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The conquest (and avoidance?) of the brackish environment by Ponto-Caspian amphipods: A case study of the German Baltic Sea

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Abstract

Although an invasion of the brackish water biotopes was to be expected with the appearance of several Ponto-Caspian amphipods in German freshwaters two decades ago (and earlier), only recently (two years ago) the conquest of the mesohaline Baltic Sea could be observed. This discrepancy is *a fortiori* of interest as previous experimental studies showed that species like *Dikerogammarus villosus* and *Obesogammarus crassus* were able to tolerate both mesohaline and also polyhaline conditions. Two decades of invasion history in rivers and lakes have led to drastic faunal changes. If similar or analogue shifts will happen in brackish environments and if estuaries like the Stettin lagoon function not only as "a gate to the Baltic Sea" but also as a "catalyser" or acclimatisation area for invasive species remains to be seen. Simultaneously the question came up, why other also potentially brackish water species failed to colonise mesohaline waters although they partially arrived in the investigation area several decades ago (e.g. *Chelicorophium curvispinum* and *Echinogammarus ischnus*).

Key words: Baltic Sea, salinity, non-indigenous species (NIS), *Dikerogammarus*, *Obesogammarus*, *Echinogammarus*, *Chelicorophium*

Introduction

The invasion of Ponto-Caspian species into the inland waters of Central Europe since the mid of the 19th century involved a dramatic faunal change. Due to the construction of artificial waterways (and their function as corridors between river drainage areas formerly disconnected) and the increasing ship traffic as vector for non-indigenous species natural biogeographic borders (e.g. watersheds, mountains, and continents) were negotiated. A prominent "pioneer" was the zebra mussel (*Dreissena polymorpha* (Pallas, 1771)) arriving in Central Europe around 200 years ago (Minchin et al. 2002). At the beginning of the 20th century the amphipod *Chelicorophium curvispinum* (Sars, 1895) was the second successful invader from the same origin (Grabowski et al. 2007b). Several other species of different taxonomical orders (six amphipods among them) have followed in the last decades. Bij de Vaate et al. (2002) describe three different introduction routes for aquatic invertebrates of Ponto-Caspian origin: the northern corridor (from the River Volga via River Neva to the Baltic Sea), the central corridor (from the River Dnieper via River Weichsel and Oder to the Baltic Sea and further via the rivers Elbe and Rhine to the North Sea) and the southern corridor as youngest connection (Main-Danube channel since 1992) from the River Danube into the tributaries of the North and Baltic Seas. Additionally, the active transport of species into lakes and rivers by human activities, e.g. tourism or fishery aspects is of importance (Gasiūnas 1963; Rewicz et al. 2014). The opening of the Main-Danube-channel in 1992 has accelerated the introduction and dispersal of allochthonous species significantly. The most prominent and successful species using this way is the amphipod *Dikerogammarus villosus* (Sowinsky, 1894) (see Rewicz et al. 2014). This euryoecious species
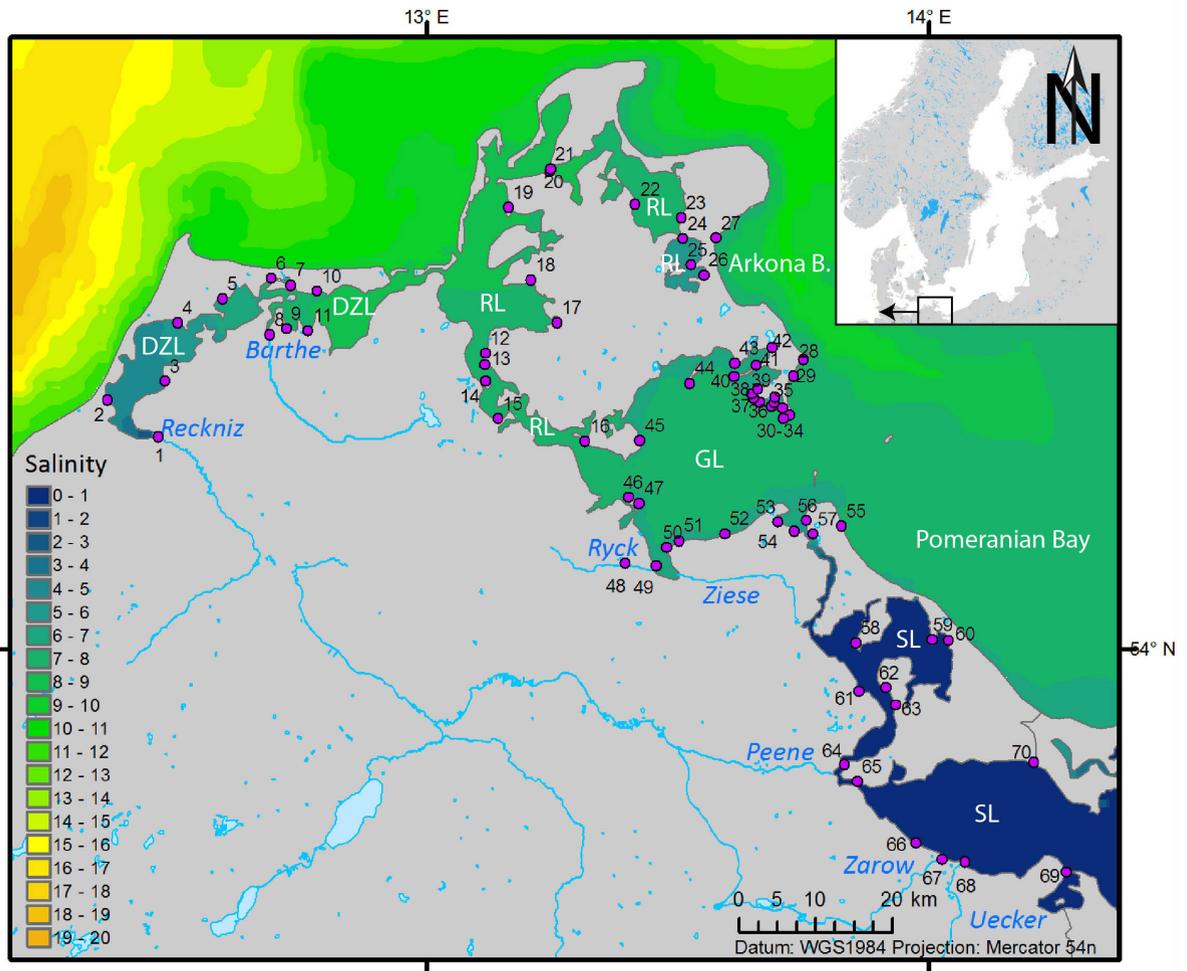
Figure 1. Investigation area of Western Pomerania with all sampling stations of the years 2016 and 2017. Several stations were sampled repeatedly. The mean salinity is indicated. [DZL = Darß-Zingst-Lagoon; RL = Rugia Lagoons; GL = Greifswald Lagoon; SL = Stettin Lagoon].

