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Distribution and habitat preferences of species within the genus *Elaphoidella* Chappuis, 1929 (Crustacea: Copepoda: Harpacticoida) in Slovenia

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Abstract

Twelve species of the harpacticoid genus *Elaphoidella*, most of them exclusively groundwater species, have been recorded in Slovenia (SE Europe). Their distribution and ecology are reviewed with the aim of evaluating distribution patterns, species preferences for groundwater habitats, ecological preferences and interactions with other copepod species at regional scale. Data on *Elaphoidella* species were obtained partly from the existing literature and partly from the author's (AB) own sampling campaigns carried out together with his co-workers. During the rich history of collecting copepods in Slovenia (from the 1920s to present), *Elaphoidella* species were recorded at 78 sampling sites altogether. The majority of collecting was conducted in the southern (Dinaric region) and north-western (Alpine region) Slovenia. The most intensively sampled habitats were porous aquifers of alluvial plains, springs in the karstic unsaturated zone and percolation water in caves. The highest species richness of *Elaphoidella* was recorded in the southern Slovenia, where 10 species were found. The strictly "Dinaric" species are *E. charon*, *E. franci*, *E. karstica*, *E. stammeri*, *E. sp. 1* and *E. sp. 2*, while *E. phreatica* and *E. bidens* were found exclusively in the north-western Slovenia. From the latest data on the copepod distributions (2002–2004), where the environmental characteristics of sampling sites were also measured, the relationship between selected environmental characteristics of the habitats and the presence of *Elaphoidella* species was analysed. The distribution of *Elaphoidella* species in Slovenia was found to be related with the region, habitat type, altitude, conductivity and pH of the water.

Keywords: *Elaphoidella*; Copepoda; Habitat preference; Distribution; Ecology; Slovenia

1. Introduction

The cosmopolitan genus *Elaphoidella* Chappuis, 1929, which inhabits fresh waters and semi-terrestrial habitats, belongs to the family Canthocamptidae Sars 1903 (Copepoda: Harpacticoida). It is the second-largest harpacticoid freshwater genus after the genus *Parastenocaris* Kessler, 1913. Species of the genus *Elaphoidella* are known from several freshwater habitats – surface sediment layers of rivers and lakes (Rundle et al. 2000a; Jersabek et al. 2001) and alluvial groundwater (Pesce et al. 1987; Rouch 1991) to karstic rheocrene springs (Brancelj 1997a) and small crevices in dissolved karst rock (= epikarst) (Petkovski 1983; Brancelj 2002; Pipan and Brancelj 2003; Brancelj and Pipan 2004).

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They have been collected even in wet moss and small pools in leaf-pits of Bromeliacea (phytotelmata) (Chappuis 1928a). In addition, some species inhabit semi-terrestrial and terrestrial habitats (Dumont and Maas 1988).

At present about 200 species and subspecies are known (for a complete list see G.L. Pesce's groundwater biology homepage-http://www.geocities.com/~mediaq/elaph.html). About one-third of all known *Elaphoidella* species (71 species) have been recorded from Europe (Fauna Europaea Service-http://www.faunaeur.org). In most countries the number of known species varies between 0 and 5, and only in a few countries does the number exceed 10 (Bulgaria: 18, France: 14, Italian peninsula: 21, Romania: 10 and Slovenia: 12).

Some species of the genus exhibit wide geographical distributions, such as *Elaphoidella bidens* (Schmeil, 1893), a benthic species that inhabits continental fresh water worldwide (Reid and Ishida 1993). On the other hand, several groundwater species of *Elaphoidella* show "spot" distributions, sometimes confined to a single habitat of the locality where the species was first found and described (Galassi 2001). The genus successfully colonised ground waters, with more than 134 stygobiotic species living exclusively in the subsurface (Galassi 2001). Lewis (1986) postulated that the genus originated in the tropics with primarily widespread species, living in surface fresh water; some of them dispersed northwards during the Miocene. Some ancestral populations are thought to have entered groundwater before or after the Quaternary glaciations and further speciation may have occurred, leading to the present-day diversification of the genus in groundwater. Species distributions within geographical regions have been shaped by the influence of glaciation, by present-day variations in climate and ecology (Strayer 1994; Rundle et al. 2002) and, not less important, by habitat availability (Rouch 1991; Danielopol and Rouch 1991). For small-scale distributions (river basin or within river basin scales) species distribution is mainly influenced by physical and chemical characteristics of the environment as well as by species interactions (Dole-Olivier 1998; Galassi 2001).

