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Distribution and conservation status of fairy shrimps (Crustacea: Anostraca) in the astatic soda pans of the Carpathian basin: the role of local and spatial factors

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ABSTRACT

The distribution of Branchinecta orientalis, B. ferox *and* Chirocephalus carnuntanus *was assessed in the natural and semi-natural astatic soda pans of the Carpathian basin. In Europe, these habitats are exclusively restricted to Hungary (Great Hungarian Plain), Austria (Seewinkel) and Serbia (Vojvodina). The present research is the first comprehensive large-scale study – covering an area of approximately 125,000 km² – on these three fairy shrimp species in the region, and it is important especially in the case of* Branchinecta *spp., due to former taxonomical uncertainties. The local, land use and spatial effects on the species distribution were also analysed. The three anostracans were found to adopt different strategies, mainly according to the salinity of the pans. The apparently halophilous* B. orientalis *tolerated higher salinities than the other species, which can be regarded as habitat-generalist halotolerants, showing a high preference for soda waters in Central Europe. The density of the species was significantly affected only by local factors, while their occurrence was influenced also by pan isolation. Land use did not explain a significant amount of variation in either case. In conclusion, soda pans with a wide range of different salinities constitute a suitable habitat for all the three species. Also, protected areas with high number of pans – as Seewinkel (in Austria) or Kiskunság (in Hungary) – can play an essential role in the long-term conservation of these anostracans. Finally, we suggest that these species should be legally protected, primarily because the number of their habitats in the basin is seriously declining.*

Key words: Pannonian plain, salinity, Branchinecta, Chirocephalus*, isolation.*

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INTRODUCTION

Large branchiopods (Anostraca, Notostraca, Spinicaudata and Laevicaudata) are important flagship species of temporary waters (Belk, 1998). Human disturbance and destruction of their often neglected natural habitats caused them to be globally vulnerable and to undergo a serious decline of their distribution (Löffler, 1993; Petrov and Petrov, 1997; Belk, 1998; Damgaard and Olesen, 1998; Samraoui *et al*., 2006; Brendonck *et al*., 2008; Demeter and Stoicescu, 2008). Moreover, as our knowledge about this group is still scarce, not only is it important to monitor them, but also to study their ecological needs and roles (Forró, 2000; Mura, 2001; Demeter and Stoicescu, 2008). In Austria, they have been recently studied in depth (*e.g*., Metz and Forró, 1991; Eder *et al*., 1996, 1997; Gottwald and Eder, 1999; Eder and Hödl, 2002, 2003), but their investigation in Serbia began only in the 1970s (Petrov and Petrov, 1997). Likewise, they have not been surveyed since the 1990s, except for some faunistical notes from the south-eastern part of the country (Miličić and Petrov, 2007). In Hungary, only one investigation has targeted large branchiopods since the 1960s (Boven *et al*., 2008), and a very few studies included them with new occurrences (*e.g*., Forró, 1990, 2003; Boros *et al*., 2006; Horváth and Vad, 2010).

In the astatic soda pans of the Carpathian basin, three Anostraca species were recorded: *Branchinecta ferox* (Milne-Edwards, 1840), *B. orientalis* Sars, 1901 and *Chirocephalus carnuntanus* (Brauer, 1877) (Petkovski, 1991; Löffler, 1993; Eder *et al*., 1997; Petrov and Petrov, 1997). Although other large branchiopods are testified to occur, *e.g*. in the Seewinkel and Kiskunság areas, these flagship species were mainly registered in temporary puddles, flooded meadows, or sometimes in former pans that had already lost the characteristics of astatic soda pans (Eder *et al*., 1996; Boven *et al*., 2008). There are no occurrences of any other species from natural, saline soda pans. The three anostracans under discussion are mainly univoltine (Löffler, 1993; Eder, *et al*., 1997) as they generally occur in early spring and disappear as water temperature increases. Eder *et al*. (1997) found them in Austria exclusively in spring, but Petkovski (1991) noted that *B. orientalis* can sometimes be present also in late autumn.

The *Branchinecta* species have a disjunct distribution

(Alonso, 1985; Brtek and Thiéry, 1995). *B. orientalis* is a Mongolian-steppic element (Brtek and Thiéry, 1995), but it is also present in the Asian high mountains (Brtek and Thiéry, 1995; Manca and Mura, 1997). *B. ferox* occurs in the temporary waters of steppes and steppe-like habitats across the Mediterranean Europe and in North Africa (Dimentman, 1981; Fryer, 1983; Alonso, 1985), but it also lives in some parts of Asia (Brtek and Thiéry, 1995). *C. carnuntanus* also inhabits astatic habitats (Eder *et al*., 1997), but with a much more restricted distribution. Apart from two exceptions [Moscow and the no-longer-existing northern Bohemian lowland (Brtek and Thiéry, 1995; Lukáš Merta, personal communication)], it is only present in the Carpathian basin (Brtek and Thiéry, 1995), and Löffler (1993) regarded it as an endemic Pannonian species. Before Petkovski's (1991) taxonomical revision, some former studies from the region did not differentiate between *B. orientalis* and *B. ferox*; therefore, Eder and Hödl (2003) suggested using Austrian data published before 1991 as *Branchinecta* spp.

Given the biogeographical importance of the Carpathian basin in the distribution of the three species (meaning presumably the exceptional area of occurrence for *C. carnuntanus* and the main European patch for the *Branchinecta* species) and the former uncertainties regarding the taxonomy of the two *Branchinecta* species before Petkovski (1991), a comprehensive survey of this region is needed.

In our study, we aimed to: i) update knowledge on the distribution of the three anostracan species in the European astatic soda pans (which unique habitat type is now restricted exclusively to Hungary, Austria and Serbia); ii) assess their current conservation status; and iii) determine the local, land use and spatial effects on their distribution.

METHODS

Study area

Shallow astatic soda pans are typical examples of steppic aquatic habitats in the lowland territory of the Carpathian basin; also, they are a special type of inland athalassohaline waters (Hammer, 1986). They have notable seasonal water level fluctuations and frequently dry out entirely in midsummer or autumn. Their high pH and salinity is caused by a high amount of dissolved sodium-hydrogen-carbonate, and their salinity varies between hypo- and meso-saline ranges, depending on the water level (Metz and Forró, 1991; Boros, 1999; Dvihally, 1999). Most of them are highly turbid because of permanently suspended colloidal ion complexes and/or high concentration of dissolved humic substances (Boros, 1999; V.-Balogh *et al*., 2010). Along the shoreline, characteristic sodic-alkaline soils can be found with the typical sodic marshland and wet meadow vegetation (*e.g.*, *Bolboschoenus-Phragmitetum* and *Lepidio-Puccinellietum* associations). Conversely, no vegetation is present in the major part of the lakebed during the wet periods (Boros, 1999).

