INVASION HISTORY, BIOLOGY AND IMPACTS OF THE BAIKALIAN AMPHIPOD *GMELINOIDES FASCIATUS*

VADIM E. PANOV* & NADYA A. BEREZINA
Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia
*Corresponding author *gaas@zin.ru*

Abstract
During the 1960s and 1970s the Baikalian amphipod *Gmelinoides fasciatus* (Stebbing) was intentionally introduced into more than 20 lakes and reservoirs outside its native range in Siberia and European Russia, in order to enhance fish production. Abilities of *Gmelinoides* to spread within the basins and to compete with native amphipods were neglected. In the European Russia this species successfully established in the Volga River basin, in such large lakes as Lake Ladoga, Lake Onega, Lake Peipsi, Lake Ilmen and their basins, and in the Neva Estuary (Baltic Sea). In most cases the native amphipods were completely replaced by *Gmelinoides*, and negative impact on other aquatic invertebrate species is also likely because direct predation by *Gmelinoides*. Studies of *Gmelinoides* biology, including experimental estimation of its salinity and temperature resistance, showed that this invasive amphipod tolerates wide range of environmental conditions and potentially is able to invade other parts of the Baltic Sea and inland waters within its basin. Considering intensive shipping activity in the Neva Estuary, and high densities of *Gmelinoides* in the St.Petersburg harbour area, introduction of this species into the North American Great Lakes and estuarine ecosystems with ballast waters of ships via existing invasion corridor is likely.

1 Introduction

During 1960-1985 intentional introductions were one of the main vectors of aquatic species invasions into inland waters of Siberia and European Russia. Facilitation of fish production was the principal reason for these large-scale introduction efforts (Zadoenko et al. 1985). High productivity and growth potential of the selected species were considered as the most important justifications of species introductions into aquatic ecosystems with “empty” niches. Possible adverse impacts of introduced species, like competition with native species and transfer of parasites, were generally neglected. Studies of biology of the organisms, considered for intentional introductions (“acclimatization”), were specifically focused on the species productivity and, in less extent, on their role in fish diet. Studies of the functional role of these species in the communities, and even studies of their foraging behavior and interactions with other species were lacking. Such examples of large-scale headlong efforts to fill an “empty” niche are well known for North America and Europe (Nesler & Bergersen 1991).

Large-scale introductions of the Baikalian amphipod, *Gmelinoides fasciatus*, in the lakes and reservoirs in European Russia can serve as one more example of headlong intentional introduction with initially unexpected, long-term and generally unwanted consequences. The present paper provides a first attempt to review existing published and, in some extent, author’s unpublished data on the *Gmelinoides* invasion history, biology and impacts.

Taxonomy of *Gmelinoides* is described elsewhere (Bazikalova 1945; Panov & Berezina 2001). This species belongs to the gammaridean crustaceans and was first described for

Lake Baikal in 1874 by B. N. Dybowsky as *Gammarus zebra* for its specific striped colour pattern (Panov & Berezina 2001).

2 Invasion history

Gmelinoides fasciatus, a gammaridean amphipod of Baikalian origin, is a common species in freshwater ecosystems in Lake Baikal basin. In Siberia this species is found in Lake Baikal, and also in lakes and rivers in basins of the Angara, Lena, Yenisey, Irtysh, Pyasina, Tunguska, Selenga and Barguzin (Bekman 1962). *Gmelinoides* was considered as one of the most suitable species for intentional introductions aimed to enhance fish production in lakes and water reservoirs, mainly because of its high environmental plasticity and generally high abundances within its native range (Bekman & Bazikalova 1951; Greze 1951). Abilities of *Gmelinoides* to spread within the basins and to compete with native amphipods were neglected.