In this paper, we have analysed all existing published and unpublished data on the geographical distribution of the genus *Elaphoidella* in Slovenia and have extracted data on the habitat types where species were found, together with the relevant environmental variables and accompanied copepod species where those data were available. The main objectives were to investigate the distribution of *Elaphoidella* in Slovenia, to analyse species preferences for different habitats within the study area and species interactions with the concurrent copepod assemblages.

2. Material and methods

2.1. Study area

Slovenia is located in south-eastern Europe, adjacent to Italy, Croatia, Hungary and Austria. The Alpine, sub-Mediterranean, Dinaric and sub-Pannonian region meet in this area (Fig. 1). The area is composed mainly of sedimentary rock (limestone and clastic rocks), only the eastern-most part of the Alpine region (Pohorje) is composed of magmatic rock. The climate of most of the country is moderately warm and humid. The mean temperature of the coldest month (January) never drops below −3 °C and of the warmest month (July) never exceeds 22 °C. The rainfall (up to 3000 mm in the west and 800 mm in the east) is distributed uniformly throughout the year (Fridl et al. 1998).

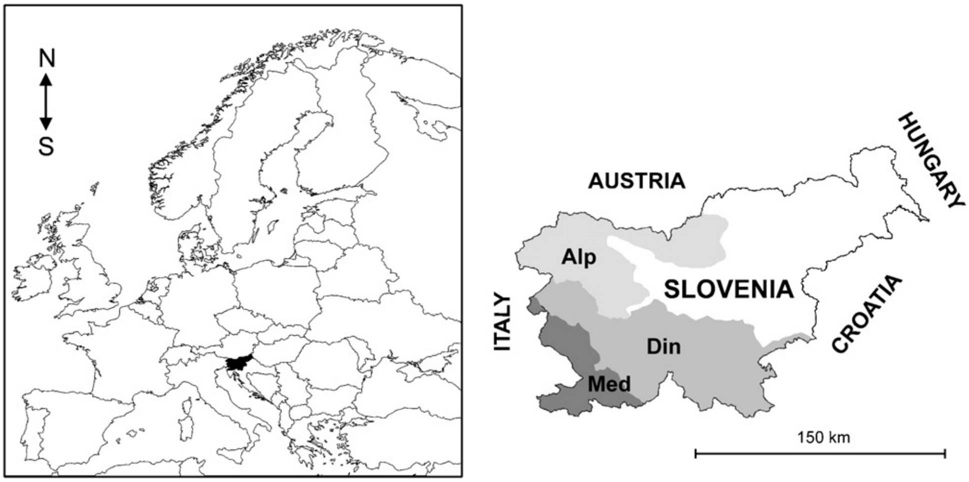

Fig. 1. Location of Slovenia in Europe (left, in black) and the investigated areas in Slovenia (right) (Alp, Alpine region; Din, Dinaric area; Med, sub-Mediterranean region).

2.2. Sampling methodology

Within each region, we defined several habitat types inhabited by *Elaphoidella* species. Waters from unconsolidated sediments (i.e. alluvium = porous aquifer) were distinguished from those in the karstic aquifer. In unconsolidated sediments, saturated interstitial areas beneath the stream bed, containing some proportion of channel water (i.e. hyporheic zone), were distinguished from true groundwater (i.e. phreatic zone). In caves, species found in dripping water, or water in the pools on the floor of the galleries, were considered as species living in the unsaturated zone of the karst (epikarst and vadose zone). Species collected in permanent cave streams or rivers were considered as species living in saturated (i.e. phreatic) zone of the karst. Springs were divided in springs fed by karstic and from porous aquifers, respectively. We further differentiated between springs emerging from the saturated zone of both porous and karstic aquifers and springs occurring within the unsaturated zone of the karstic aquifers.

Several sampling methods were used by authors and their co-workers accordingly to the different habitat types defined. Benthos was sampled with a kick-sampling method up to a depth of 5 cm into the sediment (Peckarsky 1984). Surface sediment layers were kicked for 1 min and a hand net (mesh size 100 μm) was used to collect the fauna. Springs were sampled by the same method. Percolating water in the caves and from the pools was filtered by specially designed filter bottle (Brancelj 2004) and water from the unconsolidated sediments was extracted with a piston-pump according to the Bou–Rouch method (Bou and Rouch 1967).

