

Invasions of alien amphipods (Amphipoda: Gammaridea) in aquatic ecosystems of North-Western Russia: pathways and consequences

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Abstract Since the middle of the 20th century, six species of Ponto-Caspian amphipods (*Chaetogammarus ischnus*, *C. warpachowskyi*, *Chelicorophium curvispinum*, *Dikerogammarus haemobaphes*, *Obesogammarus crassus*, *Pontogammarus robustoides*), one Baikalian amphipod *Gmelinoides fasciatus* and one amphipod of Atlantic origin *Gammarus tigrinus* have expanded in Russia and adjacent regions. A wide variety of human mediated vectors such as deliberate and accidental introductions, natural migration via constructed inland waterways and high rates of spread, survival and reproduction in these species have facilitated rapid dispersal and successful establishment of these alien species. Causes of successful establishment of these invaders and potential consequences of the invasions including extinctions of native species in rivers, lakes and estuaries of north-western Russia are discussed.

Keywords Alien amphipods · Human mediated vectors · Waterways · Invasion success · Species replacements

Introduction

At present, the number of non-indigenous invertebrates in different parts of the world has increased, resulting in structural and functional changes of aquatic ecosystems (Cohen & Carlton, 1998; Lepäkoski et al., 2002). For example, during the last decade, five new amphipod species have been added to the list of fauna for Poland (Jażdżewski et al., 2002). The dispersal rate of a species and the ability to survive and reproduce in new conditions are important characteristics of invading species. As a rule, the dispersion of euryoecious species, including most amphipods, in different directions is a rapid process owing to the ability of a species to migrate great distances and successfully establish under new conditions. The aim of this paper is to analyse the possible pathways for recent amphipod invaders to European Russia, focusing mainly on the north-western region. Fundamental causes of invasion, or why a species was transported; possible invasion routes including known invasion corridors; vectors of invasions, or how a species is transported and consequences of their successful establishment are discussed.

Alien species of amphipods in inland waters of north-western Russia

There are eight amphipod species that have invaded north-western Russia and adjacent areas

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of the Baltic Sea basin (Table 1). Amphipods of the so-called Ponto-Caspian complex (*Chaetogammarus ischnus* (Stebbing), *Chaetogammarus warpachowskyi* (Sars), *Chelicorophium curvispinum* (Sars), *Dikerogammarus haemobaphes* (Eichwald), *Obesogammarus crassus* (Sars), *Pontogammarus robustoides* (Sars)) are the leading group in terms of number among these invaders. Three Ponto-Caspian species (*C. curvispinum*, *O. crassus*, *P. robustoides*) and one North-American *Gammarus tigrinus* Sexton have established in aquatic ecosystems of the Kaliningrad province in Russia (Ezhova et al., 2005). At least three species, *C. warpachowskyi*, *P. robustoides* and Baikalian *Gmelinoides fasciatus* (Stebbing) were recorded in the Gulf of Finland and aquatic ecosystems of the Leningrad province in Russia (Berezina & Panov, 2003a; Alimov et al., 2005). Findings of *C. warpachowskyi* were also reported from the Curonian Lagoon in Lithuania (Olenin & Leppäkoski, 1999; Jankauskienė, 2002). Recently, *G. tigrinus* was found along the Finnish coast in the Gulf of Finland (Pienimäki et al., 2004), from which it can penetrate the Russian area of the gulf. *C. ischnus* (Stebbing) was not found in the Russian part of the Baltic Sea, but presence of this species in the Vistula River (Poland) and in the Curonian Lagoon (Lithuania)

was recorded (Jażdżewski, 1975; Jażdżewski & Konopacka, 2002; Jankauskienė, 2002). At present, two species *D. haemobaphes* and *G. fasciatus* are widely distributed in central Russia, including the Upper Volga basin. These species have the status of active migrants and may appear in other areas of Russia and adjacent countries in the next few years.

The uncontrolled spread of invasive amphipods, such as *G. fasciatus* and *P. robustoides* in aquatic ecosystems of Russia has had a high ecological impact, leading to changes in pre-existing biota, losses of species diversity and destabilization of recipient ecosystems through food web alterations. Other non-indigenous species belong to invaders with medium and low ecological impacts on the ecosystems, as they do not have the potential to dominate the ecosystems and often coexist with populations of native species without affecting the dynamic structure and stability of the ecosystem.

Causes for the increasing rate of amphipod invasions in Russia and the former USSR

Factors influencing the dispersal rate of alien amphipods, as well as, many other groups of

Table 1 Alien amphipod species in the Russian part of the Baltic Sea basin and adjacent areas (according to Gasiunas, 1972; Olenin & Leppäkoski, 1999; Jadzewski & Konopacka,

2000; 2002; Arbaciauskas, 2002; Bakanov, 2003; Berezina & Panov, 2003; Ezhova et al., 2005; Jażdżewski et al., 2002; Bij de Vaate et al., 2002)

