, lp
Candoninae juv.	Cae juv	12,23	0,53	0,85	45,00	22,95	0,96	1,53	80,00	**13,28**	0,19	0,22	**12,10**	7,84	10,00	10,00	11,11	0,04	-0,09	-0,07	0,17	e
Candonopsis kingslei (Brady &Robertson, 1870)	Can kin	0,02			0,11	0,04			0,20	0,02			0,03	1,96			11,11	0,01			**0,21**	t/p, l, p, sw
Cyclocypris globosa (Sars, 1863)	Cyc glo				0,11				0,20				0,03				11,11				**0,32**	–
Cyclocypris laevis (O.F. Müller, 1776)	Cyc lae	7,01	45,55	2,27	18,81	11,97	71,89	3,43	24,08	7,61	**16,36**	0,59	5,06	23,53	46,67	30,00	**66,67**	-0,09	0,16	-0,07	0,00	ll, p, sw
Cyclocypris ovum (Jurine, 1820)	Cyc ovu	0,31	3,17	4,00	70,57	0,55	4,88	5,20	111,76	0,33	1,14	1,03	**18,98**	9,80	30,00	35,00	**66,67**	-0,12	-0,05	-0,03	**0,35**	t/p, p, l, sw
Cypria ophtalmica (Jurine, 1820)	Cyp oph	0,86	38,77	313,58	19,26	1,49	63,46	562,08	29,96	0,94	**13,92**	**81,05**	5,18	13,73	43,33	**55,00**	22,22	-0,12	-0,04	**0,22**	-0,03	e
Cypridopsis vidua (O.F. Müller, 1776)	Cyp vid	1,45	10,27	0,50	23,59	1,98	11,92	0,85	25,99	1,58	3,69	0,13	6,34	37,25	70,00	15,00	55,56	**-0,24**	**0,19**	-0,15	**0,35**	e
Cyprois marginata (Straus, 1821)	Cyp mar				0,06				0,10				0,01				11,11				**0,32**	e
Darwinula stevensoni (Brady & Robertson, 1870)	Dar ste	0,02	0,03			0,04	0,06			0,02	0,01			1,96	3,33			0,01	0,07			e, v
Eucypris virens (Jurine, 1820)	Euc vir			2,95	0,44			5,31	0,69			0,76	0,12			10,00	22,22			**0,21**	-0,01	t, sw, v
Fabaeformiscandona acuminata (Fischer, 1851)	Fab acu				1,00				1,78				0,27				11,11				**0,32**	e
Fabaeformiscandona alexandri (Sywula, 1981)	Fab ale	0,31	0,75			0,62	1,45			0,34	0,27			1,96	3,33			-0,01	0,09			t, p, sw
Fabaeformiscandona fabaeformis (Fischer, 1851)	Fab fab	1,04				2,00				1,13				3,92				0,14				t/p, p, v
Fabaeformiscandona fragilis (Hartwig, 1898)	Fab fra	0,08	0,13	2,80	1,15	0,15	0,25	5,12	2,04	0,09	0,05	0,72	0,31	5,88	6,67	15,00	11,11	-0,11	-0,06	**0,19**	0,03	ll
Fabaeformiscandona juv	Fab juv	0,20	1,17	0,20	8,85	0,36	2,18	0,36	15,74	0,21	0,42	0,05	2,38	7,84	6,67	10,00	11,11	-0,11	0,00	-0,06	**0,28**	t, p, sw
Fabaeformiscandona protzi (Hartwig, 1898)	Fab pro	0,02		0,43		0,04		0,78		0,02		0,11		1,96		10,00		-0,10		**0,26**		t/p, p, sw
Herpetocypris reptans (Braid, 1835)	Her rep	0,30	3,30			0,54	5,67			0,32	1,18			9,80	20,00			-0,09	0,18			–
Heterocypris incongruens (Ramdohr, 1808)	Het inc	0,15	0,03			0,30	0,06			0,17	0,01			1,96	3,33			0,09	-0,04			p, l, sw
Ilyocypris bradyi Sars, 1890	Ily bra	0,16	0,50	0,20		0,30	0,97	0,38		0,17	0,18	0,05		5,88	6,67	5,00		-0,09	0,16	-0,05		e, v
Limnocythere inopinata (Baird, 1843)	Lim ino	6,78	5,27			9,91	8,28			7,36	1,89			39,22	26,67			-0,04	0,09			t/p, p
Neglecandona lindneri (Petkovski, 1969) Krstić 2006	Can lin		0,07				0,13				0,02	0,00	0,00	0,00	3,33				0,16			e
Neglecandona neglecta (Sars, 1887) Krstić 2006	Can neg	0,12	0,33	1,60	2,33	0,23	0,56	2,72	3,63	0,13	0,12	0,41	0,63	3,92	16,67	15,00	22,22	-0,16	-0,06	0,15	0,17	e
Notodromas monacha (O.F. Müller, 1776)	Not mon		0,77				1,43				0,28				6,67				-0,06			t/p, p, ll
Physocypria kraepelini G.W. Müller, 1903	Phy kra	2,08	2,25			3,95	4,35			2,26	0,81			5,88	3,33			0,12	0,02			e
Potamocypris juv	Pot juv		0,03				0,06				0,01				3,33				**0,22**			–
Potamocypris villosa (Jurine, 1820)	Pot vil		0,03				0,06				0,01				3,33				0,04			sp, sw
Potamocypris zschokkei (Kauffmann, 1900)	Pot zsc	0,04		0,10		0,08		0,19		0,04		0,03		1,96		5,00		-0,09		-0,05		sp
Pseudocandona albicans (Brady 1864)	Pse alb	0,71	0,43	2,63	10,74	1,20	0,78	4,38	10,58	0,77	0,16	0,68	2,89	15,69	10,00	20,00	**66,67**	-0,09	0,16	-0,05	-0,03	t/p, p, sw
Pseudocandona compressa (Koch, 1838)	Pse com	26,17	51,75			46,95	90,47			**28,42**	**18,58**			23,53	46,67			0,01	-0,08			t/p, ll
Pseudocandona juv	Pse juv	27,73	48,80	8,15	13,30	43,68	67,81	11,64	9,44	**30,11**	**17,52**	2,11	3,58	**66,67**	**76,67**	35,00	**77,78**	-0,15	-0,13	0,06	**0,40**	–
Pseudocandona pratensis (Hartwig, 1901)	Pse pra				0,07				0,13				0,02				11,11				-0,05	t, ll
Psychrodromus fontinalis Wolf, 1920	Psy fon				0,56				0,99				0,15				11,11				-0,04	sp
Schellencandona belgica (Klie, 1937)	Sch bel		2,00				3,87				0,72				3,33				-0,06			stygobiont
Other juv. Ostracoda		0,31				0,61				0,34				5,88				0,14				–
Total		**92**	**278**	**387**	**372**													-0,09	-0,06	-0,05	**0,32**	

