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Distribution, population structure and salinity tolerance of the invasive amphipod *Gmelinoides fasciatus* (Stebbing) in the Neva Estuary (Gulf of Finland, Baltic Sea)

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Abstract

In the early 1970s, the Baikalian amphipod *Gmelinoides fasciatus* (Stebbing) was intentionally introduced into several lakes in the Gulf of Finland basin in order to enhance fish production. By 1996, *G. fasciatus* successfully colonized the littoral zone of Lake Ladoga and, via the Neva River, invaded the Neva Bay, the freshwater part of the Neva Estuary. In 1999, *G. fasciatus* was first registered in the inner Neva Estuary, the very first record of the Baikalian amphipod in brackish waters of the Baltic Sea. Distribution, abundance, reproduction and population structure of *G. fasciatus* in the Neva Estuary were studied during 1998–2000. In some locations of the Neva Estuary, maximum densities of *G. fasciatus* reached 3500 ind. m^{-2}. In general, density and biomass of *G. fasciatus* in the freshwater part of the Neva Estuary were higher (around 1.5 fold) than in the brackish-water part. Fecundity of this amphipod averaged 10–20 eggs per female, depending on body size of females and season. In order to assess the possibility of further spread of *G. fasciatus* in the Baltic Sea, the salinity tolerance of this species was determined in a series of laboratory experiments. Our results showed that the invasive amphipod *G. fasciatus* is potentially able to colonize shallow coastal habitats of, for example, the Gulf of Bothnia, Gulf of Riga and other parts of the Baltic Sea with water salinities ranging from 1 to 5 psu.

Introduction

Gmelinoides fasciatus (Stebbing) is a gammaridean amphipod of Baikalian origin, which before the late 1960s was restricted to freshwater ecosystems of East Siberia, including the Lake Baikal region (Lake Baikal and upper Angara River) and the Yenisei River basin (Bazikalova, 1945; Bekman, 1962). *G. fasciatus* was described first as *Gammarus zebra* for its distinct striped colour pattern (Dybowsky, 1874), and the 'zebra amphipod' can be considered an appropriate common name for this species.

In the 1970s, *G. fasciatus* was intentionally introduced into several lakes of the Karelian Isthmus (Baltic Sea basin) in order to enhance fish production (Nilova, 1976; Arkhiptseva et al., 1977). From these lakes, *G. fasciatus* spread into Lake Ladoga (Panov, 1996) and then, via the Neva River, invaded the Neva Estuary (Gulf of Finland). In the Neva Bay, the freshwater part of the estuary, the zebra amphipod was detected for the first time in 1996 (Alimov et al., 1998). In 1999, *G. fasciatus* was first registered in the brackish-water reaches of the estuary (Panov et al., 1999). Establishment of this invasive species in the Neva Estuary may result in significant alterations of littoral communities, as has occurred already in some lakes and reservoirs of Europe and Siberia (Panov & Berezina, 2002).

The aim of the present work was to study the distribution and population structure of *G. fasciatus* in the Neva Estuary, plus the salinity tolerance of the species in order to assess the present state of the population in the estuary and the possibility of further spread of this species in the Baltic Sea.