(Grabowski et al. 2007a; Rewicz et al. 2014), often occurring in very high abundances, managed to colonise the tributaries of Central and North-West Europe connected to the Main-Danube channel within one decade. Another decade later the species had already arrived in Great Britain (Rewicz et al. 2014). The dispersal processes are highly dynamic and diverse. Even isolated waters like some alpine lakes have been populated using different vectors (e.g. fishery and tourism) (Rewicz et al. 2014). The catchment area of the Baltic Sea is occupied by several Ponto-Caspian amphipods (Zettler and Zettler 2017) with different introduction histories (e.g. Jażdżewski et al. 2005). Here the salinity plays an important role as regulation factor for dispersion regarding the osmoregulatory capacities and the changing interspecific competition. Whereas the autochthonous amphipod

fauna in surface freshwaters of the catchment area of the Baltic Sea is poor in species number (approximately 5 species) the diversity in the brackish environment, e.g. between 5 and 10 psu, is quite high (approximately 40 species) (Zettler and Zettler 2017).

Independently of their arrival, the Ponto-Caspian amphipod species have first established populations in freshwaters for a long time (several decades) and behaved as genuine freshwater species. Hitherto they have not colonised areas behind the "salty curtain" and have been found only in fresh and oligohaline waters (maximum 3 psu). They have stopped their successful invasion at these borders. In our investigation area the Stettin Lagoon (Figure 1) is a "collecting basin" for all three invasion corridors or routes (see above) and was a terminal stop for further dispersal of seven Ponto-Caspian amphipod species (Zettler 2008;

Figure 2. *Dikerogammarus villosus* from the Stettin Lagoon (Stn. 70) from 2011 (scale bar = 1 mm) (Photo: IOW).
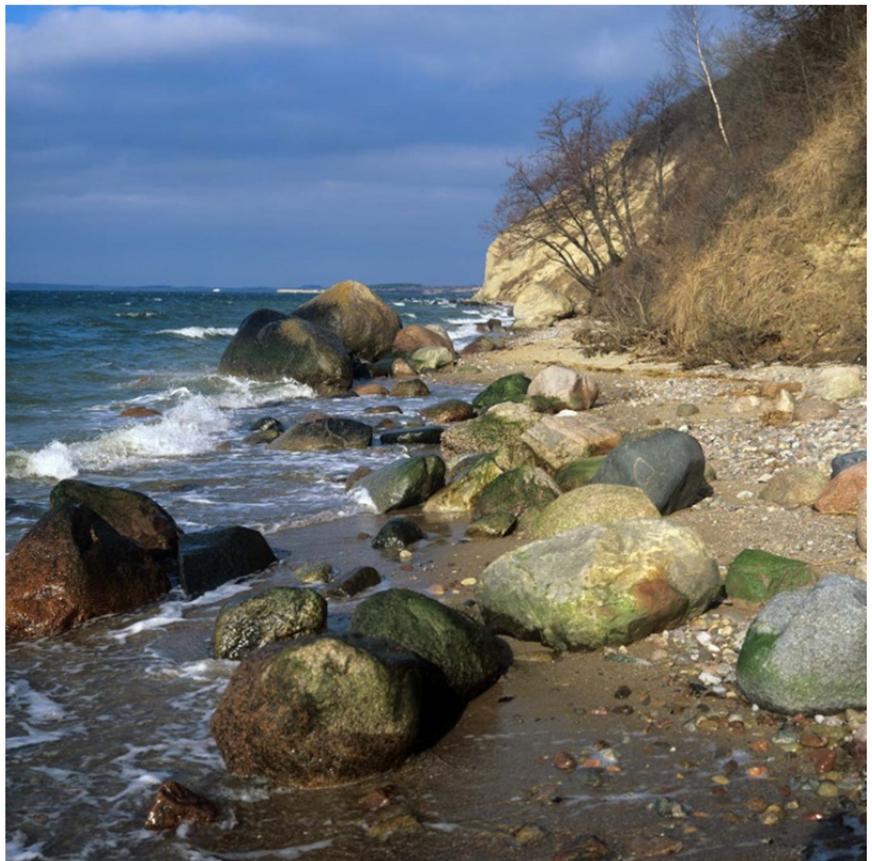
Figure 3. Typical boulder coast at the SE coast of the Island of Rugia where *D. villosus* and *O. crassus* were found in salinities around 8 psu (Photo: Rolf Reinicke).

Zettler 2015). Another donor region for non-indigenous amphipod species in our investigation area was for instance North America, where two very successful invaders came from (*Gammarus tigrinus* Sexton, 1939 and *Melita nitida* Smith, 1873) (Zettler and Zettler 2017).

The present study was motivated by a random observation of *Dikerogammarus villosus* in April 2016 in the southern Baltic Sea (Island of Rugia) (Figures 2 and 3) under mesohaline conditions (about 8 psu). Since the first occurrence of *D. villosus* in Northern Germany in 1999 (Müller et al. 2001) this species was restricted to inland waterways (freshwater) and to the oligohaline (0–3 psu) Stettin Lagoon. Additional sampling in 2016 showed an abundant population of *D. villosus* and *Obesogammarus crassus* (Sars, 1894)

in combination with several autochthonous marine species (e.g. *Gammarus salinus* Spooner, 1947; *G. zaddachi* Sexton, 1912; *Leptocheirus pilosus* Zaddach, 1844; *Microdeutopus gryllotalpa* Costa, 1853) in these mesohaline waters. It is the aim of the present study to document the current distribution of Ponto-Caspian amphipod species in the estuaries, lagoons and mesohaline waters of the Western Pomeranian area, the co-occurrence of allochthonous and autochthonous species and their salinity preference in the field (spatially and chronologically).