2.3. Data analysis

Data on copepod assemblages and *Elaphoidella* distribution were pooled from investigations conducted in the Dinaric (south Slovenia), the Alpine (northwest Slovenia) and the sub-Mediterranean (southwest Slovenia) regions (Fig. 1). Information on the distribution of *Elaphoidella* species were obtained partly from the literature (Chappuis 1928b, 1936; Stammer 1932; Petkovski 1983, 1984), and partly from the author's (AB) own sampling campaigns carried out together with his co-workers or students after 1984 (Petkovski and Brancelj 1985; Brancelj 1986, 1988, 1992, 1997a, b, 2001, 2002; Jersabek et al. 2001; Kejžar 2003; Pipan 2003; Pipan and Brancelj 2004a, b; Pipan 2005) and from the sampling campaign within the PASCALIS project (Mori 2004; http://www.pascalis-project.com). The data from before 1984 (6 records) consist solely of information on species, locality and habitat type of sampling sites, the data between 1985 and 2001 (16 records) include the information on the whole copepod assemblages collected at sampling sites and some environmental parameters, while the latest data (from 2002 to 2004) (63 records) contain information on copepod assemblages together with detailed environmental characteristics of the sampling sites. Altogether 78 sampling sites were considered; 62 in the Dinaric, 14 in the Alpine and 2 in the sub-Mediterranean regions, respectively. Some of the sampling sites were sampled more than once from different researchers. Data on geographical distribution of *Elaphoidella* and preferences for certain habitat types at regional scale were extracted from all three sets of data. The third set of data was used to analyse the relationship between *Elaphoidella* species, other copepod species and environmental characteristics of sampling sites.

Canonical correspondence analysis (CCA) (ter Braak 1986) was used to correlate species data with environmental parameters. Altogether, nine environmental parameters (region, habitat type, altitude, water temperature, conductivity, pH, nitrate, sulphate and calcium contents) were considered in the analysis. Data on the presence and absence of copepods were used, but rare species (only one individual in the sample) were excluded from the ordination analysis. The statistical significance of environmental variables in CCA was tested by the Monte Carlo permutation test (999 permutations) in forward selection of variables. CCA was run by program CANOCO 4.5 (ter Braak and Smilauer 2002). In the ordination plots, the coordinates of the sampling sites are the values of the sites on the two best synthetic gradients (axes 1 and 2), and the species are represented by their niche centre along each axis.

3. Results

The most intensively sampled were the interstitial habitats in the alluvial plains, where we recorded 21 hyporheic and 20 phreatic sampling sites inhabited by *Elaphoidella* (i.e. positive sampling sites), springs in the unsaturated zone of the karst had 19 positive sampling sites and caves 14. Two positive sampling sites were in the springs emerging from the saturated zone and two were from the lake benthos. In total, 12 *Elaphoidella* species were found (Table 1). Five of them are recognised as endemic for Slovenia (*E. charon*, *E. franci*, *E. karstica*, *E. jeanneli* and *E. stammeri*). *E. franci* and *E. karstica* are each known from only one locality (Brancelj 2001). In addition, two more species with restricted geographical distribution are not yet described, i.e. *Elaphoidella sp. 1* and *sp. 2*. *E. cvetkae* has been found outside Slovenia only in the north-eastern Italy (Pesce and Galassi 1986). *E. phreatica* is found in all of the Apennines and the Balkan Peninsula (Apostolov 1985; Karanovic 2001). Other species (*E. bidens*, *E. elaphoides*, *E. gracilis*) are distributed all over Europe, the first being cosmopolitan. In Slovenia only *E. elaphoides* is present across all three regions (Alpine, Dinaric and sub-Mediterranean), while *E. phreatica* and *E. bidens* were found only in the Alpine region, despite relatively intensive sampling in the Dinaric region and despite the fact that the latter species is known to be cosmopolitan. *E. charon*, *E. franci*, *E. karstica*, *E. stammeri*, *E. sp. 1* and *E. sp. 2* are strictly "Dinaric" species.

The species showing the highest frequency of occurrence were *E. sp. 1*, *E. elaphoides* and *E. cvetkae*, occurring at 25, 17 and 14 sampling sites, respectively (Fig. 2). The first was found in several habitats, from caves in the unsaturated zone of karst to the unconsolidated sediments of rivers. The second one inhabited habitats in unconsolidated sediments, and the third the unsaturated karst. Five species (*E. cvetkae*, *E. franci*, *E. karstica*, *E. stammeri*, *E. sp. 2*) were found only in the unsaturated zone of karst aquifer (small springs-discharge $<0.1\,\mathrm{l\,s^{-1}}$, and caves). In contrast, *E. gracilis* and *E. bidens* are found in surface waters, usually living in the sediments of rivers and lakes. *E. phreatica* was found almost exclusively in the unsaturated zone of the alpine karst, usually at higher altitudes than other species.

