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11 Longitudinal distributional patterns of Peracarida (Crustacea, Malacostraca) in the River

12 Danube

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27

28

29 **Abstract**

30

31 The River Danube plays a central role in the spread of Ponto-Caspian species as a part of the  
32 so-called southern invasion corridor (Danube-Main-Rhine system); therefore, changes in its  
33 peracarid fauna (comprising the bulk of invasives) merit special attention. The latest  
34 international research expedition (Joint Danube Survey 3, 2013) offered an opportunity for  
35 updating and synthesizing our knowledge about this group along the Danube, previously  
36 based on studies covering only certain river sections and/or dealing with a subset of species.  
37 Altogether 17 amphipod, 7 mysid, 3 isopod, and one cumacean species were recorded at 55  
38 sites investigated between Ulm (river km 2581) and the Delta. Recent large-distance  
39 expansion of additional Ponto-Caspian species was not observed, but three species  
40 (*Chelicorophium robustum*, *C. sowinskyi*, and *Echinogammarus trichiatus*) have been able to  
41 shorten their distributional gap in the Middle Danube, *E. trichiatus* being recorded for the first  
42 time in Serbia. Ponto-Caspian peracarids are still gradually advancing in the German section,  
43 as well, implying retreat of native *Gammarus* spp., and impeding the spread of non-Ponto-  
44 Caspian invaders. On the contrary, some Ponto-Caspian species seem to have declined in  
45 certain river sections; *Dikerogammarus bispinosus* was entirely missing in the Lower Danube,  
46 and several species characteristic of the lower reaches had been recorded previously much  
47 farther upstream (most notably *Chelicorophium maeoticum* and *Obesogammarus crassus*).  
48 The analysis of current and historical distributional patterns revealed that the crucial step in  
49 the large-scale spread of Ponto-Caspian species is crossing the section between Baja and the  
50 Sava estuary (rkm ~1480-1170) – characterized by an unfavorable combination of relatively

51 strong currents and fine bed material – by passive transport. Presence immediately  
52 downstream of this section does not appear to promote further expansion in most of the cases;  
53 the source region of large-distance dispersal is most likely the Delta, implying that potential  
54 future invaders cannot be identified based on their previous expansion in the lower reaches of  
55 the river.

56

57 **Key words:** Amphipoda, Cumacea, Isopoda, Mysida, Ponto-Caspian, range expansion

58

## 59 **Introduction**

60

61 The range expansion of Ponto-Caspian faunal elements has been one of the most significant  
62 biogeographical processes in inland waters of the North-Atlantic region in recent times, often  
63 having serious consequences on native fauna and ecosystem functioning (Ricciardi &  
64 MacIsaac 2000, Bij de Vaate et al. 2002, Ojaveer et al. 2002). The representatives of several  
65 metazoan groups are involved, ranging from cnidarians to fish, but in terms of species number  
66 peracarid crustaceans dominate; 19 species (13 amphipod, 5 mysid, and one isopod) have  
67 extended the limits of their distribution across river basins in Central, Western, or Northern  
68 Europe (Bij de Vaate et al. 2002, Bernerth & Stein 2003, Herkül et al. 2009, Hanselmann  
69 2010, Grabowski et al. 2012), four of which have established also in the British Isles  
70 (Gallardo & Aldridge 2015), and two have appeared even in North America (Witt et al. 1997,  
71 Pothoven et al. 2007). In addition, several other species including cumaceans have established  
72 in Eastern European reservoirs and lakes mainly by intentional introduction (Grigorovich et  
73 al. 2002, Filinova et al. 2008).

74 Europe's second longest – and most international – river, the Danube plays a central role in  
75 their spread. Emptying into the Black Sea, it has a direct connection to the Pontic Basin,

76 implying that a high number of Ponto-Caspian endemics are native to the lower reaches of the  
77 river (Lyashenko et al. 2012). The first Ponto-Caspian peracarid in the Middle Danube was  
78 detected in the 1910s (Unger 1918), and by the 1940s 7 species had established the Hungarian  
79 section (Dudich 1947, Borza 2011). The colonization of the Upper Danube was more delayed,  
80 starting only in the second half of the 20<sup>th</sup> century (Kothé 1968), parallel to the growing  
81 number of impounded sections favoring the establishment of limnophilous Ponto-Caspian  
82 elements. The next step was when in 1992 the Main-Danube canal began to operate,  
83 connecting the river to the intertwined Western European waterway network. Since then, the  
84 Danube-Main-Rhine system can be referred to as the southern invasion corridor (Bij de Vaate  
85 et al. 2002), which – based on the number of species that have passed through – can be  
86 regarded as the most important inland invasion route to Western Europe (the other candidate  
87 being the central corridor, leading from the Black Sea through the rivers Dnieper, Prypjat,  
88 Bug, Vistula, Notec, Oder, and the Mittelland Canal to the Rhine; Bij de Vaate et al. 2002).  
89 All of the Ponto-Caspian species that have reached the Upper Danube have already colonized  
90 other catchments. The most obvious way forward is the River Rhine; most of the species  
91 appeared there within a couple of years after their first record in the German Danube section  
92 (Tittizer et al. 2000, Leuven et al. 2009). Several species have continued their expansion in  
93 France (Devin et al. 2005, Wittmann & Ariani 2009, Labat et al. 2011, Forcellini 2012), and  
94 some also successfully spread eastward using the central invasion corridor, even reaching  
95 Poland (Grabowski et al. 2007, Rachalewski et al. 2013a). Due to its earlier connection to the  
96 Western European catchments, the appearance of the first Ponto-Caspian invaders overseas  
97 can be attributed to the central corridor (Crawford 1935, Cristescu et al. 2004). However, in  
98 recent times the southern corridor seems to have taken the leading role in this regard, as well;  
99 colonies of *Hemimysis anomala* G. O. Sars, 1907 and *Dikerogammarus villosus* (Sowinsky,  
100 1894) could be traced back to the Danube (Audzijonyte et al. 2008, Rewicz et al. 2015), and

101 the recently discovered population of *D. haemobaphes* (Eichwald, 1841) in England also  
102 likely derives from the southern corridor inferring from the invasion history of the species  
103 (Bij de Vaate et al. 2002, Gallardo & Aldridge 2015).

104 With regard to the role of the Danube in the range extension of Ponto-Caspian species,  
105 changes in its peracarid fauna merit special attention. The latest international research  
106 expedition, the Joint Danube Survey 3 (JDS3 henceforth) covering the entire navigable course  
107 of the river offered an opportunity for updating and synthesizing our knowledge about this  
108 group, previously based on studies covering only certain river sections and/or dealing with a  
109 subset of species. Accordingly, in the present publication we delineate and interpret the  
110 currently observable longitudinal distributions of Peracarida in the river, and provide a  
111 synthesis of the biogeographical patterns in the range expansion of Ponto-Caspian species in  
112 hope of leading to a better understanding of the processes shaping the fauna of inland waters  
113 in the North-Atlantic region.

