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INVASIVE CRUSTACEA

How to be an invasive gammarid (Amphipoda: Gammaroidea)–comparison of life history traits

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Abstract About six life history and two ecological traits of gammarid species occurring in Central European waters were compared in order to identify the characters of successful invader. The species were (1) natives: *Gammarus fossarum*, *G. pulex*, *G. lacustris*, *G. varsoviensis*, *G. balcanicus*, *G. leopoliensis*, *G. roeselii*, and (2) aliens: *Gammarus tigrinus*, *Chaetogammarus ischnus* (=*Echinogammarus ischnus*), *Pontogammarus robustoides*, *Obesogammarus crassus*, *Dikerogammarus haemobaphes*, *D. villosus*. Generally the alien species were characterised by a combination of large brood size, high partial fecundity, early maturation and by appearance of higher number of generations per year. Also, these species presented higher tolerance towards severe environmental conditions, i.e. elevated salinity and human degradation of the environment. The above features seem to facilitate the colonisation of new areas and competition with native species – a phenomenon that has been currently observed in various parts of Europe.

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Invasive Crustacea

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Introduction

Amphipods of the superfamily Gammaroidea are widespread and constitute an important functional element of fresh and brackishwater ecosystems of Europe (Jazdzewski, 1980). In terms of abundance, they are frequently dominants or subdominants in littoral communities, particularly in rivers and streams. In such environments, they contribute significantly to energy flow by decomposing dead matter and constitute a significant or even a major part of diet of many fish species (Kelleher et al., 2000; Kostrzewa & Grabowski, 2003; Grabowska & Grabowski, 2005). Within the last century, the inland amphipod fauna of Europe have been increasingly threatened by the introduction of non-native amphipod species. A number of alien species has established successfully and formed self-sustaining populations, especially in big European rivers as Rhine, Moselle, Vistula, Oder as well as in their estuarine systems (Jazdzewski, 1980; Dick, 1996; Jazdzewski & Konopacka, 2000; Bij de Vaate et al., 2002; Konopacka & Jazdzewski, 2002). In a number of cases, the newcomers were able to compete successfully with native amphipod species and eventually dominate or even replace them (Pinkster et al., 1977; Dick

& Platvoet, 1996, 2000; Van der Velde et al., 2000; Jazdzewski et al., 2004). Most often, the aliens colonized waters in which the native species could not thrive, due to pollution, leading among other things to notable increases in the salinity of rivers (Jazdzewski et al., 2002). Also, they have been incorporated in local food webs, becoming an abundant prey for local fishes, particularly of families Percidae and Gobiidae (Kelleher et al., 2000; Kostrzewa & Grabowski, 2003; Grabowska & Grabowski, 2005).

Several attempts were already made to define what determines such success of the invasive amphipod species. Among the possible factors, life history traits were listed as of potentially great importance (Rajagopal et al., 1999; Van der Velde et al., 2000; Sakai et al., 2001; Bij de Vaate et al., 2002; Kley & Maier, 2003; Devin et al., 2004; Bacela & Konopacka, 2005). Features identified as promoting invasion success of aquatic invertebrates are, among others, relatively short generation time, early sexual maturity, high fecundity, size of an animal, euryoeciousness, euryhalinity (Bij de Vaate et al., 2002).

However, despite many works concerning life cycles of both marine and freshwater gammarids, no attempt has yet been made to highlight the traits that may contrast the native versus invasive species (Steele & Steele, 1975; Kolding, 1979, 1981; Nelson, 1991; Sainte-Marie, 1991). Thus, our goal was to review critically the life histories of several invasive and native gammarids occurring in Central Europe, in order to define the traits that may promote invasion of aliens in comparison with native species.

Materials & methods

Altogether, 13 species of gammarid amphipods inhabiting inland waters of Central Europe were used for the analysis. Among them there were seven native species: *Gammarus fossarum*, *G. pulex*, *G. lacustris*, *G. varsoviensis*, *G. balcanicus*, *G. leopoliensis* and *G. roeselii*. Among the above species, there are typical dwellers of lowland and submontane waters of various characters, including springs, streams, large lowland rivers and lakes. Of six alien gammarids, there was one North American species, *Gammarus tigrinus*, and five Ponto-Caspian newcomers: *Chaetogammarus ischnus* (=*Echinogammarus ischnus*), *Pontogammarus robustoides*, *Obesogammarus crassus*, *Dikerogammarus haemobaphes* and *D. villosus*.

