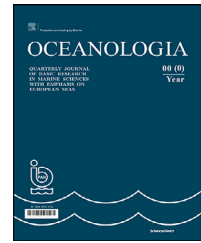


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SHORT COMMUNICATION

A substantial range expansion of alien Ponto-Caspian amphipods along the eastern Baltic Sea coast

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Abstract We report a considerable range expansion of four Ponto-Caspian amphipod species in transitional waters along the southeastern Baltic Sea coast. *Chaetogammarus warpachowskyi* and *Dikerogammarus haemobaphes* were found for the first time in Latvia, the former being common along the coast, while the latter was encountered only in the port of Riga. This indicates a 400 to 600 km expansion along the coast, assuming an origin from the Curonian or Vistula lagoons. We also officially document an expansion for *Chelicorophium curvispinum* in Latvia of ca. 300 km until Riga, confirming recent unpublished records. Moreover, we document a second invasion route of *Pontogammarus robustoides* into Estonia from nearby Latvian waters by uncovering a population at the port of Pärnu. This species was previously known in Estonia only from the Gulf of Finland (>500 km from Pärnu). With the exception of *D. haemobaphes*, all newly recorded species were represented by various life-stages and ovigerous females, indicating viable populations. Overall, our findings reveal that Ponto-Caspian amphipods are much more widespread in the Baltic area than previously known and highlight the need for more stringent monitoring.

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Alien Ponto-Caspian species are spreading at an increasing rate in European and North American fresh- and brackish water habitats, sometimes with significant ecological and economic effects (Bij de Vaate et al., 2002; Vanderploeg et al., 2002). Amphipod crustaceans are perhaps the most diverse group of Ponto-Caspian organisms (Copilaş-Ciocianu and Sidorov, 2021), and among the most common and successful aliens of Ponto-Caspian origin (Bij de Vaate et al., 2002; Cuthbert et al., 2020). It is thought that their ecological plasticity, aggressiveness and high fecundity makes them superior competitors, often driving populations of

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native species to extinction (Arbačiauskas et al., 2013; Dick and Platvoet, 2000; Grabowski et al., 2007a; Šidagytė and Arbačiauskas, 2016).

The southeastern Baltic Sea region harbors eight alien Ponto-Caspian amphipod species originating from the river mouths and lagoons draining to the northwestern Black Sea. Most have spread naturally and/or by shipping after construction of artificial canals: some since or even before the early 20th century (*Chelicorophium curvispinum* (Sars, 1895) and *Chaetogammarus ischnus* (Stebbing, 1899)), while others during the last decades (*Dikerogammarus haemobaphes* (Eichwald, 1841), *Dikerogammarus villosus* (Sowinsky, 1894) and *Trichogammarus trichiatus* (Martynov, 1932)) (Arbačiauskas et al., 2011; Bij de Vaate et al., 2002; Grabowski et al., 2007b; Rachalewski et al., 2013). In the 1960s, however, three species, namely *Chaetogammarus warpachowskyi* (Sars, 1894), *Obesogammarus crassus* (Sars, 1894), and *Pontogammarus robustoides* (Sars, 1894), were deliberately introduced and successfully acclimatized in the Lithuanian Kaunas water reservoir, and then translocated into numerous Lithuanian water bodies as well as in the nearby countries such as Latvia, Estonia and Russia (Arbačiauskas et al., 2017; Jażdżewski, 1980). From the Curonian Lagoon, the Ponto-Caspian amphipods have also dispersed along the sea coast naturally or via shipping. Namely *O. crassus* and *P. robustoides* have dispersed westward, reaching Germany (Bij de Vaate et al., 2002), the latter also making its way into the Netherlands (Moedt and Van Haaren, 2018), while *C. curvispinum*, *C. warpachowskyi*, and *P. robustoides* have spread as far north as the Gulf of Finland (Berezina, 2007; Malyavin et al., 2008).

