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BIODIVERSITY RESEARCH

Recent drastic changes in the gammarid fauna (Crustacea, Amphipoda) of the Vistula River deltaic system in Poland caused by alien invaders

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ABSTRACT

During the last decade of 20th century, the nonindigenous gammarid species *Gammarus tigrinus*, *Dikerogammarus haemobaphes*, *Pontogammarus robustoides* and *Obesogammarus crassus* invaded the lower Vistula River and its deltaic, partly brackish regions. *G. tigrinus*, an oligohaline North-American species, was introduced to western Europe in the 1950s; the remaining three species are oligohaline/freshwater Ponto-Caspian species. All these species are now invading central and western Europe using the network of man-made canals connecting different European river systems. In the Vistula River, the native European freshwater gammarid species *Gammarus pulex* and *G. varsoviensis* were replaced in the 1920s by the Ponto-Caspian *Chaetogammarus ischnus* (syn. *Echinogammarus ischnus*), which in turn has been outnumbered by the more recent invasions of *D. haemobaphes* and *P. robustoides*. In brackish waters, the native Atlantic-boreal species *Gammarus zaddachi* and *Gammarus duebeni* are replaced or at least outnumbered by *G. tigrinus*, *P. robustoides* and *O. crassus*. Possible invasion routes are discussed.

Keywords

Biological invasions, Central Europe, gammarids, Vistula River system.

INTRODUCTION

Natural changes in distributions of organisms occur slowly, being dependent on chances of crossing geographical barriers. However, increasing anthropogenic activity has created numerous opportunities for species to spread rapidly (for review see Di Castri, 1989). For fresh- and brackish-water organisms, apart from intentional introductions, transoceanic shipping and associated ballast water (Ruiz *et al*., 1997), and construction of canals joining formerly separate water catchments (Jazdzewski, 1980), are the most important vectors of species leading to spread outside their primary geographical ranges. The last decade has seen a wealth of papers reporting recent serious faunistic changes in aquatic habitats throughout central Europe. Among invertebrates, gammarid crustaceans (Amphipoda, Gammaroidea) are particularly successful invaders (Jazdzewski, 1980; Pinkster *et al*., 1992; Bij de Vaate *et al*., 2002). The present paper synthesizes information on changes in the gammarid fauna that occurred in the last few decades of the 20th century in the deltaic system of the Vistula River, i.e. in the southern Baltic inshore waters (Fig. 1).

Amphipods of the genera *Gammarus*, *Echinogammarus* and *Chaetogammarus* are common inhabitants of the shallow, offshore and littoral zones of the Atlantic and Baltic Sea, as well as of European streams and rivers. Sexton (1913) was the first to identify *Gammarus locusta* and *G. zaddachi* in the offshore waters of the Gulf of Gdansk, i.e. the area of the Vistula's mouth. Later studies (Vanhoeffen, 1917; Riech, 1926; Seligo, 1926) reported *G. zaddachi* as the only gammarid present in the Vistula Lagoon.

There are few detailed studies on the freshwater gammarids of the Vistula River. The earliest note of any gammarid species inhabiting this river is that of Seligo (1920), who observed *Gammarus pulex* in the lower Vistula. The presence of *G. pulex* in the Vistula Lagoon in the vicinity of stream mouths (near Frombork) was also mentioned by Riech (1926).

Chaetogammarus ischnus (syn. *Echinogammarus ischnus*) was the first alien gammarid invader of the Vistula's freshwater flow in 1928 (Jarocki & Demianowicz, 1931). This Ponto-Caspian fresh- and brackish-water species evidently entered the Vistula River through the Pripet–Bug canal connecting the Black Sea and the Baltic Sea basins; the Pripet River is an affluent of the Dnieper, while the Bug River is an affluent of Vistula River.