Material and methods

After the first record of *D. villosus* and *O. crassus* at the SE coast of Rugia (Figure 1, Stn. 36), a systematic mapping was conducted in the same area (Stns. 28–43) to localise their current distribution. In the years 2016 and 2017, we sampled at 65 complementary stations. The selection of the stations was based on habitat preferences from former studies. Due to similar salinities and habitats, we also sampled a few stations at the outer coast (Stns. 27–30, 55). Additionally, we used the data of five long-term monitoring stations within the investigation area (Stns. 2, 10, 14, 64, 70). For the chronological appearance in different salinities, we used all the data from our database comprising the investigation area (including rivers and lakes) from 1897 to 2017. The data are translated into a database given in Supplementary material Table S1 (non-native species) and Table S2 (native species). References within the database refer to the study of Zettler and Röhner (2004).

With few exceptions (e.g. diving) almost all sampling effort was focused on shallow waters (0 to 0.5 m). We used a hand net (sieve size 1 mm) for scratching hard substrates, macrophytes and soft sediments. We dived at one station (Stn. 37) to verify the depth distribution. Macrophytes were sampled in a depth range between 1 and 2.5 m with a net bag. At all stations the salinity was measured using a refractometer. The sampled animals were fixed in 70% ethanol. They were identified based on the amphipod key by Zettler and Zettler (2017).

Investigation area

The Western Pomeranian lagoons (Figure 1) have developed after the last glaciation by abrasion of island cores and subsequent sand drift. Depending on the tributary size, the freshwater input differs significantly.

The Darss-Zingst-Lagoon (DZL) is a chain of lagoons ("Bodden") with a strong salinity gradient (0–10 psu) from the mouth of the River Recknitz (freshwater) to the small connection with the entire Baltic Sea. The salinity can vary significantly depending on wind speed and direction. The mean water depth is very shallow (1 m) and only in some parts deeper than 5 m.

Rugia Lagoons (RL): The island of Rugia has several bays and lagoons with a small freshwater catchment area. The salinity ranges between 5 and 10 psu. Some of these lagoons are very sheltered and resemble lakes with expanded reeds (*Phragmites australis* (Cav.) Steud.). On average, the water is between 2 and 4 m deep (usually shallower).

Greifswald Lagoon (GL): The large water body has a wide connection with the Baltic Sea and moderate salinity range between 4 and 8 psu. The mean depth range lies between 2 and 4 m (> 10 m in maximum). Some coasts are very wind exposed and have a boulder and gravel dominated shoreline (see Figure 3).

Stettin Lagoon (SL): This estuary of the River Oder is very shallow (< 2 m) and only the water ways can be deeper. The salinity is very low (0–3 psu) and only at the entrance to the Greifswald lagoon the salinity can be a slightly higher. Large and wide reed belts and freshwater macrophyte weeds (*Potamogeton* spp.) indicate the "lake-conditions".

Results

The checklist of all observed amphipods and their frequency within the distinct waterbodies is shown in Figure 4. Twenty-five amphipod species were detected during the campaigns in 2016 and 2017 (three species were recorded during previous years additionally – see Table S1 and Table S2). Due to methodological reasons, talitrids are underrepresented but also present. The omnipotence of *G. tigrinus* in all subareas is obvious. Currently this species has the widest distribution and occurs frequently in all water bodies along the whole salinity gradient (Figure 5). From the autochthonous perspective *G. zaddachi* is still the characteristic species of the lagoons.