During the 1960s and 1970s, hundreds of millions of *Gmelinoides* specimens were introduced into 22 lakes and reservoirs outside its native range in Siberia and European Russia (Zadoenko et al. 1985). In the European Russia, *Gmelinoides* was introduced intentionally into Gorkovskoe Reservoir in the Volga River basin (Volkov & Potina 1977; Mordukhai-Boltovskoi & Chirkova 1979), several Karelian Isthmus lakes (Arkhiptseva et al. 1977) and Lake Ilmen (Savateeva 1985) in the Lake Ladoga basin (Fig. 1). Also, this alien amphipod was introduced accidentally in Lake Peipsi during headlong attempts to acclimatize *Gammarus lacustris* from the Siberian population in 1970-1975 (Timm & Timm 1993). *Gmelinoides* was found first in Lake Peipsi already in 1972, and by 1990 it established itself successfully in the whole littoral zone of this lake (Timm & Timm 1993; Panov et al. 2000).

First intentional introductions of *Gmelinoides* in European inland waters were conducted in 1962-1965 in Gorkovskoe Reservoir (Fig. 1), and by 1975 it successfully colonized the whole 434 km long reservoir. In 1977 *Gmelinoides* was first found in Kuibyshevskoe Reservoir (Fig. 1), around 400 km downstream from the site of intentional introduction in the Gorkovskoe Reservoir (Borodich 1979). Upstream movement of *Gmelinoides* took longer, and it was first found in Rybinskoe Reservoir 300 km upstream only in 1986 (Skalskaya 1994). By 1990 *Gmelinoides* colonized the whole Rybinskoe Reservoir and in 1994 was first found in the south part of the Beloe Lake, located in the northernmost part of the Caspian Sea drainage basin (Shcherbina et al. 1997) (Fig. 1).

In the Baltic Sea drainage basin, *Gmelinoides* was first introduced intentionally in 1971 in Lake Otradnoe (Nilova 1976), and between 1971-1975 more than 10 million specimens were introduced into five other Karelian Isthmus lakes, located close to the Lake Ladoga western shore (Fig. 1) (Arkhiptseva et al. 1977). Via rivers, connecting some of these lakes with Lake Ladoga, *Gmelinoides* invaded the Lake Ladoga. In late 1980s it was found established along western and northern shores of the lake (Panov 1996), and by 1996 it successfully colonized the whole littoral zone of this largest European lake (Panov et al. 1999). In the 1990s, via the Neva River, *Gmelinoides* invaded the Neva Bay, freshwater part of the Neva estuary (eastern Gulf of Finland), the largest estuary in the Baltic Sea (Fig. 1). In 1999 *Gmelinoides* was first registered in the inner Neva estuary, the very first record of the Baikalian amphipod in the Gulf of Finland. Results of our field survey in 2000 indicate that *Gmelinoides* established permanent population in the littoral zone of the brackish Neva estuary, almost 30 years after the first intentional introduction of this species into Karelian Isthmus lakes, located around 250 km up-stream in the Neva estuary drainage basin.

Also, our field survey of Lake Onega littoral zone in August 2001 showed, that *Gmelinoides* established dense populations along the western shore of this second largest European lake. However, the route of *Gmelinoides* invasion to Lake Onega is not clear, it might be via Svir River, connecting Lake Onega with Lake Ladoga, or the Volga-Baltic waterway, connecting Lake Beloe with Lake Onega (Fig. 1). Thus, at present *Gmelinoides* is widely distributed in the inland waters of the European part of Russia, and also in the Neva estuary (Fig. 1). Present range of *Gmelinoides* is extensive and limited by latitudes 48°-74°N and longitudes 25°-110°E (Panov & Berezina 2001).