Table 4. Average chemical and physical variables of water in different habitat types. Significant positive correlations according to Spearman's rank correlation ($p < 0.05$) are in bold, and negative correlations are underlined.

	riv lo	riv le	flo le	hel
O2 mg L^{-1}	**7,8**	7,4	4,4	5,1
SD	2,0	2,0	3,1	1,9
pH	**7,4**	7,2	6,4	6,7
SD	0,8	0,7	1,2	1,5
temp. °C	14,4	14,8	14,0	15,5
SD	2,8	2,8	3,2	2,4
Conductivity μS cm^{-1}	200	197	195	190
SD	54	53	87	101
NH4 mg L^{-1}	0,78	0,91	1,04	0,80
SD	0,56	0,70	0,74	0,36
NO_3 mg L^{-1}	1,60	1,58	1,09	0,53
SD	1,05	1,00	0,67	0,29
PO_3 mg L^{-1}	0,34	0,37	**0,63**	**0,67**
SD	0,23	0,24	0,61	0,26
Fe mg L^{-1}	0,05	0,06	**0,11**	**0,13**
SD	0,05	0,06	0,13	0,07
Turbidity mg L^{-1}	21,2	22,2	**44,8**	13,0
SD	43,0	52,9	65,1	12,2
Hardness mg L^{-1}	176	161	148	158
SD	75	68	76	73
BOD5 mg L^{-1}	**5,33**	5,19	3,71	2,98
SD	1,62	1,55	2,70	1,04