The Stettin Lagoon was dominated by allochthonous species (Figure 4) that arrived in this area in most cases via the river Oder. Only *G. tigrinus* probably used a different route via the lagoons and estuaries from the West. In 2016, we observed two Ponto-Caspian species (*Dikerogammarus villosus* and *Obesogammarus crassus*) under mesohaline conditions for the first time. The salinity of the newly spread habitats ranged between 7 and 8 psu. The populations were very abundant. They were established in 2017 (Figure 5). *D. villosus* occurs in high abundances at the SE end of the Island of Rugia (Stns. 36–38) in water depths between 0 and 0.5 m in a highly wind
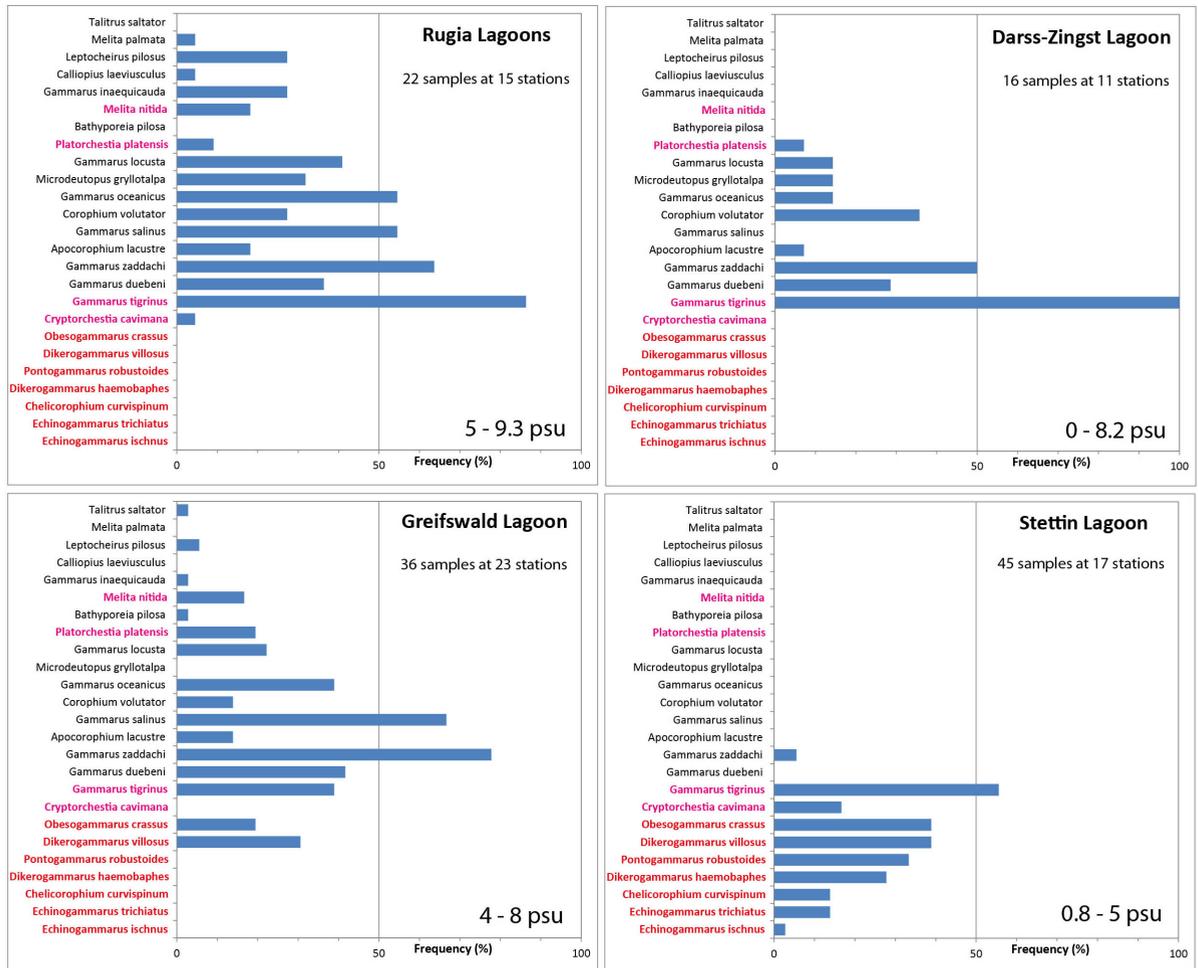
Figure 4. Frequency of amphipod species found during 119 sampling events at 66 stations between 2016 and 2017. The sampling effort, station number and the measured salinity range is given. [Red = Ponto-Caspian species; purple = non-indigenous species of other donor regions].

exposed area (see Figure 3). However, this species was also very common in the deeper vegetated zone (here *Fucus vesiculosus* L.). In the adjacent stations (e.g. 40, 43 and 44), no records were made even under very similar environmental conditions. Additionally, no Ponto-Caspian species were observed in the inner parts of the lagoon (Stns. 33–35, 39, 41–42). *Gammarus duebeni*, *G. zaddachi* and *G. oceanicus* were the dominant amphipods there. *Obesogammarus crassus* shows a very similar distributional pattern as *Dikerogammarus villosus* (Figure 6). However, it is restricted to the near shore area in water depths shallower than 20 cm.

Discussion

After first records of some Ponto-Caspian species in mesohaline conditions of Polish and Lithuanian waters of the Baltic Sea have been published recently (Santagata et al. 2008; Dobrzycka-Krahel et al. 2015; Šidagytė et al. 2017; Dobrzycka-Krahel and Graca 2018), the present study indicates a remarkable behaviour of two species (*Dikerogammarus villosus* and *Obesogammarus crassus*) as well. With about 8 psu the salinity was slightly higher than the eastern observations.