Table 1. Geographical distribution of *Elaphoidella* species in Slovenia (ALP, Alpine region; DIN, Dinaric region; MED, sub-Mediterranean region)

Species	ALP	DIN	MED
E. bidens (Schmeil, 1894)	+		
E. charon (Chappuis 1936)		+	
E. cvetkae (Petkovski 1983)	+	+	
E. elaphoides (Chappuis, 1924)	+	+	+
E. franci (Petkovski 1983)		+	
E. gracilis (Sars, 1863)	+	+	
E. jeanneli (Chappuis 1928a, b)		+	+
E. karstica (Petkovski and Brancelj 1985)		+	
E. phreatica (Sars, 1862)	+		
E. stammeri (Chappuis 1936)		+	
E. sp. 1		+	
E. sp. 2		+	

The summarised results of CCA are shown in Table 2. CCA explained 24.3% of total species variance. The percentage of the explained variance on the first two axes is 56.1%. The Monte Carlo permutation test indicated the statistical significance of habitat type, altitude, region, conductivity and pH for the distribution of *Elaphoidella* species (Table 3). Three well-separated groups of sampling sites (= habitats) can be distinguished in the ordination diagram: (a) (karstic) springs in the unsaturated zone, (b) caves and (c) interstitial habitats (Fig. 3). Springs are located at higher altitudes, in the Alpine region up to 955 m a.s.l. and in the Dinaric region up to 840 m a.s.l., while sampling sites from caves and unconsolidated sediments are located at lower altitudes (average 500 and 320 m a.s.l., respectively) (Table 4). Fluctuations in temperature are relatively low in springs (Alpine region: ±2.8 °C, Dinaric region: ±3.5 °C) and higher in caves and river sediments (±8 °C). However, maximum temperatures in the alpine springs reached 8.5 °C, in the Dinaric springs and caves 12.1 °C, while in the river sediments the maximum temperature was 20.2 °C. Water from springs in the Alpine region showed lower

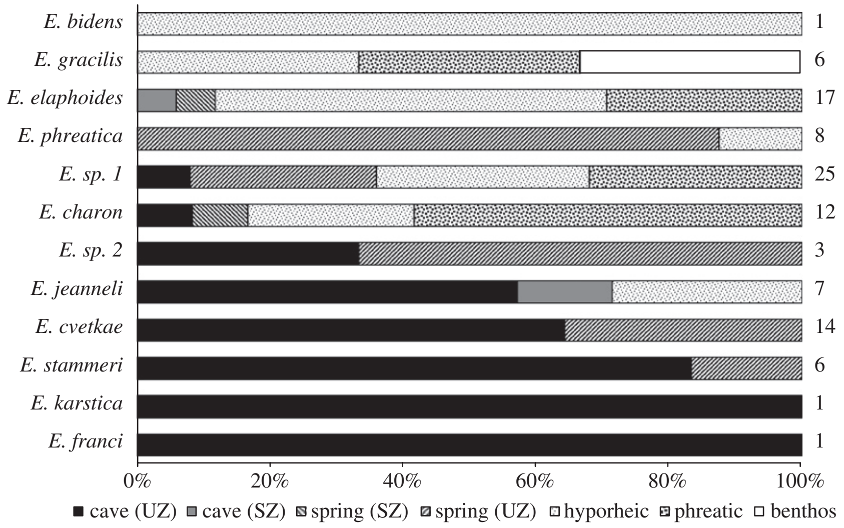

Fig. 2. Relative frequency of occurrence of *Elaphoidella* species in different habitat types in Slovenia. Numbers at the right side indicate the number of sampling sites where each species was found. UZ, unsaturated zone; SZ, saturated zone.