Species	Original area	Recipient region	First year of sighting	Vector of invasion
<i>Chaetogammarus ischnus</i>	Ponto-Caspian region	Vistula Lagoon Curonian Lagoon	1928 1960s	Construction of canals
<i>Chaetogammarus warpachowskyi</i>	Ponto-Caspian region	Curonian Lagoon Gulf of Finland	1960s 2004	Intentional introductions
<i>Chelicorophium curvispinum</i>	Ponto-Caspian region	Curonian Lagoon, Vistula Lagoon	1924 1920s	Construction of canals
<i>Dikerogammarus haemobaphes</i>	Ponto-Caspian region	Vistula Lagoon Upper Volga Reservoirs	1997 1990s	Construction of canals Range expansion
<i>Gammarus tigrinus</i>	North-American coast	Szczecin Lagoon Vistula Lagoon Gulf of Finland	1994 1998 2003	Shipping
<i>Gmelinoides fasciatus</i>	Baikal province	Gulf of Finland	1996	Intentional introductions
<i>Obesogammarus crassus</i>	Ponto-Caspian region	Curonian Lagoon Vistula Lagoon	1960s 1990s	Intentional introductions
<i>Pontogammarus robustoides</i>	Ponto-Caspian region	Curonian Lagoon Vistula Lagoon Gulf of Finland	1960s 1997 1999	Intentional introductions, shipping (?)

aquatic and terrestrial organisms are often associated with human activities. In different cases the factors can act additionally or antagonistically with each other or with natural processes.

The destruction of natural barriers between different basins of Europe in the 19th and 20th centuries is considered to be one of the most important factors, which has resulted in range expansion of many species in different directions (Jażdżewski, 1980). The majority of alien amphipods penetrated the Baltic Sea basin from basins of the Volga River, Caspian Sea, Black Sea and the Sea of Azov after the construction of artificial canals, reservoirs and drainage systems and the formation of water routes, or so-called invasion corridors (Fig. 1). At present, three inland invasion corridors are known for alien species to extend through Europe from the Ponto-Caspian basin to the Baltic Sea (Bij de Vaate et al., 2002). The Volga-Don, Volga-Baltic, Dnieper-Vistula and Danube-Rhine waterways are the most important significance corridors in the dispersal

of amphipods from the southern basin in a northern direction (Jażdżewski, 1980; Bij de Vaate et al., 2002; Slyn'ko et al., 2002). Construction of the Pripet-Bug canal (or King's Canal) connecting the Dnieper and Vistula systems has resulted in the range expansion of several Ponto-Caspian amphipods (*C. ischnus*, *C. curvispinum*, *P. robustoides*) to the Baltic Sea and western Europe (Jażdżewski, 1980; Bij de Vaate et al., 2002; Jażdżewski et al 2004). At the beginning of the 20th century, the Oginski' canal connecting the Dnieper and Neman systems facilitated the appearance of *C. curvispinum* in the Neman River and its dispersal to the Curonian Lagoon in the Baltic Sea, however, at present this old canal has no exit (Bij de Vaate et al., 2002). The Main-Danube canal, connecting the Rhine and Danube rivers, has also enabled four Ponto-Caspian species *C. curvispinum*, *Obesogammarus obesus* (Sars), *Dikerogammarus villosus* (Sowinsky), *D. haemobaphes* to enter the Rhine River from the Upper Danube River (Van der Velde

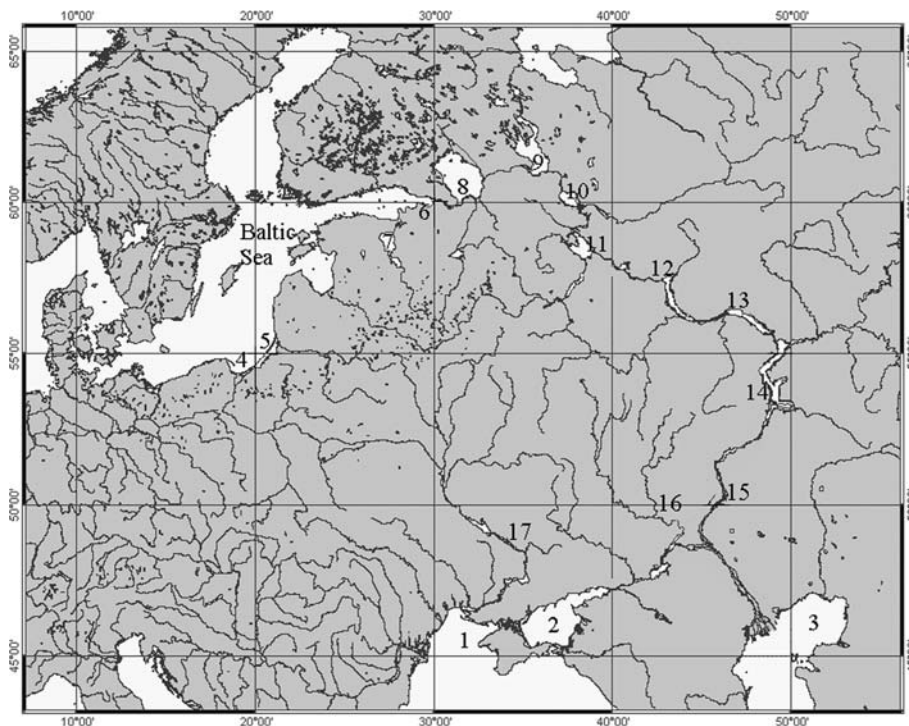


Fig. 1 Aquatic ecosystems of the north-western Russia and the Ponto-Caspian-Volga-Baltic waterway inhabited by alien amphipods: (1) Black Sea, (2) the Sea of Azov, (3) Caspian Sea, (4) Vistula Lagoon, (5) Curonian Lagoon, (6) Neva Estuary of the Gulf of Finland, (7) Lake Peipsi, (8)