All data included in the analysis were gathered through literature research, as indicated in Table 1. Taking into account the different life-cycle characteristics covered by various authors, we selected six life history traits that could be obtained for all the above species:

(a) Mean breeding female size (in mm) – measured from anterior head margin to the tip of telson.
(b) Brood size – mean number of eggs in a brood pouch.
(c) Partial fecundity index – defined as mean brood size/female size.
(d) Length of breeding period (in months).
(e) Relative age of reaching maturity – defined as minimal/mean breeding female size.
(f) Number of generations per year.

Additionally, two other variables that might possibly affect species invasiveness, were taken into account:

(g) Salinity tolerance – defined as maximum observed salinity level at which a particular species formed a self-sustaining populations in nature. Species were categorized in three classes according to that criterion: (1) salinity from 0–0.5 PSU, (2) salinity from 0.6–1 PSU, (3) salinity above 1 PSU.
(h) Tolerance to human impacts – defined as maximal level of pollution and habitat degradation in which a species may live and reproduce. As no comparable estimates exist in the literature, we identified three habitat classes with which to obtain a rough relative estimate: (1) clean or low polluted, (2) medium polluted, and (3) highly polluted.

All the above data and their sources are summarized in Table 1.

Taking into account the climatic and geographical variation, and to avoid possible differences in life cycle characteristics of the species related to geographical location of the studied populations,

Table 1 Data matrix of life history traits and ecological tolerance of analysed gammarid species

Species	Mean breeding female size (mm)	Mean brood size	Partial fecundity	Breeding period in months	Maturity index	Number of generations per year	Salinity tolerance	Human impacts	Sources
G. fossarum	10.14	16.88	1.66	10.00	0.79	2	1	1	Jazdzewski, 1975; Brzezinska-Blaszczyk & Jazdzewski, 1980
G. lacustris	11.28	18.75	1.66	4.00	0.71	1	2	2	Hynes, 1955; Hynes & Harper, 1992
G. varsoviensis	13.50	25.17	1.86	5.00	0.74	1	1	2	Jazdzewski, 1975; Konopacka, 1988
G. pulex	8.90	14.79	1.66	10.67	0.88	1	2	2	Hynes, 1955; Jazdzewski, 1975
G. leopoliensis	9.40	16.70	1.78	7.00	0.79	1	1	1	Zielinski, 1998
G. balcanicus	9.10	7.88	0.87	7.00	0.84	1	2	2	Jazdzewski, 1975; Zielinski, 1995
G. roeselii	12.55	25.60	2.04	6.00	0.68	2	1	2	Jazdzewski, 1975; Bacela, 2007
P. robustoides	12.65	64.45	5.10	7.00	0.63	3	3	3	Bacela & Konopacka, 2005; Dedju, 1966, 1967, 1980; Kasymov, 1960
D. haemobaphes	10.99	42.84	3.90	5.50	0.57	3	2	3	Musko, 1993; Kiticyna, 1980; Kurandina, 1975
D. villosus	11.39	50.66	4.45	11.00	0.57	3	2	3	Devin et al., 2004; Kley & Maier, 2003; Mordukhai-Boltovskoi, 1949
O. crassus	8.81	25.33	2.87	7.00	0.68	3	3	2	Kurandina, 1975
C. ischnus	7.83	17.33	2.21	8.00	0.64	2	2	2	Kley & Maier, 2003; Konopacka & Jesionowska, 1995; Kurandina, 1975; Mordukhai-Boltovskoi, 1949
G. tigrinus	7.94	20.31	2.56	9.00	0.50	3	3	3	Bousfield, 1958; Chambers, 1977; Pinkster et al., 1977; Steele & Steele, 1975

we concentrated on data from Central Europe (*G. fossarum, G. balcanicus, G. roeselii, P. robustoides, D. haemobaphes, C. ishnus*), from adjacent areas in Europe (*D. villosus, G. tigrinus, G. pulex*) or from areas of similar latitude (*G. lacustris).*

Data on the eight attributes for the 13 gammarid species were subjected to cluster analysis, using the Euclidean distances of the standardized (mean = 0, standard deviation = 1) variables, via the complete linkage (furthest neighbor) method. To explore patterns of association among life history traits and ordination of species, principal component analysis (PCA) was performed first on the six selected life history data, and then also with inclusion of the two additional variables for all the 13 gammarid species. Correlations between the first two principal component scores for each species and the original variables for each species were computed to provide an index of the relative importance of each variable in the ordination species into life history patterns. All the computations were performed with use of Primer 5 software.