The Carpathian basin is the westernmost occurrence of soda pans in Eurasia (parallel with the steppe biome), while it is their only occurrence in Europe (Hammer, 1986). In the last few decades soda pans have been dramatically decreased in number, and this unique habitat type is now restricted only to the lowland parts of Hungary, to Seewinkel in Austria and to Vojvodina in Serbia (Boros, 1999).

Data on sampling and species

Ninety-one astatic soda pans in the Carpathian basin were considered in the study (see Tab. 1 for their coding), in an area of approximately 125,000 km^2 (Fig. 1). We included every pan, apart from reconstruction areas and those that had already lost all their sodic characteristics, mostly by severe anthropogenetic alteration. Among the pans, 51 were located in Hungary, 31 in Austria (Seewinkel) and 9 in Serbia (Vojvodina). All of them were sampled at least twice: i) between 4th March and 9th April 2010 for the early spring sampling; and ii) between 11th May and 20th June 2009 or between 12th May and 2nd June 2010 for the early summer sampling. Sampling was conducted in the open water of all pans. As the species have a relatively short life-span, only early spring samples were included in the evaluation of the effects of environmental variables, while summer samples were used only as additional faunistic data.

Twenty litres of water for a zooplankton sample were randomly collected with a one-litre plastic beaker and sieved through a plankton net with a mesh size of 30 μm in each pan for fairy shrimp nauplii and metanauplii.

A push net – similar to the sledge dredge that Jungwirth (1973) used to collect *Branchinecta* in a soda pan – with a mesh size of 1 mm and an opening of 17 cm was used to collect anostracans. In each pan, a transect was pushed in the open water. It was 30 m in length, but it was reduced to 10 m in summer due to the very high abundances of Heteroptera. Samples were preserved in a 70% ethanol solution. Identification was based on Eder and Hödl (1996), and the numbers and densities of anostracans were also determined.

Environmental variables

Water depth and Secchi disk transparency were measured at each sampling location. Conductivity, pH, and dissolved O$_2$ concentration were determined by using a WTW Multiline P4 field equipment with TetraCon 325 and SenTix 41 electrodes (WTW Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany). Total suspended solids (TSS) concentration was measured by filtering water

Tab. 1. List of the soda pans with their location, coding and the occurrence of species.

Code*	Settlement	Pan	Latitude (N)	Longitude (E)	*B. f.*	*B. o.*	*C. c.*	Only nauplii
H01	Aba	Fényes-tó	47° 3’ 37.309”	18° 27’ 52.682”				+
H02	Aba	Sóstó	47° 3’ 13.926”	18° 28’ 20.608”				+
H03	Apaj	Alsó-szúnyog	47° 8’ 28.019”	19° 6’ 54.202”				
H04	Bácsalmás	Sóstó	46° 5’ 48.565”	19° 19’ 53.338”		+		
H05	Balástya	Müller-szék	46° 27’ 4.581”	19° 59’ 21.788”				
H06	Balástya	Ősze-szék	46° 24’ 6.123”	19° 59’ 4.185”				
H07	Csongrád	Kis-sóstó	46° 44’ 27.456”	19° 59’ 31.848”	+			
H08	Derecske	Bocskoros-szik	47° 20’ 11.583”	21° 30’ 49.906”				
H09	Derecske	Peres-szik	47° 22’ 39.048”	21° 34’ 30.972”				
H10	Dunatetétlen	Bába-szék	46° 44’ 22.275”	19° 9’ 1.597”				
H11	Dunatetétlen	Böddi-szék (N Pool)	46° 45’ 57.078”	19° 9’ 24.774”			+	
H12	Dunatetétlen	Böddi-szék (SE Pool)	46° 45’ 24.71”	19° 9’ 23.95”		+	+	
H13	Dunatetétlen	Böddi-szék (SW Pool)	46° 45’ 24.12”	19° 9’ 15.56”		+	+	
H14	Dunatetétlen	Böddi-szék (W Pool)	46° 45’ 53.15”	19° 8’ 51.91”		+	+	
H15	Dunatetétlen	Fűzfa-szék	46° 47’ 29.112”	19° 9’ 29.274”			+	
H16	Dunatetétlen	Sósér	46° 47’ 18.530”	19° 8’ 39.382”				
H17	Fülöpszállás	Fehér-szék	46° 48’ 28.496”	19° 11’ 15.912”				
H18	Fülöpszállás	Kelemen-szék	46° 47’ 50.480”	19° 10’ 59.149”	+	+	+	
H19	Gárdony	Dinnyési-fertő	47° 10’ 12.328”	18° 32’ 45.152”				
H20	Hajdúböszörmény	Móricz-szik	47° 42’ 46.801”	21° 21’ 50.606”				
H21	Hosszúpályi	Fehér-tó	47° 19’ 1.250”	21° 44’ 10.158”				
H22	Hosszúpályi	Petrovics-lapos	47° 20’ 12.572”	21° 43’ 47.257”				
H23	Jászkarajenő	Csukáséri-tó no. I	47° 1’ 3.760”	20° 3’ 32.226”		+		
H24	Jászkarajenő	Csukáséri-tó no. II	47° 1’ 5.511”	20° 3’ 40.806”				+
H25	Jászszentlászló	Kerek-tó	46° 34’ 4.091”	19° 45’ 0.619”				
H26	Kardoskút	Fehér-tó	46° 28’ 6.045”	20° 37’ 1.796”				
H27	Kaskantyú	Sárkány-tó	46° 40’ 27.500”	19° 20’ 43.023”				
H28	Királyhegyes	Csikóspusztai-tó	46° 17’ 31.291”	20° 38’ 6.123”				
H29	Kistelek	Tóalj	46° 28’ 39.234”	19° 58’ 2.616”				+
H30	Konyár	Kerek-szik	47° 20’ 23.818”	21° 39’ 10.249”	+			
H31	Mezőberény	Medvefejes-tó	46° 50’ 14.596”	21° 2’ 3.792”				
H32	Nyíregyháza	Nagy-Széksóstó	47° 55’ 8.412”	21° 37’ 58.084”				
H33	Ópusztaszer	Sárgatanyai-tó	46° 27’ 35.546”	20° 2’ 52.938”				
H34	Orosháza	Kis-sóstó	46° 31’ 25.466”	20° 37’ 48.043”				
H35	Pálmonostora	Pallagi-szék	46° 35’ 15.471”	19° 54’ 55.547”				+
H36	Pálmonostora	Kis-Péteri-tó	46° 35’ 12.738”	19° 54’ 31.950”				+
H37	Pusztaszer	Büdös-szék	46° 32’ 46.511”	20° 1’ 58.153”	+		+	
H38	Pusztaszer	Vesszős-szék	46° 31’ 27.615”	20° 2’ 20.122”				
H39	Sárkeresztúr	Sárkány-tó	46° 59’ 8.620”	18° 32’ 54.133”				+
H40	Sárszentágota	Sóstó	46° 58’ 18.426”	18° 33’ 12.224”				
H41	Solt	Bogárzó	46° 48’ 28.906”	19° 8’ 28.562”	+	+	+	
H42	Soltszentimre	unnamed	46° 45’ 48.462”	19° 10’ 50.531”		+		
H43	Soponya	Sóstó	47° 0’ 18.226”	18° 29’ 28.011”				
H44	Szabadszállás	Büdös-szék	46° 51’ 57.757”	19° 10’ 9.430”	+	+	+	
H45	Szabadszállás	Pipás-szék	46° 52’ 33.824”	19° 10’ 35.302”			+	
H46	Szabadszállás	Zab-szék	46° 50’ 15.061”	19° 10’ 11.207”	+	+	+	
H47	Tiszafüred	Meggyes-lapos	47° 33’ 25.222”	20° 53’ 51.439”				
H48	Tiszavasvári	Fehér-szik	47° 57’ 43.928”	21° 25’ 8.480”				+
H49	Tiszavasvári	Göbölyös	47° 56’ 26.217”	21° 25’ 36.453”				
H50	Tömörkény	Dong-ér	46° 34’ 7.544”	20° 3’ 46.483”				
H51	Újfehértó	Nagy-Vadas-tó	47° 51’ 31.388”	21° 39’ 24.065”		+		
				Occurrence in Hungary	7	11	11	8
A01	Apetlon	Apetloner Meierhoflacke	47° 43’ 17.673”	16° 49’ 26.545”				
A02	Apetlon	Birnbaumlacke	47° 49’ 3.775”	16° 51’ 53.678”	+			
A03	Apetlon	Darscho (Warmsee)	47° 46’ 13.079”	16° 50’ 24.694”				
A04	Apetlon	Große Neubruchlacke	47° 47’ 10.036”	16° 50’ 31.914”		+		
A05	Apetlon	Kühbrunnlacke	47° 47’ 33.848”	16° 52’ 43.053”	+	+		
A06	Apetlon	Lange Lacke	47° 45’ 26.911”	16° 52’ 43.553”		+		
A07	Apetlon	Martenhofen-lacken	47° 45’ 1.806”	16° 51’ 24.102”		+		
A08	Apetlon	Neufeldlacke	47° 45’ 52.116”	16° 50’ 24.894”				
A09	Apetlon	Ochsenbrunnlacke	47° 48’ 38.649”	16° 50’ 40.622”			+	
A10	Apetlon	Östliche Wörthenlacke	47° 46’ 24.037”	16° 52’ 48.338”				
A11	Apetlon	Östliche-Fuchslochlacken	47° 47’ 25.587”	16° 51’ 58.269”		+		

