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Invasions of alien gammarid species and retreat of natives in the Vistula Lagoon (Baltic Sea, Poland)

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Abstract During the last decades of the twentieth century, the alien gammarid species *Gammarus tigrinus*, *Dikerogammarus haemobaphes*, *Pontogammarus robustoides* and *Obesogammarus crassus* invaded the lower Vistula River and its deltaic, partly brackish regions. In brackish waters of the Vistula Lagoon the native Atlantic-boreal species *Gammarus zaddachi* and *Gammarus duebeni* have been replaced or at least outnumbered by the aliens. As compared to our earlier studies, through the years 1998–2004 we could observe nearly total decline of the native gammarid populations along the coasts of the Lagoon, and overdomination of the North-American *G. tigrinus* in most places. Possible reasons for the observed phenomena are e.g. increasing pollution and eutrophication of the Lagoon accompanied by competition between the native and the alien species.

Keywords Alien invaders · Biological invasions · Central Europe · Gammarids · Vistula River system

Introduction

In the last decade of the twentieth century several spectacular range extensions of different amphipod species have been observed. Invasions of alien gammarids in fresh- and brackish waters of the Netherlands and Germany were amply discussed (Bij de Vaate et al. 2002; Pinkster et al. 1992; Van der Velde et al. 2000). The Vistula river, the largest river of the Baltic Sea catchment area and one of the major European water-

courses, is a crucial part of the so-called central migration corridor used by Ponto-Caspian hydrobionts to invade Western Europe (Bij de Vaate et al. 2002). On the other hand, draining into the Baltic Sea, this river is also a gateway for euryhaline freshwater and brackish water alien species spreading via inshore waters of this one of the world's largest brackish waterbodies. Some of the most prominent aquatic invaders are amphipod crustaceans of superfamily Gammaroidea, commonly known as gammarids. The gammarid fauna of the Vistula River and also other Polish waters has been relatively well studied (Jazdzewski and Konopacka 1995, 2000; Konopacka 1998, 2004; Konopacka and Jazdzewski 2002). The detailed information on the periods and arrival ways of alien gammarids to Polish waters can be found in the papers by Jazdzewski et al. (2002, 2004). Clearly, the entire middle and lower sections of the river down to its mouth has been invaded by various alien gammarid species. Two of them, Ponto-Caspian *Chaetogammarus ischnus* and *Dikerogammarus haemobaphes*, have entered through the Prypet-Bug canal. The former species is an old invader, which is still present, as noted in the Vistula already in 1928 (Jarocki and Demianowicz 1931); the latter was recorded for the first time only in 1996 (Konopacka 1998). The next three species have approached from the north. Again Ponto-Caspian: *Pontogammarus robustoides* and *Obesogammarus crassus* have entered the Vistula's delta via Baltic inshore waters or through the Pregola river channels from the Nemunas river system and Curonian Lagoon, where they were introduced in the 1960s (Gasjunas 1972; Arbaciauskas 2002). The first species has successfully migrated up the freshwater course of the river colonising the artificial Włocławski and Żegrzynski reservoirs located at the middle section of the Vistula. The second, *O. crassus*, until now has not entered the purely freshwater parts of the Vistula and remained only in its delta. The third species *G. tigrinus*, is of North American origin. Introduced to German waters in the 1950s (Bulnheim 1976), the species has migrated eastwards and has colonized estuaries of major rivers along the Baltic southern shores

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including the Vistula. In the Vistula, the species still does not migrate upwards from the brackish water parts of its delta (Konopačka 2004). As one can see, the delta is a particularly interesting section of the Vistula river, possessing the richest alien gammarid fauna and invaded both from the freshwater course of the river as well as from the brackish waters of the Baltic Sea.

Despite the attention bestowed on the problem of aquatic invasive species in many countries, long-term and systematic studies on the dynamics of gammarid communities in invaded habitats are rare. Therefore, we have decided to continue and broaden our studies upon the faunal changes related to the presence of alien gammarids in the Vistula deltaic system.

