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

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Abstract

The River Danube plays a central role in the spread of Ponto-Caspian species as a part of the so-called southern invasion corridor (Danube-Main-Rhine system); therefore, changes in its peracarid fauna (comprising the bulk of invasives) merit special attention. The latest international research expedition (Joint Danube Survey 3, 2013) offered an opportunity for updating and synthesizing our knowledge about this group along the Danube, previously based on studies covering only certain river sections and/or dealing with a subset of species. Altogether 17 amphipod, 7 mysid, 3 isopod, and one cumacean species were recorded at 55 sites investigated between Ulm (river km 2581) and the Delta. Recent large-distance expansion of additional Ponto-Caspian species was not observed, but three species (Chelicorophium robustum, C. sowinskyi, and Echinogammarus trichiatus) have been able to shorten their distributional gap in the Middle Danube, E. trichiatus being recorded for the first time in Serbia. Ponto-Caspian peracarids are still gradually advancing in the German section, as well, implying retreat of native Gammarus spp., and impeding the spread of non-Ponto-Caspian invaders. On the contrary, some Ponto-Caspian species seem to have declined in certain river sections; Dikerogammarus bispinosus was entirely missing in the Lower Danube, and several species characteristic of the lower reaches had been recorded previously much farther upstream (most notably Chelicorophium maeoticum and Obesogammarus crassus).

The analysis of current and historical distributional patterns revealed that the crucial step in the large-scale spread of Ponto-Caspian species is crossing the section between Baja and the Sava estuary (rkm ~1480-1170) – characterized by an unfavorable combination of relatively
strong currents and fine bed material – by passive transport. Presence immediately
downstream of this section does not appear to promote further expansion in most of the cases;
the source region of large-distance dispersal is most likely the Delta, implying that potential
future invaders cannot be identified based on their previous expansion in the lower reaches of
the river.

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

**Introduction**

The range expansion of Ponto-Caspian faunal elements has been one of the most significant
biogeographical processes in inland waters of the North-Atlantic region in recent times, often
having serious consequences on native fauna and ecosystem functioning (Ricciardi &
MacIsaac 2000, Bij de Vaate et al. 2002, Ojaveer et al. 2002). The representatives of several
metazoan groups are involved, ranging from cnidarians to fish, but in terms of species number
peracard crustaceans dominate; 19 species (13 amphipod, 5 mysid, and one isopod) have
extended the limits of their distribution across river basins in Central, Western, or Northern
2010, Grabowski et al. 2012), four of which have established also in the British Isles
(Gallardo & Aldridge 2015), and two have appeared even in North America (Witt et al. 1997,
Pothoven et al. 2007). In addition, several other species including cumaceans have established
in Eastern European reservoirs and lakes mainly by intentional introduction (Grigorovich et
Europe’s second longest – and most international – river, the Danube plays a central role in
their spread. Emptying into the Black Sea, it has a direct connection to the Pontic Basin,
implying that a high number of Ponto-Caspian endemics are native to the lower reaches of the river (Lyashenko et al. 2012). The first Ponto-Caspian peracarid in the Middle Danube was detected in the 1910s (Unger 1918), and by the 1940s 7 species had established the Hungarian section (Dudich 1947, Borza 2011). The colonization of the Upper Danube was more delayed, starting only in the second half of the 20th century (Kothé 1968), parallel to the growing number of impounded sections favoring the establishment of limnophilous Ponto-Caspian elements. The next step was when in 1992 the Main-Danube canal began to operate, connecting the river to the intertwined Western European waterway network. Since then, the Danube-Main-Rhine system can be referred to as the southern invasion corridor (Bij de Vaate et al. 2002), which – based on the number of species that have passed through – can be regarded as the most important inland invasion route to Western Europe (the other candidate being the central corridor, leading from the Black Sea through the rivers Dnieper, Prypjat, Bug, Vistula, Notec, Oder, and the Mittelland Canal to the Rhine; Bij de Vaate et al. 2002).

