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. vilosus, 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 Wiirm 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, Birshtejn & Romanova 1968, Mor-
dukhaj-Boltovskoj et al. 1969), although already
Martynov (1924) commented some special morpho-
logical 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 “Dikerogamma-
rus-Pontogammarus complex” encompassing such
genera as Dikerogammarus, Pontogammarus, Steno-
grammarus, Niphargoides and several others as well as
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.) form-
ing together the superfamily Gammaroidea. Barnard
& Barnard (1983) have put Gammarus-like genera
in the “Gammaroid-group” (that could be possibly
situatet at the supra-familial level); in this group
these authors formally distinguished family Gamma-
ridae with genus Gammarus and several Caspian
and Baikalian genera, and 13 groups, possibly of
familial level with such master genera as Echino-
gammarus, Dikerogammarus and Pontogammarus,
among others. Until any solid cladistic analysis of
all “gammarid” genera is done, we follow the Bous-
field’s (1977, 2001) classification of Ponto-Caspi-
an 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”

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

Results of our recent studies (1997-2001), fo-
cusing on large rivers (more than 100 samples col-
lected, 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 spe-
cies was recorded in Poland in 1997 (Konopacka
1998). The range expansion of this Ponto-Caspian
invader in European waters and in Poland was al-
ready 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, Jazd-
zewski and Konopacka 2002) downstream of the
canal connecting the Oder river with the Elbe ba-
sin. 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 Mittelland-
canal joining the Rhine, Weser, Elbe and Oder basins
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,
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). Ponto-
gammarus 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 (Mordukhaj-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. oceaneicus and Chaetogammarus stoerensis. 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
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 enrich 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 invasions 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 biogegraphical 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. villus* 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
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 do we 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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