Results

Clustering of the species based on Euclidean distance with use of all the eight variables grouped the species into two major groups (Fig. 1), one consisting of all the native species, and the other all the non-native species. PCA based also on all eight variables provided a similar ordination pattern (Fig. 2A). A group of native species and group including invasive am-

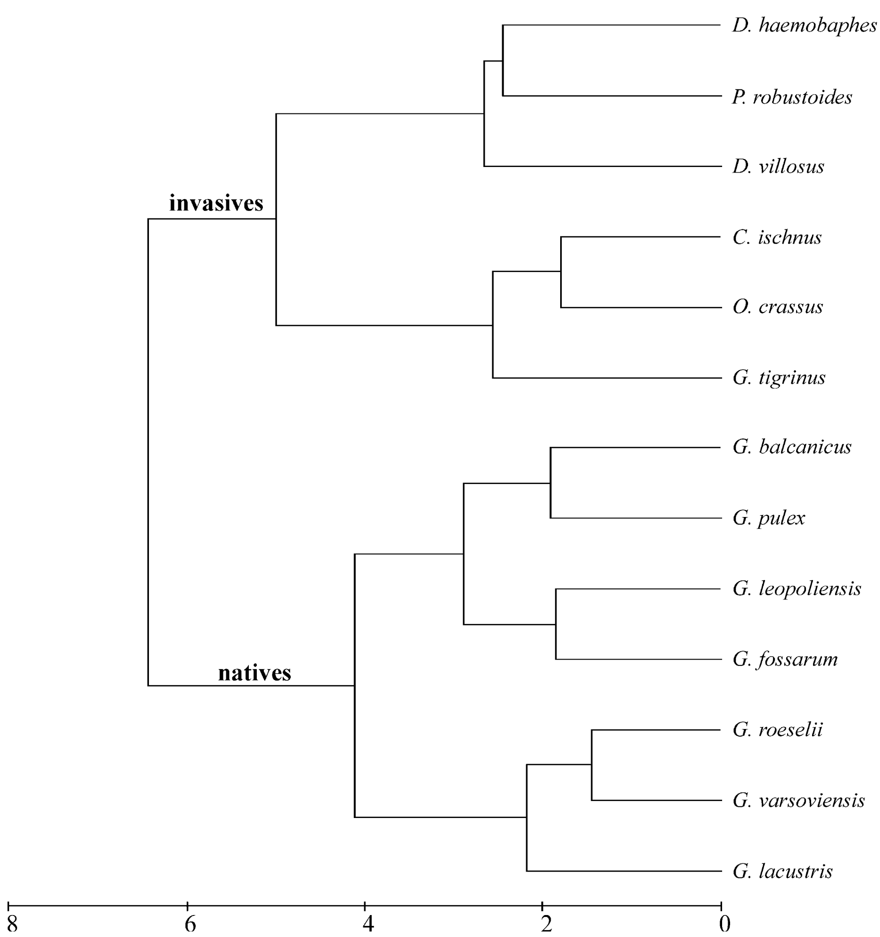

Fig. 1 Cluster diagram of 13 gammarid species based on normalized Euclidean distances counted from eight parameters

phipods can also be distinguished. Each group reflects a distinctive suite of life history attributes. In comparison with native species, the invasive species are generally characterised by larger brood sizes, higher partial fecundities, a greater number of generations per year, and earlier maturity. Also, the non-native species are able to tolerate higher salinities and greater human impact. Within both groups, assemblages related to female sizes can be observed: large invasives (*P. robustoides*, *D. villosus* and *D. haemobaphes*), smaller invasives (*G. tigrinus*, *Obesogammarus crassus*, *C. ischnus*), large natives (*G. varsoviensis*, *G. roeselii*, *G. lacustris*) and smaller natives (*G. leopoliensis*, *G. fossarum*, *G. balcanicus*, *G. pulex*). According to correlation values (Fig. 2B), the most important variable in PC1 was the breeding female size, and in PC2 – partial fecundity. Thus those variables had the highest impact on ordination pattern.