All of the Ponto-Caspian species that have reached the Upper Danube have already colonized other catchments. The most obvious way forward is the River Rhine; most of the species appeared there within a couple of years after their first record in the German Danube section (Tittizer et al. 2000, Leuven et al. 2009). Several species have continued their expansion in France (Devin et al. 2005, Wittmann & Ariani 2009, Labat et al. 2011, Forcellini 2012), and some also successfully spread eastward using the central invasion corridor, even reaching Poland (Grabowski et al. 2007, Rachalewski et al. 2013a). Due to its earlier connection to the Western European catchments, the appearance of the first Ponto-Caspian invaders overseas can be attributed to the central corridor (Crawford 1935, Cristescu et al. 2004). However, in recent times the southern corridor seems to have taken the leading role in this regard, as well; colonies of Hemimysis anomala G. O. Sars, 1907 and Dikerogammarus villosus (Sowinsky, 1894) could be traced back to the Danube (Audzijonyte et al. 2008, Rewicz et al. 2015), and
the recently discovered population of *D. haemobaphes* (Eichwald, 1841) in England also likely derives from the southern corridor inferring from the invasion history of the species (Bij de Vaate et al. 2002, Gallardo & Aldridge 2015).

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

**Material and Methods**

After 2001 and 2007, the JDS was carried out for the third time between 13 August and 26 September 2013. Macrozoobenthos samples were taken at 55 sites of the river between Ulm (river km = rkm 2581) and the Delta (rkm 18, Kiliya branch) using three different methods. (1) Based on the AQEM protocol (Hering et al. 2004), 4-7 samples were collected per site in the littoral zone (0.1-1.5 m depth) by hand net (aperture: 25 x 25 cm, mesh size: 500 μm) representing all habitat types available (multi-habitat sampling, MHS). Each sample consisted of five units covering 25 x 25 cm bottom area. On some occasions, supplementary samples were taken using a Van Veen grab (up to 5 m depth). (2) Deeper parts of the river were sampled using a triangular dredge (aperture: 25 cm, mesh size: 500 μm) towed downstream.
from a motorboat. Five tows were done per site at locations distributed evenly along the
cross-section, each yielding 1-15 dm$^3$ bed material from depths ranging between 1.1-22.7 m.

(3) In order to provide better comparability with previous datasets (JDS2) and to gather data
for methodological comparisons, additional samples were taken using the kick and sweep
(K&S) sampling technique (EN 27828:1994). Ten subsamples (each covering approx. 25 x 25
cm bottom area) representing various habitats were collected at each side of the river in the
littoral region up to 2.5 m water depth using a hand net (mesh size: 500 µm). Additional
material was gathered from stones, submerged debris, and macrophytes. At the most upstream
site only MHS was done.

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

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

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

Altogether 28 Peracarida species were recorded during the survey representing four orders (17 Amphipoda, 7 Mysida, 3 Isopoda, 1 Cumacea; Table 1). Seven of them were present along the entire course of the river without biogeographically meaningful gaps (“ubiquitous”, Fig. 1). *D. villosus* was the most prevalent among all species, occurring at all investigated sites, and *C. curvispinum* was the second, missing only at the most upstream location. Beside them, three other amphipods (*O. obesus, E. ischnus, D. haemobaphes*), one mysid (*L. benedeni*), and one isopod (*J. sarsi*) could be categorized as ubiquitous.

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

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

The distribution of ten species was limited to the lower reaches of the river (Fig. 1), among which *P. lacustris* was the most widespread, occurring downstream of the Tisza estuary (~1200 rkm). Three others; *E. sarsi, P. intermedia*, and *P. robustoides* also had a relatively wide distribution, penetrating almost 700 rkm into the river. The range of the remaining six species was more restricted; the most upstream record of *P. bakuensis* and *S. scabriusculus* was
around rkm 200, while *E. warpachowskyi, O. crassus, P. ullskyi,* and *U. spinicaudatus* were found only in the Delta during the survey.