Thus, the aim of our present paper is to deliver information on recent composition changes in the gammarid communities of the Vistula Lagoon and compare them to previous studies.

Study area

Vistula Lagoon is a brackish water body with an area of 838 sq. km. The Lagoon is divided into two parts by the Polish–Russian border (Fig. 1). It represents the easternmost part of the deltaic system of the Vistula river. Vistula empties to the Gulf of Gdansk with artificial, straight channel dug in 1895. Former main estuarine left branch now cut by a sluice, constitutes a brackish dead arm called Dead Vistula. The right branch, named Nogat, flows to the Vistula Lagoon. In medieval times this was the largest of the Vistula's arms, carrying two-thirds of its water to the Vistula Lagoon, making it a freshwater body. In the nineteenth century, due to regulatory works in the delta, this proportion between major arms changed and Nogat carried only 25% of the riverine water to the Lagoon, nevertheless still maintaining its freshwater character. Later in 1915, the sluice cut Nogat and since then only some 3% of Vistula's freshwater flow has been allowed to enter the Lagoon. It subsequently changed to a brackish water body. Now the salinity of the Vistula Lagoon amounts from some 1 PSU near the Nogat mouth to about 5 PSU at the Baltijsk Strait—the entrance to Baltic waters (Fig. 2). It is a narrow, 400 m channel in the small Russian town of Baltijsk (former German Pillau). This basin is also very shallow. Because of this small depth and large area, waters of the Lagoon are comparatively well aerated. Summer water temperatures attain over 26°C whereas in winter ice phenomena in the Vistula Lagoon may last even 3 months. The shores of the Lagoon are mostly sandy, locally with thick layer of dead zebra mussel shells and covered mostly by wide reed belt. Deeper parts of the bottom are covered with mud. Benthic fauna of the vast majority of this basin is dominated by oligochaetes and chironomid larvae with total abundance varying on average between 2,000 and 5,000 ind/m² and biomass ranging on average from 15 to 50 g/m²

(Zmudzinski 1957; Cywinska, Rozanska 1978). At the shore, in the littoral zone, practically not sampled by the mentioned authors, vagile invertebrates dominate and among them gammarid crustaceans play the major role (Jazdzewski et al. 2004).

