

Four Ponto-Caspian and one American gammarid species (Crustacea, Amphipoda) recently invading Polish waters

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Abstract

The paper discusses recent drastic changes in the composition of Polish gammarid fauna, that occurred at the end of 20th century. This change was caused by the invasion of five alien species – four of Ponto-Caspian origin (*Dikerogammarus haemobaphes*, *D. villosus*, *Obesogammarus crassus* and *Pontogammarus robustoides*) and one of American origin (*Gammarus tigrinus*). Probable invasion routes are presented.

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Introduction

Geographical ranges of animals and plants change permanently in time, however these changes, when natural, are slow from the human point of view. Even the geologically young formation of the present North-European fauna, that has begun after the last Würm glaciation and continues till now for some 15 thousands of years, from our perspective is a rather long process. The rapid development of civilisation, and especially of human intercontinental migrations commencing some 5 centuries ago, have accelerated seriously biogeographical changes by intentional acclimatisations, accidental introductions

(Di Castri 1989) and, in the case of freshwater fauna, by the construction of artificial waterways joining formerly separate river systems (Jazdzewski 1980).

Central Europe is drained by the rivers discharging into the North Sea, Baltic Sea and Black Sea. The constructions of man-made canals joining these different basins started in XVIIIth century and during two next centuries these three basins were interconnected in several ways. Major important canals to be mentioned here are those connecting the Elbe and Oder (opened in 1746), the Oder and Vistula (1774) and the Vistula and Dnieper systems (1784, Bug – Pripet' canal) (Jazdzewski 1980).

The area of Poland belongs nearly entirely to the Baltic Sea basin, and some 90% of this territory belongs to the Oder and Vistula drainage systems. Only the minor part of northern Poland is drained by smaller rivers emptying directly into the Baltic Sea.

Until recently gammarid species were usually recognised as members of the extra-large family Gammaridae. Amphipod genera ascribed to this family *sensu* Stebbing (1906) appeared to be really not related to each other, however this old familial arrangement, especially of freshwater, Holarctic Amphipoda, persisted very long. Stock (1968, 1974), Karaman (1977), Bousfield (1977, 2001) and Barnard & Barnard (1983) made attempts to group the phyletically related „gammarid” taxa using much more detailed morphological analysis.

Starting from the fundamental paper by Sars (1894-1895) the rich, originally Ponto-Caspian amphipod fauna was usually considered to form a part of the family Gammaridae *sensu lato* (i.a. Carausu

et al. 1955, Birshstejn & Romanova 1968, Mordukhaj-Boltovskoj *et al.* 1969), although already Martynov (1924) commented some special morphological features of many “gammarids” of the so called Ponto-Caspian complex – the features that he has named “pontogammarisation”. Stock (1974) has distinguished a group named “*Dikerogammarus-Pontogammarus* complex” encompassing such genera as *Dikerogammarus*, *Pontogammarus*, *Stenogammarus*, *Niphargoides* and several others as well as a newly erected *Obesogammarus*. This group was formally named “family Pontogammaridae” by Bousfield (1977) who has distinguished tentatively 10 family-groups or families (i.a. Gammaridae, Pontogammaridae, Anisogammaridae etc.) forming together the superfamily Gammaroidea. Barnard & Barnard (1983) have put *Gammarus*-like genera in the “Gammaroid-group” (that could be possibly situated at the supra-familial level); in this group these authors formally distinguished family Gammaridae with genus *Gammarus* and several Caspian and Baikalian genera, and 13 groups, possibly of familial level with such master genera as *Echinogammarus*, *Dikerogammarus* and *Pontogammarus*, among others. Until any solid cladistic analysis of all “gammarid” genera is done, we follow the Bousfield’s (1977, 2001) classification of Ponto-Caspian gammarids in the family Pontogammaridae, leaving the genera *Gammarus*, *Echinogammarus* and *Chaetogammarus* in the family Gammaridae s.str., and retaining the widely used vernacular name “gammarid” for both the superfamily Gammaroidea sensu Bousfield (1977) and a “Gammaroid-group” sensu Barnard & Barnard (1983).

Our department has studied for several decades the gammarid fauna of Poland. We have collected and determined altogether some 60,000 individuals in about 1200 samples taken in the whole country. The data obtained till 1990 were summarised in two monographs by Jazdzewski (1975) and Jazdzewski & Konopacka (1995). At that time Polish gammarid fauna encompassed 15 gammarid species.