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

**Discussion**

Present distributional patterns

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

The disjunct distribution of *C. robustum* and *C. sowinskyi* was first observed during the previous Joint Danube Survey (Borza et al. 2010) and was later confirmed by other materials (Borza 2011). Our results indicate that both species have narrowed their distributional gaps to some degree; *C. robustum* reached the upstream part of the Serbian section (rkm 1367, as compared to rkm 1533 in 2010; Borza & Puky 2012), whereas *C. sowinskyi* was recorded for the first time downstream of the Hungarian capital (rkm 1630, previously only upstream of
In the light of its recent rapid downstream spread it is reasonable to presume that the gap of *C. robustum* will soon disappear. On the contrary, in the case of *C. sowinskyi* only time will tell whether the new record is the first sign of nascent range expansion (after several years of stasis), or merely a result of occasional downstream drift.

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

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

Based on records of the three JDSs, native *Gammarus* species in the German section are retreating parallel to the gradual expansion of Ponto-Caspian invaders. In 2001 only *Gammarus pulex* (Linnaeus, 1758), *G. fossarum*, and *G. roeselii* were present at the most
upstream sampling site (Ulm, rkm 2581; Bernerth et al. 2002), whereas in 2013 the section was dominated by *D. villosus*, and *G. pulex* was not found. Similarly, *G. roeselii* disappeared at the second site (Kelheim, rkm 2415) by 2013, while the number of Ponto-Caspian species increased from 2 to 8 (Bernerth et al. 2002). Although such changes are indeed regrettable, the total extinction of native species is not likely; smaller tributaries still inhabited by them show that niche segregation is possible at the regional scale. Nevertheless, the process seems to be slowly going on, indicating that the equilibrium has not been reached yet either because of the relatively recent appearance of *D. villosus* in that river section, or perhaps due to long-term changes affecting the outcome of the interaction.

Our finding of a single specimen of the Mediterranean invader *P. coxalis* represents only the second record in the Danube. The first occurrence was detected in 2002 at rkm 2218 (unpublished data from the Federal Institute of Hydrology, Koblenz), more than 350 km downstream of the present site, indicating that although it has been present for a rather long time, it has not been able to establish viable populations in the river. Another non-Ponto-Caspian immigrant, the North-American amphipod *Crangonyx pseudogracilis* Bousfield, 1958, first recorded in the river during the previous survey (Graf et al. 2008) was missing this time. Similarly to native species, invasive Mediterranean and North American peracarids are also negatively affected by the presence of Ponto-Caspian species; they had been successful in Western Europe primarily before Ponto-Caspian invaders appeared (Tittizer et al. 2000), and subsequently their density decreased (Bernauer & Jansen 2006, Leuven et al. 2009). In the Danube, however, Ponto-Caspian species had arrived before them, which apparently precludes their establishment. *C. pseudogracilis* might be least affected; it prefers smaller stagnant or slowly flowing waters and occurs in large rivers only occasionally. Although waterways might contribute to its spread, the main means of its large-scale dispersal is assumed to be ectozoochory (Tittizer et al. 2000, Gerdes & Eggers 2007, Rachalewski et al. 2008).
2013b), which might allow its further expansion in the Danube basin. *P. coxalis* is also more prevalent in smaller waters (Kaiser 2005, Eggers 2013), but large rivers and canals are the main promoters of its spread (Van der Velde et al. 2000), so its expansion eastwards might be considerably slowed down by its exclusion from the Danube. The North-American amphipod *Gammarus tigrinus* Sexton, 1939 is more dependent on large rivers, so its conflict with Ponto-Caspian species – especially *D. villosus* – is even more pronounced (Dick & Platvoet 2000).

Accordingly, although it was present in the River Main during the 1980-90s (Tittizer et al. 2000, Bernerth et al. 2005), it has not been able to establish in the Danube after the opening of the Main-Danube canal, and has since declined in that river, as well (Bernerth et al. 2005).