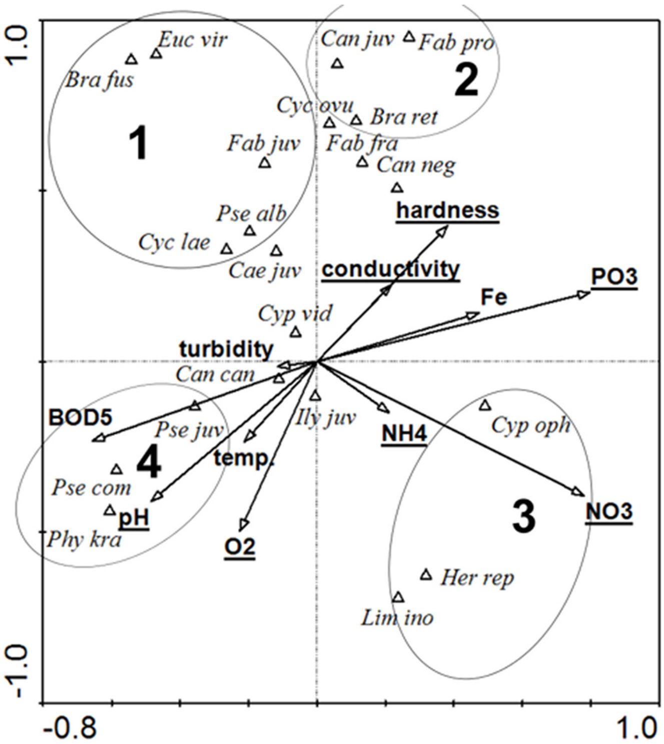

Fig. 3. Ordination diagram for ostracod species and physical and chemical water properties on the first two CCA axes for samples from the Krąpiel valley. For explanations of species abbreviations see Table 3. Statistically significant environmental variables are underlined.

Table 5. Substrate variables and other factors directly affecting the substrate in different habitat types. Significant positive correlations according to Spearman's rank correlation ($p < 0.05$) are in bold, and negative correlations are underlined. M – mean sediment grain size, W – sorting coefficient.

	velocity m s^{-1}	mineral %	organic %	M	W	insolation %	plants cover
riv lo	**0.274**	**91**	9	1.198	1.349	59	1.3
riv le	0.020	88	12	**1.496**	1.527	64	2.2
flo le	0.002	61	**39**	1.029	1.390	69	2.5
hel	0	66	**34**	1.168	1.723	19	1.4

the middle stretch, where the river is fast, with a bottom of gravel and sand and marginal pools with sand and mud. Group 3 comprises stretches of the river situated past the outflow from the lake, characterized by the high content of organic matter in the sediments and marginal pools with plants. Group 4 consists of sites from the lower gorge, with a fast current and a bottom of stones and gravel. Group 5 covers the upper course of the river, with a fast flow and a narrow channel. Group 1 in the dendrogram consists of sites with large standing water bodies in their catchment, where water can be exchanged with the main channel when the water is high. *Cyclocypris laevis* is dominant in this group; this is a eurytopic species, but it attains its greatest densities in standing water bodies. Its average density in the main river channel is 150 indiv. m^{-2}. In group 2, which has no water bodies in the catchment, juvenile *Pseudocandona* sp. accounted for the largest proportion of the fauna. These individuals were most likely of the species *P. compressa*, as only this species was abundant in the river channel. Its dominance in this stretch indicates that it is able to develop well in the river channel itself. The second dominant in this stretch, *Cypria ophtalmica*, had the density characteristic of the waters of the river channel. Group 3 is a segment fed by eutrophic oxbow lakes and thus rich in organic matter, with a dominance of *Pseudocandona compressa*, with the greatest density recorded here, 419 indiv. m^{-2}. Group 4 has no water bodies in the catchment and a very high proportion of *Limnocythere inopinata*, which may indicate that it is a species that develops in the river channel itself, *i.e.* a river species that prefers a mineral substrate. The lack of replenishment from the floodplain may explain why the total density was lowest here, at 20 indiv. m^{-2}. Group 5 is characterized by the dominance of *Cypria ophtalmica* and density at a similar level as in the water