114

## 115 **Material and Methods**

116

117 After 2001 and 2007, the JDS was carried out for the third time between 13 August and 26  
118 September 2013. Macrozoobenthos samples were taken at 55 sites of the river between Ulm  
119 (river km = rkm 2581) and the Delta (rkm 18, Kiliya branch) using three different methods.  
120 (1) Based on the AQEM protocol (Hering et al. 2004), 4-7 samples were collected per site in  
121 the littoral zone (0.1-1.5 m depth) by hand net (aperture: 25 x 25 cm, mesh size: 500 µm)  
122 representing all habitat types available (multi-habitat sampling, MHS). Each sample consisted  
123 of five units covering 25 x 25 cm bottom area. On some occasions, supplementary samples  
124 were taken using a Van Veen grab (up to 5 m depth). (2) Deeper parts of the river were  
125 sampled using a triangular dredge (aperture: 25 cm, mesh size: 500 µm) towed downstream

126 from a motorboat. Five tows were done per site at locations distributed evenly along the  
127 cross-section, each yielding 1-15 dm<sup>3</sup> bed material from depths ranging between 1.1-22.7 m.  
128 (3) In order to provide better comparability with previous datasets (JDS2) and to gather data  
129 for methodological comparisons, additional samples were taken using the kick and sweep  
130 (K&S) sampling technique (EN 27828:1994). Ten subsamples (each covering approx. 25 x 25  
131 cm bottom area) representing various habitats were collected at each side of the river in the  
132 littoral region up to 2.5 m water depth using a hand net (mesh size: 500 µm). Additional  
133 material was gathered from stones, submerged debris, and macrophytes. At the most upstream  
134 site only MHS was done.

135 All samples were preserved in 4% formaldehyde solution in the field, and stored in 70%  
136 ethanol after sorting. In several cases subsampling was necessary due to the large amount of  
137 animals in the samples; altogether ~ 70 000 Peracarida specimens were identified to species  
138 level, if possible (usually above 2 mm body length in genera represented by more than one  
139 species).

140 Regarding river sections, in the present paper we follow the traditional geographic definition  
141 (Upper/Middle Danube: Morava estuary, rkm 1880; Middle/Lower Danube: the lower end of  
142 the Carpathian Mountains, ~ Iron Gate I dam, rkm 943).

143 Although the number of sites investigated was lower than in JDS1 and JDS2, the sampling  
144 methods applied and the special attention devoted to identification make the present one the  
145 most detailed river-wide dataset on peracarids of the Danube. In the present publication we  
146 analyze presence-absence data per site based on the pooled sample of all methods (Annex 1);  
147 the full dataset is available at: <http://www.icpdr.org/wq-db>. The results of the survey on the  
148 longitudinal distribution of Ponto-Caspian gobies (Pisces: Gobiidae) are discussed by Szalóky  
149 et al. (2015).

150

151 **Results**

152

153 Altogether 28 Peracarida species were recorded during the survey representing four orders (17  
154 Amphipoda, 7 Mysida, 3 Isopoda, 1 Cumacea; Table 1). Seven of them were present along the  
155 entire course of the river without biogeographically meaningful gaps (“ubiquitous”, Fig. 1).

156 *D. villosus* was the most prevalent among all species, occurring at all investigated sites, and  
157 *C. curvispinum* was the second, missing only at the most upstream location. Beside them,  
158 three other amphipods (*O. obesus*, *E. ischnus*, *D. haemobaphes*), one mysid (*L. benedeni*), and  
159 one isopod (*J. sarsi*) could be categorized as ubiquitous.

160 Three species had a wide distribution similarly to those mentioned above, but with  
161 biogeographically interpretable gaps in between (“disjunct”, Fig. 1). *C. robustum* and *C.*  
162 *sowinskyi* were missing in certain parts of the Middle Danube (the former between rkm 1367-  
163 1159, the latter between rkm 1630-1216), but they were common in the remaining reaches of  
164 the river. *E. trichiatus* was detected in three rather separate sections; the Upper Danube, the  
165 Iron Gate I reservoir, and the Delta.

166 Four species were associated with the upstream part of the river (Fig. 1). *G. fossarum* and *P.*  
167 *coxalis* occurred only at the most upstream sampling site, whereas *G. roeselii* was found at  
168 two locations of the German section. *D. bispinosus* was common in the Upper and Middle  
169 Danube, but it was totally missing in the lower reaches (downstream of rkm 1200).

170 The distribution of ten species was limited to the lower reaches of the river (Fig. 1), among  
171 which *P. lacustris* was the most widespread, occurring downstream of the Tisza estuary (~  
172 1200 rkm). Three others; *E. sarsi*, *P. intermedia*, and *P. robustoides* also had a relatively wide  
173 distribution, penetrating almost 700 rkm into the river. The range of the remaining six species  
174 was more restricted; the most upstream record of *P. bakuensis* and *S. scabriusculus* was

175 around rkm 200, while *E. warpachowskyi*, *O. crassus*, *P. ullskyi*, and *U. spinicaudatus* were  
176 found only in the Delta during the survey.

177 Four species occurred in the river relatively rarely and without biogeographical determination  
178 („sporadic”, Fig. 1). *K. warpachowskyi* was present at 15 sites scattered along the whole  
179 course of the river, while another mysid, *H. anomala* was found only at one location. *A.*  
180 *aquaticus* and *N. hrabei* were each recorded at two rather distant sites.

181

## 182 **Discussion**

183

184 Present distributional patterns

185

186 There is no surprise among the species with a ubiquitous occurrence; they all are successful  
187 invaders with wide distributions even outside the Danube catchment (Tittizer et al. 2000, Bij  
188 de Vaate et al. 2002). It should be noted, however, that although they were found sporadically  
189 during the survey, *H. anomala* and *K. warpachowskyi* also have a more-or-less continuous  
190 distribution within the river as suggested by literature data (Wittmann 2002, 2007, 2008,  
191 Borza et al. 2011). The reason for their scarcity in the material could be that they reach their  
192 peak abundances in semi-enclosed embayments not investigated during the survey (Borza et  
193 al. 2011).