Although Lithuania and Latvia are neighboring countries with a somewhat similar history of Ponto-Caspian amphipod introductions, the latter harbors less species. Two of them, namely *D. villosus* and *P. robustoides*, are well-documented in both countries (Arbačiauskas, 2008; Arbačiauskas et al., 2011; Grudule et al., 2007; Minchin et al., 2019; Paidere et al., 2016, 2019a; Šidagytė et al., 2017). The distribution of *C. curvispinum* is well known in Lithuania (Arbačiauskas, 2008; Arbačiauskas et al., 2011), whereas in Latvia it was only reported from the Pāvilosta port half a century ago (Nikolaev, 1963), and subsequent grey literature records were reported only after 2014 (Harju et al., 2018). The remaining species, *C. warpachowskyi* and *O. crassus*, are also relatively common in Lithuania, including transitional waters (Arbačiauskas, 2008; Arbačiauskas et al., 2011), yet in Latvian inland waters they have never been officially documented (at least convincingly, see Discussion on *O. crassus* in Latvia). In Estonia the only known Ponto-Caspian amphipods are *C. curvispinum* and *P. robustoides*, occurring in a restricted area in the Gulf of Finland close to Russia (Herkül et al., 2009). Both of these species are very common in the Russian part of this gulf (Berezina, 2007; Malyavin et al., 2008).

Considering the above, a noteworthy pattern emerges. Although *C. curvispinum*, *C. warpachowskyi*, and *P. robustoides* are present in the Curonian Lagoon and the Gulf of Finland, the first two were seldom, if at all, reported in between the two regions. Such a wide distribution gap, equivalent to almost the entire Estonian and Latvian coastline, is remarkable. This pattern could be either the result of long-distance dispersal (common in invasive species) or

an artifact related to insufficient distributional knowledge. Our study agrees with the latter possibility by revealing that these amphipods are actually much more widespread than currently officially recognized, having expanded their ranges hundreds of kilometers along the eastern Baltic Sea coastline.

For this study, we collected material from 10 localities (mostly transitional waters) along the Baltic Sea coast in Latvia (8) and Estonia (2) on 11–14 August 2020 (Table 1). Samples were collected using kick-sampling with a standard benthic hand net (1 mm mesh size). All available substrates and habitats were investigated up to a depth of 1.5 m. Amphipods were fixed in 96% ethanol in the field. Specimens were dissected under a Nikon SMZ1000 stereomicroscope and identified using the keys in Bellan-Santini et al. (1982) and Copilaș-Ciocianu and Sidorov (2021). Appendages were mounted on microscope slides in glycerol and photographed using a Nikon DS-Fi2 camera attached to a Nikon SMZ1000 stereomicroscope. Previously known distribution data for the focal species was obtained from the relevant literature as well as the GBIF database (<https://doi.org/10.15468/dl.iddp60>; <https://doi.org/10.15468/dl.xmntxw>, accessed 22–23 March 2020).

Altogether we collected and identified 771 specimens belonging to seven amphipod species, five of which were aliens of Ponto-Caspian origin (*C. curvispinum*, *C. warpachowskyi*, *D. haemobaphes*, *D. villosus*, and *P. robustoides*), one of North American origin (*Gammarus tigrinus* Sexton, 1939), and one was native (*Corophium volutator* (Pallas, 1776)) (Table 1). We found that four Ponto-Caspian species (Figure 1) have expanded their previously published distribution ranges along the eastern Baltic Sea coast (Figure 2). The new findings include the first records of *C. warpachowskyi* and *D. haemobaphes* in Latvia, a new invasion route of *P. robustoides* into Estonia, and an official documentation of *C. curvispinum* expansion along the Latvian coast. Below we expand on our findings.

Our most unexpected discovery is that *C. warpachowskyi* (Figure 1A) is rather common along the Latvian coast, despite that it was never reported from this country. The previously known closest locality was in Lithuania, at the mouth of the Šventoji River (5 km from the Latvian border) (Arbačiauskas et al., 2011). We encountered this species until the port of Riga, which reveals a substantial coastal range expansion of ca. 400 km (Figure 2A). These populations were clearly established since we found male and female adults at all four localities, including ovigerous females at three of them (Table 1). Most likely *C. warpachowskyi* spread from the Šventoji river mouth or the Curonian Lagoon naturally and/or via shipping. However, it could have also spread downstream from the reservoirs on the Daugava River where it was possibly introduced during the intentional stocking campaigns in the 1960s (Arbačiauskas et al., 2017; Paidere et al., 2016). Nevertheless, despite recent sampling it has not been reported from the Daugava reservoirs (Paidere et al., 2016, 2019a, current study). Generally, *C. warpachowskyi* is among the least widespread alien Ponto-Caspian amphipods, mainly occurring in water bodies where it was deliberately introduced during the second half of the 20th century (Arbačiauskas et al., 2017, 2011; Jażdżewski, 1980).