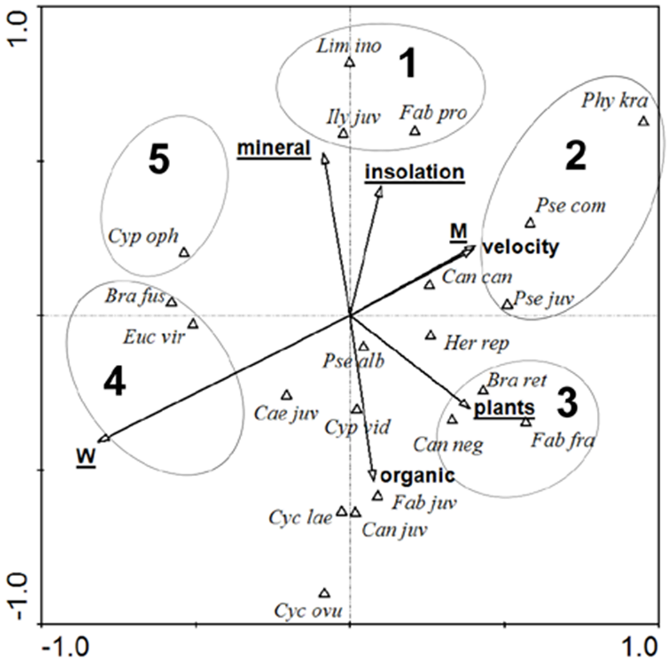

Fig. 4. Ordination diagram for ostracod species and biotic and abiotic environmental factors associated with substrate type on the first two CCA axes for samples from the Krąpiel valley. For explanations of species abbreviations see Table 3. Statistically significant environmental variables are underlined.

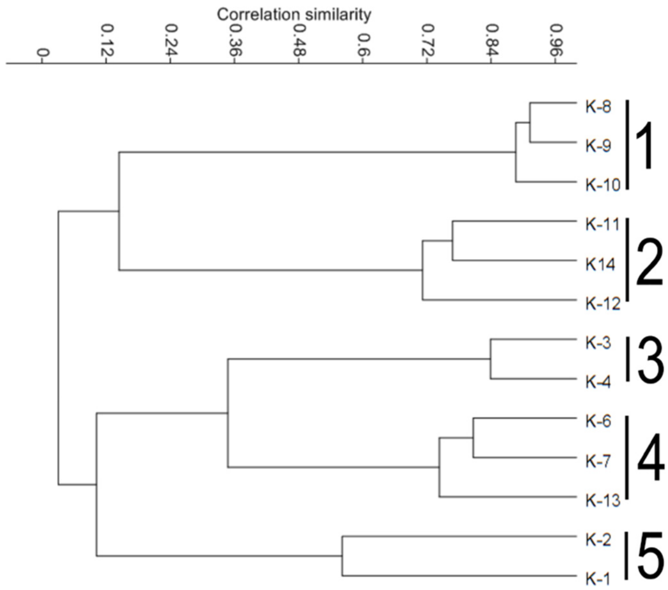

Fig. 5. Similarity dendrogram for sampling sites based on ostracod density (Unweighted Pair Group Method with Arithmetic Mean – UPGMA, using correlation similarity).

bodies of the floodplain, at 300 indiv. m^{-2}, which indicates the substantial role of surface water bodies feeding this initial stretch of the river.

4 Discussion

In the water bodies of the Krąpiel valley and in its main channel, 33 ostracod species were recorded. The checklist of ostracods of Poland, including groundwater and brackish waters, contains 140 species (Namiotko, 2008). Studies on other floodplains of European rivers have recorded 41 species in the Rhine (Scharf, 1988), 42 in the Pripyat (Nagorkaya and de Jonge, 2002), and 15 in the Danube (Kiss and Schöll 2009). Species richness in the main channels comprises 30 species in three rivers of the Iberian Peninsula (Mezquita *et al.*, 1999a), 17 in a heavily polluted river in Spain (Mezquita *et al.*, 1999b), 31 in the lower Oder (Szlauer-Łukaszewska, 2013), and 47 in a stretch of the Oder with groyne fields (Szlauer-Łukaszewska, 2015b). These data are mainly from large lowland rivers; there are no data on the ostracods occurring in small rivers like the Krąpiel, where the impact of the floodplain may be greater than in large rivers, because the river channel itself has fewer lentic areas, which are beneficial for the development of ostracods.