To be continued on next page

Tab. 1. Continued from previous page.

Code*	Settlement	Pan	Latitude (N)	Longitude (E)	*B. f.*	*B. o.*	*C. c.*	Only nauplii
A12	Apetlon	Sechsmahdlacke	47° 47’ 1.639”	16° 53’ 2.803”		+		
A13	Apetlon	Stundlacke	47° 47’ 56.054”	16° 52’ 18.143”				
A14	Apetlon	Unterer Weißsee	47° 43’ 36.432”	16° 49’ 34.386”				
A15	Apetlon	Westliche Wörthenlacke	47° 46’ 15.318”	16° 52’ 14.796”				
A16	Apetlon	Westliche-Fuchslochlacken	47° 47’ 24.276”	16° 51’ 8.458”		+		
A17	Illmitz	Albersee	47° 46’ 30.491”	16° 46’ 12.429”		+		
A18	Illmitz	Auerlacke	47° 47’ 21.015”	16° 53’ 12.400”				
A19	Illmitz	Herrnsee	47° 44’ 40.432”	16° 46’ 11.955”				
A20	Illmitz	Kirchsee	47° 45’ 31.243”	16° 47’ 7.759”		+		
A21	Illmitz	Krautingsee	47° 45’ 21.703”	16° 46’ 49.727”				
A22	Illmitz	Mittlerer Stinkersee	47° 48’ 24.332”	16° 47’ 15.079”		+		
A23	Illmitz	Obere Höllacke	47° 49’ 37.630”	16° 48’ 28.556”		+		
A24	Illmitz	Oberer Stinkersee	47° 48’ 49.544”	16° 47’ 33.062”		+		
A25	Illmitz	Runde Lacke	47° 47’ 8.681”	16° 47’ 33.877”		+		
A26	Illmitz	Südlicher Silbersee	47° 47’ 28.078”	16° 46’ 47.053”				
A27	Illmitz	Untere Höllacke	47° 49’ 19.618”	16° 48’ 23.611”				
A28	Illmitz	Unterer Schrändlsee	47° 44’ 57.014”	16° 47’ 46.915”				
A29	Illmitz	Unterer Stinkersee	47° 47’ 59.933”	16° 47’ 10.841”				
A30	Illmitz	Zicksee	47° 46’ 1.072”	16° 47’ 5.107”				
A31	St. Andrä	Baderlacke	47° 46’ 42.778”	16° 56’ 3.401”		+		
				Occurrence in Austria	2	14	1	-
S01	Baranda	Slatina	45° 4’ 58.001”	20° 29’ 29.481”				
S02	Elemir	Okanj	45° 28’ 1.793”	20° 18’ 0.262”		+		
S03	Melenci	Mala Rusanda	45° 30’ 44.80“	20° 18’ 9.50”		+		
S04	Melenci	Veliko Rusanda	45° 31’ 17.336”	20° 18’ 25.502”				
S05	Novi	Bečej Slano Kopovo	45° 37’ 30.806”	20° 12’ 36.085”		+		
S06	Čoka	Čoka Kopovo	45° 57’ 12.415”	20° 11’ 54.482”				
S07	Kanjiža	Čudotvorni Bunar	46° 3’ 38.662”	20° 0’ 3.726”				
S08	Stanišić	Bela Bara	45° 56’ 49.453”	19° 5’ 24.884”	+			
S09	Riđica	Medura	45° 59’ 31.516”	19° 7’ 59.560”		+		
				Occurrence in Serbia	1	4	-	-
				Total occurrence	10	29	12	8

**The first character of the code number stands for the country: H, Hungary; A, Austria; S, Serbia.*
N, north; E, east; SE, south-east; SW, south-west; W, west; B. f., Branchinecta ferox; B. o., Branchinecta orientalis; C. c., Chirocephalus carnuntanus.

(100-1000 mL) through *pre*-dried and *pre*-weighted cellulose acetate filters after oven-drying at 105°C.

Additional habitat characteristics were also determined. The pan area and the ratio of open water were calculated on the basis of georeferenced GoogleEarth satellite images with ArcGIS (ESRI, 2002). Two hydroperiod types with five levels were established: one for the permanence of open water in the lake bed (hydroperiod type 1) and one for the frequency of drying out (hydroperiod type 2).