Figure 1 Identification characteristics of the Ponto-Caspian amphipods that expanded their ranges in the Baltics. Scale bar = 1 mm. A) *Chaetogammarus warpachowskyi*, B) *Dikerogammarus haemobaphes*, C) *Pontogammarus robustoides*, and D) *Chelicorophium curvispinum*. Abbreviations: a1 – antenna 1, a2 – antenna 2, g2 – gnathopod 2, p3 – pereiopod 3, p7 – pereiopod 7, u3 – uropod 3.

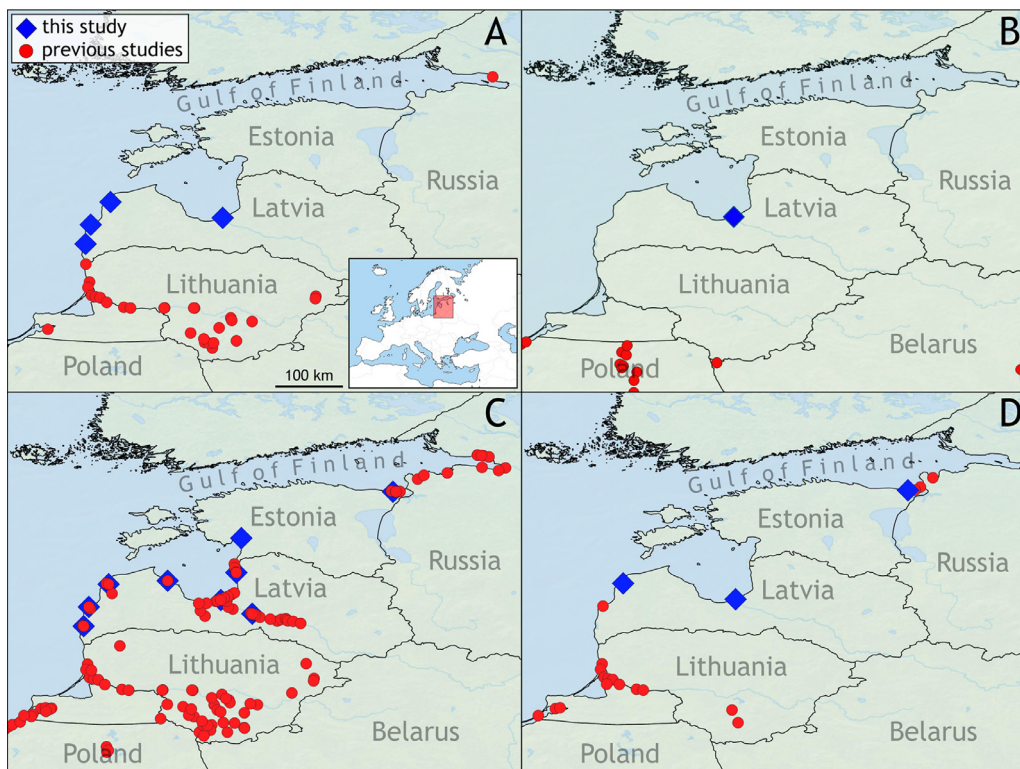


Figure 2 Baltic distributions of A) *Chaetogammarus warpachowskyi*, B) *Dikerogammarus haemobaphes*, C) *Pontogammarus robustoides*, and D) *Chelicorophium curvispinum*. Red dots and blue diamonds indicate records from the peer-reviewed literature and current study, respectively.

Table 1 Information about sampling localities, habitat and amphipod species collected. Country codes: EE – Estonia, LV – Latvia. Species abbreviations: CC – *Chelicorophium curvispinum*, CV – *Corophium volutator*, CW – *Chaetogammarus warpachowskyi*, DH – *Dikerogammarus haemobaphes*, DV – *D. villosus*, GT – *Gammarus tigrinus*, PR – *Pontogammarus robustoides* (Ponto-Caspian species are shown in boldface). Specimen stages: ovig. – a subset of ovigerous females, juv. – juveniles.