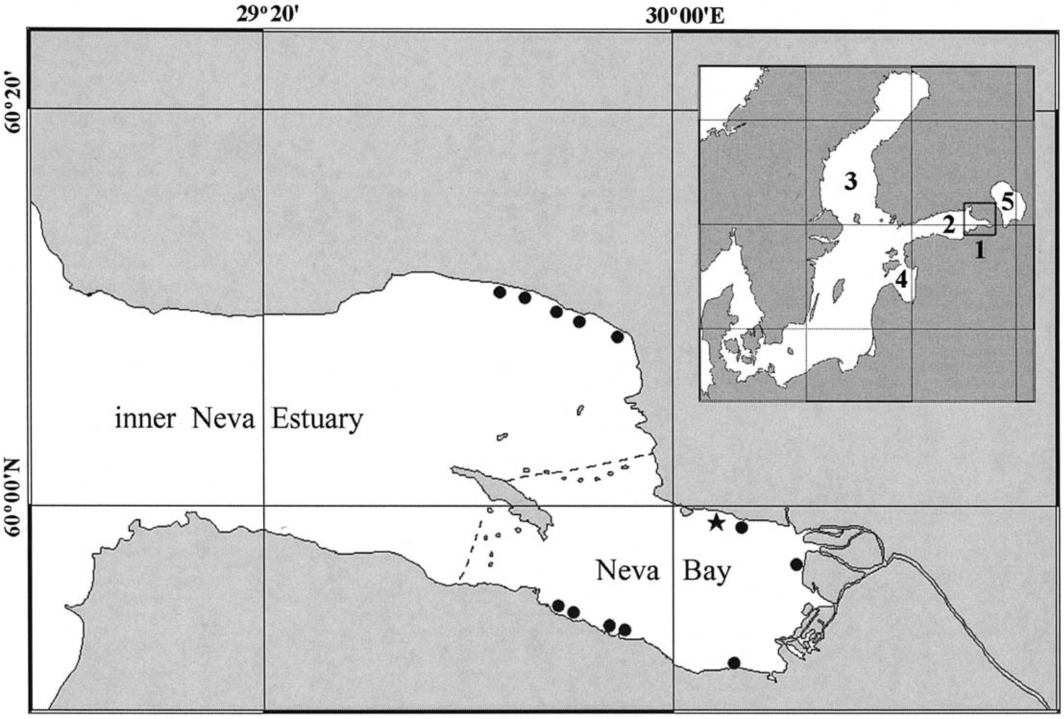

Figure 1. Distribution of the Baikalian amphipod *Gmelinoides fasciatus* in the Neva Estuary in 1998–2000. Asterisk shows the site of period of observations. The dashed line indicates the storm-surge barrier. Numbers in the inserted map of the Baltic Sea region: (1) Neva Estuary, (2) Gulf of Finland, (3) Gulf of Bothnia, (4) Gulf of Riga, (5) Lake Ladoga.

Materials and methods

Site descriptions

The Neva Estuary is the largest estuary in the Baltic Sea, the catchment area of the Neva River exceeding 280 000 km^2. The estuary consists of three main parts: the Neva Bay (400 km^2) and the inner and outer estuary (3200 km^2; Pitkänen, 1991). Our research was focused on the littoral zone (at depths from 0.2 to 1.5 m) of the Neva Bay and the northern part of the inner Neva Estuary (Fig. 1). The Neva Bay is a freshwater part of the estuary (salinity 0.06–0.30 psu). In the inner estuary, separated from the Neva Bay by a storm-surge barrier, the surface waters are brackish (0.6–2.0 psu). Description of the temperature and salinity regimes in the Neva Estuary is provided by Panov et al. (1999). In the littoral zone of the Neva Estuary, the coarse sand, gravel and stones are typical bottom substrates. Also, because of eutrophication, extensive macrophyte beds (mainly of reed *Phragmites australis* (Cav.) and bulrush *Scirpus lacustris* L.) develop during the summer in the littoral zone of the Neva Bay (Panov et al., 2002). In some locations, primary sand and gravel substrates are completely covered by macrophyte roots and debris, which provide suitable habitats for aquatic invertebrates. In the inner Neva Estuary, mats of the filamentous green alga *Cladophora glomerata* (L.), growing on hard substrates, represent the main habitat for invertebrates.

Fieldwork

Extensive biological summer surveys of the littoral communities of the Neva Estuary were conducted in 1998–2000. Also, samples of *G. fasciatus* were taken weekly from 25 May to 23 October 1998 in one location in the Neva Bay (Fig. 1). In the macrophyte beds, quantitative sampling was carried out with a cylindrical 0.125 m^2 corer (Panov & Pavlov, 1986) in two replicates. On hard substrates, quantitative samples were collected by SCUBA-divers, using 0.25 × 0.25 m metal frames in three replicates. The samples were preserved in 4% formaldehyde solution and transported to the laboratory in plastic bags. All collected amphipods were counted, measured and weighed (wet weight). Density, biomass, fecundity, size and sexual structure of the population of