4.1 Habitat types

The environmental gradient most often studied in the context of rivers is the longitudinal gradient of the main channel, from the headwaters, through the lower reaches of the river, to the mouth (Rice *et al.*, 2001). The spatial distribution of the benthos then depends mainly on the hydraulic and sedimentary conditions (Rempel *et al.*, 2000). In the case of the Krąpiel, the gradient indeed depends on the hydraulic and sedimentary conditions, but successive segments of the river do not follow one another, beginning with the coarsest sediment and the fastest current and ending with the finest sediment and the slowest current. Such a sequence is violated by the gorge in the lower course of the river (Group 4, Fig. 5). The grouping of individual segments is also significantly influenced by the character of the floodplain and the water bodies feeding each given segment of the river.

Habitat type is one of the most important environmental parameters affecting ostracod assemblages (Marmonier *et al.*, 1994; Külköylüoğlu, 2004; Nagorskaya and Keyser, 2005; Szlauer-Łukaszewska, 2015a), something that our research has also proved. Habitat type in river valleys is associated with the specific location in the river valley and connectivity with the main river channel. According to Kiss *et al.* (2014), the most important factors influencing the species richness, density, and diversity patterns of the assemblages were the occurrence of flow, connectivity with the main arm, and hydrological distance from the main arm. da Conceição *et al.* (2017), who investigated variability in ostracod communities in connected and isolated tropical floodplain lakes, were of a similar opinion. It is interesting that the number of species is greatest in the main channel of the Krąpiel, at 26, in comparison with the other habitats of the floodplain (Tab. 2). Similar observations were made by Higuti *et al.* (2009) in the tropical Brazilian River Parana, as well as by Stryjecki *et al.* (2016) in the Krąpiel, in the case of water mites. By contrast, the pattern was reversed in a study of the Danube valley by Kiss and Schöll (2009), but in that case there may have been an intensive growth in the ostracod population in the river channel itself, while the water bodies of the floodplain offered greater species richness. Over most of its course, the main channel of the

Krąpiel does not provide favourable conditions for ostracod development, due to its fast current and very narrow marginal pools areas; the mean current velocity in the lotic zone of the main channel is 0.274 $m\,s^{-1}$ (with a maximum of 1.034), and the mean content of organic matter in the sediment is only 8% (with a minimum of 0.22%) (Tab. 5). The high number of species here can be explained by the fact that the main river channel is periodically the recipient of waters from the entire floodplain, including from water bodies isolated from the main channel when the water level is low or moderate. Evidence of this is shown in the occurrence of species typical of temporary water bodies (8 species), springs (4), underground waters (1 species), small water bodies (8), and swamps (7), although these species never attained a high density and their frequency was low (Tab. 3). *Pseudocandona compressa*, which is dominant in the main river channel and absent from the water bodies of the floodplain, seems to be a typical river species, which is capable of developing in the main channel. When we consider the averages for the entire study period, the juvenile *Pseudocandona* sp., *Candona candida* and *Cyclocypris laevis* that were dominant in the river channel will account for a much lower proportion of the fauna in the water bodies of the floodplain, which also indicates the preference of these taxa for flowing water. CCA analysis identifies the following as river taxa: *P. compressa*, juvenile *Pseudocandona* sp., *Limnocythere inopinata*, *Physocypria kraepelini*, *Herpetocypris reptans*, juvenile *Ilyocypris* sp., and *C. laevis*. This is partly confirmed by studies in the Oder (Szlauer-Łukaszewska, 2015a; b), where *L. inopinata* and *P. kraepelini* were dominants. Mezquita *et al.* (2005) indicate *L. inopinata*, *Ilyocypris bradyi*, and *H. reptans* as species preferring medium-high water flows. By contrast, *Cypria ophtalmica* has a 14% share of the density in the main river channel and as much as 81% in the water bodies of the floodplain, which indicates that standing water creates better conditions for the development for this species (as in Nagorskaya and de Jonge, 2002). However, it is flexible enough that it can reach very high densities even in a river with a strong current. Mezquita *et al.* (2005) classify *Cypria ophtalmica* as a species preferring low water flows.