Results of our recent studies (1997-2001), focusing on large rivers (more than 100 samples collected, altogether around 3000 specimens), together with the results obtained by Gruszka (1995, 1999, 2001) in the Oder estuary, allowed to enrich the

list of Polish gammarids with 5 alien species, and to recognise their most probable invasion routes.

Review of recent immigrants

Dikerogammarus haemobaphes (Eichwald, 1841)
For the first time in the Baltic Sea basin, the species was recorded in Poland in 1997 (Konopacka 1998). The range expansion of this Ponto-Caspian invader in European waters and in Poland was already presented by Jazdzewski & Konopacka (2000). Recently, we discovered large population of *D. haemobaphes* in the Vistula Lagoon, Gruszka (2000) and Müller *et al.* (2001) found this species in the lower Oder river.

Dikerogammarus villosus (Sowinsky, 1894)
The species was recently recorded in the Oder river, in 1999 (Gruszka 2001, Müller *et al.* 2001, Jazdzewski and Konopacka 2002) downstream of the canal connecting the Oder river with the Elbe basin. The penetration of *D. villosus* into the Oder basin is especially interesting since it has used first the so-called southern corridor, i.e. Danube river, for westward range expansion (Bij de Vaate *et al.*, 2002). In the upper reach of Danube river *D. villosus* was first recorded by Tittizer *et al.* (1994) in 1992, and soon it has penetrated into the Rhine river via the Main – Danube canal (Bij de Vaate & Klink 1995). From the Rhine river *D. villosus* continued range expansion eastward by using the Mittellandcanal joining the Rhine, Weser, Elbe and Oder basins (Grabow *et al.* 1998, Zettler 1998, Rudolph 2000). In the lower Oder river, the species co-occurs with other alien gammarids, like *D. haemobaphes*, *P. robustoides* and *G. tigrinus* (Müller *et al.* 2001, own unpubl. data).

Pontogammarus robustoides (G.O. Sars, 1894)
First records of *P. robustoides* come from north-western Poland. Gruszka (1999) found this species in the Szczecin Lagoon and the lower Oder river in 1988. The species was also reported from the lower Vistula river (Konopacka 1998) and from the Vistula Lagoon (Jazdzewski & Konopacka 2000). *Pontogammarus robustoides* reached the Vistula and Oder deltaic systems possibly with ballast waters via

Baltic Sea from the Neman river system and Curonian Lagoon, where it was introduced in the 1960s (Gasjunas 1972, Arbaciauskas, 2002). However, the species could also have entered the Vistula Lagoon through the Pregola river system connecting the Vistula river delta with the Curonian Lagoon. More details on the origins and distribution routes of the mentioned species in Europe can be found in Jazdzewski & Konopacka (2000).

Obesogammarus crassus (G.O. Sars, 1894)

This species is most recently discovered in Polish waters, namely in the Vistula Lagoon and in the Dead Vistula in 1998 (Konopacka & Jazdzewski, 2002). Original distribution areas of *O. crassus* encompassed offshore Caspian Sea waters and lower courses of rivers emptying to this water body; in the Volga river the species penetrated upstream as far as to Volgograd (Mordukhajt-Boltovskoj 1979). In the Black Sea system *O. crassus* occurred originally in brackish lagoons and in the lower courses of large rivers (Dedju 1980, Jazdzewski 1980). In the Danube river it was noted as far upstream, as in its Yugoslavian sector (Dudich 1967). Like *P. robustoides*, *O. crassus* was transplanted in early 1960s into the Kaunas artificial reservoir on the Neman river in Lithuania and from there, after acclimatisation, it entered the Curonian Lagoon (Gasjunas 1972, Arbaciauskas, 2002). Subsequently it entered the Vistula Lagoon, most probably via the Pregel river system. However, due to its comparatively high euryhalinity, *O. crassus* could have also dispersed south-westwards along the Baltic Sea shores, with the average salinity of 7 PSU in this region.

Gammarus tigrinus Sexton, 1939

This North American euryhaline species was observed in waters with salinities ranging from 1 to 25 PSU (Bousfield 1973). Information on its introduction and distribution routes in Europe have been summarised by Jazdzewski & Konopacka (2000). First observations of *G. tigrinus* in Polish waters were done in 1988 in the Szczecin Lagoon (Gruszka 1995, 1999, Wawrzyniak-Wydrowska & Gruszka 2001). Recent survey of the entire Oder river (unpublished data) proved that *G. tigrinus* entered this river upstream as far as to the city of Opole. The

localities of the species in the Vistula Lagoon are by now the easternmost ones in Europe.