Two further species expanding from the Western Mediterranean, the amphipod *Echinogammarus berilloni* (Catta, 1878) and the isopod *Proasellus meridianus* (Racovitza, 1919) encountered Ponto-Caspian species while still being restricted to the Rhine (Tittizer et al. 2000), so their appearance in the Danube basin is even less likely.

The presence of *N. hrabei* in the German section of the river was first mentioned by Nesemann et al. (1995), but no exact occurrence data have been published so far. Since *N. hrabei* is primarily characteristic of smaller stagnant or slow-flowing waters with decaying plant material, our sporadic record in the main arm of the river can be considered as a result of drift. The location suggests that the wetlands around the Isar estuary might host self-sustaining populations. Previously, the distribution of the species was associated with the extent of the former Paratethys (Nesemann 1993), so the occurrence far beyond the Carpathian basin – parallel with records of *Synurella ambulans* (F. Müller, 1846) (Heckes et al. 1996) – poses an intriguing biogeographical question.

Our records of *P. intermedia* at rkm 686 and *P. bakuensis* at rkm 232 represent their most upstream occurrences in the river, indicating a slight headway (Table 2). Contrarily, most other species restricted to the lower parts of the river have previously been reported.
considerably farther upstream (Table 2; the only exception being *E. warpachowskyi* with all known occurrences restricted to the Delta). What is more, several Ponto-Caspian peracarids previously recorded in the Danube were not found during the survey at all. Most of these are restricted to the Delta, where obviously much more sampling effort would be needed to provide a realistic fauna list. However, there are 10 species which penetrated farther upstream in the Danube according to literature data (Table 2).

Range expansion of Ponto-Caspian peracarids

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

The second group of species has been able to penetrate several hundred kilometers into the river, but still remained restricted to the lower reaches (Table 2). A priori, the natural obstacles of the Iron Gates section could be assumed to determine their distribution; before its impoundment, the extreme currents (reaching ~ 5 m/s in the 150 m wide Kazan pass) must have represented an insurmountable barrier for all peracarids. However, if we take a look at the most upstream occurrences of the species belonging to his group (Table 2) it becomes evident, that surprisingly the narrows does not have a decisive role; several species never reached this section, while some others were present upstream of the Iron Gates even before the dams were built. The final limit to this type of distribution can be found somewhat more upstream in the Serbian section, as shown by historical records of *C. chelicorne*, *C. maeoticum*, *O. crassus*, *O. obesus*, *P. robustoides*, and *E. sarsi*, and also reflected in the
present distribution of *C. robustum*, *C. sowinskyi*, *E. trichiatus*, and *P. lacustris*. The explanation lies most likely in the flow conditions. The section immediately upstream of the Iron Gates is characterized by a low slope comparable to the Lower Danube, and since the construction of the Iron Gate I dam, current velocity is even more reduced (Fig. 2). Upstream of the Sava estuary, however, current speed attains the values characteristic of the Middle Danube (0.8-0.9 m/s). This might present a barrier in itself, but the bed material might further aggravate the situation; until approximately Baja the dominant substrate is sand, which – owing to the relatively strong currents – is very mobile, offering unfavorable conditions for most species.

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

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

Nevertheless, there are two relatively well documented cases, that of *C. maeoticum* and *O. crassus*, where it seems certain that the species considerably retreated. The reasons are unclear, but a possible explanation for such drastic changes might be the exclusion by a more successful invader, suggested by the fact that both *C. curvispinum* and *D. villosus* appeared
later in that section (Băcescu 1948, Karaman 1953; the latter mentioning *C. curvispinum*, but the figures depict *C. sowinskyi*, regarded as a subspecies of *C. curvispinum* at that time).