Lake Ladoga, (9) Lake Onega, (10) Lake Beloe, (11) Rybinsky Reservoir, (12) Gor'kovsky Reservoir, (13) Cheboksarsky Reservoir, (14) Kuibyshevsky Reservoir, (15) Volga River, (16) Don River, (17) Dnieper River

et al., 2000; Bij de Vaate et al., 2002) and allowed one gammaridean amphipod of Balkan origin *Gammarus roeselii* Gervais to potentially spread into western Europe (Jażdżewski, 1980). Most likely, the Volga-Baltic waterway has played the main role in the dispersal of some amphipods (*G. fasciatus*, *D. haemobaphes*) as well as other crustaceans (*Cornigerius maeticus*, *Cercopagis pengoi*, *Eriocheir sinensis*, *Evadne anonyx*) in aquatic ecosystems of Russia. This waterway can also be considered as a possible invasion route of *G. fasciatus* from the Upper Volga basin to the Omega Lake (Berezina & Panov, 2003b).

Climatic change, such as global warming, together with the formation of European inland waterways may also have facilitated the rapid dispersal of some aquatic species, including thermophilous amphipods from southern rivers of Ponto-Caspian and Mediterranean basins to aquatic systems of central and northern regions (Dukes & Mooney, 1999; Slyn'ko et al., 2002). Actually, during the 20th century the average temperature of the earth's atmosphere was 1.0–3.5°C higher than in the 19th century (Houghton et al., 1996; Dukes & Mooney, 1999), which has resulted in the warmer winters at high latitudes.

Natural processes, as well as the downstream drift of benthic organisms in rivers could also favour the rapid spread of many amphipod species between different basins. For example, the total biomass of drifting crustaceans, including *Corophium* spp. in the Don River averaged 9 tons (wet weight) during the summer; although this weight increased significantly during the seasonal floods (Mordukhai-Boltovskoi, 1960). During flood periods in some locations of the Volga River, amphipods *Obesogammarus sarsi* (Sowinsky), *D. haemobaphes*, *P. obesus* and *C. curvispinum* have been transported downstream at a rate of >3,000 ind. per second (or 4.6 g s⁻¹) when the width of the river is taken into account (Lyakhov, 1961).

The ability of most amphipods to migrate long distances is a common behavioural trait in freshwater, as well as, marine ecosystems and has facilitated their natural range expansion. There are vertical and horizontal migrations, with cyclic (diurnal, seasonal) or acyclic characteristics (Dedyu, 1980). It is known that *G. fasciatus*, the most active migrant in inland waters of Russia, was

recorded as a dominant species among amphipods, migrating vertically from bottom to surface waters in Lake Baikal (Bessolitsyna, 2002). According to the migration theory by Birshtein (1935), the upstream migration of species in the rivers of the Sea of Azov and the Caspian and Black seas has resulted in the rapid dispersal of many amphipods from the south to the north of the former USSR. By the middle of the 20th century, the Ponto-Caspian amphipods *C. ischnus*, *D. haemobaphes*, *D. villosus* and *O. obesus* reached the middle part of the Volga River spreading upstream more than 4,000 km from their native area (Lyakhov, 1958; Mordukhai-Boltovskoi, 1960; Dedyu, 1980). In particular, the amphipod *O. obesus* extended its distribution area 500 km upstream in the river during a short period from 1958 to 1972 (Shakhmatova & Antonov, 1988). Amphipod migration also has an important significance, not only in species dispersal, but in feeding, reproduction, defence from predators and unfavourable factors, such as hypoxia, pollution, algae blooms and storms (Dedyu, 1967, 1980; Ioffe & Maximova, 1968).

In some cases, large specimens of amphipods, which can migrate for long distances were able to transport attached invertebrates (molluscs, rotifers and infusorians etc.) and can be considered as a possible vector of accidental introductions for other species of invertebrate. For example, it is known that specimens of *D. villosus* have transported juveniles of the mollusc *Dreissena* spp. during migration upstream in the Ponto-Caspian rivers (Dedyu, 1963).

Construction of artificial water-bodies, such as artificial ponds and reservoirs of power stations on the important rivers of Russia and related changes of habitat conditions, hydrodynamic stabilization, eutrophication and appearance of “empty” niches for new species have resulted in local dispersions of euryoecious species of amphipods outside their native areas. Thus, after construction of the Dnepropetrovsky Reservoir on the Dnieper River, amphipods *P. robustoides* and *D. haemobaphes* colonized the reservoir and became the dominant species in terms of density and biomass in the macrophyte beds, although they were very rare in the former part of the river (Mordukhai-Boltovskoi, 1960). In the Dubosarsky Reservoir, the amphipod density increased

2-fold in comparison with the density in the same part of the Dnieper River before reservoir construction. Species, such as *C. curvispinum*, *C. ischnus* and *D. villosus* came out of the Ponto-Caspian basin because of active reproduction in the constructed reservoirs and their subsequent upstream migration (Dedyu, 1967).

Disturbed habitats and unfavourable abiotic conditions of the former river during construction of reservoir resulted in a decrease in the abundance of native amphipods or a contraction in their range in this basin. For example, in the 1920s, the upper border of the distribution range of *D. haemobaphes* was situated in the Volga River near Yaroslavl city (Bening, 1924) however, by 1951–1972 it had dispersed downstream to near Nizhnyi Novgorod city (Shakhmatova & Antonov, 1988). The upstream migration of the amphipods in this case was limited by constructed dams partitioning the river bed and native populations were retained, so that a so-called “mosaic” distribution range of this species was established (Mordukhai-Boltovskoi, 1960; Zhadin, 1964).