Materials and methods

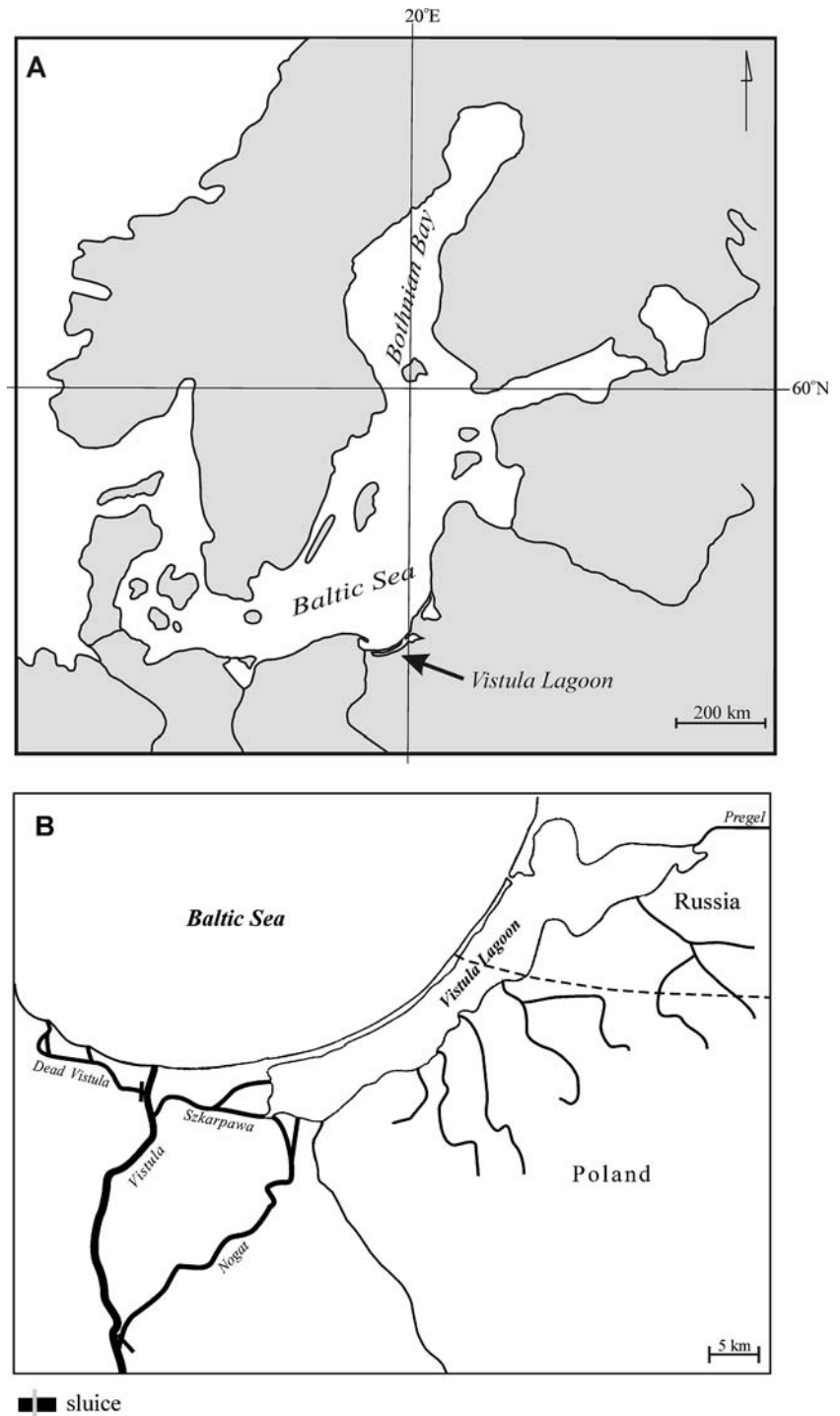
Our semi-quantitative studies of gammarids in the Vistula Lagoon were performed in six sampling sites in 2002 and in eight sites in 2004. The present sampling sites covered to a large extent those used in our earlier study. Thus, this paper presents and compares the overall results of our field investigations of the Vistula Lagoon in the period 2002–2004 with the results of our earlier comparable study in 1998–2002 (Jazdzewski et al. 2004) as well as, to some extent, with earlier results of faunistic investigations (Zmudzinski 1957; Jazdzewski 1975; Cywinska and Rozanska 1978).

With the use of a benthic hand-net, the littoral habitats were sampled for 45 min at each station (two persons' effort). This way it was possible to collect large representative samples, containing hundreds of gammarids each. Altogether, the collected material of gammarids encompassed some 7,000 individuals. Such numbers cannot be achieved using any of the quantitative methods, because of gammarid habits to hide under stones, bricks, pieces of wood, roots of trees overgrowing river banks and among dense reed or rush patches. The semiquantitative sampling method has been used for many years by our research team. It proved to be very efficient, giving reliable results in faunistic surveys performed on larger geographical scales (Jazdzewski et al. 2002, 2004). As a consequence of the above method, only the relative abundance measures (percentage of all gammarids collected at a site) were used to present the composition of gammarid communities in the figures.