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

Previous invasion success is often used in attempts for identifying potential future invaders (Ricciardi & Rasmussen 1998, Gallardo & Aldridge 2013). Accordingly, it might seem logical to assume a temporal order among the three distributional types. The connection between the estuarine and ‘lower section’ types is quite evident, but does presence in the Iron Gates section in fact portend large-scale expansion? The case of most early invaders (*D. bispinosus, D. haemobaphes, C. sowinskyi, E. ischnus*, and *J. sarsi*) is uncertain, since they were already present at the time of the first faunistic investigations both at the Iron Gates and farther upstream in the Hungarian section. Historical occurrences of *C. curvispinum, H.*
anomala, K. warpachowskyi, and L. benedeni, and present records of E. trichiatus allow the conclusion that they reached the lower Serbian section only after their establishment more upstream in the Danube (Băcescu 1948, Karaman 1953, Wittmann 2007). On the contrary, six species (C. chelicorne, C. maeoticum, O. crassus, P. lacustris, P. robustoides, and E. sarsi) having been reported in the Iron Gates section have not been able to colonize the more upstream reaches of the Danube thus far. Only in the case of three successful invaders has the appearance in this part of the river preceded the large-scale expansion, where the stepping stone role cannot be excluded. However, C. robustum and O. obesus appeared way before their respective first records upstream, so there is no indication of direct connection. In the case of D. villosus the time lag between the first records is much shorter (1968 at the Iron Gates vs. 1975 in the Hungarian section; Popescu-Marinescu 1970 cited by Petrescu 2009, Nosek & Oertel 1980) which might indicate relation, but investigations were rather rare at that time, so the colonization might have happened just as well the opposite way. Here we would like to point out that the first record of D. villosus in the Hungarian section is mistakenly dated to 1926 in some recent publications (e.g., Nesemann et al. 1995, Bij de Vaate et al. 2002, Rewicz et al. 2014). The reason for the confusion is that Dudich (1927) did not indicate the that-time subspecific rank of D. villosus bispinosus. Several independent works confirm that D. villosus was not present in the Middle Danube even in the 1950s (Dudich 1947, Karaman 1953, Ponyi 1958, Brtek & Rothschein 1964).

In conclusion, appearance upstream of the Iron Gates shows little correspondence with large-scale invasion success, establishment in this section does not appear to promote further expansion in the Danube in most of the cases. However, the species pool in the Danube reach adjacent to their estuary might be decisive for large tributaries also colonized by Ponto-Caspian peracarids. In the Drava and Sava only a subset of the third species group is present (Žganec et al. 2009, Borza 2011, Lucić et al. 2015), but the Tisza – allowing further spread of
C. maeoticum and P. lacustris – can be considered as an autonomous side-branch of the southern invasion corridor. The source region of large distance jump dispersal must have been within the Lower Danube in most of the cases at least, but further narrowing is rarely possible. The most informative in this regard is the invasion history of H. anomala, the most widespread Ponto-Caspian peracarid at present. This rheophobic species could be characterized by an estuarine distribution before its large-scale expansion began in the 1990s (Wittmann 2007), marking the Delta as the source of its invasion, and indicating at the same time that not only species occurring in the lower reaches should be considered as potential invaders, but – given the chance – estuarine species also might be able to colonize inland waters. Successful introductions or even spontaneous expansions in other rivers also prove that several species restricted to the Delta in the Danube would be able to persist at least in lakes, reservoirs, and other lentic habitats in rivers (Grigorovich et al. 2002). Nevertheless, it might not be entirely random which species are able to realize their potential; there might be traits promoting large-scale invasion success associated with the access to vectors, survival of transport, or the chance of establishment and spread.

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Authors’ contributions: BC, WG, TH, PL, MP, and JS elaborated the study design; BC, TH, PL, MP, and JS participated in the field work; PB, NR, and JS were involved in the identification and data processing; PB wrote the manuscript.