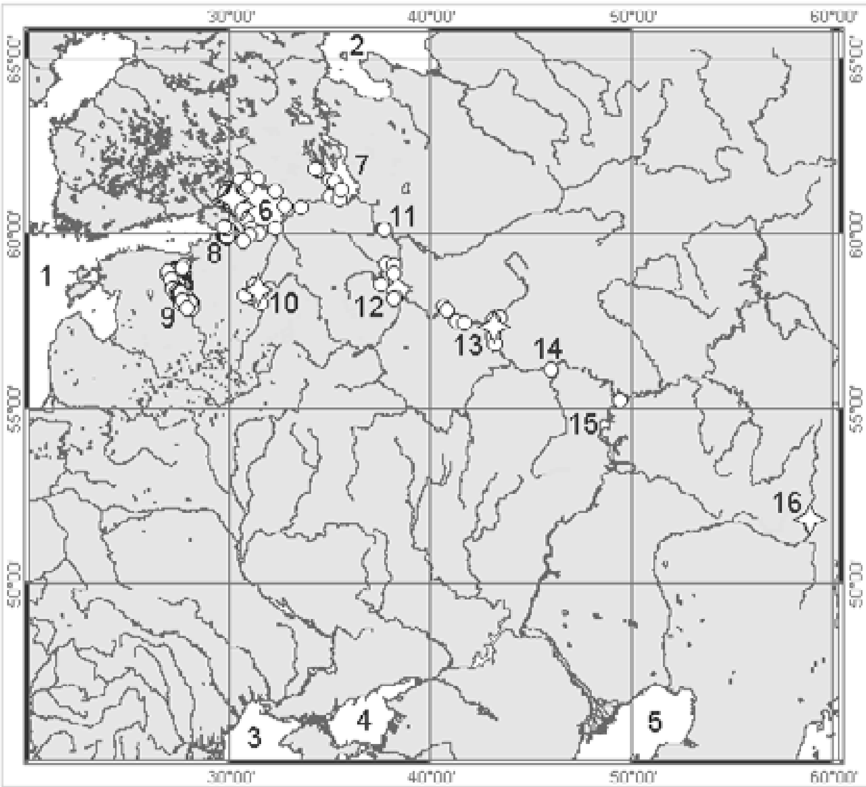

Figure 1. Distribution of *Gmelinoides fasciatus* in Europe. Asterisks indicate sites of intentional introductions, open cycles records of range expansions. (1) Baltic Sea, (2) White Sea, (3) Black Sea, (4) Azov Sea, (5) Caspian Sea, (6) Lake Ladoga, (7) Lake Onega, (8) Neva estuary, (9) Lake Peipsi, (10) Lake Ilmen, (11) Lake Beloe, (12) Rybinskoe Reservoir, (13) Gorkovskoe Reservoir, (14) Cheboksarskoe Reservoir, (15) Kuibyshevskoe Reservoir, (16) Iriklinskoe Reservoir.

3 Biology

3.1 REPRODUCTION

Reproduction in *Gmelinoides* starts early spring in shallow littoral zone at water temperatures 4-5 ^{o}C and terminates in late autumn at <10 ^{o}C. Fecundity of *Gmelinoides* averages 3-45 eggs per female, depending on female body size. Fecundity is highly variable in different ecosystems, and this likely reflects differences in local feeding conditions. Highest fecundity was found in the eutrophic Neva Bay (Fig. 2).

Our experimental studies showed that egg developmental time (hatching time τ, days) in *Gmelinoides* (period between release of fertilized eggs in brood pouch and release of new born juveniles from the pouch) is strongly temperature-dependent. This relationship at water temperatures (T, ^{o}C) range 12-24 ^{o}C can be described by equation $\tau = -26.5\ln(T)+87.8$ (n=45, R^2=0.98). At high temperatures, egg developmental time in *Gmelinoides* is rather short and averages 3-4 days at water temperature 24 ^{o}C, while at temperature 12 ^{o}C fertilized eggs develop into juveniles as long as in 21-23 days.

Laboratory observations revealed an important feature of *Gmelinoides* reproduction: after copulation females are able to lay fertile eggs in brood pouch immediately after release of developed juveniles, without copulation with males (Nilova 1976; Panov unpubl.). Along with high fecundity and high rates of eggs development at summer, it makes this invasive species enable to fast population growth during favourable conditions.