194 The disjunct distribution of *C. robustum* and *C. sowinskyi* was first observed during the  
195 previous Joint Danube Survey (Borza et al. 2010) and was later confirmed by other materials  
196 (Borza 2011). Our results indicate that both species have narrowed their distributional gaps to  
197 some degree; *C. robustum* reached the upstream part of the Serbian section (rkm 1367, as  
198 compared to rkm 1533 in 2010; Borza & Puky 2012), whereas *C. sowinskyi* was recorded for  
199 the first time downstream of the Hungarian capital (rkm 1630, previously only upstream of



200 the city, at rkm 1669; Borza 2011). In the light of its recent rapid downstream spread it is  
201 reasonable to presume that the gap of *C. robustum* will soon disappear. On the contrary, in the  
202 case of *C. sowinskyi* only time will tell whether the new record is the first sign of nascent  
203 range expansion (after several years of stasis), or merely a result of occasional downstream  
204 drift.

205 *E. trichiatus* followed a similar expansion scenario as *C. robustum*; i.e., it also reached the  
206 Upper Danube recently via jump dispersal (Weinzierl et al. 1997) and subsequently spread  
207 downstream, the latest non-native record being not far from the dam of the Gabčíkovo  
208 reservoir at Čunovo (Borza 2009). In contrast to the expectations, the present survey yielded  
209 no records further downstream in the Hungarian section; indicating that its spread stopped or  
210 considerably slowed down, at least. On the contrary, the species was found for the first time in  
211 the Iron Gate I reservoir, representing its first record for Serbia.

212 The distributional pattern of *D. bispinosus*; i.e., its total absence within its native range is  
213 arguably the most curious case of all. The previous JDSs gave similar results; the species was  
214 missing approximately downstream of the Tisza estuary (rkm 1252 and 1216 in JDS1 and  
215 JDS2, respectively) with a single record from the Delta in 2007 (Kiliya branch, rkm 18; Graf  
216 et al. 2008). Literature data suggest that it was still rather common in the lower Danube in the  
217 second half of the 20<sup>th</sup> century (Popescu-Marinescu et al. 2001), but there are some more  
218 recent records, as well (Popescu-Marinescu & Năstăsescu 2005, Petrescu 2009). It is always  
219 hard to judge the absence of a species, but data at hand indicate that *D. bispinosus* has at least  
220 seriously declined during the past decades within its native range, which is rather surprising  
221 taking its successful range expansion in Western Europe during the same period into account.

222 Based on records of the three JDSs, native *Gammarus* species in the German section are  
223 retreating parallel to the gradual expansion of Ponto-Caspian invaders. In 2001 only  
224 *Gammarus pulex* (Linnaeus, 1758), *G. fossarum*, and *G. roeselii* were present at the most

225 upstream sampling site (Ulm, rkm 2581; Bernerth et al. 2002), whereas in 2013 the section  
226 was dominated by *D. villosus*, and *G. pulex* was not found. Similarly, *G. roeselii* disappeared  
227 at the second site (Kelheim, rkm 2415) by 2013, while the number of Ponto-Caspian species  
228 increased from 2 to 8 (Bernerth et al. 2002). Although such changes are indeed regrettable,  
229 the total extinction of native species is not likely; smaller tributaries still inhabited by them  
230 show that niche segregation is possible at the regional scale. Nevertheless, the process seems  
231 to be slowly going on, indicating that the equilibrium has not been reached yet either because  
232 of the relatively recent appearance of *D. villosus* in that river section, or perhaps due to long-  
233 term changes affecting the outcome of the interaction.

234 Our finding of a single specimen of the Mediterranean invader *P. coxalis* represents only the  
235 second record in the Danube. The first occurrence was detected in 2002 at rkm 2218  
236 (unpublished data from the Federal Institute of Hydrology, Koblenz), more than 350 km  
237 downstream of the present site, indicating that although it has been present for a rather long  
238 time, it has not been able to establish viable populations in the river. Another non-Ponto-  
239 Caspian immigrant, the North-American amphipod *Crangonyx pseudogracilis* Bousfield,  
240 1958, first recorded in the river during the previous survey (Graf et al. 2008) was missing this  
241 time. Similarly to native species, invasive Mediterranean and North American peracarids are  
242 also negatively affected by the presence of Ponto-Caspian species; they had been successful in  
243 Western Europe primarily before Ponto-Caspian invaders appeared (Tittizer et al. 2000), and  
244 subsequently their density decreased (Bernauer & Jansen 2006, Leuven et al. 2009). In the  
245 Danube, however, Ponto-Caspian species had arrived before them, which apparently  
246 precludes their establishment. *C. pseudogracilis* might be least affected; it prefers smaller  
247 stagnant or slowly flowing waters and occurs in large rivers only occasionally. Although  
248 waterways might contribute to its spread, the main means of its large-scale dispersal is  
249 assumed to be ectozoochory (Tittizer et al. 2000, Gerdes & Eggers 2007, Rachalewski et al.

250 2013b), which might allow its further expansion in the Danube basin. *P. coxalis* is also more  
251 prevalent in smaller waters (Kaiser 2005, Eggers 2013), but large rivers and canals are the  
252 main promoters of its spread (Van der Velde et al. 2000), so its expansion eastwards might be  
253 considerably slowed down by its exclusion from the Danube. The North-American amphipod  
254 *Gammarus tigrinus* Sexton, 1939 is more dependent on large rivers, so its conflict with Ponto-  
255 Caspian species – especially *D. villosus* – is even more pronounced (Dick & Platvoet 2000).  
256 Accordingly, although it was present in the River Main during the 1980-90s (Tittizer et al.  
257 2000, Bernerth et al. 2005), it has not been able to establish in the Danube after the opening of  
258 the Main-Danube canal, and has since declined in that river, as well (Bernerth et al. 2005).  
259 Two further species expanding from the Western Mediterranean, the amphipod  
260 *Echinogammarus berilloni* (Catta, 1878) and the isopod *Proasellus meridianus* (Racovitza,  
261 1919) encountered Ponto-Caspian species while still being restricted to the Rhine (Tittizer et  
262 al. 2000), so their appearance in the Danube basin is even less likely.  
263 The presence of *N. hrabei* in the German section of the river was first mentioned by  
264 Nesemann et al. (1995), but no exact occurrence data have been published so far. Since *N.*  
265 *hrabei* is primarily characteristic of smaller stagnant or slow-flowing waters with decaying  
266 plant material, our sporadic record in the main arm of the river can be considered as a result of  
267 drift. The location suggests that the wetlands around the Isar estuary might host self-  
268 sustaining populations. Previously, the distribution of the species was associated with the  
269 extent of the former Paratethys (Nesemann 1993), so the occurrence far beyond the  
270 Carpathian basin – parallel with records of *Synurella ambulans* (F. Müller, 1846) (Heckes et  
271 al. 1996) – poses an intriguing biogeographical question.  
272 Our records of *P. intermedia* at rkm 686 and *P. bakuensis* at rkm 232 represent their most  
273 upstream occurrences in the river, indicating a slight headway (Table 2). Contrarily, most  
274 other species restricted to the lower parts of the river have previously been reported

275 considerably farther upstream (Table 2; the only exception being *E. warpachowskyi* with all  
276 known occurrences restricted to the Delta). What is more, several Ponto-Caspian peracarids  
277 previously recorded in the Danube were not found during the survey at all. Most of these are  
278 restricted to the Delta, where obviously much more sampling effort would be needed to  
279 provide a realistic fauna list. However, there are 10 species which penetrated farther upstream  
280 in the Danube according to literature data (Table 2).