Results

Our field surveys indicated that in both years all studied sites were completely dominated by alien gammarid species. We recorded the presence of, altogether, six gammarid species in the Polish section of the Vistula Lagoon in 2002 (Fig. 3). The general species composition was the same as observed in the year 2000. We recorded the presence of three Ponto-Caspian invaders: *D. haemobaphes*, *P. robustoides* and *O. crassus*, one North-American species—*G. tigrinus*, as well as only two native species: *Gammarus duebeni* and *Gammarus zaddachi*. The most numerous species in the southern and the western part of the Lagoon was *P. robustoides*. In the north-eastern part, closer to the Baltijsk Strait, *G. tigrinus* dominated the gammarid communities. The presence of *O. crassus* was definitely more pronounced

Fig. 1 a Baltic Sea including the study area b Vistula Lagoon



in the southern part of the Lagoon, while in the northern part its contribution was rather marginal. Nevertheless, the three above species were present in all collected samples. Some individuals of the fourth invader, *D. haemobaphes*, were found only in one sample, in the westernmost part of the Lagoon greatly influenced by the discharge of fresh water from the Vistula's channels. As far as the native species are concerned, *G. duebeni* was present in most samples along both, the southern

and the northern shores of the Lagoon with some 10% contribution with regard to relative abundance. On the other hand, *G. zaddachi* was present as a single individual in only one sampling site, closest to the Baltijsk Strait, which enables inflow of more saline waters from the Gulf of Gdansk.

In the year 2004, we could find only five species in the studied area due to lack of the native *G. zaddachi* in our samples (Fig. 3). Still the absolute dominants were the

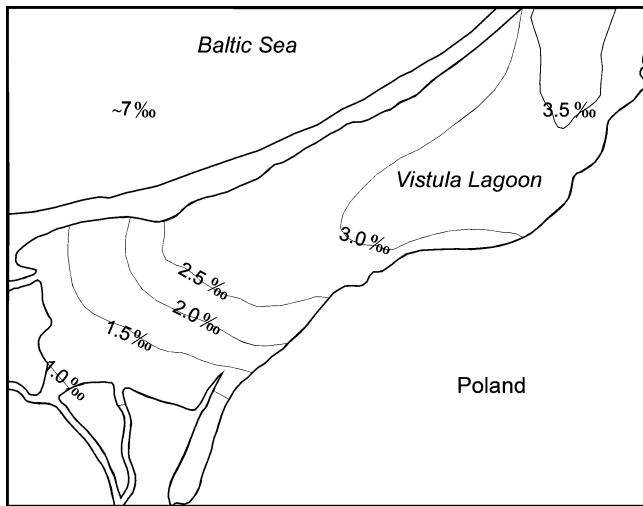


Fig. 2 Salinity of the Polish part of the Vistula Lagoon

aliens, however the dominance structure somewhat changed. The most visible change is the diminishing dominance of *P. robustoides*, most often in favour of *G. tigrinus*, or locally along the southern shores, also in favour of *O. crassus*. Another invader, *D. haemobaphes*, saved its position in the westernmost part of the Lagoon. The only remaining native, *G. duebeni*, had just a marginal contribution in only two samples—among some 4,500 gammarids collected in 2004 only 15 individuals of that species were found.

Discussion

Gammarids recorded originally in this water body in the beginning of the former century, when the basin has become already brackish, were exclusively native species. In the Lagoon itself only *G. zaddachi* was found, whereas in mouths of small rivulets entering the Lagoon, *Gammarus pulex* occurred (Vanhöffen 1917; Riech 1926; Seligo 1926). Schellenberg (1942) recorded already both *G. zaddachi* and *G. duebeni* in the Lagoon—the latter species only at the entrance to the Baltic near Pillau (now Baltijsk).

In rather thorough studies of the Vistula Lagoon benthos carried out by Zmudzinski in the early fifties of the former century (Zmudzinski 1957) only *G. zaddachi* was recorded, usually as an abundant species in the littoral zone (Fig. 4). Nevertheless, Jazdzewski (1975) has found both species at that time—the dominating *G. zaddachi*, and *G. duebeni* consisting the minor part of the sample (Fig. 4). Later, some data by Cywinska and Rozanska (1978) and own data from 1980 (Jazdzewski et al. 2004) have proven the occurrence of only the above-mentioned native species, with some dominance of *G. duebeni*.