Subsequently, *C. ischnus* remained the sole gammarid species in the whole lower Vistula River below Warsaw for five decades (Jarocki & Demianowicz, 1931; Mikulski & Tarwid, 1952; Pliszka

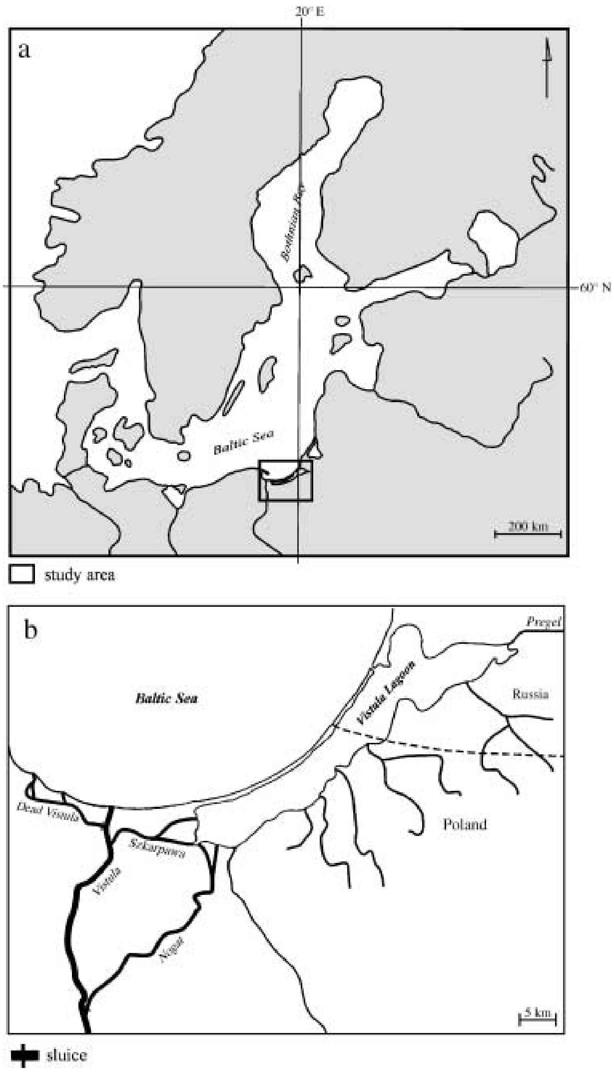

Figure 1 Baltic Sea (a) including the study area (b).

et al., 1952) and its distribution extended as far as the Vistula River's mouth (Jazdzewski, 1975) (Fig. 2a).

The brackish Vistula Lagoon was thoroughly investigated in the early 1950s by Zmudzinski & Szarejko (1955) and Zmudzinski (1957), who noted *G. zaddachi* as the sole gammarid present in abundance throughout the littoral zone. A second gammarid species, *Gammarus duebeni*, was identified in the Vistula Lagoon by Jazdzewski (1975) from samples collected in 1956 (Fig. 3a). Somewhat later, in the early 1970s, *Gammarus duebeni* was reported to dominate locally over *G. zaddachi* in the Vistula Lagoon (Jazdzewski, 1975; H. Kaczmarek, unpublished data) (Fig. 3b).

Gammarids of the Dead Vistula were studied by Arndt (1965) and somewhat later by Jazdzewski (1967, 1975), Klekot (1968, 1972, 1973) and H. Kaczmarek (unpublished data). During that time, *G. zaddachi* was the most abundant species along most of this elongated water basin, followed by *G. salinus*. *G. oceanicus* was also present, but only at the mouth to the Baltic Sea. *Gammarus duebeni* first appeared in the brackish Ptasi Raj (Messina) lake and within a decade had become more abundant near the Dead Vistula mouth, in the vicinity of a leaky dike separating the Dead Vistula from this lake (Fig. 4a).