At present, some Ponto-Caspian amphipods survive in the modern Volga River basin. For example, *D. haemobaphes* continues to migrate upstream from their known localities: in 1995–1997, it was recorded in the upper part of the Gor’kovsky Reservoir and in the Volga River near Yaroslavl city (Bakanov, 2003). Other findings of this species were reported from the Upper Moskva River in 1993 (L’vova et al., 1996), as well as in the Volga River near the site connected by a canal with the Moskva River in 1995 and finally, in the Rybinsky Reservoir in 1997 (A. Bakanov, pers. comm.). All these findings indicate an active range expansion by *D. haemobaphes* in a northern direction.

In some locations, intentional introductions of amphipods may have caused the extinction of native species. In the Gor’kovsky Reservoir, the Baikalian amphipod *G. fasciatus* was intentionally introduced for enrichment of fish production in the 1960s and has spread widely in to different biotopes over several years, replacing *O. obesus* and *D. haemobaphes* which were common species in the former part of the Volga River (Mordukhai-Boltovskoi & Chirkova, 1971; Mordukhai-Boltovskoi & Dziuban, 1976). In the 1970s, the

distribution range of both species considerably contracted in the Volga River and has been limited near Kstovo city (Shakhmatova & Antonov, 1988). At the same time, introduced *G. fasciatus* dispersed from the Gor’kovsky Reservoir to other Volga Reservoirs (Cheboksarsky, Kuibyshevsky and others), successfully established itself and became the dominant species in the majority of the aquatic ecosystems of the Upper Volga basin (Borodich, 1979; Shcherbina et al., 1997). Similarly, in the Angara River (Siberia), before construction of its reservoirs, the number of amphipod species including *G. fasciatus* was high (up to 45 species). After construction of the Angara Reservoirs, species richness significantly decreased, the amphipods *Eulimnogammarus verrucosus* (Gerstfeldt) and *E. viridis* (Dybowsky), which were leading species in the former river disappeared, whereas *G. fasciatus* survived and rapidly occupied all types of habitat between depths of 0–5 m, becoming the dominant species in terms of density and biomass among the amphipods (Erbaeva et al., 2002).

During the 1950–1980s, large-scale intentional introductions of crustaceans were a major vector of amphipod invasions in inland waters of European Russia and Siberia. Enrichment of fish production was the principal motivation for the introductions. At least 30 amphipod species of Ponto-Caspian origin, 3 species of Siberian origin and 2 species belonging to so-called “glacial relicts” were used during amphipod transportations through the former USSR area (Gordeev, 1954; Gasiunas, 1972; Pirozhnikov & Ioffe, 1974; Karpevich, 1975; Jażdżewski, 1980; Zadoenko et al., 1985; Suschenya et al., 1986; Grigorovich et al., 2002). In addition, four species (*Gammaracanthus lacustris* Sars, *Pallasea quadrispinosa* Sars, *G. tigrinus* and *G. pulex*) were introduced to aquatic ecosystems of Western Europe (Jażdżewski, 1980; Fürst, 1981). These intentional introductions (or so-called acclimatizations) resulted in a rapid change of distribution area for many native amphipods.

The large-scale mass transportation of amphipods (even unknown species), conducted in the former USSR during the second part of the last century, were often not documented, which made it difficult to determine the invasion routes of acclimatized species. For example, it is still

unclear how *P. robustoides* penetrated the eastern Gulf of Finland. This species (or mix of species) was taken from the Kaunas Reservoir for its intentional introduction into the aquatic ecosystems of the Leningrad Region in Russia (Gasiunas, 1972; Lazauskiene et al., 1995), however, the consequences of this introduction are unknown.

Accidental introductions of some alien species have taken place during contaminated acclimatizations of aquatic plants or animals. Introductions of aquatic plants have caused the invasion of *G. roeselii* from the southern Balkans to France (Jazdzewski, 1980; Jazdzewski & Roux, 1988). Baikalian *G. fasciatus* was accidentally introduced in Lake Peipsi during the intentional acclimatization of *Gammarus lacustris* Sars from the aquatic ecosystems of Siberia in the 1970s (Timm & Timm, 1993; Panov & Berezina, 2002).

Accidental introductions of species also occur with the ballast water of ships or in sediments of ballast tank, which are considered the main cause of species invasions throughout the world (Carlton, 1989; Ruiz et al., 2000). However, only a few case studies of this vector for amphipod invasions are known. For example, the North-American amphipods, *G. tigrinus* and *Crangonyx pseudogracilis* Bousfield were introduced in England with ballast water transport (Crawford, 1937; Hynes, 1955). The transoceanic transfer of the oligohaline amphipod *C. ischnus* from Europe to the Great Lakes of America occurred by the same vector (Witt et al., 1997; Cristescu et al., 2004). Despite the opening of inland waterways connecting the southern and northern regions of the European part of the former USSR and intensive shipping, introductions of amphipods are still unknown for Russia.