Both studies on osmoregulation (*D. villosus*: Dobrzycka-Krahel et al. 2015, *O. crassus*: Dobrzycka-Krahel and Graca 2018) and experiments on survival at different salinities (e.g. Bruijs et al. 2001; Brooks et al. 2008; Ellis and Macisaac 2009; Piscart et al. 2011) suggest the potential of several Ponto-Caspian amphipods to colonise brackish environments. The discrepancy between their potential in the laboratory and the real affinities in the field cannot be explained
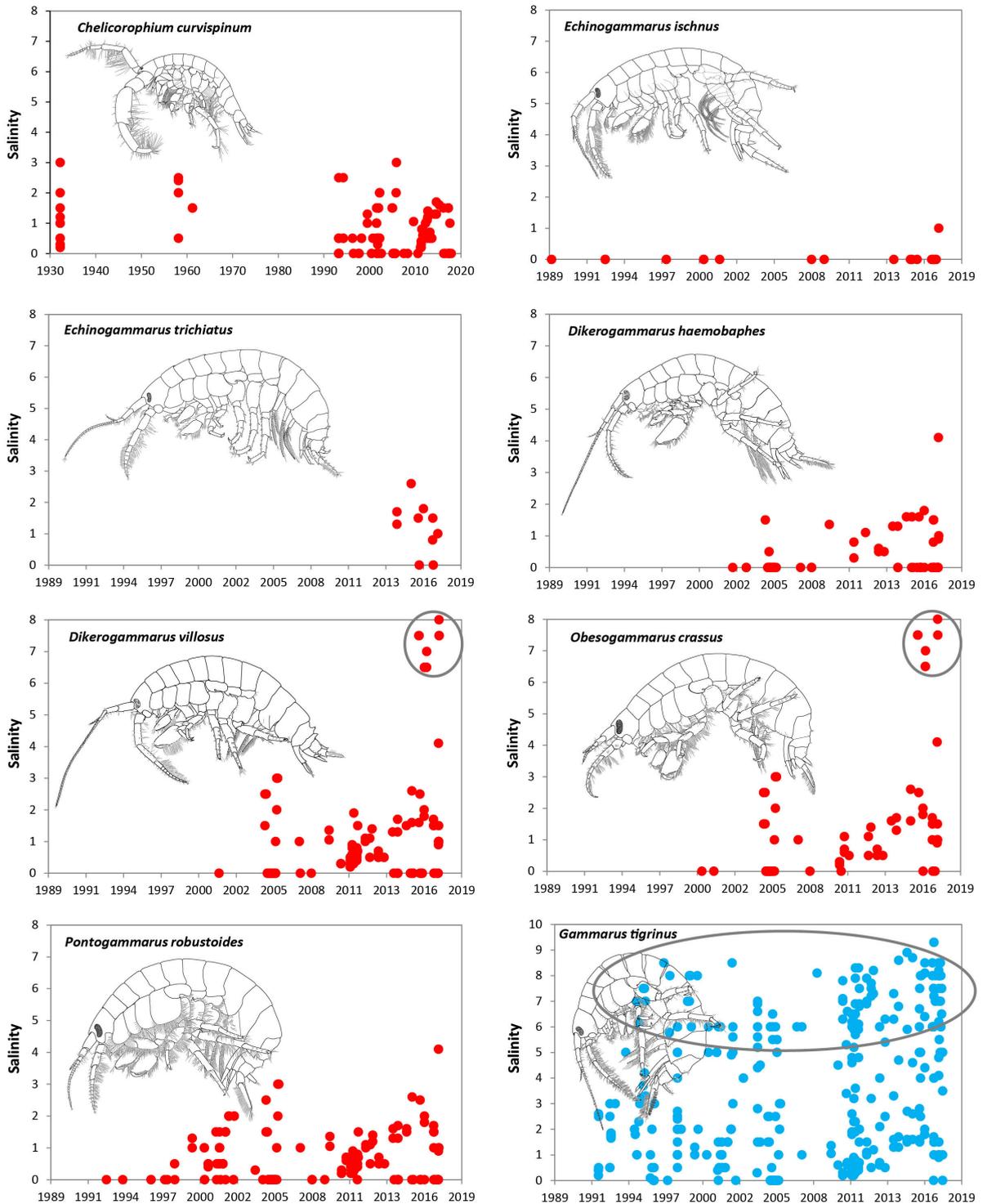
Figure 5. Invasion history of seven Ponto-Caspian (red dots) and one North-American (blue dots) amphipod species in Western Pomerania and the distribution pattern along the salinity gradient. Please note the different salinity scale between red and blue dots. [Circle = mesohaline records].
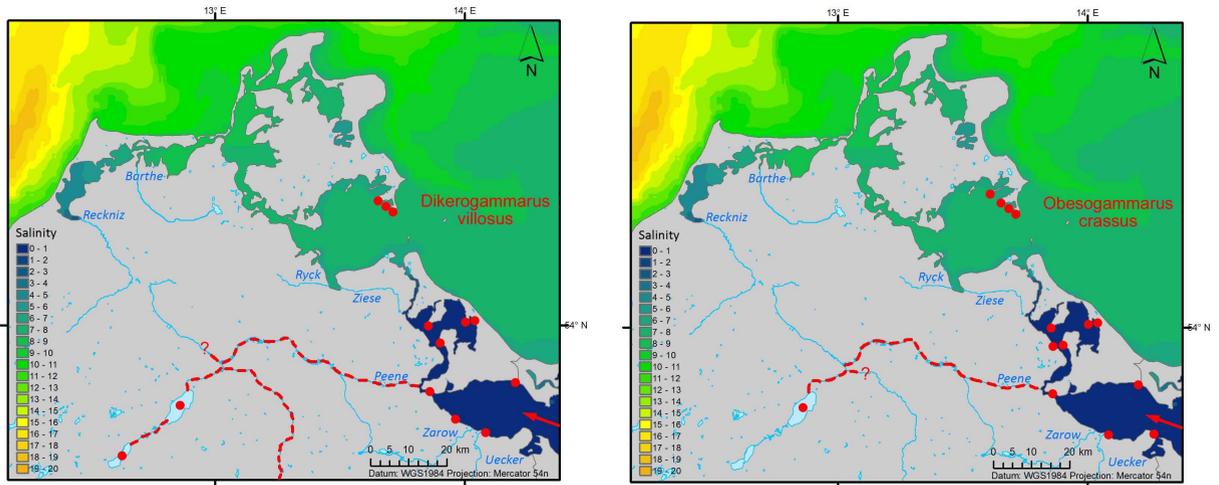
Figure 6. Distribution of *D. villosus* and *O. crassus* in Western Pomerania in 2017.

by multifactorial analysis (Devin and Beisel 2007). We are following here the definition of salinity tolerance given by Grabowski et al. (2007a): „… defined as maximum observed salinity level at which a particular species formed a self-sustaining populations in nature". The extensive research on the salinity tolerance of Ponto-Caspian amphipod species occurring in their place of origin (Black Sea, Sea of Azov, Caspian Sea) provides inconsistent and imprecise data (compare Markovski 1954; Paavola et al. 2005; Grabowski et al. 2007a; Rewicz et al. 2014). Very often we only found the salinity range of the particular sea without specific measurements from locations where the species was actually found or lived. Merely data of some species and their salinity tolerance in the estuaries of the rivers Dnieper and Bug (tributary of the Black Sea) by Markovski (1954) were more relevant. According to him, *D. villosus* and *O. crassus* live there in a salinity range between 0.5 and 5 psu, with an optimum for *D. villosus* and *O. crassus* at 0.5 psu and 1.5 to 3 psu, respectively. Paiva et al. (2018) reported observations of *O. crassus* from the southern Caspian Sea at salinities between 9 and 10.5 psu. Our own observation at the Bulgarian Black Sea coast indicate the occurrence of some Ponto-Caspian species (e.g. *Pontogammarus robustoides* (G.O. Sars, 1894) und *Echinogammarus ischnus* (Stebbing, 1899)) in the river mouths or in oligohaline coastal lakes, but not in the open mesohaline areas. Only *Pontogammarus maeoticus* (Sowinsky, 1894), not yet introduced to Central European waters, lived in the Black Sea at salinities up to 17 psu (own observations, sea also Kocataş et al. 2003 and Uzunova 1999). Very recently a study

by Paiva et al. (2018) was published, in which the salinity range of *O. crassus* in its indigenous area was given between 12 and 34 psu and of *P. maeoticus* between 0.5 and 30 psu. It is the first time that we found such a high salinity tolerance of *O. crassus* in connection with field observations. However, we entertain some doubt about the correctness of the data. We assume that for most locations, salinity was determined based on the mean annual salinity from The World Ocean Atlas database (Black Sea, Caspian Sea), which is too imprecise for coastal waters, and not on real observations of amphipods within a distinct salinity. We, at least, were not able to reproduce this large range from the given references.