When only the six life history patterns were considered, we observed a very similar tendency

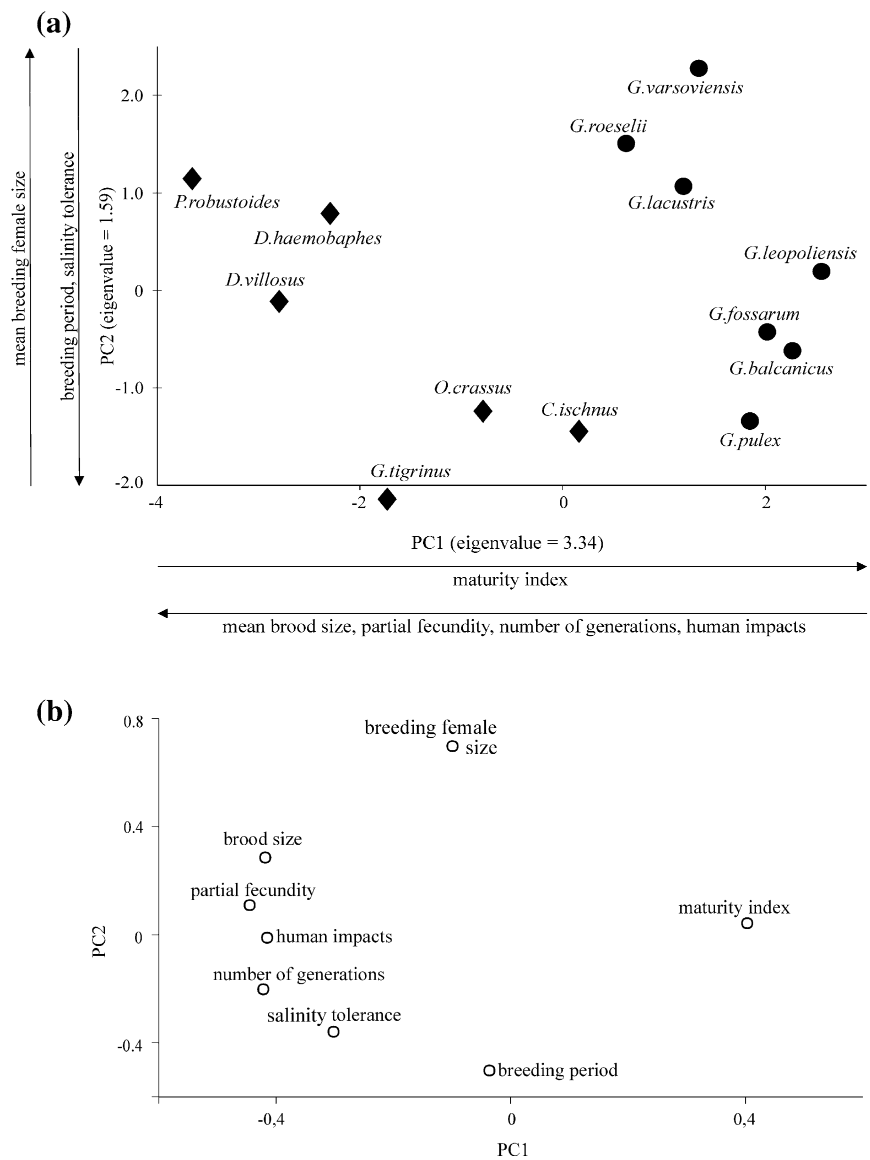

Fig. 2 (**A**) Scores for native and invasive gammarid species on the first two principal component axes based on eight life history and ecological variables. (**B**) Factor loadings of the eight life history and ecological variables used in PCA