In the last decade, five gammarid species new to the Polish fauna have been discovered: *Gammarus tigrinus*, introduced to European waters from North America, was collected from the Oder estuary (Gruszka, 1995, 1999) and from the Vistula Lagoon (Jazdzewski & Konopacka, 2000). Four gammarids of Ponto-Caspian origin have been identified: *Pontogammarus robustoides* from Szczecin Lagoon (Gruszka, 1999), the Vistula River (Konopacka, 1998) and the Vistula Lagoon (Jazdzewski & Konopacka, 2000); *Dikerogammarus haemobaphes* in the Vistula River (Konopacka, 1998); and, more recently, *D. villosus* was recorded from the lower Oder River by Müller *et al*. (2001) and Jazdzewski *et al*. (2002); *Obesogammarus crassus* in the Vistula Lagoon and in the Dead Vistula (Konopacka & Jazdzewski, 2002). These findings paralleled the recent discoveries of *G. tigrinus* and *D. villosus* in north-eastern Germany (Rudolph, 1994a,b; Zettler, 1995, 1998; Martens & Eggers, 2000), and of *Pontogammarus robustoides* in central and eastern Germany (Rudolph, 1997; Zettler, 1998; Martens *et al*., 1999).

STUDY AREA

The Vistula is one of the major European rivers, with a length of 1047 km and a drainage area of 194,400 km^2. It flows entirely through Poland and empties into the Baltic Sea in the Gulf of Gdansk (Fig. 1a,b). The Vistula's delta (18°38′–19°46′ E, 53°56′–54°22′ N) comprises several old and new river branches, some of them brackish, as well as an oligohaline water body, the Vistula Lagoon (Fig. 1b).

The Baltic Sea is a brackish, boreal, shallow inland sea, with a salinity ranging from 2 to 15 PSU (7–8 PSU on average). It is a young, postglacial basin, *c*. 16,000 years old, with an average depth of approximately 60 m (Segestråle, 1957). The fauna of this sea is seriously impoverished and mainly of North Atlantic origin; this impoverishment is well illustrated by the classical curve of Remane (1958), where the minimum of species richness falls just in the salinity range from 5 to 10 PSU, and the bulk of the fauna within this range is formed by typically mixohaline species.

Major parts of the Vistula's delta treated herein are:

1 the main Vistula River channel (freshwater);

2 the eastern arm of this freshwater flow, called Nogat, which empties to the Vistula Lagoon;

3 the western dead arm of the Vistula, called Dead Vistula (more than a century ago this water body was separated by a sluice and is now brackish); and

4 the Vistula Lagoon, which is bisected by the Polish-Russian border. This lagoon is a large, shallow (average depth of 3 m), brackish-water body (salinity from 2 to 5 PSU) with a surface area of over 800 km^2 (Zmudzinski & Szarejko, 1955; Zmudzinski, 1957). The Vistula Lagoon is connected to the Baltic Sea by a narrow strait near the Russian town of Baltijsk (Fig. 1b).

The western dead arm of the Vistula (Dead Vistula) has two connections with the Baltic Sea (Fig. 1b). One is the old Vistula