In the Baltic Sea, observations of the Ponto-Caspian species in mesohaline waters with real salinity measurements are still rare. Dobrzycka-Krahel and Rzemykowska (2010) and Dobrzycka-Krahel et al. (2015) found *D. villosus* and *O. crassus* in the Bay of Danzig at salinities between 5.8 and 6.8 psu. Šidagytė et al. (2017) indicate a salinity range between 0 and 8 psu for the investigation area of the Lithuanian waters in which *D. villosus* and *O. crassus* were recorded, but not for the records in particular.

The salinity range for the Ponto-Caspian (and one North-American) species in our study area is given in Figure 5. The North-American species (*G. tigrinus*) colonise both fresh and brackish (up to 16 psu outside the present study area) waters from the beginning of its arrival. It was observed in the Stettin Lagoon for the first time in 1992 (Rudolph 1994), in the Darß-Zingst Lagoon in 1994 (Zettler 1995), in the western Baltic Sea already in 1975 (Bulnheim 1976). Up to now,
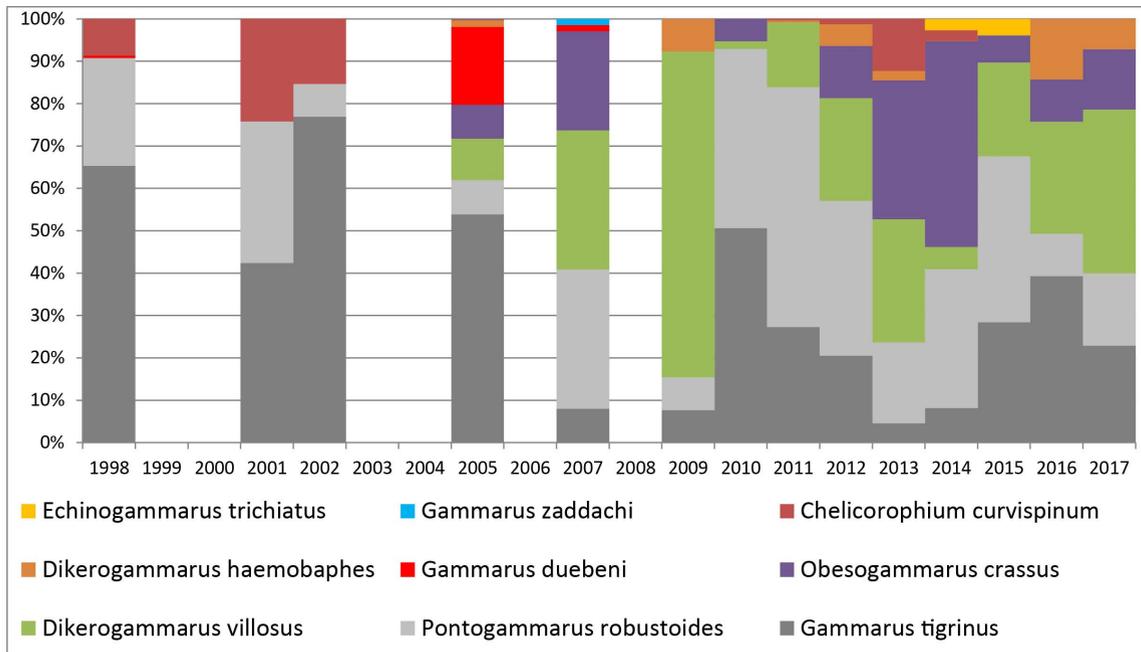
Figure 7. Relative abundance of amphipod species in the Stettin Lagoon (Stn. 70 in Figure 1) between 1998 and 2017 (gaps are not sampled years).

the seven Ponto-Caspian species have behaved like freshwater species (in rivers and lakes) and have found their distribution boundary in the oligohaline Stettin Lagoon. Although they have occurred in high numbers and frequencies for more than two decades there, no dispersal tendencies into the Baltic Sea have been observed. Only recently and for two species the conquest of the mesohaline areas has become apparent. Why did it take so long and why now? These questions cannot be answered. Long-term measurements of the Federal Agency for Environment, Nature Conservation and Geology (LUNG) show clearly that the salinity of the lagoons has not decreased between 2015, 2016 or 2017. Additionally the salinity is not highly variable among seasons with low salted periods allowing the surviving of stable population. In contrast, the annual range of salinity in exemplarily the Greifswald Lagoon is moderately low (< 0.8 standard deviation) in the last 10 years (not shown in figure). Both Gruszka and Wozniczka (2008) and Zettler (2008) stressed the rapid colonisation of the Stettin Lagoon by *D. villosus* in contrast to the outlets of the lagoon to the open Baltic Sea. The gap between the population around the SE end of Rugia and the next occurrence in the Stettin Lagoon is also interesting. Maybe other vectors (fishery, artificial construction activities) can explain this jump from the oligohaline to the mesohaline

areas. Although highly speculative separate introductions of two genetically diversified populations are also possible (see Hupało et al. 2018).

Further open questions are 1) do we now observe the starting shot for the conquest of other mesohaline areas at our coasts and 2) will other Ponto-Caspian amphipod species follow?

Dobrzycka-Krahel and Rzemykowska (2010) for instance also found *Pontogammarus robustoides* and *Dikerogammarus haemobaphes* at the outer coast in salinities between 5.8 and 6.1 psu. Markovski (1954) assigned *D. haemobaphes* to salinities between 0.2 and 5 psu with an optimum of 0.5 psu, *P. robustoides* even as stenohaline species up to 1 psu in the Dnieper-Bug estuary.