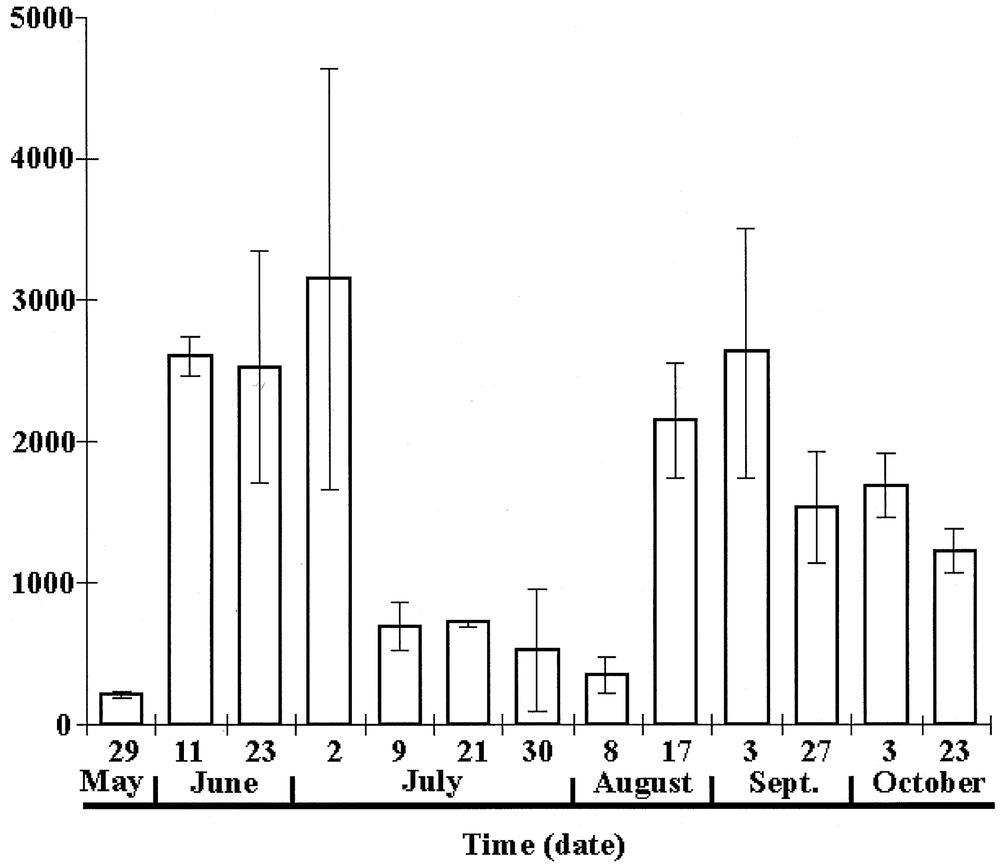

Figure 2. Seasonal dynamics of *Gmelinoides fasciatus* (mean density ± SE) in the littoral zone of the Neva Estuary in 1998.

G. fasciatus were evaluated. Density and biomass of amphipods were expressed as mean (SE: standard error).

Salinity tolerance of *G. fasciatus* at different water salinities and temperatures was determined in a series of laboratory experiments. Experiments were performed with sexually mature males with body length in the range 7.9–9.5 mm (mean 8.7 mm), sexually mature females (5.1–7.0 mm; mean 5.8 mm) and juveniles (2.6–3.3 mm; mean 2.9 mm), which were collected in the freshwater part of the Neva Estuary. The salinity tolerance of *G. fasciatus* was assessed as the survival rate of specimens transferred for 15 days from freshwater to water of different salinities (1–16 psu) and constant temperature (18 °C). The salinity was varied either abruptly (direct transfer) or in 1 psu increments at two-day intervals (stepwise adaptation; see Karpevich, 1968) or at ten-day intervals (stepwise acclimation; see Khlebovich & Kondratenkov, 1973). Also, we studied the development of eggs in females at different water salinities. Sexually mature females (body length 5.7–6.5 mm) and males of *G. fasciatus* were held together at 0.06 psu (control), and at 1, 2, 3, 5, 8, 10, 12 and 16 psu and water temperature of 18 °C. After fertilization, males were removed and fecund females were regularly examined. A separate series of experiments was conducted in order to evaluate the effects of temperature on salinity tolerance in *G. fasciatus*. The amphipods (only males) were held in experimental microcosms (volume 40 l) with various combinations of temperature and salinity (Table 3) for 30 days, before estimations of the coefficients of salinity tolerance. For estimations of these coefficients, the lethal salinity was evaluated after transfer of animals from microcosms to water with gradually increasing salinity (1 psu every 10 min). The value for the control variant (see Table 3) was taken for 1, and then the relative values of lethal salinities for other experimental variants were counted and considered as the coefficients of salinity tolerance for *G. fasciatus*.