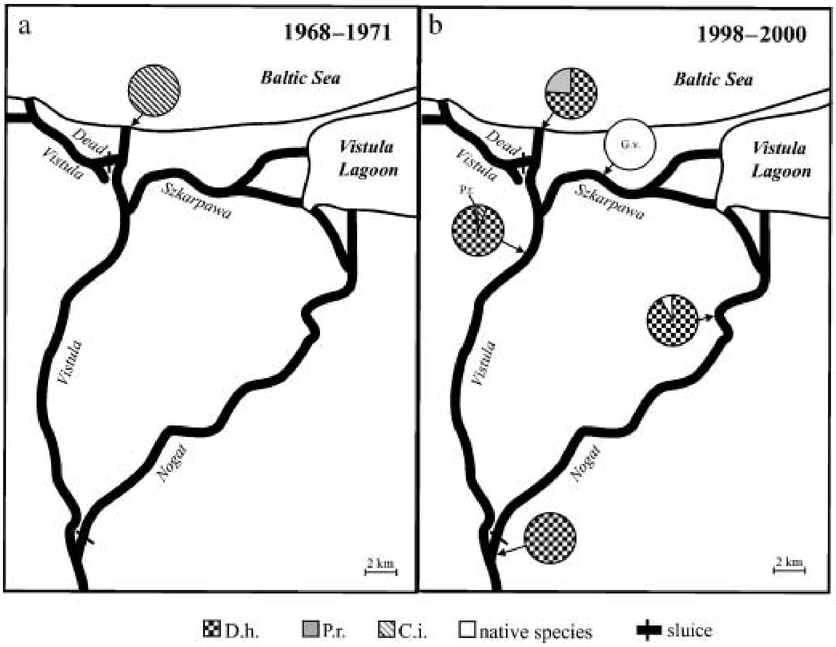

Figure 2 Species composition of gammarid communities in the lower Vistula River a. Data after Jazdzewski (1975); H. Kaczmarek, unpublished data b. Present study. Invasive species: D.h. — *Dikerogammarus haemobaphes*, C.i. — *Chaetogammarus ischnus*, P.r. — *Pontogammarus robustoides*. Native species: G.v. — *Gammarus varsoviensis*.

River mouth in the city of Gdansk, now its harbour, and the second is the old Vistula's mouth, which functioned between 1840 and 1895. By 1895, an artificial river mouth, the present main Vistula's channel, was built and the western arm sluiced. These modifications still remain in place today, creating in the Dead Vistula a salinity gradient of 2 PSU at the sluice and 7 PSU at the mouth (Klekot, 1972, 1973).

The right (eastern) Vistula's arm, Nogat, was the Vistula's main flow in the 16th and 17th centuries, and was sluiced from the present main Vistula's channel in 1915 allowing only some 10% of the river's flow to enter the Vistula Lagoon. Since then, lagoon salinity has increased from the former nearly freshwater situation to the present oligohaline conditions (on average salinity 3–4 PSU).

The present main flow of the Vistula River is a straight channel with a width of some 500 m. Its banks are protected by large boulders and concrete; this protection has been destroyed in some places, allowing the formation of shallow, lentic, sandy pools with some submerged vegetation (*Potamogeton* sp., *Ranunculus* sp., *Myriophyllum* sp.). The banks of the Nogat are richer in plant cover, and include *Typha* sp., *Scirpus* sp., *Potamogeton* sp., and *Nuphar* sp. The shores of the oligohaline Dead Vistula and Vistula Lagoon are mostly bordered by rush (*Phragmites* sp., *Typha* sp., *Scirpus* sp.).

METHODS

Our 1998–2000 sampling of gammarids in the Vistula river deltaic system had a semiquantitative character. Using a hand net and a dredge, the littoral of the basins was sampled for 45 min at each station (2 persons' effort). This way we were able to collect comparatively large and thus representative samples, sometimes containing hundreds of individuals each species. Such numbers cannot be achieved using any of the quantitative methods, because of the gammarid habits of hiding under stones, bricks, pieces of wood, roots of trees overgrowing river banks and among dense reed or rush patches. To track the faunal changes in the Dead Vistula, we have used literature data based on the gammarid materials collected in 1963–64 by Arndt (1965) and in 1968–71 by Jazdzewski (1975) and, in the Vistula Lagoon, the data of Zmudzinski (1957) based on the materials collected in 1952–56. Since various authors used different collection methods, only the relative abundance measure (percentage of all gammarids collected at a site) was used in the figures.

RESULTS AND DISCUSSION

The drastic changes in the gammarid fauna of the deltaic region of the Vistula River are evident when comparing the proportions of particular species in all parts of this delta through the different periods.

1 The main freshwater Vistula flow in its lowest, deltaic section is now inhabited almost exclusively by a new invader, *Dikerogammarus haemobaphes* (Fig. 2b), that has mostly replaced a previous invader, *Chaetogammarus ischnus* (Fig. 2a). *Dikerogammarus haemobaphes* also dominates the amphipod fauna within the eastern Vistula's arm, the Nogat, and its mouth to Vistula Lagoon; *Pontogammarus robustoides* is also present, although in lower abundance (Fig. 2b).

2 The Vistula Lagoon is presently dominated by invaders: *Gammarus tigrinus* and *Obesogammarus crassus*, but in some samples native *G. duebeni* or alien *Pontogammarus robustoides* were more numerous (Fig. 3c). Among some 2000 gammarids collected in the Vistula Lagoon in 1998–2000, only 17 specimens of the native *G. zaddachi* were found.