Table 2. Summarised results of CCA analysis

Axes	1	2	3	4	Total inertia
Eigenvalues	0.563	0.459	0.212	0.153	7.510
Species–environment correlations	0.937	0.895	0.807	0.755	
Cumulative percentage variance					
of species data	7.5	13.6	16.4	18.5	
of species–environment relation	30.9	56.1	67.7	76.1	
Sum of all Eigenvalues					7.510
Sum of all canonical Eigenvalues					1.822

Table 3. Summary of the Monte Carlo permutation test

	p	Eigenvalue	Cumulative eigenvalue	% Variance	Cumulative % variance	% Inertia	Cumulative % inertia
Habitat type	0.001	0.510	0.510	28.0	28.0	6.8	6.8
Region	0.001	0.470	0.980	25.8	53.8	6.3	13.0
Altitude	0.001	0.210	1.190	11.5	65.3	2.8	15.8
Conductivity	0.032	0.130	1.320	7.1	72.4	1.7	17.6
pH	0.010	0.120	1.440	6.6	79.0	1.6	19.2
Temperature	0.086	0.110	1.550	6.0	85.1	1.5	20.6
NO_3^-	0.219	0.090	1.640	4.9	90.0	1.2	21.8
SO_4^{2-}	0.217	0.090	1.730	4.9	95.0	1.2	23.0
Ca^{2+}	0.181	0.090	1.820	4.9	99.9	1.2	24.2

conductivity than water from caves, springs and river sediments from the Dinaric region due to fast flow of melted snow and rain water through vertical voids in cold unsaturated zone of karstic channels. Water from the Dinaric caves and springs was the richest in nitrate and sulphate contents as a result of mineralisation of rich organic material within relatively warm subterranean environment.

Different species of *Elaphoidella* and accompanied copepods (Appendix A) show different preference for the three groups of sampling sites. *E. phreatica*, accompanied by the harpacticoids *Attheyella wierzejskii* (Mrázek, 1893), *Bryocamptus rhaeticus* (Schmeil, 1893), *Moraria mrazeki* (Scott, 1903) and *Moraria radovnae* (Brancelj 1988), shows strong preference for high-altitude springs in the karstic unsaturated zone. *E. karstica* and *E. stammeri*, together with harpacticoids such as *Bryocamptus echinatus* (Mrázek, 1893), *Bryocamptus balcanicus* (Kiefer, 1933), *Morariopsis dumonti* (Brancelj 2002), *Maraenobiotus brucei* (Richard, 1898) and *Parastenocaris* sp. live in small fractures of epikarst. *E. elaphoides*, *E. gracilis*, *E. sp. 1* and *E. charon* are grouped around sampling sites from porous aquifers. The remaining species, *E. cvetkae*, *E. jeanneli* and *E. sp. 2*, are located on the border between clusters of sampling sites, indicating that they are successful in two or more different habitats.

4. Discussion

The number of *Elaphoidella* species found in Slovenia (12 species) is greater than in most other European countries. Only in mainland Italy is the number higher, mostly due to relatively intensive sampling (Pesce 1985; Pesce et al. 1987), large area (301,230 km^2 of Italy vs. 20,256 km^2 of Slovenia), and the remarkable range of groundwater environments. The considerable species richness in Slovenia is mostly due to the large number of endemic *Elaphoidella* species in groundwater of the Dinaric region.

The genus *Elaphoidella* is characterised by a high number of stygobiotic species in Slovenia as well as in other European countries and in the Holarctic region as a whole. In Slovenia, about 33% of them are located exclusively in the unsaturated zone of karst (i.e. vadose and/or epikarstic zone), characterized by a high calcium content (resulting in high conductivity and alkalinity) and intermittently interrupted by severe fluctuations in water discharge and temperature (Pipan 2005). It is highly probable that such an environment limits dispersal in the horizontal direction and consequently the exchange of genetic material within a given area. As a result there are many endemics having relatively narrow distributions in both horizontal and vertical directions. When individuals are washed out from the