Particularly due to the rapid colonisation by Ponto-Caspian amphipods (especially by *D. villosus*), significant faunal changes were observed (e.g. Bij de Vaate et al. 2002; Jażdżewski et al. 2004, 2005; Rewicz et al. 2014; Meßner and Zettler 2016). Dick and Platvoet (2000) described the disappearance of *G. duebeni* and *G. tigrinus* caused by the introduction of *D. villosus* into the Markermeer und IJsellmeer (freshwater to oligohaline). It is most likely that similar drastic faunal changes will also occur in the mesohaline areas of the Baltic Sea. Our own long-term observations in the Stettin Lagoon demonstrated significant faunal changes involving a high variability (Figure 7). Whereas

Gammarus tigrinus, *Obesogammarus crassus* and *Pontogammarus robustoides* were abundantly and frequently found since the arrival of *Dikerogammarus villosus*, the formerly very abundant non-indigenous species *Chelicorophium curvispinum* is almost disappeared. Due to changing environmental conditions (e.g. salinity, river run off, eutrophication, and temperature seasonality), the colonisation success and development vary as well. Nevertheless, it is obvious that the species composition has changed and the species number has distinctly increased during the last decades. While the non-indigenous species already prevailed at the beginning of the monitoring (3 of 4 species), we have observed an additional impulse of introduction (7 of 9 species are allochthonous) in the last 10 years. The dispersal of non-indigenous species may be affected also due to the presence of stronger or weaker competitors (sensu Kobak et al. 2016).

Conclusions

Finally, although Ponto-Caspian NIS are currently not established in higher salinity areas of the North and Baltic Seas (Casties et al. 2016; Paavola et al. 2005), we assume a noteworthy and rapid spread of *D. villosus* and *O. crassus* along the southern Baltic Sea because the populations in the investigation area have already reached a sufficient and stable size. However, a lot of other abiotic and biotic parameters affect the distribution and dispersal of species. It is high speculative to predict the areas of future occurrence, nevertheless, the present observations are evidentially signs for the conquest of the brackish environment. Additionally, other Ponto-Caspian species will probably also have the potential to colonise these mesohaline waters. Based on the experience from freshwater habitats, we expect significant faunal displacements in coastal waters of the Baltic Sea in the near future.

Acknowledgements

References

Bij de Vaate A, Jażdżewski K, Ketelaars HAM, Gollasch S, Van der Velde G (2002) Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1159–1174, https://doi.org/10.1139/f02-098

Brooks SJ, Platvoet D, Mills CL (2008) Cation regulation and alteration of water permeability in the amphipod *Dikerogammarus villosus*: an indicator of invasion potential. *Archiv für Hydrobiologie* 172: 183–189, https://doi.org/10.1127/1863-9135/2008/0172-0183

Bulnheim HP (1976) *Gammarus tigrinus*, ein neues Faunenelement der Ostseeförde Schlei. *Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein* 46: 79–84

Bruijs MCM, Kelleher B, Van der Velde G, Bij de Vaate A (2001) Oxygen consumption, temperature and salinity tolerance of the invasive amphipod *Dikerogammarus villosus*: indicators of further dispersal via ballast water transport. *Archiv für Hydrobiologie* 152: 633–646, https://doi.org/10.1127/archiv-hydrobiol/152/2001/633

Casties I, Sebens H, Briski E (2016) Importance of geographic origin for invasion success: A case study of the North and Baltic Seas versus the Great Lakes–St. Lawrence River region. *Ecology and Evolution* 6: 8318–8329, https://doi.org/10.1002/ece3.2528

Devin S, Beisel JN (2007) Biological and ecological characteristics of invasive species: a gammarid study. *Biological Invasions* 9: 13–24, https://doi.org/10.1007/s10530-006-9001-0

Dick JT, Platvoet D (2000) Invading predatory crustacean *Dikerogammarus villosus* eliminates both native and exotic species. *Proceedings of the Royal Society of London B: Biological Sciences* 267: 977–983, https://doi.org/10.1098/rspb.2000.1099

Dobrzycka-Krahel A, Graca B (2018) Effect of salinity on the distribution of Ponto-Caspian gammarids in a non-native area – environmental and experimental study. *Marine Biology Research* 14: 183–190, https://doi.org/10.1080/17451000.2017.1406666

Dobrzycka-Krahel A, Rzemykowska H (2010) First records of Ponto-Caspian gammarids in the Gulf of Gdańsk (southern Baltic Sea). *Oceanologia* 52: 727–735, https://doi.org/10.5697/oc.52-4.727

Dobrzycka-Krahel A, Melzer M, Majkowski W (2015) Range extension of *Dikerogammarus villosus* (Sowinsky, 1894) in Poland (the Baltic Sea basin) and its ability to osmoregulate in different environmental salinities. *Oceanological and Hydrobiological Studies* 44: 294–304, https://doi.org/10.1515/ohs-2015-0028

Ellis S, MacIsaac HJ (2009) Salinity tolerance of Great Lakes invaders. *Freshwater Biology* 54: 77–89, https://doi.org/10.1111/j.1365-2427.2008.02098.x

Gasiūnas I (1963) The acclimatization of fodder crustaceans (of the Caspian relict type) into the reservoir of Kaunas Hydroelectric power station and the possibility of their transference into other water bodies. *Proceedings of the Lithuanian Academy of Sciences Series C* 1(30): 79–85 [in Russian]

Grabowski M, Bącela K, Konopacka A (2007a) How to be an invasive gammarid (Amphipoda: Gammaroidea) – comparison of life history traits. *Hydrobiologia* 590: 75–84, https://doi.org/10.1007/s10750-007-0759-6

Grabowski M, Jażdżewski K, Konopacka A (2007b) Alien Crustacea in Polish waters – Amphipoda. *Aquatic Invasions* 2: 25–38, https://doi.org/10.3391/ai.2007.2.1.3

Gruszka P, Woźniczka A (2008) *Dikerogammarus villosus* (Sowinski, 1894) in the River Odra estuary – another invader threatening Baltic Sea coastal lagoons. *Aquatic Invasions* 3: 395–403, https://doi.org/10.3391/ai.2008.3.4.4

Hupało K, Riss HW, Grabowski M, Thiel J, Bącela-Spychalska K, Meyer EI (2018) Climate change as a possible driver of invasion and differential in HSP70 expression in two genetically distinct populations of the invasive killer shrimp, *Dikerogammarus villosus*. *Biological Invasions*, https://doi.org/10.1007/s10530-018-1679-2