No.	Locality	Coordinates	Date	Habitat	Species	Number of specimens
EE 1	Sillamäe, Sõtke stream mouth	59°23'56"N, 27°46'12"E	11 August 2020	Depth: 0.1–1.5 m Substrate: stones, sand, detritus	CC GT PR	3♀, 1♂ 4 (2 ovig.)♀, 6♂ 28 (12 ovig.)♀, 29♂, 3 juv.
EE 2	Pärnu, Pärnu river mouth	58°23'17"N, 24°29'00"E	11 August 2020	Depth: 0.1–0.4 m Substrate: stones, sand	CV GT PR	2♀ 13 (8 ovig.)♀, 11♂ 32 (17 ovig.)♀, 18♂, 49 juv.
LV 1	Vitrupe, Vitrupe river mouth	57°38'13"N, 24°22'31"E	11 August 2020	Depth: 0.1–0.5 m Substrate: sand, plants	PR	8 (5 ovig.)♀, 8♂, 4 juv.
LV 2	Kegums Reservoir	56°44'21"N, 24°43'14"E	12 August 2020	Depth: 0.1–1.5 m Substrate: stones	PR	5 (2 ovig.)♀, 2♂, 6 juv.
LV 3	Riga, Daugava river mouth	57°02'18"N, 24°02'22"E	12 August 2020	Depth: 0.1–1.5 m Substrate: boulders, stones, sand, plants	CC CV CW DH DV GT PR	18 (6 ovig.)♀, 2♂ 3♀, 3♂ 2♀, 1♂ 1♀, 2♂ 4 (2 ovig.)♀, 6♂, 1 juv. 3♀, 1♂ 30 (8 ovig.)♀, 15♂, 32 juv.
LV 4	Kaltene, sea shore	57°27'34"N, 22°53'09"E	12 August 2020	Depth: 0.1–0.5 m Substrate: stones, pebbles	GT PR	47 (26 ovig.)♀, 45♂, 5 juv. 6 (1 ovig.)♀, 8♂, 5 juv.
LV 5	Ventspils, Venta river	57°22'58"N, 21°36'23"E	13 August 2020	Depth: 0.1–1 m Substrate: sand, plants, detritus	CC CV CW GT PR	8 (2 ovig.)♀, 2♂ 2♀ 35 (27 ovig.)♀, 32♂ 3♀, 3♂ 7♀, 4♂, 12 juv.
LV 6	Pāvilosta, Saka river mouth	56°53'17"N, 21°10'40"E	13 August 2020	Depth: 0.1–1 m Substrate: stones, sand, plants, detritus	CV CW DV GT PR	5 (3 ovig.)♀, 3♂, 1 juv. 11 (9 ovig.)♀, 6♂ 27 (15 ovig.)♀, 16♂, 6 juv. 1♀, 3♂
LV 7A	Liepāja, Lake Liepāja	56°30'30"N, 21°02'18"E	14 August 2020	Depth: 0.1–1 m Substrate: stones, mud	GT	9 (2 ovig.)♀, 8♂, 2 juv. 22 (9 ovig.)♀, 16♂
LV 7B	Baidzele, Lake Liepāja	56°28'08"N, 21°03'57"E	14 August 2020	Depth: 0.1–1 m Substrate: sand, plants	CW PR	15 (11 ovig.)♀, 6♂ 6 (3 ovig.)♀, 4♂, 24 juv.

The appearance of *D. haemobaphes* in the port of Riga (Figure 1B) is enigmatic since this species does not seem to occur anywhere along the Baltic coast eastwards from Poland (Figure 2B). Few individuals have been recently recorded in Belarus, close to the Lithuanian border (Lipinskaya et al., 2021), and since 2019 viable populations have been observed in the upper Lithuanian part of the Nemunas River, but never below the Kaunas Reservoir (Šidagytė-Copilas and Copilaş-Ciocianu, in preparation). Therefore, the most likely origin of the Latvian specimens remains the Vistula Lagoon, located ca. 600 km away.