For land use effects, we used water supply (artificial inflow), drainage melioration channelling (artificial outflow), disturbancy of the structure, grazing pressure (density of mainly Hungarian grey cattle or water buffalos on the pan and in the catchment area), grazing time (from no grazing through a few spring months to year-round), and catchment characteristics. Water supply, channelling, disturbancy of the lake bed, grazing pressure and time were determined with the help of information collected from managers of the pans (mainly workers of the national park directorates). The ratios of natural habitats (meadows, swamps, forests, *etc*.), agricultural fields and human settlements in the catchment area of each pan were calculated on the basis of georeferenced GoogleEarth satellite images with ArcGIS (ESRI, 2002).

For spatial effects, we calculated the nearest distance to the next pan, pan density (number of pans within an area with a radius of 20 km around each pan), and isolation (average distance of a pan from all the other sites).

Statistical analysis

All environmental variables (Tab. 2) were used in a forward selection procedure of redundancy analysis (RDA) to explore those variables which significantly explain the distribution of the three anostracan species. First, we identified the most important factors in determining the occurrence (presence-absence data) of each species. Forward selection revealed significant effects both among the habitat characteristics (conductivity, pan area and Secchi disk transparency) and spatial variables (isolation), which were used

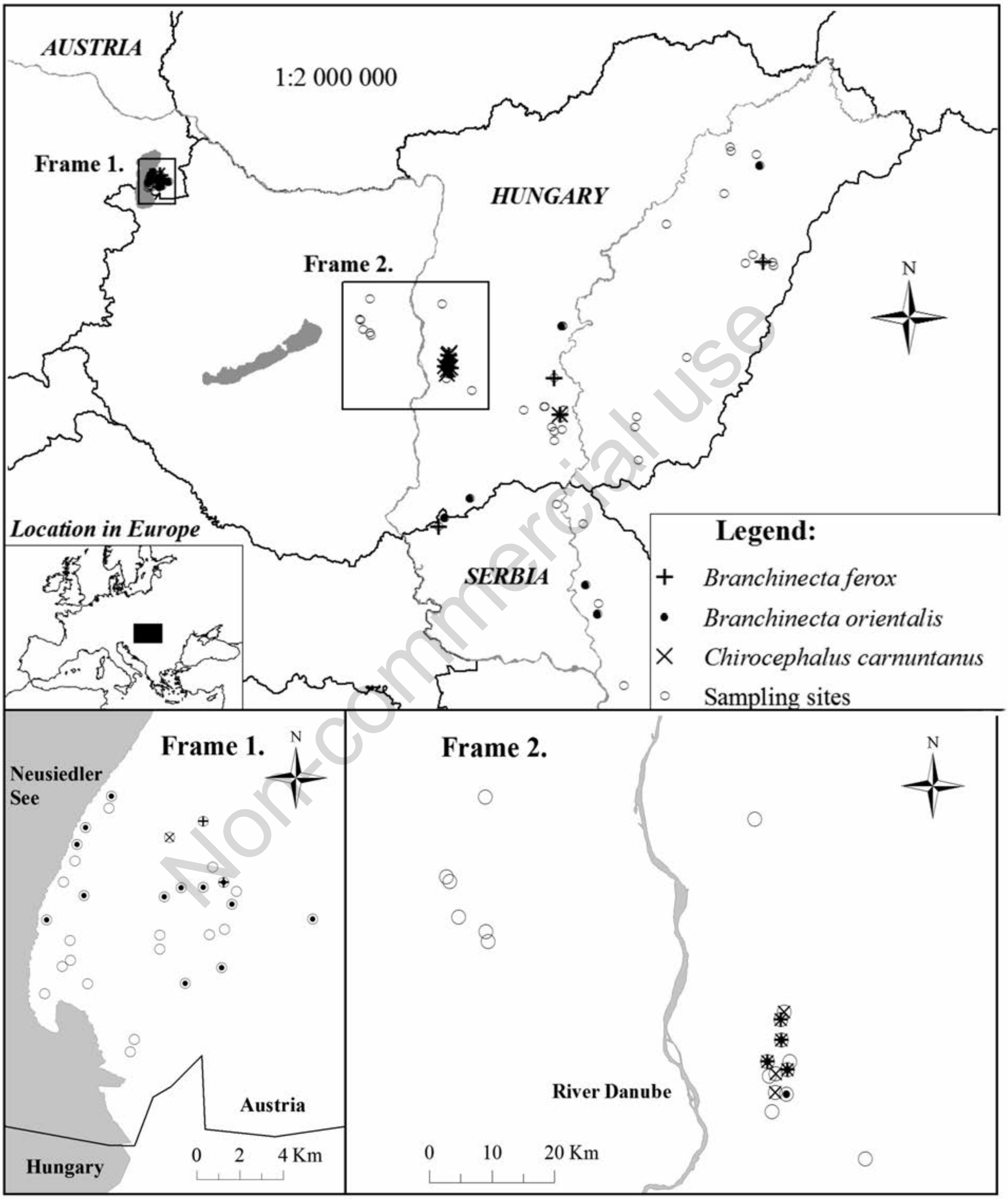

Fig. 1. Location of the soda pans in the Carpathian basin (open circles) and the distribution of the three Anostraca species. The enlarged frames show the clutches of soda pans: in Seewinkel in Austria (Frame 1); and in the middle section of the Danube valley in Hungary, with the pans of Kiskunság east of the Danube (Frame 2).

in variance partitioning models (Borcard *et al*., 1992). Another RDA model was constructed according to the abundance of species [$\log_{10}(x+1)$ transformed data]. In this analysis, only local effects proved to have a significant contribution to variance (conductivity, pan area and Secchi disk transparency), hence no variation partitioning was performed. The significance of the models were tested by n=999 unrestricted Monte-Carlo permutations under the reduced model. All analyses were performed with inter-sample scaling and centring by species using Canoco software for Windows 4.5 (Lepš and Šmilauer, 2003).

In order to fit generalised additive models (GAM) of density data, we first used the variables serving as significant predictors in our RDA models. Among them, compared to the linear model with the Akaike information criterion, the best models were chosen for each species and used for predictions, which meant only the ones with Secchi disk transparency and conductivity (with $\log_{10}$ transformed environmental data). For *B. orientalis*, both variables were chosen as smooth variables, while for *C. carnuntanus* and *B. ferox*, only Secchi disk transparency was selected. These analyses were carried out in R (R Development Core Team, 2009).

RESULTS

Distribution and co-occurrence

Anostracans were found in half of the investigated pans: 47 out of 91 (Fig. 1, Tab. 1). We recorded all the three species that were formerly known to inhabit soda pans. Among them, *B. orientalis* was by far the most frequent. Its collected individuals were six times more numerous in our samples than the specimens of the other two species, and they were present in all the three countries in 29 pans (Tab. 1) as well as in the three major parts of the basin: east of the river Tisza, in the Danube-Tisza interfluve, and in Seewinkel, in Transdanubia.