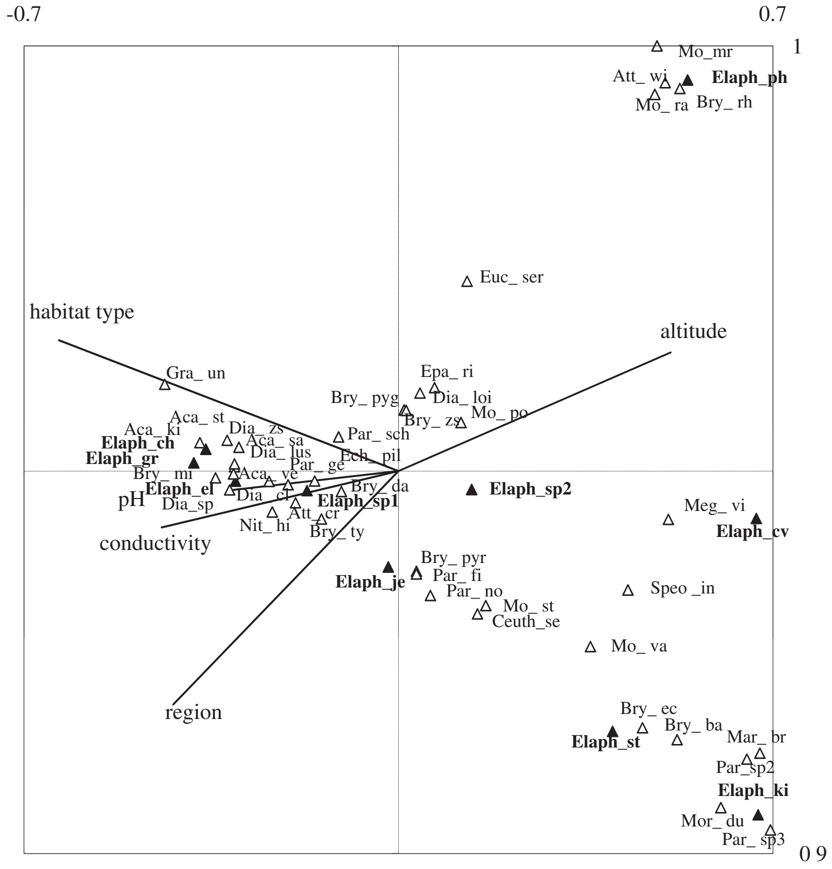

Fig. 3. Ordination diagrams based on canonical correspondence analysis (CCA) of copepod species scores (above) and sampling site scores (below) with respect to environmental variables (lines). Species abbreviations are listed in Appendix A. Filled triangles (above) refer to *Elaphoidella* species.

Table 4. Maximum, mean and minimum values of environmental parameters of different habitats where *Elaphoidella* species were sampled

Region	Habitat		Altitude (m a.s.l.)	Water temperature (°C)	pH	Conductivity (μS cm^{-1})	NO$_3^-$ (mg l^{-1})	SO$_4^{2-}$ (mg l^{-1})	Ca^{2+} (mg l^{-1})
Alpine	Spring (UZ)	Max	955	8.5	8.1	368	4.8	10.2	54.3
		Mean	618	6.9	7.8	280	2.4	5.6	39.6
		Min	410	5.7	7.5	162	1.1	0.4	25.0
Dinaric	Cave (UZ)	Max	680	12.3	8.4	548	36.9	10.2	60.7
		Mean	499	8.6	7.9	388	4.9	6.8	37.2
		Min	320	4.5	7.5	256	0.2	2.3	19.6
	Spring (UZ)	Max	840	12.1	8.3	532	10.2	9.2	46.9
		Mean	547	10.8	7.8	464	5.0	7.3	37.0
		Min	362	8.6	7.5	383	0.4	5.1	28.8
	Hyporheic	Max	384	20.2	8.4	555	6.4	11.4	57.1
		Mean	320	14.6	8.1	444	3.7	8.4	44.2
		Min	290	11.4	7.7	390	0.9	6.9	28.3
	Phreatic	Max	375	19.6	8.4	731	6.7	27.1	61.3
		Mean	323	15.0	8.1	459	3.9	8.7	44.0
		Min	295	11.9	7.7	267	0.9	4.9	29.7

UZ, unsaturated zone.

unsaturated karstic zone they are normally out-competed by more aggressive species (Brancelj 2002).