3 The Dead Vistula is now dominated by the North American *G. tigrinus*. In the Ptasi Raj lake, this species was found along with the native *G. zaddachi*, though neither species was numerous.

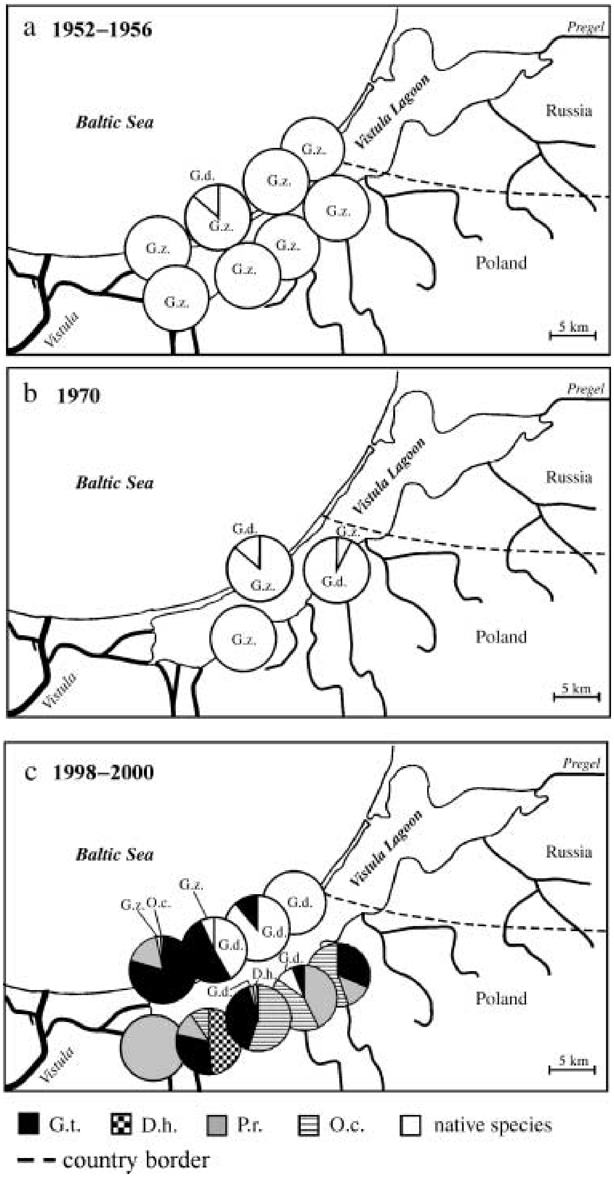

Figure 3 Species composition of gammarid populations in Vistula Lagoon a. Data after Zmudzinski (1957); Jazdzewski (1975) b. Data after Jazdzewski (1975); H. Kaczmarek, unpublished data c. Present study. Invasive species: D.h. — *Dikerogammarus haemobaphes*, O.c. — *Obesogammarus crassus*, P.r. — *Pontogammarus robustoides*, G.t. — *Gammarus tigrinus*. Native species: G.d. — *Gammarus duebeni*, G.z. — *Gammarus zaddachi*.