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Captions

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

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

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

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

Annex 1. Records of peracarids during JDS3 (2013). A: species with occurrences at more than 2 sites. CC – *Chelicorophium curvispinum* (G. O. Sars, 1895); CR – *Chelicorophium robustum* (G. O. Sars, 1895); CS – *Chelicorophium sowinskyi* (Martynov, 1924); DB – *Dikerogammarus bispinosus* Martynov, 1925; DH – *Dikerogammarus haemobaphes* (Eichwald, 1841); DV – *Dikerogammarus villosus* (Sowinsky, 1894); EI – *Echinogammarus*
ischnus (Stebbing, 1899); ET – Echinogammarus trichiatus (Martynov, 1932); ES – Euxinia sarsi (Sowinsky, 1898); JS – Jaera sarsi Valkanov, 1936; KW – Katamysis warpachowskyi G. O. Sars, 1893; LB – Limnomysis benedeni Czerniavsky, 1882; OO – Obesogammarus obesus (G. O. Sars, 1894); PB – Paramysis bakuensis G. O. Sars, 1895; PI – Paramysis intermedia (Czerniavsky, 1882); PL – Paramysis lacustris (Czerniavsky, 1882); PR – Pontogammarus robustoides (G. O. Sars, 1894); SS – Schizorhamphus scabriusculus (G. O. Sars, 1894), B: species with occurrences at 1 or 2 sites. Coordinates are indicative of the sites (i.e., cross-sections of the river); individual samples were collected at slightly different localities. ¹: Kiliya arm, ²: Sulina arm, ³: Sf. Gheorghe arm.
Fig. 2

Grain size (84% percentile, mm)

Mean current velocity (m/s)

River km

Baja Sava estuary

Bed material grain size

Mean current velocity
Table 1

**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* (Cărăuşu, 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

*Limnomyis benedeni* Czerniavsky, 1882

*Paramysis bakuensis* G. O. Sars, 1895

*Paramysis intermedia* (Czerniavsky, 1882)

*Paramysis lacustris* (Czerniavsky, 1882)

*Paramysis ullskyi* (Czerniavsky, 1882)
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<thead>
<tr>
<th>Species</th>
<th>Most upstream occurrence (rkm)</th>
<th>Reference</th>
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</thead>
<tbody>
<tr>
<td><em>Paramysa lacustris</em> (Czerniavsky, 1882)</td>
<td>1199</td>
<td>Present survey</td>
</tr>
<tr>
<td><em>Obesogammarus crassus</em> (G. O. Sars, 1894)</td>
<td>18 (Kiliya arm)</td>
<td>Previously</td>
</tr>
<tr>
<td><em>Chelicorophium maeoticum</em> (Sowinsky, 1898)</td>
<td>not found ~1116/ ~178 (Tisza)</td>
<td>Karaman (1953)/ Borza (2011)</td>
</tr>
<tr>
<td><em>Euxitia sarsi</em> (Sowinsky, 1898)</td>
<td>686</td>
<td>Present survey</td>
</tr>
<tr>
<td><em>Pontogammarus robustoides</em> (G. O. Sars, 1894)</td>
<td>686</td>
<td>Present survey</td>
</tr>
<tr>
<td><em>Echinogammarus placidus</em> (G. O. Sars, 1896)</td>
<td>not found 834</td>
<td>Russev (1966)</td>
</tr>
<tr>
<td><em>Stenogammarus carausi</em> (Derzhavin &amp; Pjatakova, 1962)</td>
<td>not found 834</td>
<td>Russev (1966)</td>
</tr>
<tr>
<td><em>Paramysa ullskyi</em> (Czerniavsky, 1882)</td>
<td>104 (Sf. Gheorghe arm)</td>
<td>Present survey</td>
</tr>
<tr>
<td><em>Paramysa intermedia</em> (Czerniavsky, 1882)</td>
<td>686</td>
<td>Present survey</td>
</tr>
<tr>
<td><em>Pontogammarus maeoticus</em> (Sowinsky, 1894)</td>
<td>not found 552</td>
<td>Russev (1966)</td>
</tr>
<tr>
<td><em>Paraniphargoides motasi</em> (Cărăuşu, 1943)</td>
<td>not found 552</td>
<td>Russev (1966)</td>
</tr>
<tr>
<td><em>Niphargogammarus intermedius</em> (Cărăuşu, 1943)</td>
<td>not found 495</td>
<td>Russev (1966)</td>
</tr>
<tr>
<td><em>Schizorhamphus scabriusculus</em> (G. O. Sars, 1894)</td>
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<td>Present survey</td>
</tr>
<tr>
<td><em>Pontogammarus borceae</em> Cărăuşu, 1943</td>
<td>not found 375</td>
<td>Russev (1966)</td>
</tr>
<tr>
<td><em>Pontogammarus aestuarius</em> (Derzhavin, 1924)</td>
<td>not found ~375</td>
<td>Prunescu-Arion &amp; Elian (1965)</td>
</tr>
<tr>
<td><em>Uroniphargoides spinicaudatus</em> (Cărăuşu, 1943)</td>
<td>104 (Sf. Gheorghe arm)</td>
<td>Prunescu-Arion &amp; Elian (1965)</td>
</tr>
<tr>
<td><em>Paramysa bakuensis</em> G. O. Sars, 1895</td>
<td>232</td>
<td>Present survey</td>
</tr>
<tr>
<td><em>Paramysa kessleri sarsi</em> (Derzhavin, 1925)</td>
<td>not found 150</td>
<td>Present survey</td>
</tr>
</tbody>
</table>
## Annex 1A