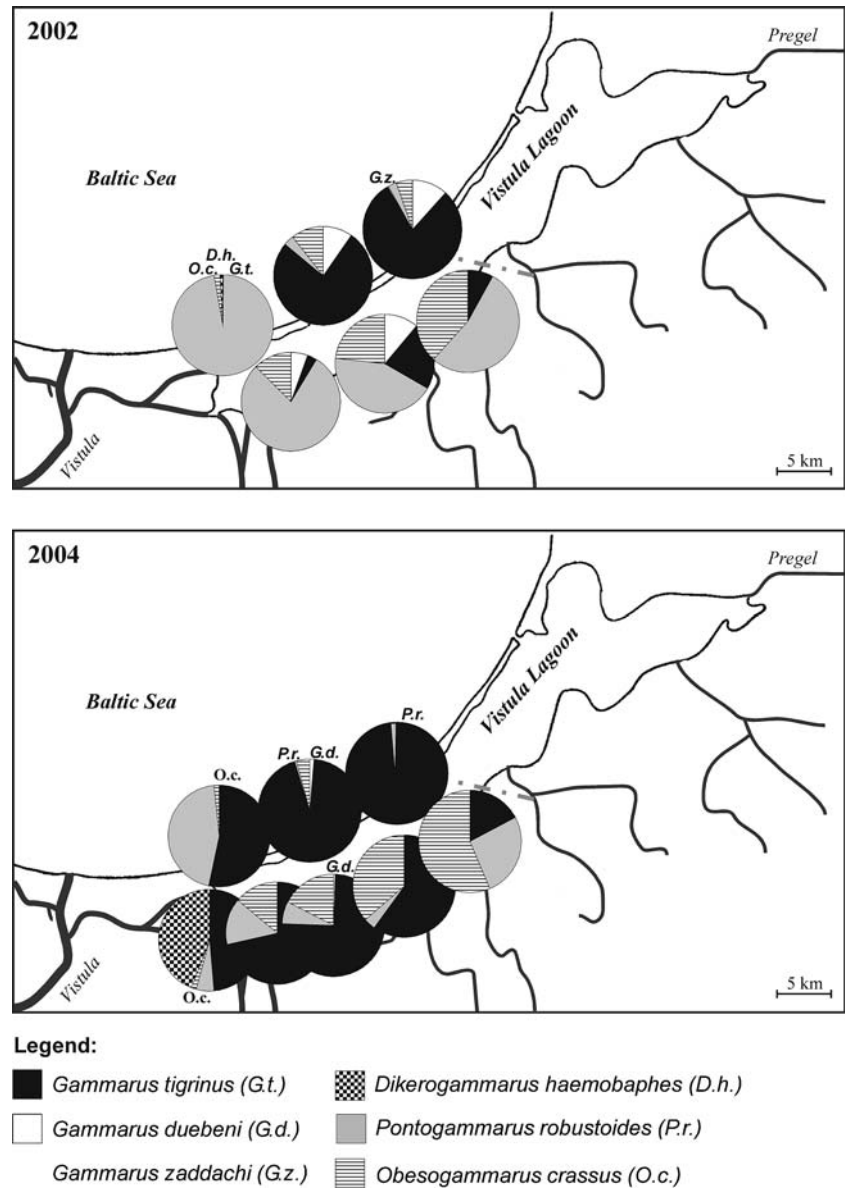
Our team has undertaken more regular sampling in the Vistula Lagoon at the break of the century, already knowing that the Vistula river has been invaded by alien