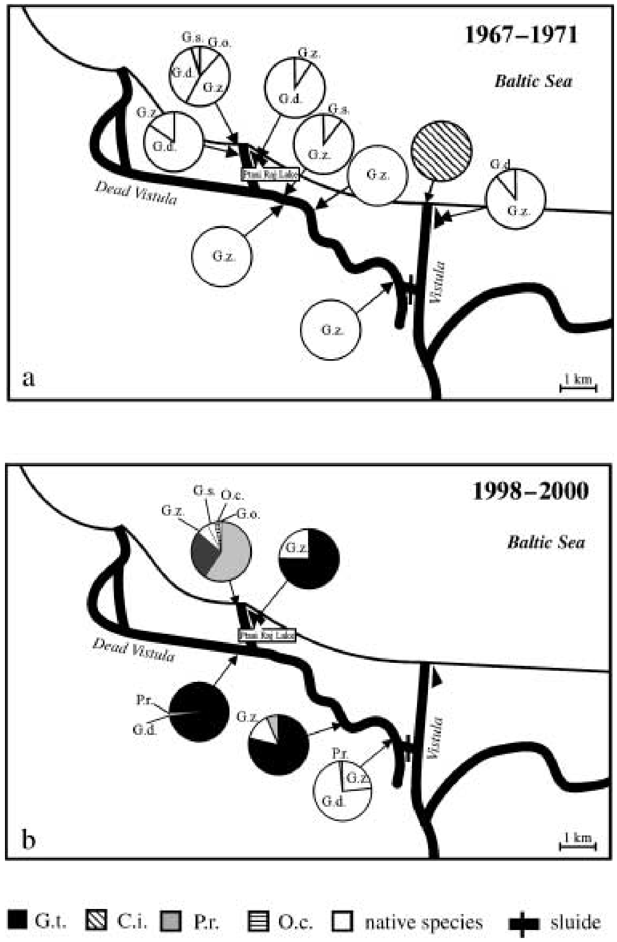

Figure 4 Species composition of gammarid populations in the Dead Vistula a. Data after Jazdzewski (1975); H. Kaczmarek, unpublished data b. Present study. Invasive species: C.i. — *Chaetogammarus ischnus*, O.c. — *Obesogammarus crassus*, P.r. — *Pontogammarus robustoides*, G.t. — *Gammarus tigrinus*. Native species: G.d. — *Gammarus duebeni*, G.z. — *Gammarus zaddachi*, G.s. — *Gammarus salinus*, G.o. — *Gammarus oceanicus*.

Native *G. duebeni* was found infrequently and mainly in the easternmost part of Dead Vistula, near the sluice. *G. zaddachi* was still numerous near the sluice. Non-indigenous *O. crassus* and *P. robustoides* were noted in the Dead Vistula only in 2000, the latter being rather numerous in one sample (Fig. 4b).

The above changes may be summarized as follows (Fig. 5):

1 At the beginning of the 20th century, in the freshwater flow of the Vistula River, the native *G. pulex* (and possibly also *G. varsoviensis*) was replaced by the Ponto-Caspian invader, *C. ischnus*. By the end of the millennium, a new Ponto-Caspian invader, *Dikerogammarus haemobaphes*, using the same corridor (i.e. the Pripet–Bug canal), had to a large extent replaced *C. ischnus*, the former being now the dominant species in the lower Vistula (including its deltaic area) and also having entered the Vistula Lagoon at its least saline part.

2 Near the end of the 20th century, *Pontogammarus robustoides* and *Obesogammarus crassus* invaded the Vistula Lagoon, most probably from the Curonian Lagoon in Lithuania where they were introduced in the 1960s (Gasjunas, 1968). During that time, Soviet mass-introductions of Ponto-Caspian species into rivers, lakes and other reservoirs occurred commonly (Karpevich, 1975). The Curonian Lagoon is connected with the Vistula Lagoon by the freshwater system of the Pregola (Pregel) River. Both species tolerate freshwater and brackish conditions, and could easily have also used the littoral Baltic waters of salinity around 7 PSU as a migration route. Another, somewhat less possible route of *P. robustoides* arrival might have been the