The present state of Polish gammarid fauna

The gammarid fauna of Poland is comparatively well known (Jazdzewski & Konopacka 1995, Gruszka 1995, 1999, Konopacka 1998, Konopacka & Jazdzewski 2002). Native freshwater taxa are *Gammarus pulex*, *G. fossarum*, *G. lacustris*, *G. varsoviensis*, *G. leopoliensis* and *G. balcanicus*, whereas the Baltic autochthonous species are *G. zaddachi*, *G. salinus*, *G. duebeni*, *G. locusta*, *G. inaequicauda*, *G. oceanicus* and *Chaetogammarus storerensis*. *Gammarus roeselii* was recognized by Jazdzewski & Roux (1988) as a species of Balkan origin, possibly recently (in XIX century?) entering western and northern Europe via the Danube system. It has possibly used the Danube-Rhein canal and Mittelland-canal in its westward and then eastward range expansion. Until recently the only evidently alien gammarid species was *Chaetogammarus ischnus*, discovered in the Vistula river in 1928 (Jarocki & Demianowicz 1931). This species has surely used the Bug-Prypet' canal for range extension from the Dnieper system westward. In the last decades we face an increasing number of invasions of new alien species in Polish waters (Fig. 1). In quite a short time Polish gammarid fauna has been enriched by 5 species: four of Ponto-Caspian origin (*Dikerogammarus haemobaphes*, *D. villosus*, *Pontogammarus robustoides* and *Obesogammarus crassus*) and one from North America (*Gammarus tigrinus*). Two of these immigrants, *G. tigrinus* and *D. haemobaphes*, dominate now the gammarid fauna of lotic environments in the Oder and Vistula rivers, respectively. In the Oder river *G. tigrinus* is the most common and widespread species, entering upstream as far as nearly to the city of Opole, being the only gammarid species there. In the lower Oder river, especially downstream of its connection with Spree – Havel system and of the Warta river mouth, *Dikerogammarus haemobaphes* joins *G. tigrinus*, and, according to Müller *et al.* (2001) could be even a dominant gammarid in mixed populations. On the other hand *D. haemobaphes* has conquered nearly the entire Vistula river, occurring