The experimental water solutions were prepared by diluting artificial sea water (32 psu) with freshwater

Table 1. Average density, biomass and fecundity of *Gmelinoides fasciatus* in the littoral zone of the Neva Estuary.

Part of the estuary	Density, ind. m^{-2}	Biomass, g m^{-2}	Fecundity, eggs per female
Brackish water	1100 ± 700	2.95 ± 1.50	12.47 ± 2.12
Freshwater	1550 ± 1050	3.75 ± 3.00	12.67 ± 3.96

from the Neva River. The total mineral content of the Neva water was 0.05–0.06 psu. The salinity of experimental solutions was determined with an ATAGO S-10 refractometer to the nearest 0.05 psu. The water in the experimental vessels was changed every three days. Experiments were performed in triplicates. The oxygen concentrations in the water ranged from 7.2 to 8.6 mg l^{-1}. Amphipods were kept in 200-ml flat vessels and fed on a mixture of algae (mainly *Cladophora glomerata*), aquatic moss (*Drepanocladus* spp.) and dried birch leaves (*Betula* spp.).

Results

Distribution and population structure of G. fasciatus in the Neva Estuary

Results of the field surveys in 1998–2000 indicate that *G. fasciatus* established permanent populations in the littoral zone of both freshwater and brackish-water parts of the Neva Estuary (Fig. 1). During the reproductive period from May to October, most of the *G. fasciatus* population concentrates in the shallow near-shore habitats at depths less than 3 m. Maximum density of the zebra amphipod in the littoral zone of the inner Neva Estuary exceeded 1600 ind. m^{-2}. In some locations of the Neva Bay, maximum densities of *G. fasciatus* reached 3500 ind. m^{-2}. Average density and biomass of *G. fasciatus* in the Neva Bay were higher (around 1.5 fold) than in the brackish-water part of the estuary (Table 1).

Our results showed that *G. fasciatus* in the Neva Estuary possesses a one-year life cycle with 2 peaks in density during the season in 1998 (Fig. 2). Significant increase in density of the amphipod population, up to 3400–4800 ind. m^{-2} in late June and early July (first peak), was attributed to the appearance of large numbers of juveniles. The midsummer period was characterized by comparatively low population density (500–800 ind. m^{-2}), a decline in the number of overwintering adults and domination by immature females of the first generation (Fig. 3). Beginning in the first week of August, amphipods of the first summer generation became mature and started to reproduce, which resulted in the second peak of amphipod density up to 2800–3800 ind. m^{-2} in mid-August and September (Fig. 2). Fecund females were present in the *G. fasciatus* population until late September (Fig. 3). Thus, reproduction of the zebra amphipod in the shallow littoral zone of the Neva Bay started in 1998 in early spring at temperatures of 4–5 °C and terminated in October at water temperatures below 10 °C.

The fecundity of *G. fasciatus* averaged 8–36 eggs per female, depending on female body size (Fig. 4). During the reproductive period, from May to September, the mean size of fecund females and their fecundity decreased. In early July, their mean fecundity averaged 20 eggs per female, in early September it decreased to 10–11 eggs per female, and during this period mean sizes of females decreased from 7.3 ± 1.5 to 5.9 ± 1.1 mm.

Experimental study of salinity tolerance in G. fasciatus

After direct transfer from freshwater, during 15 days all males of *G. fasciatus* survived at salinities from 1 to 4 psu, while females were more resistant, tolerating salinities up to 6 psu. The salinity for 100% mortality was 13–16 psu for males and 15–18 psu for females. The salinity tolerance in juveniles was significantly lower, 50% of them dying within one day at 4–5 psu. Their mortality was not significant at 1–2 psu, rising to more than 50% at 3–5 psu (Fig. 5). Thus, sexually mature specimens of *G. fasciatus* tolerate salinities of 4–6 psu, which is the upper limit for this species.