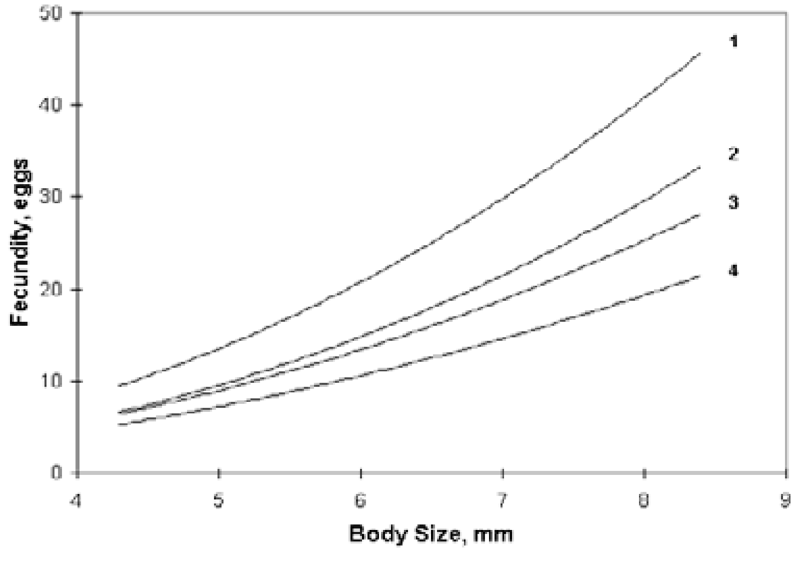

Figure 2. Mean fecundity in females of *Gmelinoides fasciatus*, related to body length: (1) – in the Neva Bay, Gulf of Finland; (2) in Baikal and Ladoga lakes; (3) in Rybinskoe Reservoir and Lake Otradnoe; (4) in Gorkovskoe Reservoir and Lake Ilmen (calculated from Bekman 1962; Mitskevich 1980; Savateeva 1985; Skalskaya 1996; Volkov & Potina 1977; Panov & Berezina unpubl).

3.2 LIFE CYCLE AND ABUNDANCE

Sizes of newborn specimens of *Gmelinoides* ranged from 1.2 to 1.4 mm. Sizes of mature females ranged from 4 to 10 mm in different locations, with smallest fecund females found at higher temperatures. Sizes of mature males ranged from 4-16 mm. As in females, at high temperatures males develop in mature specimens faster and reach maturity at smaller sizes. For instance, in spring, at mean water temperature 11 °C, 6-7 mm is minimum size of mature *Gmelinoides*, while in summer, at mean water temperature 25 °C, the minimum size of mature individuals decreases to 4-5 mm (Vershinin 1967).

For development of newborn amphipods into adults, around 1,000-1,250 day-degrees is needed (around 55-65 days at water temperature 18.5 °C). Because strong temperature effect on the development, number of generations per season is temperature-dependent and ranges from 1-3 (Fig. 3), with 1 generation in aquatic habitats with summer day-degrees < 1,200 (Lake Baikal littoral zone), 2 generations in locations with 1,500-2,000 day-degrees (Lake Ladoga, Lake Peipsi and Lake Otradnoe), and 3 generations in locations with > 2,200 day-degrees during season (Upper Volga reservoirs).

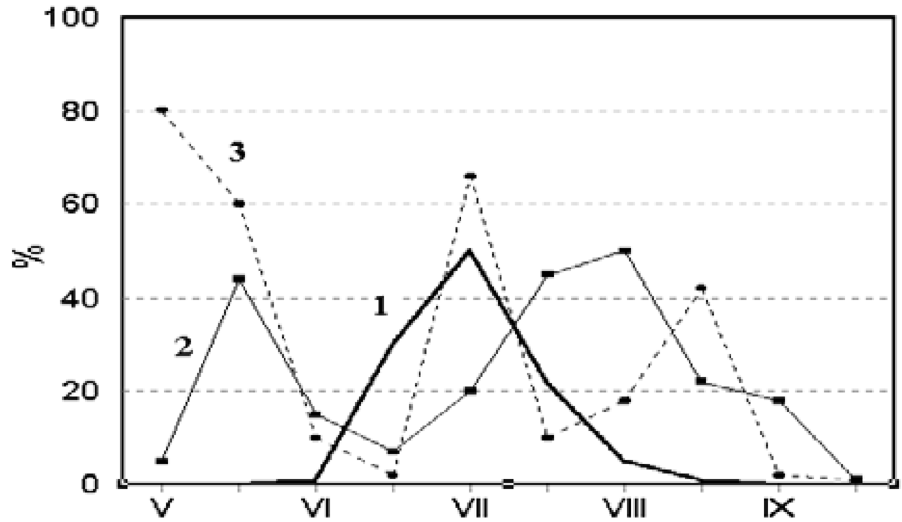

Figure 3. Ratio (%) of immature specimens (body length 1.5-3.0 mm) in *Gmelinoides* populations during season in Lake Baikal (1), Lake Otradnoe (2), and Rybinskoe Reservoir (3) (calculated from Bekman 1962; Nilova 1976; Skalskaya 1994, 1996).