In Hungary, *B. orientalis* was found in 9 middle-Hungarian pans in Kiskunság (H12, H13, H14, H18, H23, H41, H42, H44, H46), one pan near the Serbian border (H04) and another one in the northern part of the Great Hungarian Plain (H51). *B. orientalis* was the most frequent species in both Austria and Serbia. Localities of this species were all across Seewinkel. In Serbia, *B. orientalis* was present in a small northern pan – Medura (S09) – near the Hungarian border, and in three southern ones near the river Tisza (S02, S03, S05).

C. carnuntanus was found only in 12 pans and its distribution was almost restricted to Hungary. Indeed, it was present only in one Austrian pan [Ochsenbrunnlacke (A09)] and was missing from the 9 Serbian pans. On the other hand, like the most common *B. orientalis,* it was recorded in the same number of Hungarian pans, though its distribution was restricted to Kiskunság in the Danube-Tisza interfluve.

B. ferox was the rarest species both in relative abundance and distribution (only in 10 pans). However, its distribution included all three countries: it was found mostly in Hungary, in two Austrian pans in Seewinkel [Birnbaumlacke (A02) and Kühbrunnlacke (A05)], and in

Tab. 2. List of the environmental variables used in the statistical analysis.

Spatial variables	Nearest pan (km) Isolation (km) Pan density (no. of pans within an area with a radius of 20 km)
Habitat characteristics (local effects)	Water depth (cm) Secchi disk transparency (cm) Conductivity (mS cm^{-1}) TSS (mg L^{-1}) pH DO (%) DO (mg L^{-1}) Pan area (ha) Hydroperiod type 1 (nominal) Hydroperiod type 2 (nominal) Ratio of open water (%)
Land use effects	Water supply (binomial) Channelling (binomial) Disturbancy of structure (binomial) Ratio of natural habitats in catchment area (%) Ratio of agricultural fields in catchment area (%) Ratio of human settlements in catchment area (%) Grazing pressure (nominal) Timing of grazing (nominal)

TSS, total suspendid solids; DO, dissolved oxygen.

Northern Serbian Bela Bara (S08), near the Hungarian border.

The survey of 8 Hungarian pans resulted in only anostracan nauplii that could not be identified to species level. Ten of the investigated 91 pans proved to be disturbed (H06, H19, H31, H32, H33, H36, A03, A27, S01, S07), *e.g.* because of illegal fish stocking or probable inflow of pesticides. None of them was inhabited by adult fairy shrimps, and nauplii were found only in one of them (Kis-Péteri-tó; H36), with a very low abundance (0.15 ind L^{-1}).

In spring, usually only one species was present in a pan (28 pans, 76% of all pans with at least one species), but sometimes two were counted (7 pans, 19%), or even all the three species at a time [2 pans, Kelemen-szék (H18) and Zab-szék (H46) in Kiskunság, 5%]. Apart from the last two cases, *B. ferox* and *B. orientalis* co-occurred only in the case of the Austrian Kühbrunnlacke (A05), while the other two pairs occurred in three additional Hungarian pans in Kiskunság: *C. carnuntanus* was found together with *B. ferox* in pans H37, H41, H44, and with *B. orientalis* in three separate pools of Böddi-szék.

In summer, only *C. carnuntanus* and *B. orientalis* were found: the former in one (H44) and the latter in six pans (H04, H18, H41, H44, H45 in the Danube-Tisza interfluve in Hungary along with pans A06 and A22 in Seewinkel).

The role of the environmental factors

The three species were clearly separated into two groups in both RDA models (Fig. 2). *B. orientalis* was always positively associated with high conductivity, and the range of conductivity of the three species also showed a similar difference (Tab. 3). Conductivity, together with pan area and Secchi disk transparency, significantly affected density, which local variables together explained 27% (F=10.73, P=0.001) of variance. In the case of presence-absence data, pure spatial effect (isolation) also explained a significant variation (2.6%, F=2.93, P=0.045). Nevertheless, presence was also predominantly determined by the local habitat characteristics (Tab. 4). Land use did not explain significant amount of variation in any of the models.

The GAM models also well illustrated the different strategies among the species (Fig. 3). While *B. orientalis* was predicted to have high densities only in the case of high conductivity and low Secchi disk transparency, the other two species could also be found lower along the conductivity gradient and even in relatively more transparent waters.

DISCUSSION

Ecological factors

Our results show different strategies in the case of the three species, mainly related to the salinity of the pans. Eder (2006) regarded both *Branchinecta* species as obligatory inhabitants of saline waters in Seewinkel, and considered *C. carnuntanus* as a facultative element. According to our data, *B. orientalis* seems to tolerate higher salinities than *C. carnuntanus* and *B. ferox*. Fur-

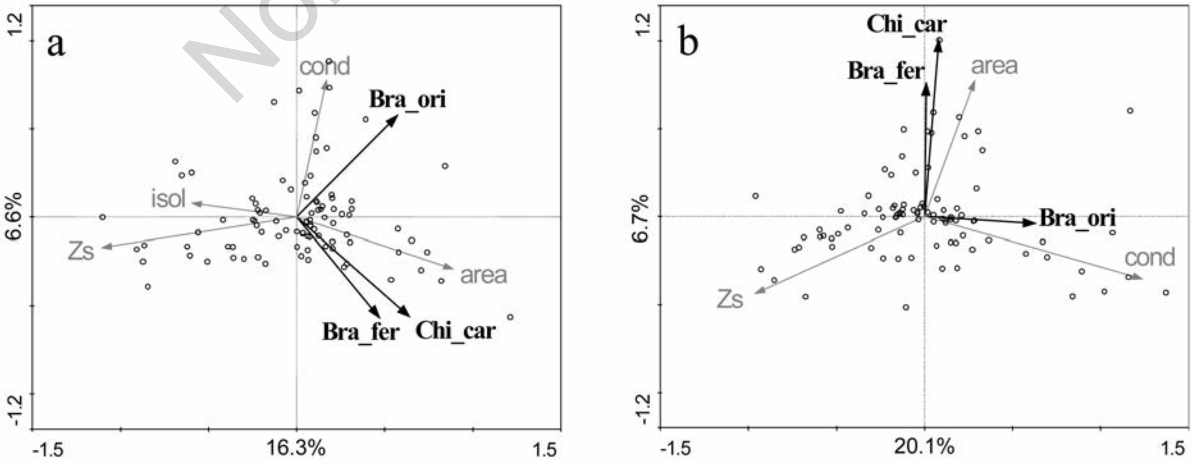

Fig. 2. Redundancy analysis (RDA) models illustrating the relationships between the presence-absence (a) and density (b) data of each species (black arrows) and the significant explanatory variables (grey arrows). Labels used in the figure are: Bra_fer, *Branchinecta ferox*; Bra_ori, *Branchinecta orientalis*; Chi_car, *Chirocephalus carnuntanus*; cond, conductivity; Zs, Secchi disk transparency; area, pan area; isol, isolation.

thermore, the latter species disappeared in early summer, somewhat earlier than the other two, possibly as a result of the increasing salinity of the pans. In their studies in Spain, Alonso and Comelles (1981) and Alonso (1985) also showed that *B. ferox* preferred cold and not very highly mineralised waters and that the species disappeared as salt concentration increased in the lagoons. Alonso (1985) found the two *Branchinecta* species to be similar in the persistence of their environment as both occupied mainly temporary waters. Yet, while *B. ferox* tolerated lower salinity and a turbidity ranging from low to high, *B. orientalis* preferred higher salinity and only low turbidity [the latter species is mentioned in the study as *B. cervantesi*, which is a synonym according to Brtek and Thiéry (1995)]. Conversely, Petkovski (1991) reported that *B. ferox* also preferred rain pools where soil had a high content of mineral salts – especially natron and chlorate –, though exact values of salinity tolerance were not mentioned. Fryer (1983) suggested *B. ferox* to have a wide eco-physiological tolerance because of the different morphological specialisations of its various life stages.