281

282 Range expansion of Ponto-Caspian peracarids

283

284 Based on their penetration into the Danube, three major groups of Ponto-Caspian peracarids  
285 can be distinguished. Firstly, almost half of the approximately 60 species present in the  
286 Danube system (Lyashenko et al. 2012) have never been recorded upstream of the Delta,  
287 indicating that even if adapted to freshwater, the ability to persist in fluvial environment is not  
288 trivial among crustaceans originating from the sea.

289 The second group of species has been able to penetrate several hundred kilometers into the  
290 river, but still remained restricted to the lower reaches (Table 2). A priori, the natural  
291 obstacles of the Iron Gates section could be assumed to determine their distribution; before its  
292 impoundment, the extreme currents (reaching ~ 5 m/s in the 150 m wide Kazan pass) must  
293 have represented an insurmountable barrier for all peracarids. However, if we take a look at  
294 the most upstream occurrences of the species belonging to his group (Table 2) it becomes  
295 evident, that surprisingly the narrows does not have a decisive role; several species never  
296 reached this section, while some others were present upstream of the Iron Gates even before  
297 the dams were built. The final limit to this type of distribution can be found somewhat more  
298 upstream in the Serbian section, as shown by historical records of *C. chelicorne*, *C.*  
299 *maeoticum*, *O. crassus*, *O. obesus*, *P. robustoides*, and *E. sarsi*, and also reflected in the

300 present distribution of *C. robustum*, *C. sowinskyi*, *E. trichiatus*, and *P. lacustris*. The  
301 explanation lies most likely in the flow conditions. The section immediately upstream of the  
302 Iron Gates is characterized by a low slope comparable to the Lower Danube, and since the  
303 construction of the Iron Gate I dam, current velocity is even more reduced (Fig. 2). Upstream  
304 of the Sava estuary, however, current speed attains the values characteristic of the Middle  
305 Danube (0.8-0.9 m/s). This might present a barrier in itself, but the bed material might further  
306 aggravate the situation; until approximately Baja the dominant substrate is sand, which –  
307 owing to the relatively strong currents – is very mobile, offering unfavorable conditions for  
308 most species.

309 Some of the species have probably been able to colonize the lower reaches actively and have  
310 been present there for a long time, as indicated by a considerable genetic divergence between  
311 fluvial and estuarine populations of *E. ischnus* in the Dniester and Dnieper rivers, for example  
312 (Cristescu et al. 2004). On the other hand, it is likely that passive transport also contributed to  
313 the expansion of some species, especially those present upstream of the Iron Gates.

314 In several cases, discrepancy is high between the most upstream occurrences and recent  
315 records, leaving an impression of fluctuating ranges. In part, this might be an artefact arising  
316 from different sampling effort and different methods used, assuming patchy or simply rare  
317 occurrence of certain species. However, it is likely that the range of some species has actually  
318 been constricted. Some of the previous records (especially those without subsequent  
319 confirmation) might reflect temporary establishment; i.e., the presence of a small population  
320 developing as a result of passive transport, but later collapsing (e.g., due to a flood).

321 Nevertheless, there are two relatively well documented cases, that of *C. maeoticum* and *O.*  
322 *crassus*, where it seems certain that the species considerably retreated. The reasons are  
323 unclear, but a possible explanation for such drastic changes might be the exclusion by a more  
324 successful invader, suggested by the fact that both *C. curvispinum* and *D. villosus* appeared

325 later in that section (Băcescu 1948, Karaman 1953; the latter mentioning *C. curvispinum*, but  
326 the figures depict *C. sowinskyi*, regarded as a subspecies of *C. curvispinum* at that time).  
327 The species having successfully crossed the barrier of the Serbian section represent the third  
328 group. They have not only populated the whole navigable course of the river, but all of them  
329 have already invaded other catchments, as well. Their establishment also seems more stable  
330 compared to the species of the previous group; no retreats have been observed in terms of  
331 distance to the sea, but *C. sowinskyi* and *D. bispinosus* serve as intriguing examples for  
332 decline in more downstream parts of their range. The large distances involved and the lack of  
333 records in the intermediate river sections leave jump dispersal by ships as the only viable  
334 explanation for their arrival (e.g., Wittmann 2002). Remarkably, the target region of invasions  
335 went through a distinct change during time; previously all species appeared in the Middle  
336 Danube, but since the mid-1990s all four novel invaders were first detected in the Upper  
337 Danube, or even outside the Danube basin, as in the case *C. robustum* (Weinzierl et al. 1997,  
338 Wittmann et al. 1999, Wittmann 2002, Bernerth & Stein 2003). This might be in connection  
339 with the presumable rearrangement in shipping activity after the opening of the Main-Danube  
340 canal, but unfortunately no comprehensive datasets allowing the analysis of the question are  
341 available.

342 Previous invasion success is often used in attempts for identifying potential future invaders  
343 (Ricciardi & Rasmussen 1998, Gallardo & Aldridge 2013). Accordingly, it might seem  
344 logical to assume a temporal order among the three distributional types. The connection  
345 between the estuarine and ‘lower section’ types is quite evident, but does presence in the Iron  
346 Gates section in fact portend large-scale expansion? The case of most early invaders (*D.*  
347 *bispinosus*, *D. haemobaphes*, *C. sowinskyi*, *E. ischnus*, and *J. sarsi*) is uncertain, since they  
348 were already present at the time of the first faunistic investigations both at the Iron Gates and  
349 farther upstream in the Hungarian section. Historical occurrences of *C. curvispinum*, *H.*