Jażdżewski K, Konopacka A, Grabowski M (2004) Recent drastic changes in the gammarid fauna (Crustacea, Amphipoda) of the Vistula River deltaic system in Poland caused by alien invaders. *Diversity and Distributions* 10: 81–87, https://doi.org/10.1111/j.1366-9516.2004.00062.x

Jażdżewski K, Konopacka A, Grabowski M (2005) Native and alien malacostracan Crustacea along the Polish Baltic Sea coast in the twentieth century. *Oceanological and Hydrobiological Studies* 24: 195–208

Kobak J, Rachalewski M, Bącela-Spychalska K (2016) Conquerors or exiles? Impact of interference competition among invasive Ponto-Caspian gammarideans on their dispersal rates. *Biological Invasions* 18: 1953–1965, https://doi.org/10.1007/s10530-016-1140-3

Kocataş A, Katağan T, Özbek M, Sezgin M (2003) A new amphipod for the Turkish fauna: *Pontogammarus maeoticus* (Sowinsky, 1894). *Crustaceana* 76: 879–884, https://doi.org/10.1163/156854003 60730651

Markovski YM (1954) Fauna bespozvonochnykh nizoviev rek Ukrainy [Invertebrate fauna of the lower reaches of the Ukrainian rivers, in Russian]. Part II. Kiev, 206 pp

Meßner U, Zettler ML (2016) Die Amphipodenfauna (Crustacea) zwischen Plauer See und Müritz (Mecklenburgische Seenplatte). *Archiv Natur- und Landeskunde Mecklenburg-Vorpommern* 54: 43–55

Minchin D, Lucy F, Sullivan M (2002) Zebra mussel: impacts and spread. In: Leppäkoski E, Gollasch S, Olenin S (eds), Invasive Aquatic Species of Europe, Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 135–146, https://doi.org/10.1007/978-94-015-9956-6_15

Müller O, Zettler ML, Gruszka P (2001) Verbreitung und Status von *Dikerogammarus villosus* (Sovinski 1894) (Crustacea: Amphipoda) in der mittleren und unteren Strom-Oder und den angrenzenden Wasserstraßen. *Lauterbornia* 41: 105–112

Paavola M, Olenin S, Leppäkoski E (2005) Are invasive species most successful in habitats of low native species richness across European brackish water seas? *Estuarine, Coastal and Shelf Science* 64: 738–750, https://doi.org/10.1016/j.ecss.2005.03.021

Paiva F, Barco A, Chen Y, Mirzajani A, Chan FT, Lauringson V, Baltazar-Soares M, Zhan A, Bailey SA, Javidpour J, Briski E (2018) Is salinity an obstacle for biological invasions? *Global Change Biology*, https://doi.org/10.1111/gcb.14049

Piscart C, Kefford BJ, Beisel JN (2011) Are salinity tolerances of non-native macroinvertebrates in France an indicator of potential for their translocation in a new area? *Limnologica-Ecology and Management of Inland Waters* 41: 107–112, https://doi.org/10.1016/j.limno.2010.09.002

Rewicz T, Grabowski M, MacNeil C, Bącela-Spychalska K (2014) The profile of a 'perfect' invader – the case of killer shrimp, *Dikerogammarus villosus*. *Aquatic Invasions* 9: 267–288, https://doi.org/10.3391/ai.2014.9.3.04

Rudolph K (1994) Erstnachweis des Amphipoden *Gammarus tigrinus* Sexton, 1939 (Crustacea: Gammaridea) im Peenestrom und Achterwasser (südliche Ostseeküste). *Naturschutzarbeit in Mecklenburg-Vorpommern* 37: 23–29

Santagata S, Gasiūnaite ZR, Verling E, Cordell JR, Eason K, Cohen JS, Bącela K, Quilez-Badia G, Johengen TH, Reid DF, Ruiz GM (2008) Effect of osmotic shock as a management strategy to reduce transfers of nonindigenous species among low-salinity ports by ships. *Aquatic Invasion* 3: 71–76, https://doi.org/10.3391/ai.2008.3.1.10

Šidagytė E, Solovjova S, Šniaukštaitė V, Šiaulys A, Olenin S, Arbačiauskas K (2017) The killer shrimp *Dikerogammarus villosus* (Crustacea, Amphipoda) invades Lithuanian waters, South-Eastern Baltic Sea. *Oceanologia* 59: 85–91, https://doi.org/10.1016/j.oceano.2016.08.004

Uzunova S (1999) On the biodiversity of the Ponto-Caspian Amphipoda (Crustacea) from the Bulgarian Black Sea coast. *Proceedings of the Institute of Fisheries Varna* 25: 175–186

Zettler ML (1995) Erstnachweis von *Gammarus tigrinus* Sexton, 1939 (Crustacea: Amphipoda) in der Darss-Zingster Boddenkette und seine derzeitige Verbreitung an der deutschen Ostseeküste. *Archiv der Freunde der Naturgeschichte in Mecklenburg* 34: 137–140

Zettler ML (2008) Veränderungen einer litoralen Amphipoda-Gemeinschaft am Beispiel einer Langzeitstudie im Oderhaff. *Lauterbornia* 62: 27–32

Zettler ML (2015) Kurze Notiz über die Ankunft von *Echinogammarus trichiatus* im Ostseegebiet und den Erstnachweis von *Paramysis lacustris* in Deutschland. *Lauterbornia* 79: 151–156

Zettler ML, Röhner M (2004) Verbreitung und Entwicklung des Makrozoobenthos der Ostsee zwischen Fehmarnbelt und Usedom - Daten von 1839 bis 2001. In: Bundesanstalt für Gewässerkunde (Hrsg.), Die Biodiversität in Nord- und Ostsee, Band 3. Bericht BfG-1421, Koblenz, 175 pp

Zettler ML, Zettler A (2017) Marine and freshwater Amphipoda from the Baltic Sea and adjacent territories. Conchbooks, Harxheim, 845 pp

Supplementary material

The following supplementary material is available for this article:

Table S1. Data on non-native amphipod species in the Western Pomeranian Lagoons area.

Table S2. Data on native amphipod species in the Western Pomeranian Lagoons area.

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