The survival of amphipods during transportation in ballast tanks (water or sediments) is possible in most cases because of the high tolerance of this group of animals to different abiotic factors, mainly salinity. All Ponto-Caspian amphipods are characterized by high euryhalinity, surviving in the range of 0.1–20‰ (Romanova, 1959; Mordukhai-Boltovskoi, 1960; Bruijs et al., 2001). The freshwater amphipod *G. fasciatus*, which is widely spread throughout Russia are able to survive at salinities less than 7–8‰ (Berezina

et al., 2001; Berezina & Panov, 2003a). Another invader in the European waters, *G. tigrinus*, has been recorded along the coastal zone of North America, where water salinity changes from 1‰ to 25‰ (Bousfield, 1973).

Establishment of alien amphipods in aquatic ecosystems of Russia and the former USSR

Transfers of amphipods were frequently accompanied by physiological adaptations and changes in life cycle traits of introduced species in recipient ecosystems. Some authors (Mordukhai-Boltovskoi, 1960; Dedyu, 1967; Mordukhai-Boltovskoi & Chirkova, 1971) also recorded the significant morphological variability for *C. warpachowskyi*, *G. fasciatus*, *P. robustoides*, *O. obesus*, *O. crassus* and *D. villosus* in new conditions. This variability is a common feature for the majority of amphipods exposed to different conditions. A significant difference in body size, number of setae and structure of pereopods, uropods and telson were found in specimens of *G. fasciatus* within one region (Mekhanikova, 2000), which suggested a high molecular genetic polymorphism in this species.

Life cycle traits can change in response to the conditions of the recipient ecosystem. It is known that 1,000–1,250 day-degrees (or approximately 55–65 days at a temperature of 18.5°C) are needed for oogenesis of *G. fasciatus*. The number of generations, in the case of *G. fasciatus*, is temperature-dependent and ranges from 1 to 3 per year, with one generation in the littoral zone of Lake Baikal with day-degrees less than 1,200 during summer, two generations in north-eastern lakes with 1,500–2,000 day-degrees (Lake Ladoga, Lake Peipsi and Lakes of Karelian Isthmus) and three generations in the Upper Volga reservoirs with the total day-degrees more than 2200 (Panov & Berezina, 2002).

In the recipient ecosystem, introduced species can occupy new types of habitats. For example, populations of *D. haemobaphes*, *D. villosus* and *O. obesus* are mainly concentrated in the deep-water habitats of southern rivers (Mordukhai-Boltovskoi, 1960; Dedyu, 1980), while in recipient reservoirs and estuaries of Russia they inhabit

shallow areas with favourable trophic, oxygen and temperature conditions. At the same time, during storm or other unfavourable conditions, the amphipods are able to migrate into deeper water. In water-bodies of ancestral areas, the bulk of the *G. fasciatus* population is concentrated mainly into depths of 0.5–5.0 m, although it can inhabit depths up to 14 m, where its density is low (Bekman, 1962). The biomass of *G. fasciatus* had been recorded as extremely high (up to 5 kg m⁻²) during the summer in shallow zones of small water-bodies of the Baikalian basin. In contrast, in reservoirs and small rivers of the Upper Volga basin, this species was the most abundant in biocenosis of *Dreissena* spp. at depths of 6–10 m (Shcherbina et al., 1997).

The abrupt transfer of some species from one climatic geographic zone to another, without preliminary acclimation during intentional or accidental introductions, does not always result in successful establishment. Thus, introductions of *Micruropus possolskii* Sowinsky from the Angara River basin to reservoirs of Siberia and the Volga River (Ioffe, 1968; Volkov & Potina, 1977; Zadoenko et al., 1985) failed, as well as those of *Gammarus lacustris* from Siberia to Lake Peipsi (Timm & Timm, 1993; Panov et al., 2000) and *P. robustoides* from the Ponto-Caspian basin to the Simferopolsky and Kakhovskiy reservoirs (Mordukhai-Boltovskoi, 1960). The transfer of some species within one region has also ended in the failure to establish. Such examples are known for *Gammarus lacustris* in some lakes of Ural and Siberia, including Lake Baikal (Deksbakh, 1952; Bekman, 1954; Safronov, 1993) and for the relict amphipods *Gammaracanthus lacustris* and *Pallasea quadrispinosa* in 40 % of Swedish lakes (Fürst, 1981; Hill et al., 1990). The cause of unsuccessful introductions is a discrepancy of hydrological, hydrochemical and trophic characteristics of recipient lakes and the ecological requirements of the introduced species. Nevertheless, the relict amphipods *P. quadrispinosa* and *Gammaracanthus lacustris* were successfully established in several lakes in Sweden (Hill et al., 1990) and *Monoporeia affinis* in Russia (Greze, 1958).

What life cycle traits are facilitating successful invasion of alien amphipods in new habitats?

Alien species of amphipods, which belong to opportunistic or r-strategic species, will be able to increase their density over a short period, becoming leading species in recipient ecosystems. As a rule, high fecundity, fast growth and maturation of juveniles, wide food spectrum, high genetic variability and tolerance to different factors, including pollutants are the main characteristics of this alien amphipod species (Dennert, 1974; Dedyu, 1980; Van den Brink et al., 1993; Dick et al., 1999; Holdich et al., 1999; Berezina & Panov, 2003a).