gammarids. First results from 1998–2000 samplings were summarised by Jazdzewski et al. (2004) (Fig. 4). That time, of the two native gammarids, *G. duebeni* was still abundant in some samples. Especially in the northern part of the Lagoon, this native species was an important, and sometimes even dominant element in gammarid communities, with low contributions in only two samples in its southern part. Whereas, *G. zaddachi* was totally absent along the Lagoon's southern shore and only marginally present in two samples along the northern shore. Generally, all sampling sites in the southern part of the Lagoon were clearly overdominated by Ponto-Caspian aliens: *O. crassus* and *P. robustoides* in most cases and by *D. haemobaphes* near the freshwater mouth of Nogat, with North-American *G. tigrinus* also being quite abundant. Along the northern shore of the Lagoon only the latter species played an important role, with some *P. robustoides*, and marginal number of *O. crassus* present in only one sample in north-western part of the Lagoon.

Looking at the results obtained and comparing them to the earlier studies, several patterns of gammarid distributions can be seen. First, is the case of *D. haemobaphes*. Since its discovery in 1998, the species occurs exclusively in the westernmost section of the Lagoon, usually near the mouths of various freshwater channels. Due to a significant freshwater discharge, salinity in this area is usually between 1–1.5 PSU. Our other studies show that *D. haemobaphes* is an abundant species in the lowest freshwater course of the Vistula, and also in the mouth section of the Nogat branch. On the other hand, we did not observe this gammarid in definitely more saline (2–7 PSU) Dead Vistula (Jazdzewski et al. 2002, 2004). Our extensive field observation of the species occurrence in the Vistula system shows that usually it is more abundant in running waters, especially if compared with *P. robustoides* (unpublished data). However, Ponomareva (1976) indicates that it may tolerate salinities from freshwater up to 8 PSU; our findings lead us rather to a conclusion that *D. haemobaphes* is predominantly a riverine, freshwater species, that does not adopt well in brackish conditions above 1.5 PSU. That is also supported by our findings in the Szczecin Lagoon, where the species occurs in its least saline regions, and in the mouth section of the Oder river; also no *D. haemobaphes* was found in the 7–8 PSU inshore Baltic waters along the Polish coast (Jazdzewski et al. 2005). Its distribution limited by salinity conditions in the Vistula deltaic system may thus explain why the species migrates westwards through the central corridor, using only inland watercourses (see Bij de Vaate et al. 2002).

The situation looks quite different with the two other Ponto-Caspian, *P. robustoides* and *O. crassus*. It is clear that both species may tolerate higher salinities—they were found also in the more saline sections of the delta (Jazdzewski et al. 2004). Besides, they were recorded in the Szczecin Lagoon as well as in some brackish coastal lakes and channels along the Polish Baltic coast (Jazdzewski et al. 2005). However, we did not observe