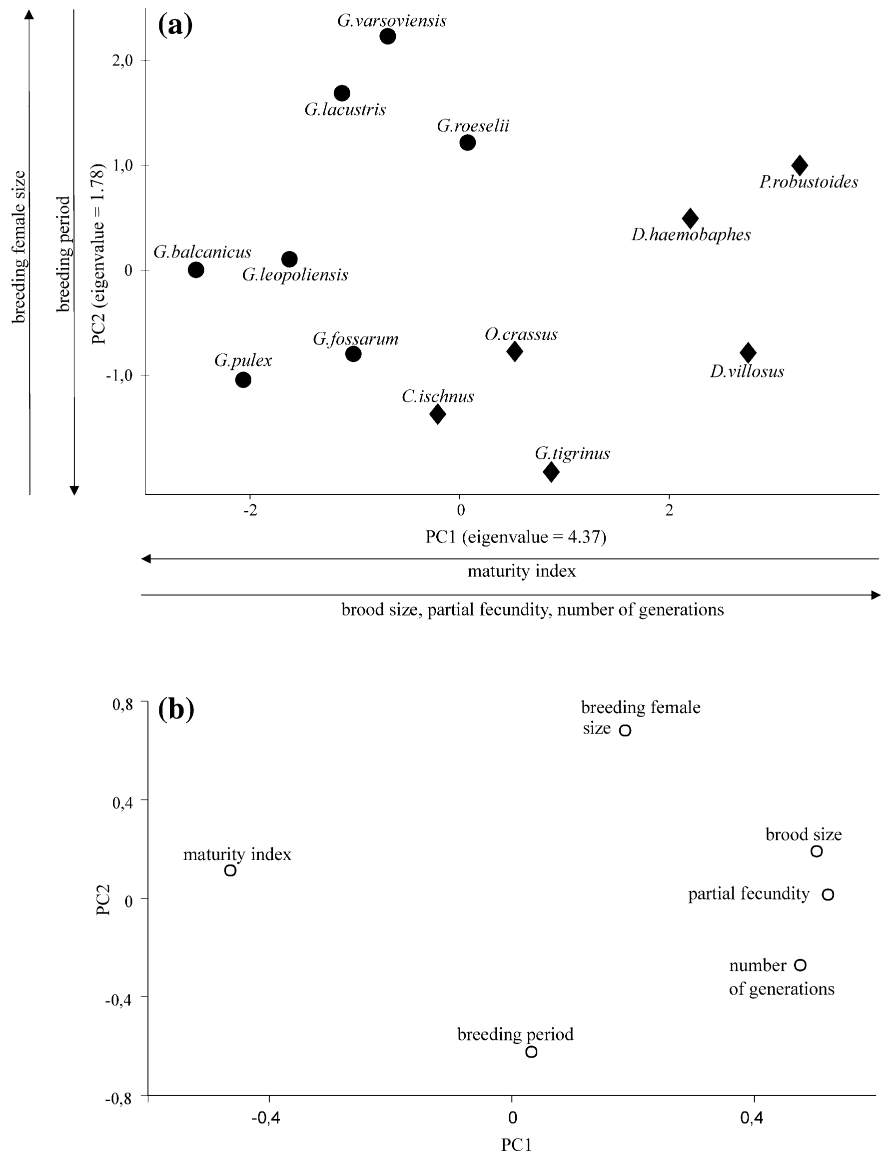

Fig. 3 (**A**) Scores for native and invasive gammarid species on the first two principal component axes based on six life history variables. (**B**) Factor loadings of the 6 life history variables used in PCA

(Fig. 3A), however the separation of invaders versus native species is not so well pronounced along the axes. In this case, the strongest variable in PC1 was fecundity, and in PC2 both correlated variables (breeding female size and breeding period) were of equal importance (Fig. 3B).

When data set consisting all the eight parameters were considered, the first two axes of the PCA modelled 76.9% of the total variation in the data set. In the case of six parameters, the first two axes explain 82.2% of the variation.

Discussion

Ecological tolerance is amongst the most important features of biological invasions in European rivers (Lozon & MacIsaac, 1997; Bruijs et al., 2001). Eurytopicity and euryoecious-ness are crucial for species' range extension (Lodge, 1993; Moyle & Light, 1996). As seen from our results, the life history parameters are crucially important for species establishment in a new environment and for population development. In numerous case studies, in particular the rivers Vistula, Oder, Rhine and Moselle, alien amphipods have successfully outnumbered and eventually replaced native species, especially in degraded and polluted habitats with elevated salinity (Van der Velde et al., 2000; Devin et al., 2004; Jazdzewski et al., 2002, 2004).

When omitting the ecological parameters in analysis, we obtain very similar order in grouping. The results suggest the type of life history can be as much important as ecological tolerance. The competition between two related species for resources is well known. The higher productivity of a species is a result of fecundity, embryological development time, time of gaining the ability to reproduce, mortality of juveniles etc. It enables one species to outnumber another species with lower potential (Poeckl & Humpesch, 1990; Poeckl & Timischl, 1990; Costello, 1993; Kley & Maier, 2003; Poeckl, 1993), such as is suggested in our analyses. Invasive species such as *P. robustoides*, *D. villosus* and *D. haemobaphes* have very high productive potential, which is expressed by very high fecundity, early maturity, and repeated reproduction (three generations) each year.