Possessing the majority of the above-mentioned characteristics, the Baikalian amphipod *G. fasciatus* could be considered as one of the most successful invaders in inland waters of Russia. Characteristic features of its life history facilitate successful adaptation and rapid population growth in recipient ecosystems. Reproduction of this species in the Neva Estuary and lakes of the Baltic Sea basin begins in March–April at a water temperature of 4–5°C. At 14–15°C, copulation of the amphipods lasts for 2 days; in 11–15 days fecund females produce fertile eggs in the brood pouch, and then after a further 15–18 days the females release juveniles (Nilova, 1976). Under favourable conditions, each mature female produces a maximum of 8–10 broods per season. Maximum clutch size in *G. fasciatus* is 34–36 eggs (sometimes up to 46 eggs) (Bekman, 1962; Vershinin, 1967; Savateeva, 1985; Skalskaya, 1996; Berezina, 2005).

During the reproductive period, the population structure of *G. fasciatus* is characterized by females prevailing over males, which can facilitate rapid population growth. This phenomenon is a common adaptation for many amphipod species and has been described for *G. fasciatus* populations in the Angara River reservoirs (Vershinin, 1967), Rybinsky Reservoir (Skalskaya, 1996), Lake Onega (Berezina & Panov, 2003b) and Neva Bay (Berezina, 2005). High summer temperatures can result in the rapid maturation of amphipods, with females producing their first clutch when their body size is only slightly larger than the juveniles. For example, 3.4 mm females of *G. fasciatus* were found with fecund eggs in July 2001 in the Neva Estuary at a water temperature of 27°C. In addition, in Lake

Baikal (Posolskyi Bay), ovigerous females with a body length of 3.5 mm were recorded in late August (Bekman, 1962).

Gmelinoides fasciatus is able to survive at a wide range of temperatures, oxygen concentrations and ionic water content. This species, of freshwater origin, is widely spread in different aquatic ecosystems from oligotrophic Lake Onega, with a very low salt content to the oligohaline Neva Estuary (Baltic Sea). It inhabits silt, sandy, stony and woody substrates and concentrates in macrophyte and macroalgae beds (*Phragmites*, *Eleocharis*, *Scirpus*, *Potamogeton*, *Cladophora* and *Nitella*) (Panov & Berezina, 2002).

The important trait of alien species is the ability to adapt to conditions where food resources are limited by mixing feeding strategies. Omnivorous *G. fasciatus* consumes detritus, algae and aquatic plants. In addition, it preys upon small benthic and zooplankton organisms (Berezina et al., 2005). *Gmelinoides fasciatus* also tolerates moderate pollution and severe eutrophication. It was found to be among the first invertebrates to re-colonize previously lifeless locations caused by pulp mill discharges in Lake Ladoga (Panov, 1996). Similarly, other invasive species *G. tigrinus* and *C. curvispinum* were also found in ecosystems disturbed by anthropogenic pollution (Van den Brink et al., 1993; Lee & Bell, 1999). *Gmelinoides fasciatus* tolerates concentrations of oil products 5-times higher than the amphipod *Hyaella azteca*, and 20-times higher than the chironomid *Chironomus riparius* (Tomilina, 2000). *Gmelinoides fasciatus* was more tolerant to toxic concentrations of potassium than the molluscs *Bithynia tentaculata*, *Planorbis planorbis*, *Sphaerium* sp., *Dreissena* sp. and the isopod *Asellus aquaticus*. The tolerance range of *G. fasciatus* for potassium in water is 0.3–200 mg l⁻¹ and LC₅₀ for 240 h is 400–500 mg l⁻¹. According to Makrushin (1998), the LC₅₀ of the mollusc *D. polymorpha* for 240 h is 57 mg l⁻¹ and the LC₅₀ for the molluscs *Unio* sp. and *Anodonta* sp. is 170 mg l⁻¹.

The main natural barriers for the establishment of *G. fasciatus* in new habitats are low pH (<6.0) (Nilova, 1976; Berezina, 2001) and salinity higher than 2‰ (Berezina et al., 2001), which prevents the successful completion of oogenesis. Soft water

with a calcium content less than 5–7 mg l⁻¹ and low pH have also terminated normal moulting in specimens (Bekman, 1962; Berezina, 2003). In addition, hypoxia in water and sediments is an unfavourable factor for the development of *G. fasciatus* (Bekman & Bazikalova, 1951).

The high resistance of other amphipod species to different unfavourable factors allows them to survive in many cases even at a lethal dose. For example, at oxygen concentrations of 0.1–0.3 mg l⁻¹ for 1 h, specimens of *D. villosus* and *C. ischnus* became motionless, but after transfer to water with normal conditions they revived within 1 h (Mordukhai-Boltovskoi, 1960). It was revealed that *P. robustoides* was not able to reproduce successfully in water with potassium concentrations less than 10–15 mg l⁻¹ (Berezina & Panov, 2003a), however, adult specimens were able to survive in distilled water for 1 week.

Introductions of a successful invader into new habitats, where limits for its range expansion such as predation, parasites and food competition are insignificant, result in rapid population growth of the invader. When the invader is introduced to such conditions, the classic ecological scenario begins (see Odum, 1975), where density (or biomass) initially increases slowly and imperceptibly, indicating the phase of “positive acceleration”. The following phase of population growth, the so-called “logarithmical phase”, is characterized by accelerated population growth rate and may result in a density explosion. As a rule, different environmental factors limit the logarithmical population growth, which results in the beginning of growth rate deceleration. The deceleration rate can be attributed to the phase of density stabilization, when the population size reaches a maximum level and may fluctuate slightly near this level. Population dynamics of alien amphipods in new habitats are often characterized by the above-mentioned scenario and this is demonstrated by the example of density growth in the Neva Estuary (Fig. 2). At the same time, the abrupt decline in the density of the first invader can be induced by new species invasions, especially in the case of species inhabiting the same niche (Fig. 3). Later, the density of both species can be stabilized near a certain level, which allows their coexistence.