Fig. 3 Composition of gammarid communities in the Vistula Lagoon in 2002–2004



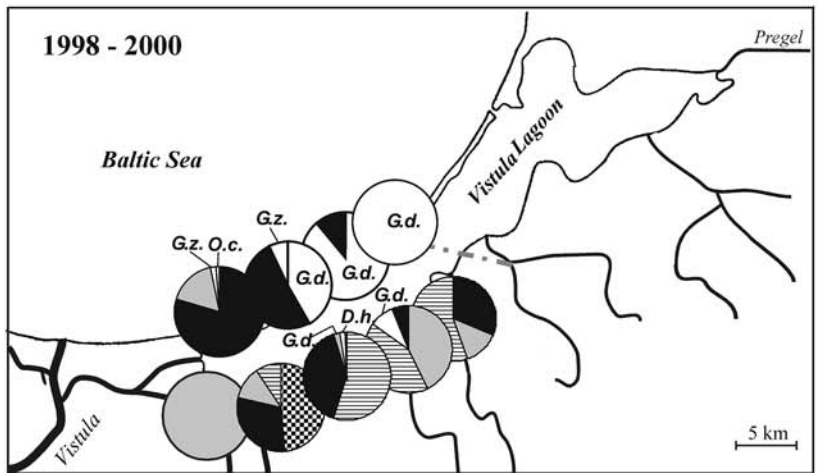
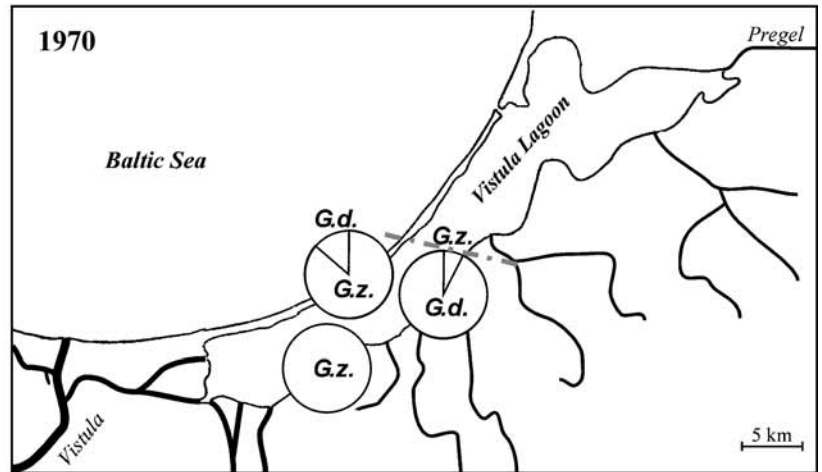
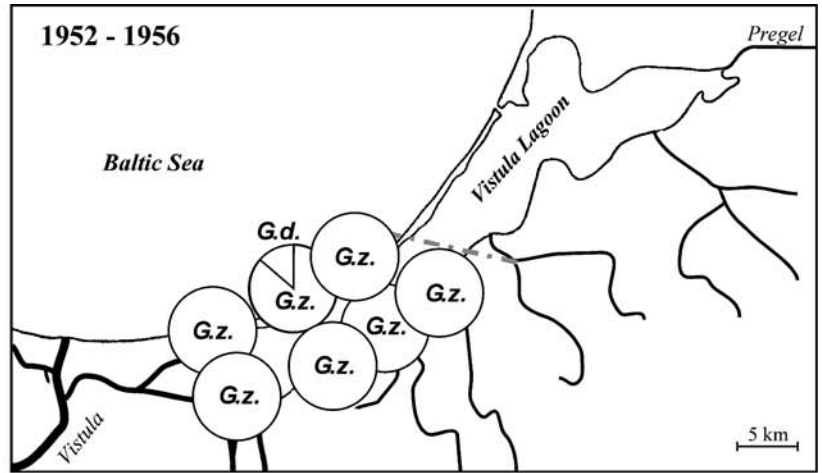
this species in also brackish, but more saline (6–7 PSU) Bay of Puck (Jazdzewski et al. 2005). *Pontogammarus robustoides* occurs also in the purely freshwater sections of the Vistula River, particularly in the more lentic waters of artificial dam reservoirs (Jazdzewski et al. 2002). The distribution we observe seems to prove that the species may spread in the Baltic offshore waters, however, it thrives well and builds stable populations only in salinities not exceeding 3–4 PSU. The same is very much true for *O. crassus*; however, this species occurs exclusively in the brackishwater parts of the Vistula and Oder systems, namely in their deltas (Konopacka 2003; Jazdzewski et al. 2004, 2005).

The most versatile alien species (in terms of salinity tolerance) seems to be *G. tigrinus*. It is known to occur in habitats from freshwater to nearly marine conditions (Bousfield 1973). Also, in Poland, this species occurs in

the Baltic itself, i.e. in the Bay of Puck (Szaniawska et al. 2003) in the brackish parts of the Oder and Vistula deltas and also in the freshwater course of the Oder River penetrating up to the city of Opole, some 600 km from the river mouth. This wide tolerance probably enables the species to dominate in almost all sites in the Vistula Lagoon. However, interestingly, this species, for some unknown reasons, has not yet colonized the freshwater parts of the Vistula's delta and has not penetrated up the freshwater course of this river.