So far, five species from Slovenia are restricted to the unsaturated zone in the Dinaric karst, either in percolating water or in small springs in the unsaturated zone (*E. cvetkae*, *E. franci*, *E. karstica*, *E. stammeri* and *E. sp. 2*). These species are restricted to one or a few sites at moderate altitude (between 300 and 600 m a.s.l.). They can be considered as highly endemic species. The exception is *E. cvetkae*, which has a wider geographical distribution (Brancelj 2001), ranging from the Dinaric to the Alpine region in Slovenia and in northern Italy (Pesce and Galassi 1986), inhabiting areas between 200 and 700 m a.s.l., but in Slovenia predominantly found in waters with lower temperatures (below 8 °C). On the other hand, there are three, morphologically similar (= cryptic), species (*E. charon*, *E. jeanneli* and *E. sp. 1*) all first discovered in the unsaturated karstic zone, but recently recorded from interstitial habitat along the river beds in the Dinaric region (Mori 2004). These three stygobiotic species definitively occupy two different habitats at least: the unsaturated/vadose zone in the karstic aquifer, and porous aquifer in contact with the karstic one. This indicates that they have sufficient dispersal ability to migrate between two systems with quite different hydrological and geomorphological characteristics. An interesting species is *E. phreatica* which, despite intensive sampling campaigns in Slovenia, has been found exclusively in the Alpine region, mostly in springs located in the unsaturated karstic zone but never in the phreatic zone of the Dinaric karst. The species is considered common in southern and central Europe (Ilies 1978; Apostolov 1985), inhabiting predominantly porous aquifers (as indicates its name = *phreatica*). In Montenegro, this species was reported from the hyporheic zone (Karanovic 2001) and in central and northern Italy was collected from both phreatic and hyporheic habitats (Pesce and Galassi 1986). *E. elaphoides* may be considered to be stygophile species, which recently immigrated into subterranean biotopes (Pesce et al. 1987). However, its ecology is still open to question. In Europe it is widespread in both epigean and hypogean waters. Our results suggest that *E. elaphoides* prefers epigean waters and hyporheic zone, and is only occasionally or accidentally washed downstream by sinking rivers into cave environment.

At scale of the river basins the distribution of *Elaphoidella* (and other aquatic organisms) is governed by environmental characteristics together with habitat availability. Measurements of environmental parameters in ground waters, especially in unsaturated zone, are difficult. Animals collected by filtration in caves or springs are the result of drift through a whole system of fractured rock (Rouch and Danielopol 1997) and it is therefore difficult to describe their true environment by measurement of physical and chemical parameters of percolation or spring water. The results of CCA showed the importance of pH and conductivity in the distribution of *Elaphoidella* in Slovenia. At least in epigean environments those two factors were found to play an important role. Rundle and Hildrew (1990) reported that the species richness and density of benthic harpacticoids in some southern English and Welsh streams were positively correlated with pH and conductivity. During sampling of unsaturated zone in the karstic aquifer, Pipan (2005) found statistically significant positive correlations between copepod communities collected by filtration and the concentrations of some ions (Na^+, NO_3^- and K^+) in the percolation water.

The two main factors controlling the presence of species at given sampling sites in Slovenia resulted to be the geographical region and the habitat type. One of the most important elements governing the differences in the species richness and the occurrence of *Elaphoidella* species are probably the differences in the geological and climatological history of each region, along with diversity of habitats. In the karstic environments, horizontal dispersion was constrained due to rather intensive geological, i.e. seismic, activity which separate limestone blocks in rather isolated blocks which act in unsaturated karstic zone as islands (Brancelj 2002), resulting in several endemic species. Rundle et al. (2000) pointed out the importance of glaciation for differences in harpacticoid diversity in freshwater streams across Europe. In the north, diversity is much lower than in the south, where many endemic species live. Those species were prevented from re-colonisation in the Holocene by their poor dispersal ability. Analogously, the majority of species from the Dinaric region in Slovenia were prevented from re-colonising the Alpine region. The Quaternary glaciation may have played an important role in increasing colonisation and speciation in the groundwater of the Dinaric region. The process involved active and passive dispersion, and the initial part of the process of colonisation might have taken place before the appearance of ‘environmental constraint’ (Galassi 2001; Stoch 2004).

Important properties differentiating habitat types are their physical characteristics – differences in geomorphology, hydrology and degree of connectivity within and between habitats. Creuzé des Chatelliers (1991) demonstrated the importance of geomorphology and hydrology for the distribution of interstitial fauna in the alluvial sediments. The structure of the sediments and their connectivity with surface water or groundwater determines the community composition. Rouch (1991) demonstrated that distribution of harpacticoid species in the interstitial habitats of the Lachein Creek (French Pyrenees) is a function of streambed permeability. Other important factors for differences in species richness are environmental stability and predictability of habitats (Stoch 1995). In interstitial habitats, physical inertia increases with depth. The karst is more heterogeneous, with the saturated zone storing large water reserves with long retention times and the unsaturated zone characterised by low water availability with short retention time (Gibert et al. 1994). If some environmental parameters fluctuate in a regular and predictable way, organisms may evolve some degree of dependence and specialisation on temporal patterns of resource availability, enhancing diversity (Stoch 1995). This is in a good agreement with rather high diversity of Copepoda in unsaturated zone of karst (Brancelj 2002), including high number of *Elaphoidella* species. Shallow alluvial sediments and springs are more connected with the surface and therefore host fewer species of *Elaphoidella* than karstic habitats.