<p>| Site ID | Date     | Lat (N) | Lon (E) | Rkm  | CC | CR | CS | DB | DH | DV | El | 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| 19.56178| 1300 | *  | *  | *  | *  | *  | *  | *  | *  | *  |    |    |    |    |    |    |    |    |    |
| Site ID | Date     | Lat (N)     | Lon (E)    | Rkm | CC | CR | CS | DB | DV | El | 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$^1$ | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  |
| 67      | 25-Sep   | 45.19450    | 28.95933   | 31$^2$ | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  |
| 68      | 25-Sep   | 45.15953    | 28.90893   | 104$^2$ | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  | *  |</p>
<table>
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<tr>
<th>Species</th>
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<th>Lon (E)</th>
<th>Rkm</th>
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<tr>
<td><em>Asellus aquaticus</em> (Linnaeus, 1758)</td>
<td>5</td>
<td>16-Aug</td>
<td>48.68595</td>
<td>13.10883</td>
<td>2258</td>
</tr>
<tr>
<td></td>
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<td>44.72470</td>
<td>21.00068</td>
<td>1107</td>
</tr>
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<td><em>Echinogammarus warpachowskyi</em> (G. O. Sars, 1894)</td>
<td>66</td>
<td>24-Sep</td>
<td>45.39553</td>
<td>29.58547</td>
<td>18</td>
</tr>
<tr>
<td><em>Gammarus fossarum</em> Koch, 1836</td>
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<td>10.02761</td>
<td>2581</td>
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<td><em>Gammarus roeseli</em> Gervais, 1835</td>
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<td>48.42419</td>
<td>10.02761</td>
<td>2581</td>
</tr>
<tr>
<td></td>
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<td>16-Aug</td>
<td>48.68595</td>
<td>13.10883</td>
<td>2258</td>
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<td>24-Sep</td>
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<td>29.58547</td>
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<tr>
<td><em>Paramysis ullskyi</em> (Czerniavsky, 1882)</td>
<td>68</td>
<td>25-Sep</td>
<td>45.15953</td>
<td>28.90893</td>
<td>104</td>
</tr>
<tr>
<td><em>Proasellus coxalis</em> (Dollfus, 1892)</td>
<td>1</td>
<td>13-Aug</td>
<td>48.42419</td>
<td>10.02761</td>
<td>2581</td>
</tr>
<tr>
<td><em>Uroniphargoides spinicaudatus</em> (Cărăuşu, 1943)</td>
<td>68</td>
<td>25-Sep</td>
<td>45.15953</td>
<td>28.90893</td>
<td>104</td>
</tr>
</tbody>
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