In experiments on stepwise adaptation in *G. fasciatus*, adult amphipods tolerated salinities up to 7–8 psu with 100% survival (Table 2). At salinities of 9–10 psu, their survival decreased to 50–60%. Mortality of 100% was observed at salinities of 11–12 psu. Similar results were obtained with juveniles, whose mortality was in the range 5–25% at salinities of 7 psu and less. After stepwise acclimation in *G. fasciatus*, all females and juveniles tolerated salinity of 7 psu, while males tolerated salinity of 5–6 psu (Table 2). These estimates correspond to the potential salinity tolerance or 'potential euryhalinity' according to Khlebovich (1974) for this species.

We revealed that the reproductive ability of the amphipod *G. fasciatus* significantly decreased at higher

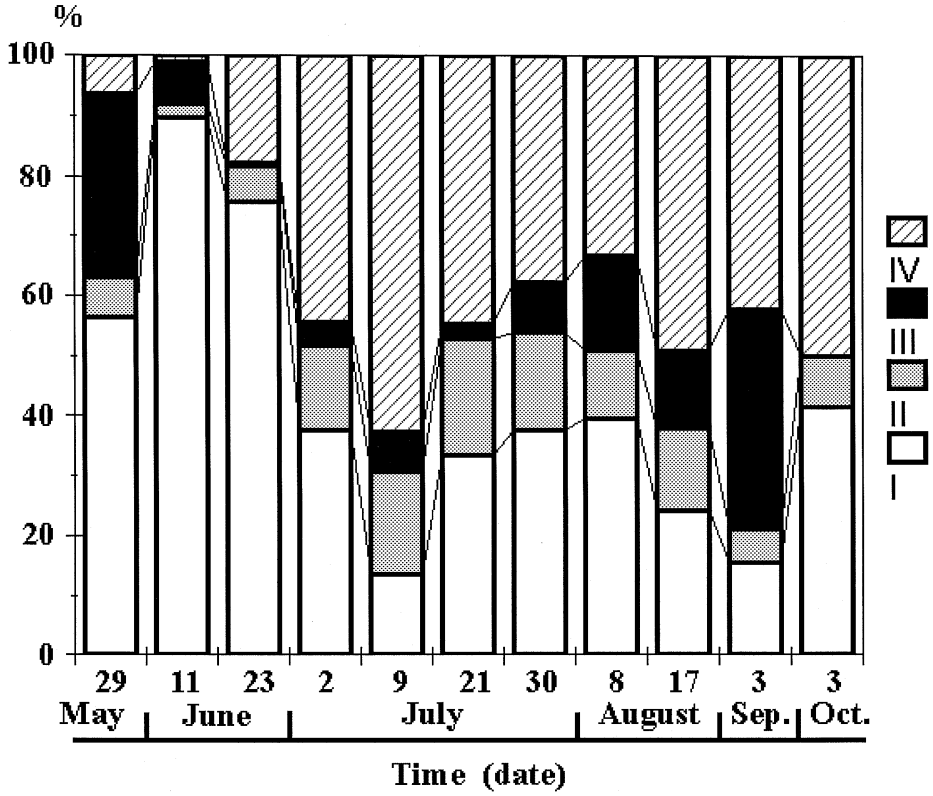

Figure 3. Population structure of *Gmelinoides fasciatus* in the littoral zone of the Neva Estuary in 1998: (I) juveniles, (II) males, (III) females with brood, (IV) females.