Alonso (1985, 1990) observed that *B. orientalis* at salinity ranges between 0.5 and 4.5% and that the species did not inhabit freshwater habitats at all, thus he considered it halophilous. Its halophilous characteristic is also confirmed by our results. In soda pans, the total ion concentration (mg L^{-1}) can be calculated by multiplying the conductivity values (expressed in µS cm^{-1}) by 0.774 (Boros and Vörös, 2010). According to this, the highest concentration at which *B. orientalis* was found was 7.85 g L^{-1} (lowest: 0.62), which is a hypo-saline value (Hammer, 1986). Recently, Boronat (2003) found this species in a similar environment in a salt pan in Central Spain, where salinity was 6 g L^{-1}. The species is also known from Mongolian salt lakes with salinities ranging from 4.8 to 12.7 g L^{-1} (Alonso, 2010). These waters are also hypo-saline (Hammer, 1986). On the other hand, our results contradict those of Angeler *et al*. (2008), where *B. orientalis* density correlated negatively with conductivity in some Spanish salt pans.

C. carnuntanus occurred at salinities ranging from 0.54 to 2.48 g L^{-1} and *B. ferox* from 0.46 to 1.94 g L^{-1}, in sub-saline pans (Hammer, 1986). In accordance with its former occurrences in temporary freshwater habitats, we can confirm the generalist feature of *C. carnuntanus* suggested by Eder (2006). Boven *et al*. (2008) also noted that *C. carnuntanus* could be a habitat generalist, but their results only included five occurrences of the species. *B. ferox* may also be a habitat generalist, but in the Carpathian basin it seems to be highly associated with sodic waters. As the vast majority of Pannonian soda pans belong to the sub-saline lakes and the remaining ones are mainly hypo-saline (Boros, 1999), they represent a suitable habitat for all three anostracans (some pans can even reach the hyper-saline range in summer but these cold-water species disappear by then).

The occurrence of the species was also significantly affected by isolation. Anostracans are passive dispersers, mainly dispersed by wind (Vanschoenwinkel *et al*., 2008a) and waterbirds (Green *et al.*, 2005). Amphibians (Vanschoenwinkel *et al.*, 2008b) and insects (Beladjal and Mertens, 2009) can also act as vectors, while human-mediated dispersal occurs as well (Waterkeyn *et al*., 2010). Waterbirds can act as long-distance dispersal vectors (Figuerola and Green, 2002), for instance by linking different pans in the Carpathian basin, especially during migration. On the other hand, our results suggest that the species are less likely present in isolated pans. Moreover, the highest ratios of occupied pans were found in the Seewinkel and Kiskunság areas, having high numbers of pans in restricted areas (although pan density itself was not a significant variable in our models). Similarly, Demeter (2005) found the highest species richness in areas with high number of habitats. This may not be detectable in the case of restricted areas, which can be a reason why Boven *et al*. (2008) did not find any significant effect of isolation on large branchiopods in Kiskunság. Land use characteristics did not show significant effect in the explanation of variance in the models. This is in line with the results by Angeler *et al*. (2008), as no effect of regional land use on

Tab. 3. Environmental features of the pans inhabited by the three species in spring.

	Branchinecta ferox	*Branchinecta orientalis*	*Chirocephalus carnuntanus*
Water depth (cm)	5-60	5-60	9-60
Secchi disk transparency (cm)	0.5-5	0.5-27	0.5-12
Conductivity (mS cm^{-1})	0.59-2.1	0.8-10.1	0.7-3.2
TSS (mg L^{-1})	302-13,922	62.5-29,360	498-22,156
pH	8.5-10.2	8.7-10	8.5-10
DO (%)	83.3-115.4	88-139	67.8-102
DO (mg L^{-1})	9.1-12.9	8.3-14.3	8.3-12.9
Pan area (ha)	5.8-180	0.5-180	5-180
Ratio of open water (%)	30-90	10-90	5-90

TSS, total suspendid solids; DO, dissolved oxygen.

B. orientalis density in Spanish habitats, neither on a small nor on a larger scale, was detected.

Pan area also appeared to have a significant effect on the two least frequent species, *B. ferox* and *C. carnuntanus*. This can presumably be a pattern caused by their large-scale distribution rather than any *real* effect of pan area on these species, since they were primarily found in in the Kiskunság area of Central Hungary which has many large pans. In this region, though, they can also be found in very small astatic habitats, *e.g.* sodic puddles or wheel tracks (Boven *et al*., 2008; E. Boros personal communication).

Co-occurrences of the species

Co-occurrence of fairy shrimps in the soda pans (24%) was relatively low compared to other habitats: Petrov and Cvetković (1997) observed a co-occurrence of 42% in early spring and Waterkeyn *et al*. (2009) of 79%. The co-occurrence recorded by Boven *et al.* (2008), instead, was 31%, thus similar to ours. Still, in the latter two cases, total large branchiopod co-occurrence included Notostraca, Spinicaudata and Laevicaudata species as well.

As the three fairy shrimps are all – at least in the first stages of their life-cycle – filter feeders, they can be competitors when occurring together. Temporal differences in life cycle can play an important role in avoiding inter-species competition in a shared habitat, which is a widely observed phenomenon among anostracans (Petrov and Cvetković, 1997; Abatzopoulos *et al*., 1999; Moscatello *et al*., 2002; Thiéry and Puente, 2002; Waterkeyn *et al*., 2009). According to Thiéry (1991), simultaneous differences in body length can also contribute to resource partitioning as such species presumably feed on particles with different size. Other authors similarly observed that co-occurring fairy shrimp species belonged to different

Tab. 4. Results of the variance partitioning on the presence-absence data.

	Presence-absence		
	Explained variance (%)	F	P
[H]	20.4	7.45	0.001
[S]	3.0	7.74	0.061
[HUS]	23.1	6.44	0.001
[H/S]	20.1	7.48	0.001
[S/H]	2.6	2.93	0.045
[H∩S]	0.4		
100-[HUS]	76.9		

[H], variation explained by habitat characteristics with no covariables; [S], variation explained by the spatial effect with no covariables; [HUS], variation explained by habitat characteristics and spatial effects; [H/S], pure variation explained by habitat characteristics; [S/H], pure variation explained by spatial variables; [H∩S], variation shared by habitat characteristics and spatial variables; 100-[HUS], total unexplained variance.