4.2 The physical and chemical properties of the water

The chemical and physical variables of the water are clearly among the most important environmental parameters affecting the ostracod assemblages, as has been demonstrated by numerous publications (Mezquita *et al.*, 2005; Külköylüoğlu and Sari, 2012; Szlauer-Łukaszewska, 2015b; Conceição *et al.*, 2017; and many others). The results of the CCA analysis showed that those variables were responsible for 28.7% of the total variance in the ostracod assemblages in the Krąpiel valley, with nitrates, phosphates, and conductivity most strongly affecting the ostracod assemblages. According to various authors, ostracod assemblages are most influenced by temperature, pH, conductivity, and oxygen (Külköylüoğlu and Sari, 2012); oxygen and water flow (Mezquita *et al.*, 2005); temperature, oxygen and nitrates (Szlauer-Łukaszewska, 2015b); oxygen and pH (Conceição *et al.*, 2017); and COD, phosphates and inorganic nitron ions (Mazzini *et al.*, 2014). The impact of individual parameters on particular species varies. Our results show that the occurrence of *Cypria ophtalmica* is related to a high content of nutrients (NO_3 and PO_3), while that of *Physocypria kraepelini* and *Pseudocandona compressa* is associated with a low nutrient content, higher pH and better oxygenation, while avoiding waters with high conductivity and PO_3. Other dominants, such as *Cyclocypris laevis* and *Candona candida*, do not show clear preferences in relation to these environmental parameters. A comparative analysis with the findings of other authors reveals quite different relationships (Mezquita *et al.*, 2005; Külköylüoğlu and Sari, 2012; Szlauer-Łukaszewska, 2015b). It seems that the relationships obtained by various authors are strongly determined by the type of environment studied and by the species that are characteristic of a given geographic region, rather than by individual physical and chemical parameters. This type of data cannot be compared with the results obtained from different areas and habitat types.

4.3 Features of the microhabitats

Environmental factors associated with the substrate type were responsible for 23% of the total variance in the ostracod assemblages in the valley of the Krąpiel (CCA analyses). In the case of the ostracods in the Oder, the substrate was responsible for 5.69% (Szlauer-Łukaszewska, 2015b), in the River Parana 11% (Higuti *et al.*, 2010), and in Lake Świdwie 20% (Szlauer-Łukaszewska, 2012). Other authors have also described the ostracod assemblages that are characteristic of different substrate types (Kamiya, 1988; Benzie, 1989; Szlauer-Łukaszewska, 2012, 2013, 2015b; Mazzini *et al.*, 2014). In our study, *Limnocythere inopinata*, *Ilyocypris bradyi* and *Fabaeformiscandona protzi* were associated with a mineral substrate, while vegetation habitats were typical for *Cypridopsis vidua*, *Herpetocypris reptans*, *Fabaeformiscandona fragilis*, *Bradleystransesia reticulata*, Neglecandona *neglecta*, *Cyclocypris laevis* and *C. ovum*. *Physocypria kraepelini*, and *Pseudocandona compressa* preferred a larger grain size and a stronger current (as shown by CCA analysis). The relationship between vegetation and *C. vidua* is widely known (Benzie, 1989; Meisch, 2000; Frenzel *et al.*, 2010; Szlauer-Łukaszewska, 2012, 2015b, Mazzini *et al.*, 2014), as in the case of *Herpetocypris reptans* (Benzie, 1989; Meisch, 2000; Frenzel *et al.*, 2010; Szlauer-Łukaszewska, 2015b). The occurrence of *B. reticulata* in phytal substrates has been reported by Szlauer-Łukaszewska (2013, 2015b), *N. neglecta* by Szlauer-Łukaszewska (2012, 2015b), *C. leavis* and *C. ovum* by Frenzel *et al.* (2010); Szlauer-Łukaszewska (2013, 2015b), and *F. fragilis* by Frenzel *et al.* (2010); Szlauer-Łukaszewska (2013). *L. inopinata* prefers a mineral substrate (sand or gravel), as confirmed by Benzie (1989); Nagorskaya and de Jonge (2002); Scharf and Brunke (2013); Szlauer-Łukaszewska (2013, 2015b). The same has been found for *I. bradyi* (Szlauer-Łukaszewska, 2015b) and *F. protzi* (Szlauer-Łukaszewska, 2013).