350 *anomala*, *K. warpachowskyi*, and *L. benedeni*, and present records of *E. trichiatus* allow the  
351 conclusion that they reached the lower Serbian section only after their establishment more  
352 upstream in the Danube (Băcescu 1948, Karaman 1953, Wittmann 2007). On the contrary, six  
353 species (*C. chelicorne*, *C. maeoticum*, *O. crassus*, *P. lacustris*, *P. robustoides*, and *E. sarsi*)  
354 having been reported in the Iron Gates section have not been able to colonize the more  
355 upstream reaches of the Danube thus far. Only in the case of three successful invaders has the  
356 appearance in this part of the river preceded the large-scale expansion, where the stepping  
357 stone role cannot be excluded. However, *C. robustum* and *O. obesus* appeared way before  
358 their respective first records upstream, so there is no indication of direct connection. In the  
359 case of *D. villosus* the time lag between the first records is much shorter (1968 at the Iron  
360 Gates vs. 1975 in the Hungarian section; Popescu-Marinescu 1970 cited by Petrescu 2009,  
361 Nosek & Oertel 1980) which might indicate relation, but investigations were rather rare at that  
362 time, so the colonization might have happened just as well the opposite way. Here we would  
363 like to point out that the first record of *D. villosus* in the Hungarian section is mistakenly  
364 dated to 1926 in some recent publications (e.g., Neesemann et al. 1995, Bij de Vaate et al.  
365 2002, Rewicz et al. 2014). The reason for the confusion is that Dudich (1927) did not indicate  
366 the that-time subspecific rank of *D. villosus bispinosus*. Several independent works confirm  
367 that *D. villosus* was not present in the Middle Danube even in the 1950s (Dudich 1947,  
368 Karaman 1953, Ponyi 1958, Brtek & Rothschein 1964).

369 In conclusion, appearance upstream of the Iron Gates shows little correspondence with large-  
370 scale invasion success, establishment in this section does not appear to promote further  
371 expansion in the Danube in most of the cases. However, the species pool in the Danube reach  
372 adjacent to their estuary might be decisive for large tributaries also colonized by Ponto-  
373 Caspian peracarids. In the Drava and Sava only a subset of the third species group is present  
374 (Žganec et al. 2009, Borza 2011, Lucić et al. 2015), but the Tisza – allowing further spread of

375 *C. maeoticum* and *P. lacustris* – can be considered as an autonomous side-branch of the  
376 southern invasion corridor. The source region of large distance jump dispersal must have been  
377 within the Lower Danube in most of the cases at least, but further narrowing is rarely  
378 possible. The most informative in this regard is the invasion history of *H. anomala*, the most  
379 widespread Ponto-Caspian peracarid at present. This rheophobic species could be  
380 characterized by an estuarine distribution before its large-scale expansion began in the 1990s  
381 (Wittmann 2007), marking the Delta as the source of its invasion, and indicating at the same  
382 time that not only species occurring in the lower reaches should be considered as potential  
383 invaders, but – given the chance – estuarine species also might be able to colonize inland  
384 waters. Successful introductions or even spontaneous expansions in other rivers also prove  
385 that several species restricted to the Delta in the Danube would be able to persist at least in  
386 lakes, reservoirs, and other lentic habitats in rivers (Grigorovich et al. 2002). Nevertheless, it  
387 might not be entirely random which species are able to realize their potential; there might be  
388 traits promoting large-scale invasion success associated with the access to vectors, survival of  
389 transport, or the chance of establishment and spread.

390

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392

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400

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404

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622 Captions

623

624 Fig. 1. A: Sampling sites on the Danube during JDS3 (site codes are shown for the sake of  
625 comparability with the online dataset; numbers are not necessarily consecutive). Shaded area:  
626 Danube catchment, ISO codes of riparian countries: DE – Germany, AT – Austria, SK –  
627 Slovakia, HU – Hungary, HR – Croatia, RS – Serbia, RO – Romania, BG – Bulgaria, MD –  
628 Moldova, UA – Ukraine. B: Distribution of Peracarida species in the Danube during JDS3. ○:  
629 multi-habitat sampling, ◇: dredge, ×: kick-and-sweep, neighbouring records are connected  
630 with grey line.

631

632 Fig. 2. Mean current velocity and bed material grain size (84% percentile) in the Danube  
633 during JDS3.

634

635 Table 1. Peracarid taxa recorded during JDS3. Classification follows the World Register of  
636 Marine Species (WoRMS 2014), taxa above family level indicated only if relevant.