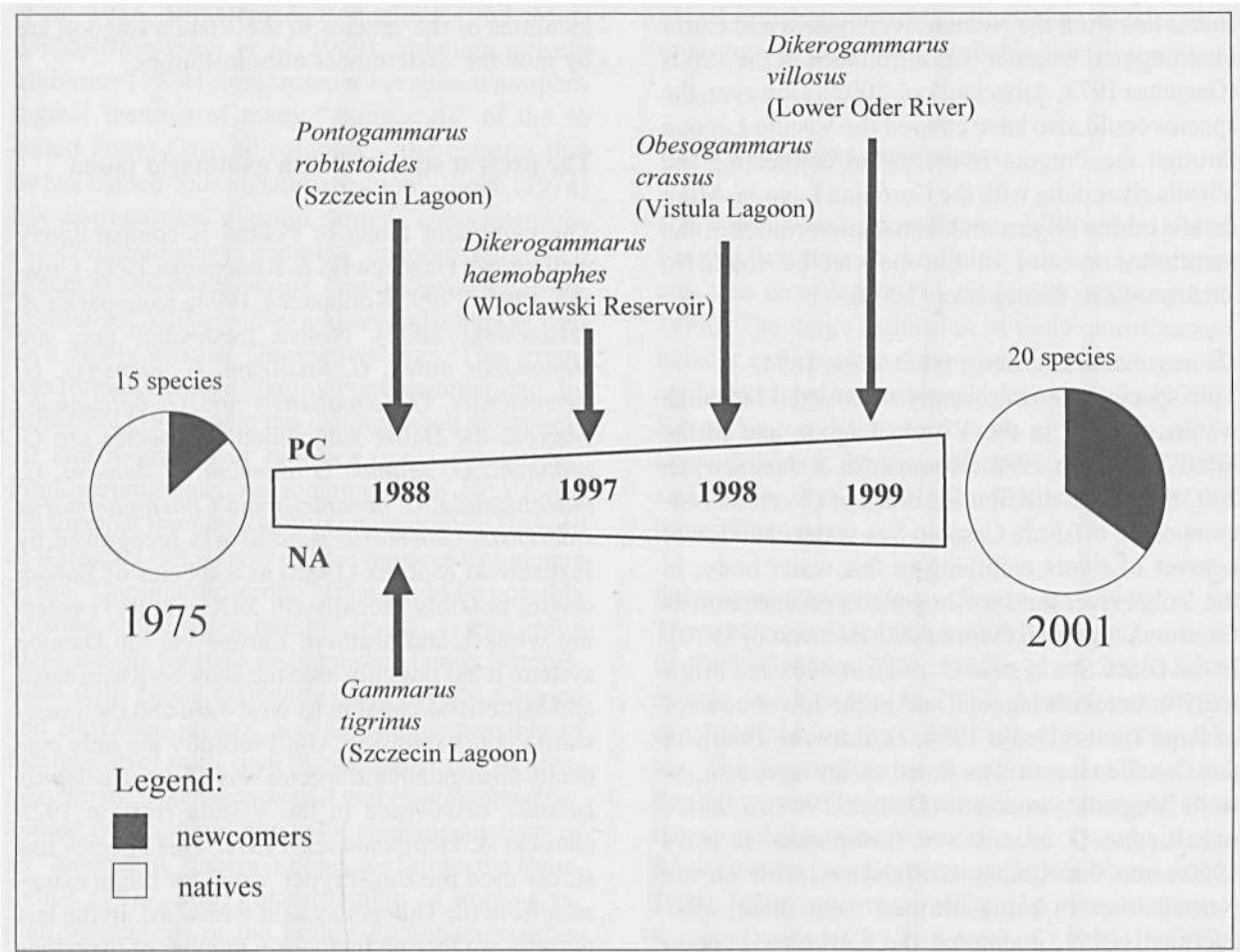


Fig. 1. Changes in gammarid fauna of Polish waters. Place of first record indicated in brackets. PC – Ponto-Caspian species. NA – North American species.

usually as an only gammarid species as far upstream as about 100 km below Cracow. In the lentic conditions of the artificial Wloclawek reservoir in the middle/lower Vistula section, *D. haemobaphes* was outcompeted by *Pontogammarus robustoides*. Downstream of this reservoir the more rheophilous *D. haemobaphes* regained its dominance.

Populations of native gammarid species – *Gammarus pulex*, *G. fossarum*, *G. varsoviensis*, and the earlier immigrant *G. roeselii* – were only recorded in some tributaries.

In the β -oligohaline waters of the Szczecin Lagoon two alien species dominated the gammarid fauna – *G. tigrinus* and *P. robustoides* (Wawrzyniak-Wydrowska & Gruszka 2001). In the mostly α -oligohaline Vistula Lagoon, in its southern part,

the gammarid fauna was dominated by either *Obesogammarus crassus* and *G. tigrinus* or *P. robustoides* and *O. crassus*. In both cases a small admixture of *Gammarus duebeni* occurred. *D. haemobaphes* also occurred in numbers in the less saline (β -oligohaline) part of the Lagoon influenced by the Nogat arm of the Vistula. The gammarids occurring along the northern shores of the Vistula Lagoon were mostly dominated by *G. duebeni* or by *G. tigrinus*, other species found were *P. robustoides*, *Gammarus zaddachi* and *O. crassus*. In brackish water of the former Vistula section, called the Dead Vistula (salinity 2-7 PSU) the most common and usually dominant gammarid is *G. tigrinus*, most often accompanied by *G. zaddachi*, sometimes by *D. haemobaphes* and rarely by *G. duebeni*, which was, however,

the dominant species at the least saline station near the dam separating Dead Vistula from the Vistula river. It is worth while to note, that these same brackishwater bodies – Vistula Lagoon and Dead Vistula – at least till the 1970s, were mainly inhabited by *G. zaddachi* and *G. duebeni* with varying dominance of one or another species and a very rare presence of *Gammarus salinus* and *G. oceanicus* at the entrance of Dead Vistula to the Baltic Sea (Zmudzinski 1957, Arndt 1965, Jazdzewski 1975, and unpubl. observations).