However, given that we have found only three individuals (Table 1), it is unclear whether this is an established population or not. Future sampling in the area is therefore necessary. At a broad scale, *D. haemobaphes* is among the most successful and widespread Ponto-Caspian amphipods (Bacela-Spychalska and Van der Velde, 2013; Bij de Vaate et al., 2002; Jażdżewska et al., 2020). As such, its further northward dispersal is to be expected.

Within this paper, we provide the first report of *P. robustoides* from the Estonian port of Pärnu (Figure 1C). It was the most abundant amphipod at this locality and

all life stages were observed, including ovigerous females (Table 1). Almost certainly *P. robustoides* reached this area from Latvia, as it was reported a few kilometers from the Estonian border in 2011, but not from Pärnu Bay (Strode et al., 2013). This established population clearly demonstrates that the species expanded northwards by up to 70 km and exposes a second invasion route of *P. robustoides* into Estonia (Figure 2C). The previously known route was a westward dispersal from Russia along the shore of the Gulf of Finland, the invader being discovered for the first time close to the border in 2006 (Herkül et al., 2009). Herein, we further confirm its presence in this area, and also in various places throughout Latvia (Table 1, Figure 2C). At a broader geographic scale, *P. robustoides* is relatively widespread in Europe, although not nearly as much as some other Ponto-Caspian species. Its current range is a result of both natural dispersal and deliberate introductions (Arbačiauskas et al., 2011; Bij de Vaate et al., 2002; Moedt and Van Haaren, 2018).

Our study also clarifies the expansion of *C. curvispinum* in the eastern Baltic Sea (Figure 1D). In Latvia, it was first reported from the port of Pāvilosta in the 1960s (Nikolaev, 1963). Since 2014 it was reported from the ports of Liepāja, Ventspils, and Riga, however, only in the grey literature (Grudcina, 2018; Harju et al., 2018). We confirm this spread of ca. 300 km northwards along the Latvian coast, as we also observed *C. curvispinum* in Ventspils and Riga (Figure 2D). Specimens of both sexes as well as ovigerous females were collected, thus confirming its establishment (Table 1). We also confirm its presence on the Estonian shore of the Gulf of Finland (Sõtke stream mouth) where it was hitherto reported (Herkül and Kotta, 2007). Being encountered in almost all major European watersheds (Figure 2F) (Bij de Vaate et al., 2002), *C. curvispinum* is one of the most widely distributed Ponto-Caspian amphipods. Most likely its dispersal began in the early 20th century, or even earlier, and was facilitated by artificial canals that connected previously isolated watersheds (Arbačiauskas et al., 2011; Jażdżewski, 1980).

We sampled *D. villosus* only within its previously reported range (Minchin et al., 2019; Šidagytė et al., 2017), confirming its establishment with records of adult specimens, ovigerous females, and juveniles (Table 1). This dispersal stagnation is only apparent given that just a couple of years passed between our current sampling and that of the most recent study (Minchin et al., 2019). It is therefore still highly likely that *D. villosus* will spread further north, and its presence in Estonia (especially Pärnu Bay) should soon be expected.

Recently, *O. crassus* has been reported (mainly in the grey literature) from the Latvian ports of Liepāja, Ventspils, and Riga (Grudcina, 2018; Harju et al., 2018; Paidere et al., 2019b). Nevertheless, we could not confirm these reports. Firstly, we did not manage to collect this species in our current study although the sampling localities roughly coincided. Secondly, the only accessible evidence for the identification of the Latvian *O. crassus* provided by the authors is a habitus photograph of a highly damaged specimen (Harju et al., 2018), making a full validation impossible. Our doubts, of course, do not exclude the species' occurrence in Latvian waters.

Overall, our findings indicate that several Ponto-Caspian alien amphipods are substantially more widespread than previously known, inevitably dispersing northwards along the eastern Baltic Sea coast. The expanding distribution is most likely a result of natural spread combined with shipping activity. It remains to be seen whether the southern (from Latvia) and northeastern (from Russia) invasion fronts will ever meet in Estonia. We recommend more stringent monitoring activities, especially in the transitional waters, to better understand the dispersal of these species and their impact on the local biota.

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