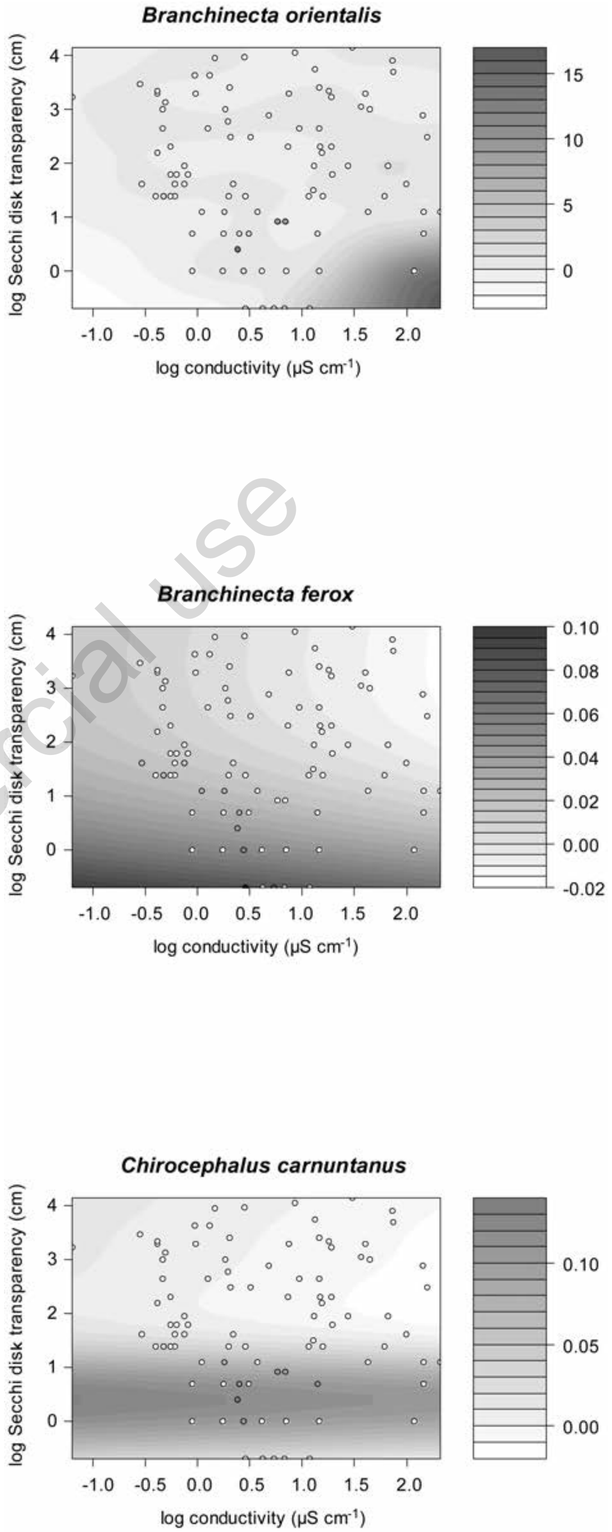

Fig. 3. Generalised additive models (GAM) models for density data (ind L^{-1}) of the three species. Points illustrate the original data obtained from the samples, while background shows the predicted values. Colour coding for both variables can be found on the right side of the plots.

size and/or age classes (Mura, 1991; Hathaway and Simovich, 1996; Thiéry and Puente, 2002; Beladjal *et al*., 2003), as it is resulted also from this study. The adult sizes of the three species differ: *B. ferox* has a maximal length of 52 mm, *B. orientalis* 41 mm, while the utmost limit of *C. carnuntanus* is only 20 mm (Petkovski, 1993). Additionally, we observed considerable size differences among co-occurring species in the same sample, with a minimum of 1.5 mm and a maximum of 22.7 mm (average difference was 8.1 mm). This, together with the high amount of available suspended particles, could enable the coexistence of the different species.

Historical and current distribution

C. carnuntanus was not recorded in Seewinkel between 1968 and 1995 (Eder and Hödl, 2003), and therefore it was considered to be extinct (Löffler, 1993). In 1995, it was rediscovered in Illmitzer Zicksee and Östliche Hutweidenlacke (Eder and Hödl, 1995; Eder and Aescht, 1996; Eder *et al*., 1996). In 2009-2010, we did not find this species in the former pan (A30), while the latter was part of Lange Lacke in spring 2010 due to the high amount of precipitation. There, instead of *C. carnuntanus*, *B. orientalis* was found. However, we registered the species in a new site, *i.e*., in Ochsenbrunnlacke (A09).

During our study, *C. carnuntanus* was absent from the Serbian pans, although it had been formerly recorded from temporary waters of the region. Petkovski (1993) described three localities of this species in Vojvodina: two in the vicinity of Melenci (registered in 1965 and 1989) and the pan Okanj (registered in 1971). The former habitats were proved to exist also later on by Petrov and Cvetković (1997). Nonetheless, we found *B. orientalis* instead of *C. carnuntanus* in Okanj (S02).

In Hungary, *C. carnuntanus* was documented in the Danube-Tisza interfluve and the eastern part of the Great Hungarian Plain (Forró, 2000). Yet, these records are mainly from 1890-1959, and the description of the exact locality is usually missing. Recently, the species appeared only in Kiskunság (Forró, 1987; Boven *et al*., 2008), which highlights the conservational importance of this area. As temporary waters that could also be inhabited by this species are under decline, astatic soda pans are essential habitats for *C. carnuntanus*. Other recent European findings of the species were only in three sites in Romania, by Băile Calacea, Sânnicolau Mare and Timişoara, near the Hungarian and Serbian borders (Demeter and Stoicescu, 2008) and in one site in Western Slovakia in 1996, near Vysoká pri Morave (Lukáš, 2000).

Being the most frequent species in the pans, *B. orientalis* had the widest distribution in the Carpathian basin. Our data included many new localities. In Serbia, it was formerly recorded only in Mala Rusanda (S03) (Petkovski, 1991). We found the species in this pan again in 2010 and documented three new localities: Slano Kopovo (S05), Medura (S09) and Okanj (S02), the latter being the southernmost occurrence of this species in the central European area.