Discussion

There are several possibilities for gammarid species to extend their original distribution areas. Quite natural way is their upstream migration, especially in large rivers. Segerstrale (1954) suggested that, at least in the case of *Gammarus lacustris*, the transport by birds could be responsible for the wide distribution of this species in Holarctic. However, in most of the cases discussed we have to do with various kinds of human impact. The construction of canals connecting different drainage areas is one of fundamental reasons of the penetration of particular species into sometimes distant regions. Another factor, often connected with the former one, are intentional introductions of species aimed at the enrichment of fish food resources (Karpevich 1975, Arbaciauskas 2002). In Europe the impact of these both factors upon the range extensions of various amphipod species were amply discussed by Jazdzewski (1980) and, more recently, various alien freshwater invertebrates penetration in western Europe as well as the ecological impact of these invaders were summarised, i.a., by Kinzelbach (1995), Tittizer (1996), Jazdzewski & Konopacka (2000), Van der Velde *et al.* (2000), Tittizer *et al.* (2000) and Bij de Vaate *et al.* (2002).

One should consider of course, also the possibility of introductions of alien gammarids, for instance by the transfer of aquatic plants; such possibility was suggested for *Gammarus roeselii* by Jazdzewski & Roux (1988).

The ballast water transport also cannot be excluded as a factor accelerating gammarid range extensions and, in the case of transatlantic, inva-

sions of freshwater or oligohaline species (e.g. the case of *Chaetogammarus ischnus*, Witt *et al.* 1997) such transport seems to be the major possibility.

However, in European waters, after breaking physical barriers, migrations through canals and along the brackish Baltic Sea littoral waters were the most important way of range extensions. This semi-natural penetration can occur within the same or adjacent biogeographical province of identical or similar climatic conditions.

Recent invasion routes of alien gammarid species in Polish waters are illustrated by Fig. 2. This scheme is based upon the distribution of new and old records of alien gammarids along the Polish river courses given in detail by Jazdzewski & Konopacka (2002).

The invasion of many Ponto-Caspian species in European freshwaters, and, via freshwaters, into brackish coastal waters of the Baltic and North Seas, is related to their typically oligohaline preferences and relatively high euryhalinity. Most of these species originally live in estuaries and lagoons of the Black and Azov Seas of a low salinity (0.1-7 PSU but mostly 0,5-5 PSU (Mordukhaj-Boltovskoj *et al.* 1969, Dedju 1980)) as a relict fauna of the Sarmatian or Pontian Age.

The endemic Ponto-Caspian crustacean fauna is probably of a freshwater origin; at present various species exhibit various grades of euryhalinity. In the Caspian Sea itself over 70 endemic malacostracan species were recorded, of them some 15 species (mostly amphipods) penetrated in different distances upstream the Volga river – those being the most euryhaline taxa (Mordukhaj-Boltovskoj & Dzjuban 1976).

Gammarid species of the so-called Ponto-Caspian complex (see Mordukhaj-Boltovskoj 1964) in general do not occur in the open (central) Baltic Sea of the surface salinity 7-8 PSU, or at least do not compete with native fauna. On the other hand such species, like *Chaetogammarus ischnus*, *Pontogammarus robustoides*, *Dikerogammarus haemobaphes*, *D. villosus* and *Obesogammarus crassus* are found only in freshwaters or in oligohaline lagoons like Vistula Lagoon (salinity 2-5 PSU) or Szczecin Lagoon (0,5-1,5 PSU) and only there they really may compete with success with native fauna; the same is true for Curonian Lagoon, possibly for