Obesogammarus crassus, *G. tigrinus* and *C. ischnus* are not so clearly distinguished from native species when only life history traits are considered (Fig. 3A). This may be explained by the very strong correlation of brood size with PC1 and breeding female size with PC2. These non-indigenous species are the smallest amongst all species analyzed, alien and native. They cannot produce large broods, being limited by the size of the brood pouch. However, they produce broods of sizes almost equal to those of much larger native gammarids (Table 1), which enables them to thrive in areas already inhabited by other species.

When comparing the fecundity parameters (brood size and partial fecundity) in species of similar size (i.e. *Dikerogammarus haemobaphes* versus *Gammarus fossarum*, *Pontogammarus robustoides* versus *G. varsoviensis*, or *Obesogammarus crassus* versus *G. pulex* and *G. balcanicus*), all of the non-native species are more fecund. For example, *P. robustoides* is up to three times more fecund than the indigenous *G. varsoviensis* (Table 1). When we add the ability to breed earlier, non-native populations can expand in a very short time, eventually outnumbering the natives, such as observed elsewhere (Kley & Maier, 2003).

All but one of the accounted alien amphipods are Ponto-Caspian endemics. Owing to complex geological history and changing environments of Caspian and Black Sea region, all of these gammarids are relatively euryhaline, euryoecious, omnivorous organisms – features making them preadapted to invade new environments (Dumont, 1998). It seems their invasions have possibly been aided by human impacts to European waters (e.g. eutrophication, pollution), which have led to a deterioration of the native fauna and to increased salinity levels, which have facilitated the establishment of the euryhaline, alien species (Bij de Vaate et al., 2002; Jazdzewski et al., 2004). *Gammarus tigrinus* is also an extremely euryoecious species, occuring in salinities from 0 to 25 PSU, e.g. all along the North American coast from Newfoundland to the Gulf of Mexico (Bousfield, 1958).

In conclusion, the life history traits and environmental parameters that distinguish the invasive versus native gammarids consist mainly of high fecundity (big brood size and high partial fecundity), early maturity, and elevated reproductive rate (large numbers of generations per year). These traits facilitate the invasion of European waters by alien species, which are also possess relatively high tolerances to environmental stressors such as salinity, pollution and habitat degradation. In contrast, native gammarid species are characterized by relatively small brood size, much lower partial fecundity and late reproductive ability. In most native species, we can observe only one generation per year, and their ecological tolerance is low compared to the non-native species.

Nonetheless, some species of gammarid native to Central Europe appear to be colonizing other territories as is e.g. in the case of *G. pulex*, which is an invasive species in Ireland (Costello, 1993; Dick et al., 1990, 1995), and is progressively colonizing areas of Brittany west of its previous range limit, coinciding with a westward regression in range by *G. duebeni celticus* (Piscart et al., 2007). Also *G. roeselii*, is expanding its range in fresh waters of Western Europe (Jazdzewski, 1980). Thus, it is always necessary to define the biological/ecological potential of the alien in the particular context, i.e. versus the species native to the area. Only this approach will permit determination of whether the alien may become a permanent element of the local fauna and of what may be its possible impact on the local amphipod communities.

Apart of the life history traits considered here, another factor promoting the successful invasion of the alien gammarids may be predation. This aspect of alien gammarid biology is still insufficiently studied. Until now, invasive *Gammarus pulex* in Ireland have been observed to prey efficiently on the native endemic *G. duebeni celticus* (Dick et al., 1990, 1995). Also, in the Netherlands and in Germany, *Dikerogammarus villosus* has been found to be a voracious predator responsible for the extermination of other macroinvertebrate species (Dick & Platvoet, 2000; Krisp & Maier, 2005). This lends support to our observations of *D. villosus* displacing *G. tigrinus* in the Oder River (unpublished data). However, despite the above data, the predatory abilities of other alien species, or their predation pressure on the local fauna has not yet been studied. Also there is no data upon possible displacement through predation among the native gammarid species, and therefore it was not possible to speculate further on this factor.

To estimate the entire biological potential and life strategy of a species, more detailed studies upon parameters (e.g. egg size, embryological development time, mortality of juveniles, life fecundity, feeding behaviour) should be conducted.

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