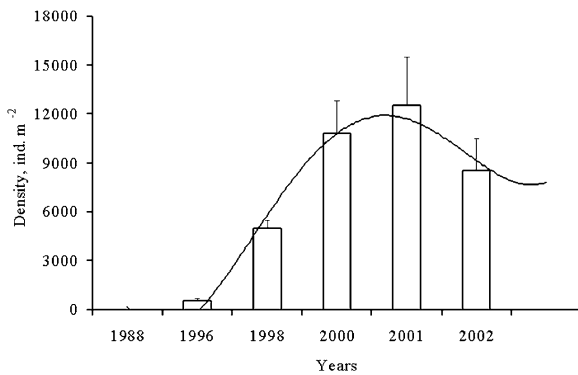


Fig. 2 Increase in mid-summer density of the Baikalian amphipod *Gmelinoides fasciatus* in *Phragmites* beds in the northern part of the Neva estuary (Gulf of Finland, Baltic Sea)

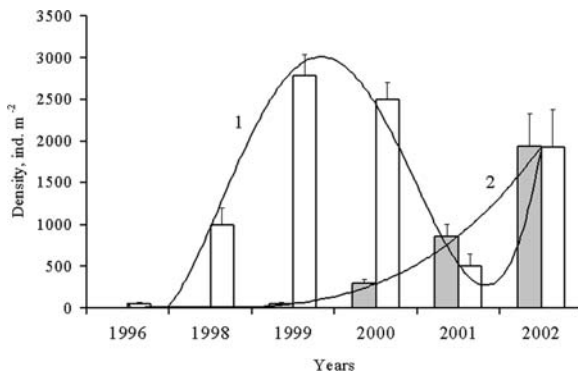


Fig. 3 Change in the dynamics of the mid-summer density of *Gmelinoides fasciatus* (1) after invasion and successful establishment of *Pontogammarus robustoides* (2) in stony littoral zone of the southern Neva estuary (Gulf of Finland, Baltic Sea)

Consequences of amphipod invasions in different aquatic ecosystems

The number of alien amphipods in Europe has considerably increased in recent years, however, only a few species can be considered as invasive or hazardous. According to the rule formulated by Williamson (Williamson & Fitter, 1996), only 10% (and 5–20% in the case of aquatic species) of established species can increase their density up to a significantly high level that they have an impact on the recipient ecosystem by facilitating a decrease its biodiversity and stability. However, we do not have universal criteria for the assessment of the minimum damage of an alien species, which defines it as harmful. One thing is clear;

even a small number of specimens, possessing low genetic variability and low population density, may be sufficient for a generation to cause severe damage in a recipient ecosystem (Mack et al., 2000). According to Elton (1958), each introduction of a new species, whether an explosion of population density takes place or not, influences native populations and results in ecosystem destabilization.

Invasive species can interact with native species by predation, resource competition, habitat modification, causing the disappearance of species (or races) and irreversible losses of genetic diversity. The loss, or addition, of functionally dominant species, such as keystone species, ecosystem engineers or species with many trophic relations, can have a strong impact, inducing rapid losses of local biodiversity. Invasiveness of the alien species is mainly related to species characteristics, hierarchical complexity of the recipient ecosystem and its vulnerability. The vulnerability of the ecosystem increases depending on the degree of anthropogenic disturbance (Elton, 1958; Simberloff, 1981; Kinzelbach, 1995; Lozon & MacIsaac, 1997).

Although patterns of amphipod invasions in the Baltic Sea basin and Europe are well-known, processes of alien species interactions with native species and impacts on the environment are poorly understood. It is known that the impact of established invaders may be positive, neutral or negative and dependent on characteristics of the invader (Holdich et al., 1999; Westman, 2002). As for amphipods, these characteristics may include a larger body, faster growth, more aggressive behaviour, greater fecundity or better tolerance to unfavourable abiotic factors and pollution than in native species (discussed by Mordukhai-Boltovskoi, 1960; Dennert, 1974; Dedyu, 1980; Dick et al., 1999; Van der Velde et al., 1999).

After establishment of an alien species, its population size, feeding habits and its position in the food web may be significant in determining the type and strength of effect on the invaded community (Nyström et al., 1999). Most amphipod species are omnivorous, and the food preferences of each species may differ and be dependent on food resources in the invaded habitat. Adult specimens of different amphipod

species are able to predate. Some species of the family Corophiidae, including *C. curvispinum* are suspension-feeders. Large-sized species *D. villosus* and *Pontogammarus robustoides* can be considered as the most effective predators (Berezina & Panov, 2003a; Krisp & Maier, 2005). *Pontogammarus robustoides* start to predate at a young age (body length of 6–7 mm), attacking the larvae of chironomids and oligochaetes, which are often larger than itself. In experiments, it was shown that specimens of *D. villosus* actively attacked *Asellus sp.*, *Gammarus duebeni*, larvae of mayflies, chironomids and even aquatic beetles (Dick et al., 2002). Isotope analysis ($\delta^{15}\text{N}$) revealed that *D. villosus* has the same trophic status as the benthivorous fish level (Marguillier et al., 1998).