The high number of *Elaphoidella* species recorded and their distribution in Slovenia indicate that events in the past on macro-scale (glaciation) as well as the physical structure of the habitats favoured the speciation and shaped the distribution of species. Although fauna of Copepoda in Slovenia is relatively well known, more new species, also in the genus *Elaphoidella*, are expected to be found in the future, especially in the unsaturated zone of karst and in porous aquifers along small and middle-size rivers.

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5. Appendix A. List of abbreviations used in the CCA ordination diagram (Fig. 3)

Att_cr	*Attheyella crassa* (Sars, 1863)	Mo_mr	*Moraria mrazeki* (Scott, 1903)
Att_wi	*Attheyella wierzejskii* (Mrázek, 1893)	Mor_ra	*Moraria radovnae* (Brancelj 1988)
Bry_ba	*Bryocamptus balcanicus* (Kiefer, 1933)	Mor_st	*Moraria stankovitchi* (Chappuis, 1924)
Bry_da	*Bryocamptus (L.) dacicus* (Chappuis, 1923)	Mor_va	*Moraria varica* (Graeter, 1910)
Bry_ec	*Bryocamptus (L.) echinatus* (Mrázek, 1893)	Mor_du	*Morariopsis dumonti* (Brancelj 2002)
Bry_mi	*Bryocamptus minutus* (Claus, 1863)	Nit_hi	*Nitocrella hirta* (Chappuis, 1923)
Bry_pyg	*Bryocamptus pygmaeus* (Sars, 1863)	Par_sch	*Paracamptus schmeili* (Mrázek, 1893)
Bry_pyr	*Bryocamptus pyrenaicus* (Chappuis, 1923)	Par_ge	*Parastenocaris gertrudae* (Kiefer, 1968)
Bry_rh	*Bryocamptus (A.) rhaeticus* (Schmeil, 1893)	Par_no	*Parastenocaris nolli* (Kiefer, 1938)
Bry_ty	*Bryocamptus typhlops* (Mrázek, 1893)	Pa_sp2	*Parastenocaris sp. 2*
Bry_zs	*Bryocamptus zschokkei* (Schmeil, 1893)	Par_sp3	*Parastenocaris sp. 3*
Ceuth_se	*Ceuthonectes serbicus* (Chappuis, 1924)	Aca_ki	*Acanthocyclops kieferi* (Chappuis, 1925)
Ech_pil	*Echinocamptus pilosus* (Van Douwe, 1910)	Aca_sa	*Acanthocyclops sambugarae* (Kiefer, 1981)
Elaph_ch	*Elaphoidella charon* (Chappuis 1936)	Aca_st	*Acanthocyclops stammeri* (Kiefer, 1930)
Elaph_cv	*Elaphoidella cvetkae* (Petkovski 1983)	Aca_ve	*Acanthocyclops venustus* (Norman and Scott, 1906)
Elaph_el	*Elaphoidella elaphoides* (Chappuis, 1924)	Dia_cl	*Diacyclops clandestinus* (Kiefer, 1926)
Elaph_gr	*Elaphoidella gracilis* (Sars, 1863)	Dia_loi	*Diacyclops languidoides* (Lilljeborg, 1901)
Elaph_je	*Elaphoidella jeanneli* (Chappuis, 1928)	Dia_les	*Diacyclops languidus* (Sars, 1863)
Elaph_ki	*Elaphoidella karstica* (Petkovski and Brancelj 1985)	Dia_zs	*Diacyclops zschokkei* (Graeter, 1910)
Elaph_ph	*Elaphoidella phreatica* (Sars, 1862)	Dia_sp	*Diacyclops* sp.
Elaph_st	*Elaphoidella stammeri* (Chappuis 1936)	Euc_ser	*Eucyclops serrulatus* (Fischer, 1851)
Elaph_sp1	*Elaphoidella sp. 1*	Gra_un	*Graeteriella unisetigera* (Graeter, 1908)

Elaph_sp2	*Elaphoidella sp. 2*	Meg_vi	*Megacyclops viridis* (Jurine, 1820)
Epa_ri	*Epactophanes richardi* (Mrázek, 1893)	Par_fi	*Paracyclops fimbriatus* (Fischer, 1853)
Mar_br	*Maraenobiotus brucei* (Richard, 1898)	Speo_in	*Speocyclops infernus* (Kiefer, 1930)
Mor_po	*Moraria poppei* (Mrázek, 1893)		

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