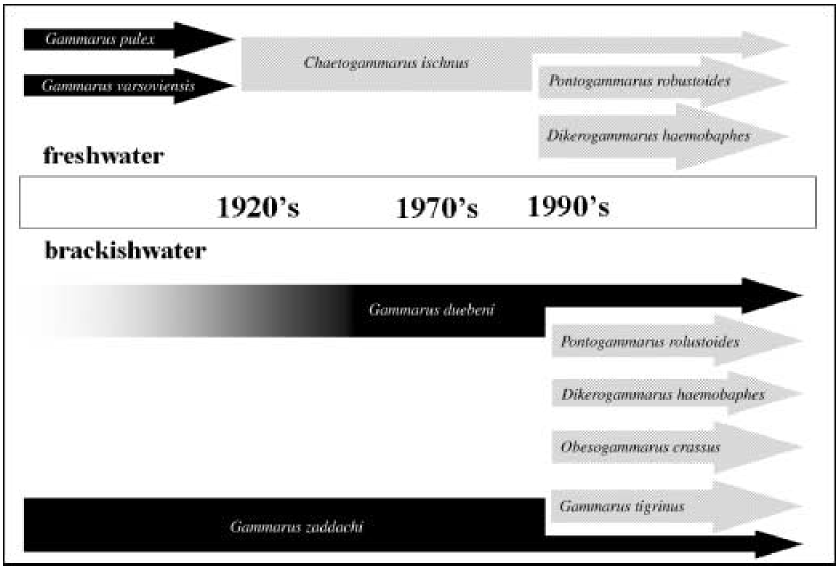

Figure 5 Sequential replacement of native gammarid species by invader gammarids in the Vistula deltaic system.

Pripet–Bug canal, as this species was noted in the lower Vistula flow in 1998 (Jazdzewski & Konopacka, 2000).

3 In the 1950s, a North American brackish-water species, *G. tigrinus*, was introduced to western European waters (Pinkster *et al*., 1980, 1992; Platvoet, 1989). This species has extended its range from the west to the east, most likely via the Baltic Sea coast (Bulnheim, 1976), but also possibly through the German Mittelland-canal (Martens & Eggers, 2000). *G. tigrinus* thrives especially well in oligohaline waters, and is very successful in the Dead Vistula, and in the Vistula Lagoon. Due to eutrophication of these water bodies, the native *G. zaddachi* was first replaced in the 1970s by *G. duebeni*, a species which tolerates wide fluctuactions in temperature, oxygen content, and salinity better than other gammarid species (Segerstråle, 1947; Kinne, 1959; Rygg, 1972). The second step is the more or less contemporaneous invasion of *G. tigrinus* from the west and *P. robustoides* and *O. crassus* from the east (and possibly south). These nonindigenous species are now conspicuous in gammarid zoocenoses in brackish basins of the Dead Vistula and Vistula Lagoon. The prevalence of one or another species in particular samples from these two basins may depend on local, variable conditions, and/or their life cycles. Mechanisms of the coexistence and competition of these native and invader gammarids of brackish-waters is of great interest and needs further studies.

Why we do observe this quite recent success of invasive gammarids in Baltic inshore waters (particularly lagoons and estuaries as well as in many large European rivers (Vistula, Elbe, Danube, Rhine and its delta) (Bij de Vaate *et al*., 2002)?

All the newcomers to the Vistula River deltaic region discussed are brackish-water species originally inhabiting the mixohaline zone of the PSU (practical salinity units) usually between 1 and 10 (Mordukhai-Boltovskoi, 1960, 1964; Bousfield, 1973). In that salinity range, and sometimes even beyond this range, these gammarid species exhibit considerable euryhalinity. A likely reason allowing such species to penetrate rivers and canals could be the increase of ionic concentration in large European rivers caused by agricultural and industrial pollution throughout the 20th century. That could be a trigger for the wave of invasions especially in the case of Ponto-Caspian species. One should remember that, for them, the physical barriers between different European catchment areas were broken long ago, by the construction of canals in 19th or even 18th century (Jazdzewski, 1980). Similar suggestions can be found in the recent paper by MacIsaac *et al*. (2001).

On the other hand, we also have to consider the recent climate warming tendency which could widen the geographical ranges of Ponto-Caspian species, which originate from warmer areas than the North European boreal climatic conditions.

In general, we would favour the opinion expressed by Ricciardi & MacIsaac (2000) that '*aquatic invasions are modified more by dispersal opportunity and favourability of abiotic conditions … than by the composition of the recipient community …*', and not the suggestion by Wolff (1999) that the enhanced number of nonindigenous species in European brackish-waters comes from the presence of empty niches in these habitats; native gammarids occupy in principle the same ecological niche as invaders which clearly dominate at present in the deltaic Vistula River waters and also other southern Baltic lagoons and estuaries.

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