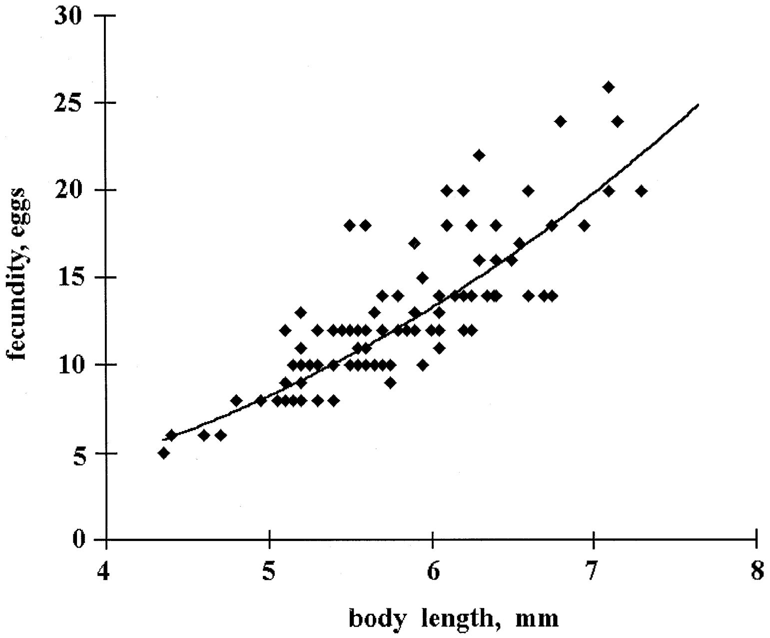

Figure 4. Fecundity (E) in *Gmelinoides fasciatus* females, related to body length (L), in the littoral zone of the Neva Estuary (E = 0.124 $L^{2.61}$, $R^2 = 0.70$, $n = 120$).

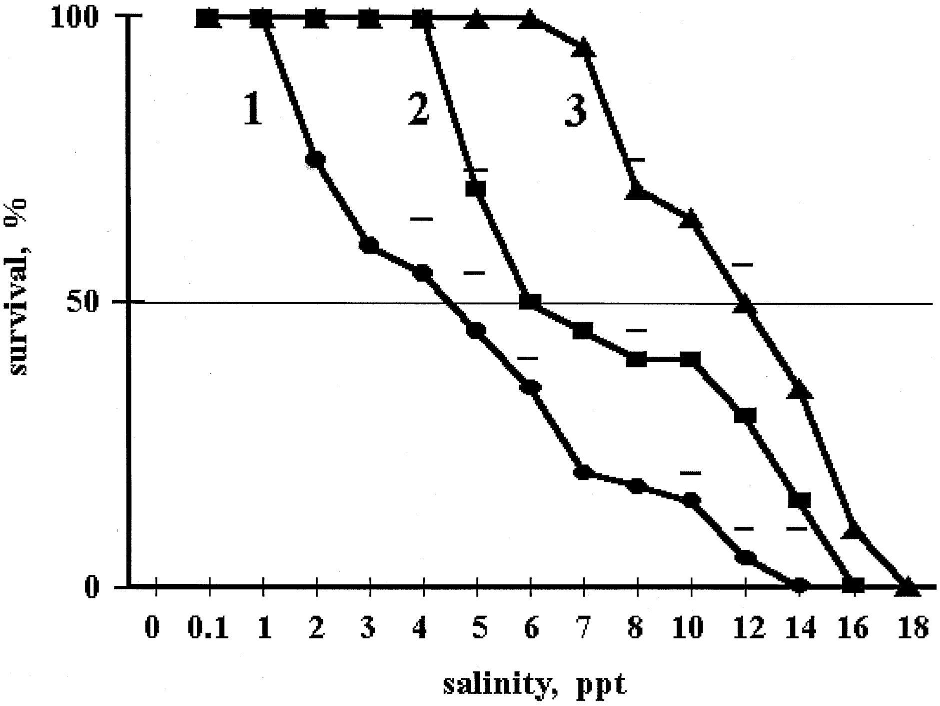

Figure 5. Survival of the amphipod *Gmelinoides fasciatus* after 15 days at various salinities: (1) juveniles, (2) males, (3) females.

Table 2. Salinity tolerance in *Gmelinoides fasciatus*.

Experimental conditions	Upper salinity level, psu	
	Females	Males
Stepwise adaptation (in 1 psu increments at two-day intervals)	7–8	7
Stepwise acclimation (in 1 psu increments at ten-day intervals)	7	5–6

salinities. In freshwater and at 1 and 2 psu, juveniles appeared 11–12 days after fertilization of the eggs. However, in freshwater and at 1 psu, the ratio of hatched juveniles to number of eggs in clutch was 1, while it was only 0.4–0.6 at 2 psu. The juveniles were viable, and their growth and development were normal during the experiment (30 days). At 3–8 psu, females survived for several weeks, but no egg development in their brood pouches was observed. Females either lost their eggs or embryos died at early stages of development.

Experimental studies further showed that the salinity tolerance of *G. fasciatus* depends on water temperature. Survival of amphipods decreased along with increasing temperature (Table 3). At water salinity of 5 psu, the maximum survival in this amphipod (50%) occurred at the lowest experimental temperatures of 12–14 °C. Adult amphipods did not survive in experiments with water temperature of 23–26 °C and salinity of 5 psu. Estimated coefficients of salinity tolerance of *G. fasciatus* decreased with increasing salinity and temperature. This is likely a result of decrease of total adaptive potential of the amphipods during acclimation in brackish waters. At that in water with salinity of 2 psu and 5 psu, the coefficients were higher at low temperatures (12–14 °C) than at medium (16–22 °C) and high (23–26 °C) temperatures (Table 3).