4.4 Seasonal variability and the supply of the main channel from the floodplain

The occurrence of ostracods in the main channel may depend on the character of the floodplain and the water bodies feeding any given segment of the river. Following the occurrence of species at different times of the year with different water levels leads to the same conclusions regarding the genesis of ostracod fauna in the main river channel. After flooding in April, water from the floodplain returned in May to the main river channel. Nevertheless, in all the water bodies of the floodplain, different taxa were dominant than in the river channel. In many cases this tendency persisted into August, when the water level was very low, the exchange of water was substantially limited, and nearly all of the helocrenes feeding the river had dried up, and was even seen in October, when the water level had risen somewhat but the helocrenes were still dried up. Note that in May the habitats of the river channel had a much greater ostracod density than the water bodies of the floodplain, and that the situation was reversed in August and October. Thus, the floodplain is as a refugium supplying the river (Sedell *et al.*, 1990). The various ostracod taxa that entered the river from other water bodies were quickly selected by the current in terms of tolerance to this factor, and thus the taxonomic composition of the river channel was different from that of the water bodies. The densities in the water bodies were low in May because the fauna had to be regenerated after the spring flood. Densities in floodplain water bodies can be very significant, reaching as much as an average of 1300 indiv. m^{-2} (with a maximum of 5568 indiv. m^{-2}). The number of individuals can increase not only due to reproduction, but also to the decrease in the area of the water body and the concentration of fauna in a smaller amount of water. The low densities in the river channel in the summer and autumn were probably due to the ostracods being eaten by young fish (Neale, 1964), a lack of or limited numbers of individuals from the water bodies of the floodplain, and the small area of the marginal pools in which the ostracods could reproduce and develop. During floods, water bodies with distinct hydrological characteristics tend to become joined and as a consequence, ecological processes and biological communities tend to be more similar among the distinct habitats that comprise a river-floodplain system (Thomaz *et al.*, 2007). The supply of the main river channel with floodplain fauna has also been observed in the Krąpiel in the case of water mites (Zawal *et al.*, 2017), caddisflies (Buczyńska *et al.*, 2016a), and molluscs (Zawal *et al.*, 2016a), and in the Oder in the case of ostracods (Szlauer-Łukaszewska, 2013). The reverse effect, *i.e.* the fauna of the Krąpiel feeding its floodplain, has been reported for caddisflies (Buczyńska *et al.*, 2016b), water beetles (Pakulnicka *et al.*, 2016a, 2016b), and water mites (Stryjecki *et al.*, 2016; Zawal *et al.*, 2018).

5 Conclusions

1. Significant differences were found in terms of the number of taxa, the mean density, and the evenness index of the ostracod assemblages from the lotic habitat of the main river channel, the lentic habitat of the main river channel, the helocrenes, and the other lentic waterbodies of the floodplain.
2. CCA analyses showed that habitat types were responsible for 17% of the total variance in the ostracod assemblages, while the chemical and physical variables of the water explained 29%, and factors associated with substrate type were responsible for 23%.
3. Among the factors associated with the substrate, sediment sorting, plant coverage and insolation were the most important in determining the composition of the ostracod assemblages.
4. There are few ostracod species capable of developing in the main river channel: *Pseudocandona compressa*, *Cypria ophtalmica*, *Limnocythere inopinata* and *Physocypria kraepelini*. Other species occurring in this habitat should be considered eurytopic, capable of development in both lentic and lotic habitats, or assumed to have been supplied from the waterbodies of the floodplain.
5. Species characteristic of the lentic environments of the floodplain and the helocrenes include *Bradleystrandesia fuscata*, *Eucypris virens*, *Cyclocypris globosa*, *Cyprois marginata, Fabaeformiscandona acuminata*, *Pseudocandona pratensis* and *Psychrodromus fontinalis.*
6. The abundance and diversity of ostracod fauna in the water bodies of the floodplains is mainly determined by the hydrobiological characteristics of the water bodies and the rate of reproduction of the ostracods living in them. The inflow of individuals from outside the water bodies is not as significant as it is in the case of the river channel.

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