Life cycles in *Gmelinoides* can be of 4 different types, varying in the amphipod life duration and number of generations per season. First, a three-year life cycle with 1 generation per season and newborn amphipods developing into mature amphipods in 17-18 months (Lake Baikal) (Bazikalova 1945; Bekman 1962). Second, a one-year life cycle with 2 generations per season, 1 summer peak in abundance and 2-3 sequential breeds in females (lakes and reservoirs in Lake Baikal basin) (Bekman & Bazikalova 1951; Bekman 1962; Mekhanikova 1982). Third, a one-year life cycle with 2 summer peaks in abundance and 6-8 sequential breeds in females (Lake Ladoga and Lake Otradnoe, Neva Bay) (Nilova 1976; Zadoenko et al. 1986; Berezina & Panov unpubl). Fourth, a one-year life cycle with 3 summer peaks in abundance and 8-10 sequential breeds in females (Upper Volga reservoirs) (Volkov & Potina 1977; Skalskaya 1996).

During reproduction period, most part of *Gmelinoides* population concentrates in shallow near shore habitats. Maximal abundances of this amphipod during summer were found at depths less than 2 m (Table 1). During winter period, abundance of *Gmelinoides* decreases 4-5 fold (Mekhanikova 1982).

Table 1. Maximal abundances and biomasses of *Gmelinoides* in different locations.

Location	Abundance, ind m^{-2}	Biomass, g m^{-2}	Reference
Lake Baikal	10,000-20,000	63-100	Bekman & Bazikalova 1951; Bekman 1962
Lake Ladoga	37,000-54,000	121-160	Panov 1996
Lake Otradnoe	1,600	4,3-4,7	Mitskevich 1980
Lake Peipsi and Narva River	14,000-29,500	57-102	Timm & Timm 1993; Panov et al. 2000
Rybinskoe Reservoir	6,800	19,8	Skalskaya 1994, 1998
Gorkovskoe Reservoir	15,000	66	Volkov & Potina 1977

3.3 FEEDING

Gmelinoides is a nektobenthic omnivorous amphipod, and able to prey effectively upon small benthic and zooplankton organisms. Some authors, who suggested *Gmelinoides* as object for intentional introductions, considered this amphipod as mainly detritivorous animal, feeding on detritus, filamentous and diatom algae, and consuming animal food only accidentally (Nilova 1976). However, other authors found *Gmelinoides* to be an active predator, effectively foraging on small zooplankton crustaceans (Bekman 1962; Panov 1996).

Our study of gut content in *Gmelinoides* revealed significant difference in food composition for small (5-7 mm) and large (> 9 mm) amphipods. Filamentous, diatom and unicellular green algae along with remnants of small oligochaetes comprised the main part of gut content in small amphipods. In large amphipods, guts were empty or filled with mixture of algae and remnants of oligochaetes, chironomids and caddis flies, with dominance of animal food (up to 80% of gut content biomass) (Berezina unpubl.).

Quantitative estimates of food selectivity, feeding rates, functional response and food assimilation rates for *Gmelinoides* are not present in the literature and need further study.

3.4 EFFECTS OF ENVIRONMENTAL FACTORS

Gmelinoides is able to survive at variable range of temperatures, oxygen content in water and water mineralization (total content of salts in water). However, soft water with calcium content less than 5-7 mg l^{-1} and low pH (< 6.0) terminate normal moulting in *Gmelinoides* and can be limiting factors (Bekman 1962; Berezina unpubl). *Gmelinoides* colonizes a wide range of bottom substrates and macrophytes, reaching highest abundances in shallow waters (< 2 m). *Gmelinoides* tolerate moderate pollution, and were found among the first invertebrates re-colonizing previously lifeless location of pulp-mill discharges in Lake Ladoga (Panov 1996). However, this amphipod avoids localities with heavy toxic pollution and sites impacted by warm water from power plants in Volga River reservoirs (Skalskaya 1998).