637

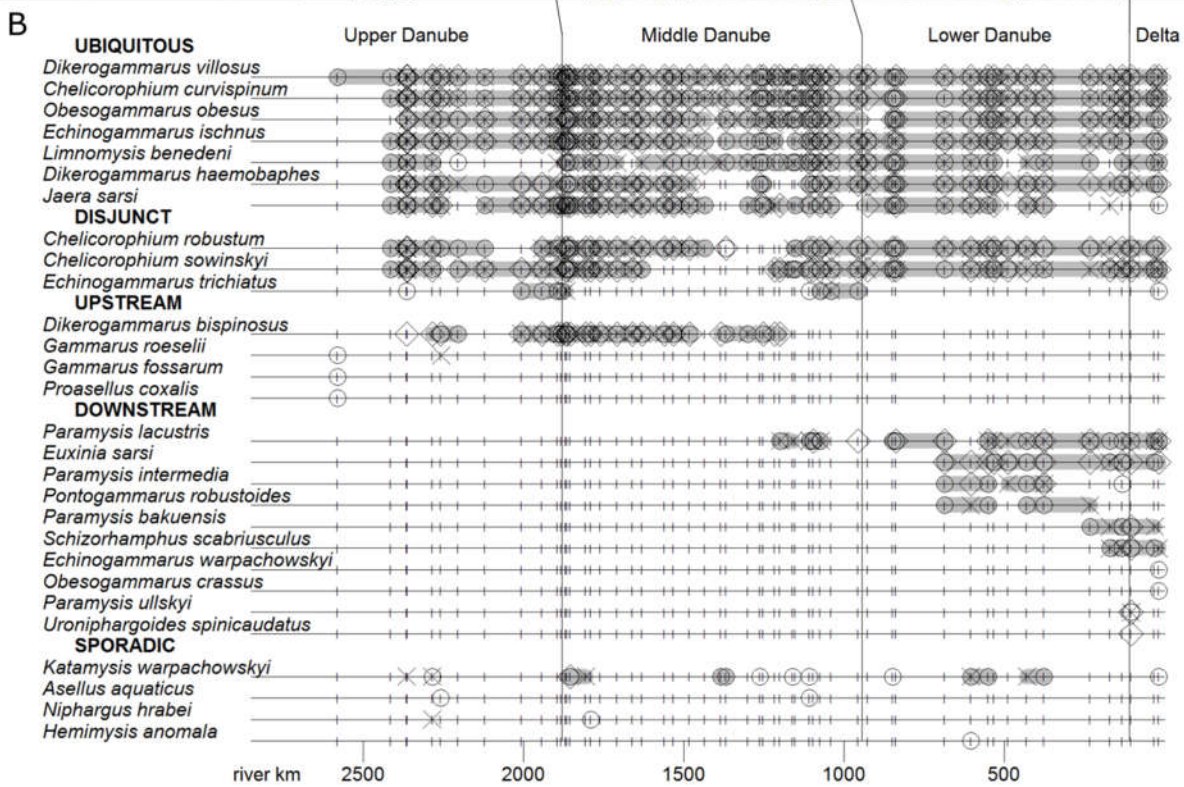
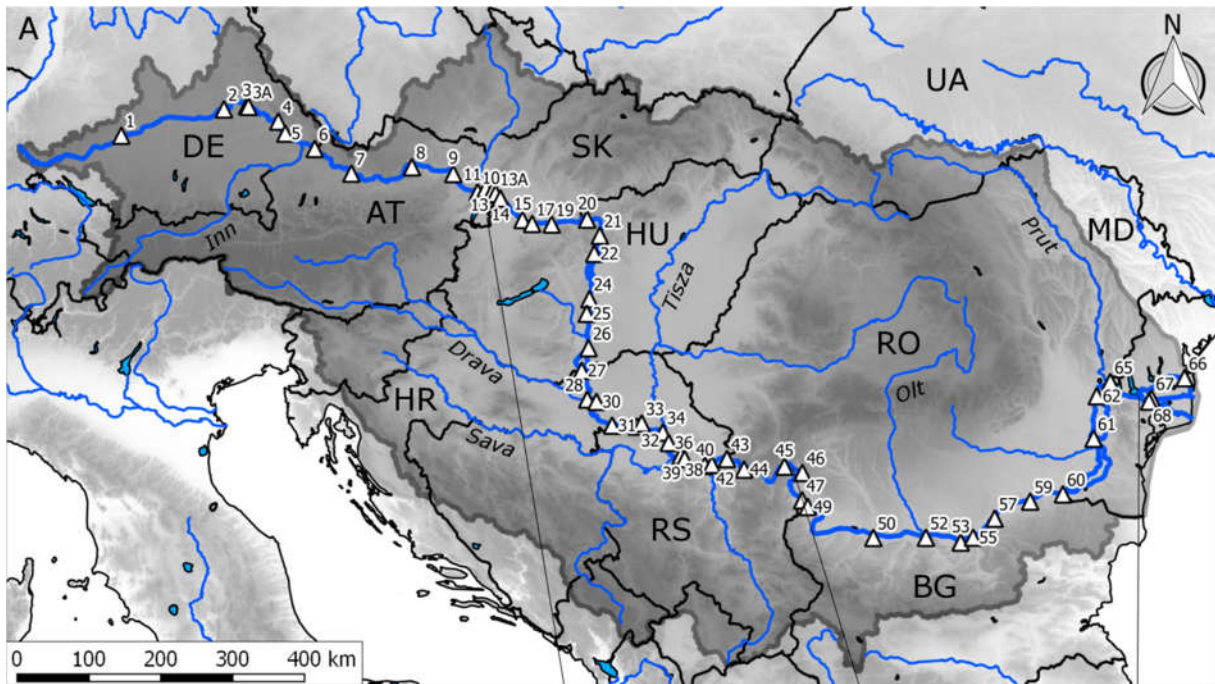
638 Table 2. Peracarid species penetrating into the lower reaches of the Danube (ordered by their  
639 most upstream occurrence ever). ~: estimated value based on geographic name. \*: Wittmann  
640 (2007) recorded a single specimen of *P. lacustris* near Vienna (rkm 1930).

641

642 Annex 1. Records of peracarids during JDS3 (2013). A: species with occurrences at more than  
643 2 sites. CC – *Chelicorophium curvispinum* (G. O. Sars, 1895); CR – *Chelicorophium*  
644 *robustum* (G. O. Sars, 1895); CS – *Chelicorophium sowinskyi* (Martynov, 1924); DB –  
645 *Dikerogammarus bispinosus* Martynov, 1925; DH – *Dikerogammarus haemobaphes*  
646 (Eichwald, 1841); DV – *Dikerogammarus villosus* (Sowinsky, 1894); EI – *Echinogammarus*

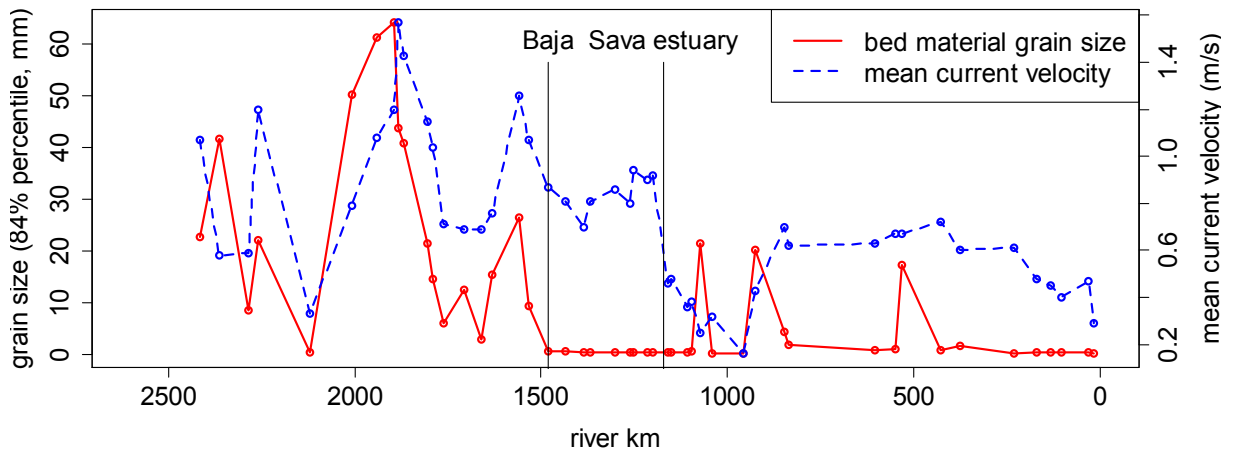
647 *ischnus* (Stebbing, 1899); ET– *Echinogammarus trichiatus* (Martynov, 1932); ES – *Euxinia*  
648 *sarsi* (Sowinsky, 1898); JS – *Jaera sarsi* Valkanov, 1936; KW – *Katamysis warpachowskyi*  
649 G. O. Sars, 1893; LB – *Limnomysis benedeni* Czerniavsky, 1882; OO – *Obesogammarus*  
650 *obesus* (G. O. Sars, 1894); PB – *Paramysis bakuensis* G. O. Sars, 1895; PI – *Paramysis*  
651 *intermedia* (Czerniavsky, 1882); PL – *Paramysis lacustris* (Czerniavsky, 1882); PR –  
652 *Pontogammarus robustoides* (G. O. Sars, 1894); SS – *Schizorhamphus scabriusculus* (G. O.  
653 Sars, 1894). B: species with occurrences at 1 or 2 sites. Coordinates are indicative of the sites  
654 (i.e., cross-sections of the river); individual samples were collected at slightly different  
655 localities. <sup>1</sup>: Kiliya arm, <sup>2</sup>: Sulina arm, <sup>3</sup>: Sf. Gheorghe arm.