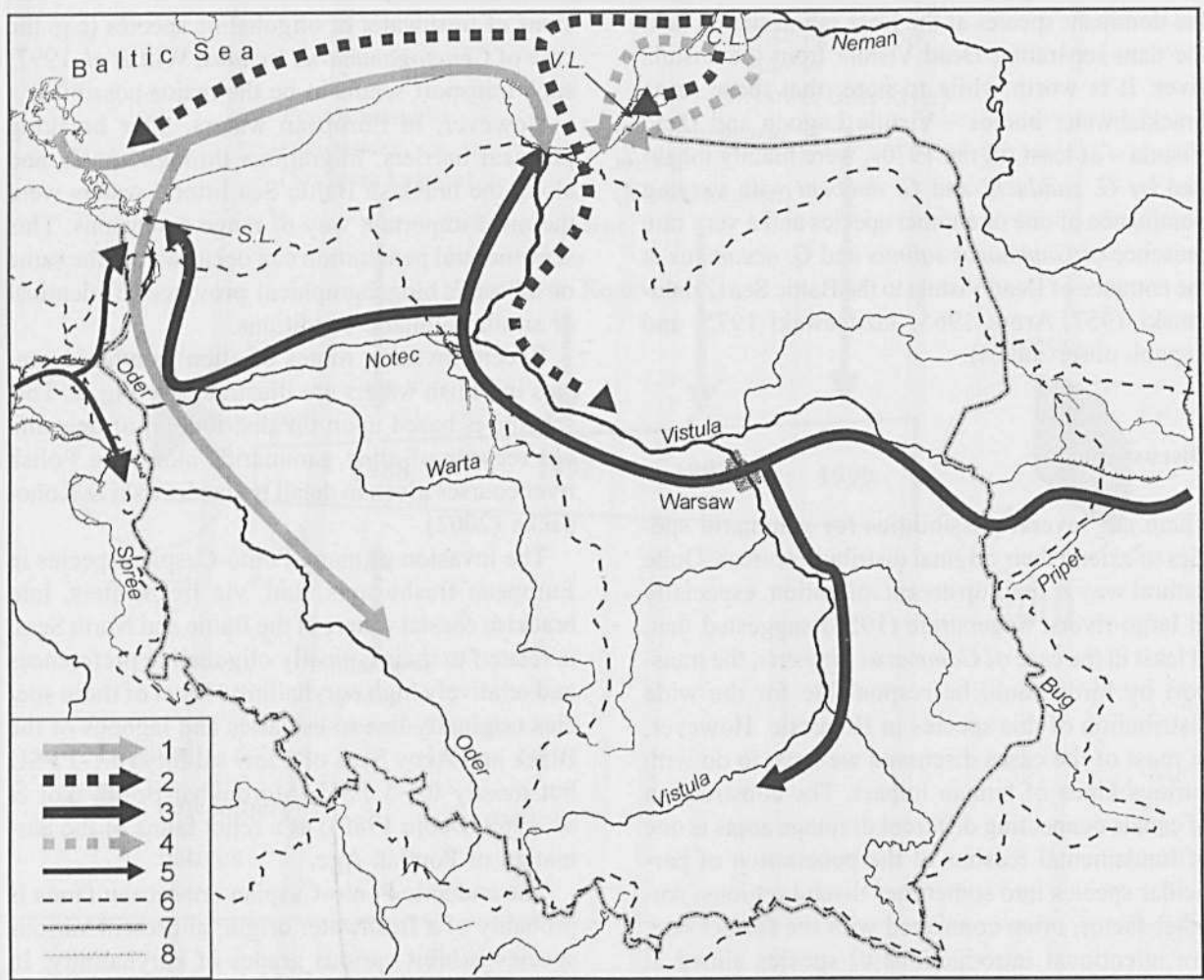


Fig. 2. Immigration routes of invasive gammarid species in Polish waters. 1 – *Gammarus tigrinus*, 2 – *Pontogammarus robustoides*, 3 – *Dikerogammarus haemobaphes* (and *Chaetogammarus ischnus*, except upstream of Warsaw), 4 – *Obesogammarus crassus*, 5 – *D. villosus*, 6 – basin boundaries, 7 – country borders, 8 – artificial waterways, V.L. – Vistula Lagoon, S.L. – Szczecin Lagoon, C.L. – Curonian Lagoon.

Gulf of Riga and Gulf of Finland.

Similar oligohaline preferences of *Gammarus tigrinus* have been mentioned several times in the literature (Bulnheim 1976, Pinkster *et al.* 1992).

Although the first record of the invading species may be somewhat delayed and the really first occurrence of a taxon in new place surely precedes this first record, one can assume that this delay is not longer than, say, 3-5 years, taking into account still more and more detailed monitoring of European rivers.

An interesting question arises – why we do observe this rather recent massive invasions of various Ponto-Caspian species in central and western

Europe? (Jazdzewski & Konopacka 2000, Tittizer *et al.* 2000, Bij de Vaate *et al.* 2002, and unpubl. 2000/2001 observations). In Poland one of the reasons can be the increasing ionic content of large rivers in last decades, caused by the industrial pollution (Dojlido & Woyciechowska 1985, Szymanska 1990, Ficek & Ficek 1994). This rise in the „salinity” of such rivers like Vistula and Oder would finally reach the „critical point” allowing several species of oligohaline preferences to start their rather quick conquest of new basins. Obviously the increasing transport is also responsible, but when looking for a „trigger” of these invasions and attaining rich populations in the whole river flows in

comparatively short period the present authors would rather favor the above mentioned hypothesis.

Serious studies on the ecological impact of alien species upon the native fauna in the Vistula and Oder systems are still not undertaken. Quantitative studies on the fish and invertebrates diet are urgently needed to estimate this impact. The present paper shows merely the qualitative aspect of these invasions indicating their possible routes and actual faunistic changes.

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