Predation of alien amphipods on small benthic organisms is often considered to be the main negative effect observed in a recipient community. In the stony littoral zone of the Neva Bay, predation of *P. robustoides* on benthic organisms (isopods, oligochaetes, aquatic insects) resulted in a significant decrease in their density (Berezina & Panov, 2003a). The intraguild predation was the primary mechanism, whereby the abundance of native amphipods (or earlier invaders) dropped abruptly after the establishment of a new amphipod species. This mechanism was found experimentally, in the case of the replacement of *G. duebeni* by *G. pulex* (Dick & Platvoet, 1996; Dick et al., 1999) as well as in two other cases of replacement, including *G. fasciatus* by *P. robustoides* (Berezina & Panov, 2003a) and *G. lacustris* by *G. fasciatus* (Berezina, pers. obs.). The phenomenon of the replacement of one amphipod species by another is a common trait for this group. Species interactions among amphipods of different origins have been observed in many cases (Martynov, 1932; Mordukchai-Boltovskoi, 1960; Dedyu, 1980). Antagonistic relationships have been distinguished between the species pairs of *G. fasciatus* and *G. pulex*, *G. duebeni* and *G. pulex* (Hynes, 1954; Dick et al., 1994), *G. duebeni* and *G. salinus* (Kinne, 1954), *D. villosus* and *G. duebeni*, *D. villosus* and *G. tigrinus* (Dick et al., 2002), *G. lacustris* and *G. fasciatus*, *G. fasciatus* and *P. robustoides* (Berezina & Panov, 2003a).

As a rule, the species which occurred in conditions within its tolerance range was more

successful during species interactions. This scenario is illustrated by the example of the oligohaline amphipod *G. tigrinus* and the freshwater *G. pulex* interaction, when the displacement of the first species by the second was observed in waters with low ionic content, and the second by first ones in oligohaline estuaries (Van der Velde et al., 2000). In different aquatic ecosystems in Russia, a considerable decline in density or even the disappearance of the native *G. lacustris* was recorded in the case of *G. lacustris* and *G. fasciatus* coexistence (Panov, 1996; Panov et al., 2000; Berezina, 2005). Whilst *G. fasciatus* has a short life cycle and high fecundity that allows it to reach high densities in a short-term period, *G. lacustris* is characterized by low density, a longer life cycle, low reproductive potential and, in most cases, low density. Also, *G. lacustris* is less tolerant to storm activity (Bekman, 1954), which may limit its spread to the exposed littoral zone of large lakes and estuaries.

High densities of alien amphipods can facilitate the transformation and mineralization of organic matter and energy mediation in the coastal zone of the Baltic Sea estuaries (Berezina & Panov, 2003a). The intensity of these processes can be related to the consumption rates, depending on water temperatures, type of food items, age and consumer weight (Greze, 1977; Sushchenya, 1975). At 20°C, the rates of *G. fasciatus* and *P. robustoides* comprised 20–130% of individual consumer weight per day (Berezina & Panov, 2003a). Fecal pellets of amphipods consist of incompletely digested remains of animal and plant origin, and associated bacteria groups, which can be used by detritivorous invertebrates (oligochaetes, insect larvae and juveniles of amphipods and isopods). In addition, grazing by the amphipods *G. fasciatus* and *P. robustoides* can control the biomass of filamentous algae that is a cause of pollution in the coastal zone of the Gulf of Finland (Berezina et al., 2005). Similarly, Gasiunas (1975) revealed that the established population of *P. robustoides* with densities up to 4,980 ind. m⁻², feeding on *Cladophora* algae, contributed to the disappearance of the algae in some lakes of Lithuania 5 years after introduction.

The successful invasion of alien amphipods in communities with low species diversity, have

often resulted in enrichment of food resources for fish. It is known that the amphipod *Gmelinoides fasciatus* is a favourite food item for many fish species, such as perch, roach, bream, dace and whitefish (*Leuciscus leuciscus*). According to Mitskevich (1981), *G. fasciatus* played a significant role in feeding of benthophagous fish from Lake Otradny (Baltic Sea basin). *Gmelinoides fasciatus* juveniles were also a regular component, comprising 8.2–10% of the diet of bream and roach. In addition, these amphipods constituted about 65% of the biomass ingested by perch *Perca fluviatilis*.

Alien species inhabiting new ecosystems can transfer new species of parasites to vertebrates, as well as fish, birds and mammals. Amphipods are intermediate hosts for certain species of Acanthocephala, trematodes and microsporidia (Baldanova & Pronin, 2001). The Baikalian amphipod *G. fasciatus* is able to transfer the parasite *Polymorphus magnus* which can cause disease in ducks (Sidorov, 1963).

Conclusion

The major factors accelerating the dispersal process of many amphipods in European Russia are related to human activity. The destruction of natural barriers between the different basins of Europe is considered to be one of the most important factors, which has resulted in the range expansion of many amphipod species in different directions. Disturbed habitats are more often invaded by new species than well-balanced, undisturbed ones. The destruction of natural habitats will increase ecosystem invasiveness and facilitate the successful invasion of undesirable euryoecious species. The success of invading species strongly depends on life cycle traits, including reproduction rate, tolerance to environmental factors and the strength of their interactions with other species. In the recipient ecosystem, the established alien species can become the dominant species which can strongly influence the ecosystem. The consequences of amphipod introductions need further assessment, because it is clear that the impact of alien species

on invading ecosystem can result in the serious loss of biodiversity and the destruction of system stability.

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