656 Fig. 1  
657



658

659 Fig. 2



660

661

**Order Amphipoda****Infraorder Corophiida****Family Corophiidae***Chelicorophium curvispinum* (G. O. Sars, 1895)*Chelicorophium robustum* (G. O. Sars, 1895)*Chelicorophium sowinskyi* (Martynov, 1924)**Infraorder Gammarida****Parvorder Crangonyctidira****Family Niphargidae***Niphargus hrabei* S. Karaman, 1932**Parvorder Gammaridira****Family Gammaridae***Dikerogammarus bispinosus* Martynov, 1925*Dikerogammarus haemobaphes* (Eichwald, 1841)*Dikerogammarus villosus* (Sowinsky, 1894)*Echinogammarus ischnus* (Stebbing, 1899)*Echinogammarus trichiatus* (Martynov, 1932)*Echinogammarus warpachowskyi* (G. O. Sars, 1894)*Gammarus fossarum* Koch, 1836*Gammarus roeselii* Gervais, 1835**Family Pontogammaridae***Euxinia sarsi* (Sowinsky, 1898)*Obesogammarus crassus* (G. O. Sars, 1894)*Obesogammarus obesus* (G. O. Sars, 1894)*Pontogammarus robustoides* (G. O. Sars, 1894)*Uroniphargoides spinicaudatus* (Cărăușu, 1943)**Order Cumacea****Family Pseudocumatidae***Schizorhamphus scabriusculus* (G. O. Sars, 1894)**Order Isopoda****Family Asellidae***Asellus aquaticus* (Linnaeus, 1758)*Proasellus coxalis* (Dollfus, 1892)**Family Janiridae***Jaera sarsi* Valkanov, 1936**Order Mysida****Family Mysidae***Hemimysis anomala* G. O. Sars, 1907*Katamysis warpachowskyi* G. O. Sars, 1893*Limnomysis benedeni* Czerniavsky, 1882*Paramysis bakuensis* G. O. Sars, 1895*Paramysis intermedia* (Czerniavsky, 1882)*Paramysis lacustris* (Czerniavsky, 1882)*Paramysis ullskyi* (Czerniavsky, 1882)

Species	Most upstream occurrence (rkm)		Reference
	Present survey	Previously	
<i>Paramysis lacustris</i> (Czerniavsky, 1882)	1199	1300*	Paunović et al. (2007)
<i>Obesogammarus crassus</i> (G. O. Sars, 1894)	18 (Kiliya arm)	~1258	Dudich (1947)
<i>Chelicorophium maeoticum</i> (Sowinsky, 1898)	not found	~1116/ ~178 (Tisza)	Karaman (1953)/ Borza (2011)
<i>Euxinia sarsi</i> (Sowinsky, 1898)	686	~1116	Karaman (1953)
<i>Chelicorophium chelicorne</i> (G. O. Sars, 1895)	not found	~1072	Popescu-Marinescu & Năstăsescu (2005)
<i>Pontogammarus robustoides</i> (G. O. Sars, 1894)	686	1072-943	Popescu-Marinescu et al. (2001)
<i>Echinogammarus placidus</i> (G. O. Sars, 1896)	not found	834	Russev (1966)
<i>Stenogammarus carausui</i> (Derzhavin & Pjatakova, 1962)	not found	834	Russev (1966)
<i>Paramysis ullskyi</i> (Czerniavsky, 1882)	104 (Sf. Gheorghe arm)	747	Russev (1966)
<i>Paramysis intermedia</i> (Czerniavsky, 1882)	686	644	Băcescu (1954), Wittmann (2007)
<i>Pontogammarus maeoticus</i> (Sowinsky, 1894)	not found	552	Russev (1966)
<i>Paraniphargoides motasi</i> (Cărbăușu, 1943)	not found	552	Russev (1966)
<i>Niphargogammarus intermedius</i> (Cărbăușu, 1943)	not found	495	Russev (1966)
<i>Schizorhamphus scabriusculus</i> (G. O. Sars, 1894)	170	450	Băcescu (1951)
<i>Pontogammarus borceae</i> Cărbăușu, 1943	not found	375	Russev (1966)
<i>Pontogammarus aestuarius</i> (Derzhavin, 1924)	not found	~375	Prunescu-Arion & Elian (1965)
<i>Uroniphargoides spinicaudatus</i> (Cărbăușu, 1943)	104 (Sf. Gheorghe arm)	~375	Prunescu-Arion & Elian (1965)
<i>Paramysis bakuensis</i> G. O. Sars, 1895	232	80	Băcescu (1954)
<i>Paramysis kessleri sarsi</i> (Derzhavin, 1925)	not found	150	Băcescu (1954)