Discussion

Our study shows that at present the invasive amphipod *G. fasciatus* is an abundant species in the studied habitats in the Neva Bay and some locations in the inner Neva Estuary. In the 1980s in littoral communities of the Neva Bay, the amphipod *Gammarus lacustris* Sars was the common and abundant species, with densities of up to 700 ind. m^{-2} in some locations (Panov, 1988). This native amphipod became locally extinct by the period of our study (1998–2000), and we suggest that this was a result of the zebra amphipod invasion.

Table 3. The survival and tolerance to salinity in *Gmelinoides fasciatus* at different salinity-temperature conditions.

Variant	Salinity, psu	Temperature, °C	Survival, %	Coefficient of salinity tolerance
Control	0.2	16.3–22.0	100	1
I	2.0	23.2–25.6	100	0.5 ± 0.05
II	2.0	16.2–21.9	100	0.65 ± 0.05
III	2.0	12.3–14.3	100	0.7 ± 0.1
IV	5.0	23.2–26.0	0	0
V	5.0	16.3–22.1	25	0.5 ± 0.1
VI	5.0	12.1–14.2	50	0.65 ± 0.1

Mechanisms of replacement of the native species by *G. fasciatus* are not clear and require further study. We suppose that two mechanisms are likely. First, adult zebra amphipods are active predators (Bekman, 1962; Panov, 1996) and may prey on juveniles of *G. lacustris*. On the other hand, the invasive species appears more resistant to unfavorable environmental and anthropogenic factors than *G. lacustris*. Perhaps along with it high fecundity and fast population growth, this makes *G. fasciatus* able to successfully replace the native species.

The capacity to tolerate a wide range of salinities is typical for many amphipod species (Kinne, 1970; Khlebovich, 1974). As shown by Bazikalova et al. (1946), *G. fasciatus*, which is a homoiosmotic organism in freshwater, cannot maintain a constant body fluid osmotic pressure at high salinities (i.e. brackish and sea waters) and acquires the features of a poikilosmotic organism. Our experimental results showed that the adult zebra amphipod tolerates brackish water with salinity 5–7 psu, but they are not able to reproduce successfully at salinities higher than 2 psu, because their embryos die. Bazikalova (1945) suggested that *G. fasciatus* is a species of marine origin, because the adult amphipods are able to survive in a wide range of water salinities, and the species is morphologically similar to the Caspian amphipod of the genus *Gmelina*. However, our experimental results showed that development of eggs in *G. fasciatus* was successful only at low salinities, which is in contradiction with the suggestion of a marine origin of this species. These data also indicate that *G. fasciatus* is potentially able to invade parts of the Baltic Sea where salinities do not exceed 5 psu. Because successful reproduction of the species is possible only at water salinities below 2 psu, establishment of permanent populations will be limited to habitats with salinities less than this critical level.

Our experiments also revealed that salinity tolerance in *G. fasciatus* depends on water temperature, with highest tolerance at low temperatures. At a salinity of 5 psu and temperatures of 23–26 °C, the amphipods are not able to survive. Decreasing salinity tolerance with increase in temperature of water has also been found for molluscs (Komendantov et al., 1985). In accordance with Kinne (1964), the tolerance of aquatic animals for salinity decreases at temperatures different from optimum, thus unfavorable salinities are best tolerated at the temperature optimum. We assume that temperatures below 22 °C are more suitable for the acclimatization of zebra amphipod in brackish-water habitats, and this species will not be able to colonize brackish-water areas with high summer temperatures.

The results of the present study indicate that certain salinity and temperature limits exist for zebra amphipod spread in the Baltic Sea. However, considering the ability of amphipods, including *G. fasciatus*, to actively migrate into habitats with favorable environmental conditions (Lindstrom, 1991; Bessolitsyna at al., 2000), the establishment of the zebra amphipod in the brackish coastal habitats of the Baltic Sea, such as the Gulf of Bothnia and Gulf of Riga, is likely in near future.

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