In experiments on salinity resistance in *Gmelinoides*, amphipods tolerated increase in salinity up to 5-7 PSU (at constant temperature 18 ^{o}C). Successful reproduction in *Gmelinoides* occurred at salinities from 0.06 to 2 PSU, but development of eggs in fecund females terminated at salinities > 2 PSU. At experimental water salinity 2 PSU, mortality of eggs was significant (60-70%). Most likely expansion of *Gmelinoides* in brackish waters will be limited to salinities < 2 PSU (Berezina et al. 2001).

Also, experimental studies show that survival in *Gmelinoides* at salinities 2-5 PSU decreased significantly with increase in water temperature. At temperatures 22-26 ^{o}C, adult amphipods were not able to acclimate to salinities > 2 PSU, and their survival rates ranged from 0 to 30%. Maximum resistance (50%) of *Gmelinoides* to salinity 5 PSU occurred at the lowest experimental temperatures of 12-14 ^{o}C. Most likely high water temperatures will limit distribution of *Gmelinoides* in brackish waters (Verbitsky & Berezina 2002).

4 Impacts

In both Lake Ladoga and Neva Bay *Gmelinoides* almost completely replaced the native amphipod, *Gammarus lacustris*. From Gorkovskoe Reservoir, the site of its intentional introduction in the River Volga basin, *Gmelinoides* spread both to upstream and downstream reservoirs, and to some rivers and lakes in the basin. Drastic decline in Caspian amphipod populations was observed in Gorkovskoe Reservoir after introduction of *Gmelinoides* (Mordukhai-Boltovskoi & Chirkova 1971). In Lake Peipsi *Gmelinoides* was first found in 1972, and established itself successfully in the littoral zone of the lake by 1990, replacing completely the native population of *Gammarus lacustris* along with possible successors of Siberian specimens (Panov et al. 2000). Significant negative impact of *Gmelinoides* on local populations of other amphipod species was also found in Lake Baikal basin (Saphronov 1993). For instance, after construction of reservoirs on Angara River, rich fauna of other Baikalian amphipods, formerly characteristic for the river, was almost completely replaced by *Gmelinoides* (Saphronov & Erbaeva 1998). At present *Gmelinoides* is actively replacing local populations of *Gammarus lacustris* in lakes in Lake Baikal basin (Erbaeva pers. comm.), likely as a result of increasing anthropogenic disturbance of their ecosystems.

Mechanisms of replacement of other amphipod species by *Gmelinoides* are not clear and require further study. Most likely this is a result of predation by *Gmelinoides* on juveniles of other species. Predation could be also a main reason of negative impact of *Gmelinoides* on isopod *Asellus aquaticus* in Lake Ladoga littoral zone (Panov unpubl.).

5 Conclusions

Large-scale intentional introductions of *Gmelinoides* into inland waters of European Russia, conducted between 1960-1975, resulted in significant range expansion in this species. By 2000, *Gmelinoides* successfully established in the Upper Volga basin, in

Lake Ladoga, Lake Onega, Lake Peipsi, Lake Ilmen and their basins, and invaded the largest Baltic estuary. In most cases the native amphipods were completely replaced by their aggressive Baikalian congener, and negative impact on other aquatic invertebrate species is likely because predation by *Gmelinoides*. However, mechanisms of effective replacement of relative species by *Gmelinoides* are not clear and require further study.

Recent studies of *Gmelinoides* biology, including experiments on its salinity and temperature resistance, showed that this invasive Baikalian amphipod is potentially able to invade other parts of the Baltic Sea and inland waters within its basin. Considering intensive shipping activity in the Neva Estuary, and high densities of *Gmelinoides* in the St. Petersburg harbour area, invasion of this species to the North American Great Lakes and estuarine ecosystems via existing invasion corridor is likely.

Acknowledgements

The present study was supported by the Russian Federal Contract 43.073.1.1.2511, grants from the Presidium of the Russian Academy of Sciences on Biodiversity Conservation, Maj and Tor Nessling Foundation and INTAS grant 99-00674.