In Seewinkel, *B. orientalis* has been recorded from several pans, being the most common fairy shrimp of the Austrian pans. We found *B. orientalis* in 14 Austrian pans, 4 of which (A07, A11, A22, A31) were new records for the species (Eder *et al*., 1996; Eder and Hödl, 2002). We confirmed 6 formerly known localities (A04, A06, A16, A23, A24, A25; Eder *et al*., 1996), and discovered this fairy shrimp in Kühbrunnlacke (A05), Sechsmahdlacke (A12), Albersee (A17), and Kirchsee (A20). The latter localities were documented as habitats of *Branchinecta* spp., but the most recent investigation conducted in 1994-1995 did not result in any specimens. As former studies in the area often considered *B. orientalis* and *B. ferox* one species before Petkovski (1991), several previous data are uncertain on the species and therefore indicated here as *Branchinecta* sp. Among its formerly known Austrian habitats, *B. orientalis* was only missing from Illmitzer Zicksee (A30) in 2009-2010. Löffler (1959) found the species in 15 pans, while Metz and Forró (1991) in 14. According to Eder and Hödl (2003), though, this data should all be treated as *Branchinecta* spp., due to the uncertainties. On the other hand, considering the taxonomical changes (*i.e*., some of the above mentioned records may mean *B. ferox* instead of *B. orientalis*) and the disappearance of some pans like Huldenlacke or Martenthaulacke, which were formerly inhabited by one of the *Branchinecta* species, we can conclude that *B. orientalis* has a very stable population in Seewinkel.

In Hungary, *B. orientalis* has formerly been recorded from several pans on the southern and north-eastern parts of the Great Hungarian Plain and the Danube-Tisza interfluve (Forró, 2000). Many of them, though, have disappeared by now, mainly due to the significant fall of the groundwater level. Recent occurrences of the species are only known from Central Kiskunság (Forró, 2003; Boros *et al*., 2006), similarly to *C. carnuntanus*. Our results include some new data for the current Hungarian distribution of *B. orientalis*, involving the pans H04, H23 and H51, along with some new localities in Central Kiskunság (H12-14, H41, H42, H44). In the other neighbouring countries, *B. orientalis* was only recorded from the eastern part of Romania in 1953, outside the Carpathian basin (Demeter and Stoicescu, 2008).

As the rarest fairy shrimp, *B. ferox* was proved to occur in three Austrian pans in 1994-1995: Birnbaumlacke (A02), Martenhofen-lacken (A07), and Ochsenbrunnlacke (A09) (Eder *et al*., 1996). We registered the species in two pans: one of them was Birnbaumlacke (A02) while the other, Kühbrunnlacke (A05), was a locality where one of the *Branchinecta* species had been formerly recorded, but it was not confirmed later by the study of Eder *et al*. (1996). In the light of both our results and those of Eder *et al*. (1996), we can conclude that a relatively small area (approximately 3×3 km) including three of the above mentioned 4 pans (A02, A05, A09) presumably maintains a stable population of *B. ferox* in Seewinkel.

B. ferox was recorded in Serbia only from pools in the vicinity of Melenci in 1965, 1989 and 1991-1995 (Petkovski, 1991, 1993; Petrov and Cvetković, 1997). Therefore, the Northern Bela Bara (S08) is its second registered occurrence in Vojvodina and in Serbia, and the first record for Serbian soda pans.

Hungarian literature on *B. ferox* is mainly from 1858 to 1959 (Forró, 2000). Megyeri (1975) reported new data in the 1970s, but the material he collected was from pans that have dried out and disappeared since then. In the following 40 years, the occurrence of *B. ferox* was registered only in a wheel track (Boven *et al*., 2008) and in three astatic soda pans [Kelemen-szék (H18), Zab-szék (H46), Böddi-szék (H11-14)] in Kiskunság (Forró, 2003), along with the pan Göbölyös (H49) in the north-eastern part of the Great Hungarian Plain (Forró *et al*., 1996). Although we did not find *B. ferox* in Böddi-szék (H11-14) or any fairy shrimp in Göbölyös (H49), we confirmed the presence of *B. ferox* in Kelemen-szék (H18) and Zab-szék (H46) and additionally registered 5 new localities for the species near the river Tisza (H34, H37), in eastern Hungary (H30) and in the western part of the Danube-Tisza interfluve (H41, H44). Recently, Kerek-szik (H30) is the easternmost occurrence of the species in the region, as its next habitat is in Southern Ukraine by the Black sea, more than 600 km eastward (Brtek, and Thiéry 1995). In the Carpathian basin, there is no data on *B. ferox* from Romania (Demeter and Stoicescu, 2008), Slovenia (Brancelj and Gorjanc, 1999), Croatia (Petrov and Marinček, 1991), eastern Czech Republic (Brtek and Thiéry, 1995) or the western part of Ukraine (Brtek and Thiéry, 1995), and, although the species is known from several localities in South-Western Slovakia, its last observation there dates back to 1976 (Brtek, 2005).

CONCLUSIONS

The two *Branchinecta* spp. have disjunct distributions in Europe with very similar patterns. Their central European range in the Carpathian basin is the greatest among the patches (Brtek and Thiéry, 1995). This means that our data approximately covers the recent distribution of both species in their central European area, and particularly of *B. orientalis*, as this species has only been documented here in soda pans for a long time. The main and presumably exclusive area of *C. carnuntanus* is also the Carpathian basin and this is the first large-scale study on its actual distribution in the region. Seewinkel and Kiskunság play an essential role in conserving the three fairy shrimp species. Indeed, they conserved stable populations of all species, presumably because they have been part of the Neusiedler See-Seewinkel and Kiskunság National Parks for a long time. Moreover, they also conserved a high number of pans within relatively small areas. In Hungary, extensive studies on the historical distribution of the species are available. Still, as we could not prove their occurrence in many of their formerly reported habitats – especially in the eastern part of the country – a probable decline in their area of occupancy may have occurred.

Moreover, local land use management seems to have no direct effect on the anostracans, though it can still have a role in changing local conditions, *e.g.* conductivity, which occurred in the case of the disturbed pans. Our results suggest that habitat management, including grazing and agriculture which are quite regular in the case of most pans (especially in the Hungarian national parks), does not have a side effect on fairy shrimps as long as it does not alter any of the local environmental factors, *e.g*. salinity or turbidity.

However, the drastic decrease in the number of soda pans threatens the survival of the species in the region, especially that of the halophilous *B. orientalis*. This habitat loss in Kiskunság has been 80% since the 18th century, and it is mainly due to climatic changes and former human disturbance, primarily drainage, flood control, and irrigation before the establishment of the Kiskunság National Park (Boros and Biró, 1999). In Seewinkel, a similar tendency was observed with the disappearance of approximately 70-85% of the pans between 1850 and the end of the 20th century (Kohler *et al*., 1994; Zulka and Milasowszky, 1998).

In Hungary, all soda pans are now protected by law, which provides a good basis for the conservation of the species in the long-term. However, in Serbia, only Slano Kopovo and Okanj are under protection (with plans on the future protection of Rusanda). This calls for conservational measures to save the vulnerable habitats of these fairy shrimps, which are also unique representatives of athalassohaline soda waters in Europe. On the other hand, to conserve them efficiently, it would be highly desirable to nationally protect these anostracans and to include them in the vulnerable category of the IUCN Red List, given their rarity, vulnerability and the decline in their extent of occurrence, especially in the Hungarian part of the Carpathian basin.

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