Looking at the ecological characteristics of the above alien species, and at the environments the species inhabit within their natural distribution limits it is not surprising why they have colonized the Vistula Lagoon successfully. All of them are euryoecious, highly fertile species of wide salinity tolerance, thriving well in various conditions and able to compete with local fauna (Grabowski

Fig. 4 Former species composition of gammarid populations in Vistula Lagoon (modified from Jazdzewski et al. 2004). 1952–1956: data after Zmudzinski 1957; Jazdzewski 1975, 1970: data after Jazdzewski 1975 and unpublished data, 1998–2000: data after Jazdzewski et al. 2004



Legend:

- Gammarus tigrinus* (G.t.)
- Gammarus duebeni* (G.d.)
- Pontogammarus robustoides* (P.r.)
- Dikerogammarus haemobaphes* (D.h.)
- Gammarus zaddachi* (G.z.)
- Obesogammarus crassus* (O.c.)

et al. 2006). Due to their evolutionary inheritance and geological history of the Ponto-Caspian area, this feature is particularly well expressed in the Ponto-Caspian

fauna, a relict of the Sarmatian Sea, living naturally in coastal Lagoons (limans) and lower sections of large rivers emptying to Black and Caspian seas.

Why we do observe such a dramatic decline of native *G. duebeni* and *G. zaddachi* in the Vistula Lagoon? Zmudzinski (2000) points out that although the salinity of the Lagoon has slightly increased since 1950s until mid-1990s, the bottom fauna richness decreased, showing loss of several brackish water species (including corophiid amphipods). It is worth noting that in samples from 1988–1994, this author has not recorded the presence of any alien amphipod species, whereas the frequency of *G. zaddachi* clearly dropped down, and *G. duebeni* was not found at all. The reason for that may be severe eutrophication and pollution of the Lagoon (Rozanska and Wieclawski 1978; Glasby and Szefer 1998; Anonymous 2000) that is supposed to have an effect e.g. on the fish assemblages (Psuty-Lipska and Borowski 2003). Also, prior to the invasion of alien gammarids, the bottom macrofauna of the Vistula Lagoon has been considerably reduced, with the biomass of Crustacea diminishing, due to the introduction of *Marezzelleria* cf. *viridis*, an alien polychaete species (Zmudzinski 1996). As seen from the above, there are several reasons that may stand behind the decline of native gammarid species. Most probably the process has started with the pollution and eutrophication of the Lagoon and has enhanced through expansion and activity of *M. cf. viridis*. Competition or even predation pressure of the alien gammarids may be another factor reducing populations of native gammarids. In fact, studies in the lower Rhine River revealed that introduction of Ponto-Caspian *Dikerogammarus villosus* caused the vanishing of previously present gammarid assemblages (Van der Velde et al. 2000). Similar patterns of replacing native gammarid assemblages by alien species has been observed also in other Baltic Lagoons and estuaries, e.g. in the Szczecin Lagoon, Dead Vistula (Gruszka 1999; Konopacka 2003; Jazdzewski et al. 2004, 2005) and in the Puck Bay (Szaniawska et al. 2003; Jazdzewski et al. 2005).

Generally, the true reasons and mechanisms behind the above changes still remain obscure and demand further and detailed investigation. Also, it is hard to anticipate how the gammarid fauna will change in the future. With a high degree of probability, we can say that the alien gammarids will become dominant and stable elements as it happened in other European countries (Konopacka 2004). Also other Ponto-Caspian species as e.g. *Obesogammarus obesus* may be expected to enter the Vistula Lagoon (Eggers and Martens 2001).

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