Annex 1A

Site ID	Date	Lat (N)	Lon (E)	Rkm	CC	CR	CS	DB	DH	DV	EI	ET	ES	JS	KW	LB	OO	PB	PI	PL	PR	SS
1	13-Aug	48.42419	10.02761	2581						*												
2	13-Aug	48.90874	11.90123	2415	*	*	*		*	*	*			*		*						
3	14-Aug	48.97915	12.33248	2365	*	*	*	*	*	*	*	*		*	*	*	*					
3A	14-Aug	48.97389	12.36222	2363	*	*	*		*	*	*			*		*	*					
4	15-Aug	48.82700	12.95435	2285	*	*	*	*	*	*	*			*	*	*	*					
5	16-Aug	48.68595	13.10883	2258	*	*		*	*	*	*			*								
6	17-Aug	48.52750	13.68978	2205	*	*	*	*	*	*	*					*	*					
7	18-Aug	48.25643	14.41622	2121	*	*	*		*	*	*			*								
8	18-Aug	48.38720	15.54578	2007	*		*	*	*	*	*	*		*								
9	19-Aug	48.33132	16.33048	1942	*	*	*	*	*	*	*	*		*								
10	20-Aug	48.11658	16.80312	1895	*	*	*	*	*	*	*	*		*		*	*					
11	21-Aug	48.16607	16.95138	1882	*	*		*	*	*	*	*		*								
13	21-Aug	48.14224	17.08258	1868	*	*	*	*		*	*	*		*		*	*					
13A	21-Aug	48.10639	17.14056	1860	*	*	*	*	*	*	*			*		*	*					
14	22-Aug	48.04858	17.23590	1855	*	*	*	*	*	*	*			*	*	*	*					
15	23-Aug	47.79092	17.65987	1806	*	*	*	*	*	*	*			*	*	*	*					
17	23-Aug	47.74393	17.84257	1790	*	*	*	*	*	*	*			*		*	*					
19	24-Aug	47.74400	18.20568	1761	*	*	*	*	*	*	*			*		*	*					
20	25-Aug	47.81490	18.86405	1707	*	*	*	*	*	*	*			*		*	*					
21	25-Aug	47.61418	19.10332	1660	*	*	*	*	*	*	*			*								
22	26-Aug	47.38657	19.00443	1630	*	*	*	*	*	*	*			*		*	*					
24	28-Aug	46.81755	18.92853	1560	*	*		*	*	*	*			*		*	*					
25	29-Aug	46.63305	18.88267	1532	*	*		*	*	*	*			*		*	*					
26	29-Aug	46.20115	18.92518	1481	*	*		*	*	*	*			*		*	*					
27	30-Aug	45.91557	18.80750	1434	*	*				*	*			*		*	*					
28	31-Aug	45.55618	18.91455	1384	*			*		*					*	*						
30	31-Aug	45.52952	19.07842	1367	*	*		*		*	*				*	*	*					
31	1-Sep	45.23288	19.36178	1300	*			*		*	*			*		*	*					

Site ID	Date	Lat (N)	Lon (E)	Rkm	CC	CR	CS	DB	DH	DV	EI	ET	ES	JS	KW	LB	OO	PB	PI	PL	PR	SS
32	2-Sep	45.22340	19.80373	1262	*				*	*	*			*	*	*	*					
33	3-Sep	45.26162	19.88713	1252	*			*	*	*	*			*		*	*					
34	3-Sep	45.14825	20.26202	1216	*			*		*	*			*		*	*					
36	4-Sep	45.01687	20.36708	1199	*		*	*		*				*		*	*				*	
38	6-Sep	44.85318	20.57685	1159	*	*	*			*					*	*	*				*	
39	6-Sep	44.81287	20.64495	1151	*	*	*			*	*			*		*	*					
40	7-Sep	44.72470	21.00068	1107	*	*	*		*	*	*	*		*	*	*	*				*	
42	7-Sep	44.73655	21.12330	1095	*	*	*		*	*	*					*	*				*	
43	8-Sep	44.80508	21.38992	1073	*	*	*		*	*	*	*		*		*	*				*	
44	9-Sep	44.66830	21.68792	1040	*	*	*		*	*	*	*		*		*	*					
45	9-Sep	44.69203	22.39952	956	*	*	*		*	*	*	*				*	*				*	
46	10-Sep	44.60565	22.71053	926	*	*	*		*	*	*			*		*						
47	12-Sep	44.26088	22.68898	847	*	*	*		*	*	*			*	*	*	*				*	
49	13-Sep	44.17505	22.78380	837	*	*	*		*	*	*			*		*	*				*	
50	14-Sep	43.74992	23.89870	686	*	*	*		*	*	*	*		*		*	*		*	*	*	*
52	15-Sep	43.71322	24.80642	604	*	*	*		*	*	*	*		*	*	*	*		*	*	*	*
53	15-Sep	43.62342	25.40175	550	*	*	*		*	*	*	*		*	*	*	*		*	*	*	*
55	16-Sep	43.67415	25.61943	532	*	*	*		*	*	*	*		*		*	*			*	*	
57	18-Sep	43.89015	26.01707	488	*	*	*		*	*	*	*		*		*	*		*	*	*	
59	19-Sep	44.06632	26.65588	429	*	*	*		*	*	*	*		*	*	*	*		*	*	*	*
60	19-Sep	44.11870	27.23455	375	*	*	*		*	*	*	*		*	*	*	*		*	*	*	*
61	20-Sep	44.77473	27.86305	232	*	*	*		*	*	*	*		*		*	*	*		*	*	*
62	21-Sep	45.30087	27.99493	170	*	*	*		*	*	*	*		*		*	*	*		*	*	*
65	22-Sep	45.45785	28.26178	132	*	*	*		*	*	*	*		*		*	*	*	*	*	*	*
66	24-Sep	45.39553	29.58547	18 <sup>1</sup>	*	*	*		*	*	*	*	*	*	*	*	*			*	*	*
67	25-Sep	45.19450	28.95933	31 <sup>2</sup>	*	*	*		*	*	*	*	*	*	*	*	*	*		*	*	*
68	25-Sep	45.15953	28.90893	104 <sup>3</sup>	*	*	*		*	*	*	*	*	*	*	*	*	*		*	*	*

1 Annex 1B

Species	Site ID	Date	Lat (N)	Lon (E)	Rkm
<i>Asellus aquaticus</i> (Linnaeus, 1758)	5	16-Aug	48.68595	13.10883	2258
	40	7-Sep	44.72470	21.00068	1107
<i>Echinogammarus warpachowskyi</i> (G. O. Sars, 1894)	66	24-Sep	45.39553	29.58547	18
<i>Gammarus fossarum</i> Koch, 1836	1	13-Aug	48.42419	10.02761	2581
<i>Gammarus roeselii</i> Gervais, 1835	1	13-Aug	48.42419	10.02761	2581
	5	16-Aug	48.68595	13.10883	2258
<i>Hemimysis anomala</i> G. O. Sars, 1907	52	15-Sep	43.71322	24.80642	604
<i>Niphargus hrabei</i> S. Karaman, 1932	4	15-Aug	48.82700	12.95435	2285
	17	23-Aug	47.74393	17.84257	1790
<i>Obesogammarus crassus</i> (G. O. Sars, 1894)	66	24-Sep	45.39553	29.58547	18
<i>Paramysis ullskyi</i> (Czerniavsky, 1882)	68	25-Sep	45.15953	28.90893	104
<i>Proasellus coxalis</i> (Dollfus, 1892)	1	13-Aug	48.42419	10.02761	2581
<i>Uroniphargoides spinicaudatus</i> (Căraușu, 1943)	68	25-Sep	45.15953	28.90893	104

2

3