Spatial distribution of Gmelinoides fasciatus Steb. in Thermally Polluted Water (Belovo Reservoir, Southwest Siberia)

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ABSTRACT: Gmelinoides fasciatus (Stebbing, 1899) is a Baikal endemic amphipod that has recently become widespread in Eurasia. This species accidentally entered the cooling reservoir of the Belovo power plant and became successfully naturalised there. This study describes the peculiarities of G. fasciatus distribution in reservoir sites with different thermal regimes and analyses the environmental factors that limit its spread. The use of heating areas for prevernal breeding promoted the rapid expansion of G. fasciatus in the cooling reservoir. Silted soils, depths greater than 1 m and water heating above 26°C limit the dissemination of G. fasciatus in the reservoir. Invasion of G. fasciatus in the Belovo reservoir has not caused the extinction of the indigenous species Gammarus lacustris. The structural characteristics of aboriginal communities at unpopulated and populated by G. fasciatus zone of reservoir were not statistically different. Invasion of G. fasciatus did not aggravate the competitive interactions in the benthic communities.

Key words: Invasion, Macroinvertebrate, Power plant

INTRODUCTION

Among aquatic macroinvertebrates, Crustaceans most actively invade areas beyond their natural habitats (Karatayev et al., 2009; Leuven et al., 2009). Crustaceans account for 53% of alien species in the Ponto-Caspian region (Grigorovich et al., 2002), 55% in Spain (García-Berthou et al., 2007; Oscoz, 2010), 52% in Belarus (Semenchenko et al., 2009) and 51% in the upper reaches of the Rhine (Bernauer & Jansen, 2006). Similar relations find in the marine ecosystems as well. Of 115 alien species registered in the Baltic Sea, 40% and more fall on crustaceans (Leppakoski et al., 2002).

Gmelinoides fasciatus (Stebbing, 1899) is one of the most dispersed alien species in Eurasian freshwater ecosystems. In its natural habitat, this species inhabits the shallow coastal areas of Baikal. This eurybiontic species is tolerant to various types of pollution and is found in disturbed habitats (Panov, 1996). By feeding type it refers to euryphage consuming micro- and macroalgae, detritus, bacteria, invertebrates and their corpses (Panov & Berezina, 2002; Berezina et al., 2005; Berezina, 2007; Pankova & Berezina, 2007; Kestrup et al., 2011). This eurybiontic species tolerant to various types of pollution (Panov, 1996). Gmelinoides fasciatus is the most widespread acclimatised invertebrate and was introduced into 22 reservoirs of European Russia, the Urals, Siberia, Kazakhstan and Central Asia to improve the food supply for fish. The introduction of this species into fresh water bodies contributed to its spread in Eurasian reservoirs (Panov & Berezina, 2002). In recent decades, G. fasciatus has actively settled across Eurasia; there are numerous reports of its presence in lakes (Ladoga, Onega, Peipsi, Ilmen), reservoirs (the Volga and the Angara) and in Baltic Sea (Panov, 1996; Panov & Berezina, 2002; Kangur et al., 2010). The invasion of G. fasciatus into new ecosystems can lead to strained competitive relationships and direct aggressive contacts with native species. There are cases of the displacement of indigenous species (mainly crustaceans), biodiversity loss and changes in the structure of natural communities caused by G. fasciatus invasion (Panov & Berezina, 2002).

Prior to our research, data on G. fasciatus in the Ob River basin were available only for the Novosibirsk Reservoir, where the species was introduced from Posolsky sor of Baikal in the 1960s. In the Novosibirsk reservoir, it was primarily found in the littoral zone on sandy and submerged woody

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debris. At some sites, it dominated up to 50–80% of the biomass and 40% of the invertebrate density (Yanygina, 2011a).

In 2002, we recorded this species in the cooling reservoir of the Belovo power plant for the first time. Probably, *G. fasciatus* was introduced into the Belovo reservoir together with young fishes from the hatchery of a fish farm located downstream from the Novosibirsk Reservoir. The aim of this study was to investigate the biology of *G. fasciatus*, to analyse the environmental factors that limit the spread of the species and to assess the after-effects of its invasion into the Belovo cooling reservoir. The particular interest of the study of the *G. fasciatus* population from the cooling reservoir relates to the sporadic data available concerning the biology of this species from thermally polluted waters. The study of its spatial distribution in heated water enables predictions to be made concerning its dispersal ability under climate-change conditions and following its introduction into water bodies with different thermal regimes.

MATERIALS AND METHODS

The reservoir was created in 1964 by flow regulation of the Inya River (the right tributary of the Ob) near the town of Belovo (Kemerovo Region), to cool the heated water of the Belovo power plant. The length of the Belovo reservoir is 10 km, the maximum width is 2.3 km and the maximum and mean depth are 12.0 and 4.4 m, respectively. The water surface area of the reservoir comprises 13.6 km² and the area of a shallow site (up to 2.0 m) reaches 5.4 km². It is a small reservoir according to its water surface, and shallow in terms of its mean depth. The Inya catchment (up to the plant site) is approximately 1,760 km², and the river length is 116 km. The reservoir is used to supply water to the Belovo power plant and industrial enterprises of the town of Belovo, as well as for growing fish in the rearing channel, and for irrigation and recreation.

The bottom sediments in the reservoir’s littoral, diversion and discharge channels are predominantly rocky at Inya River, and are sandy and silty in other parts of the reservoir.

The water from the dam area arrives at the power plant via a diversion channel and then enters the central part of the reservoir through a 6.45-km-long channel. Thus, a circulation of a cooling flow is formed in 40% of the reservoir area. The water temperature in the circulation flow can exceed +30°C in the summer and vary from +5.4 to +10.1°C in the winter (Yanygina et al., 2010).

According to the heating effect, three zones can be defined: zone 1 of permanent maximum heating is situated directly in the area of water discharge and includes the discharge channel and the reservoir site near its mouth. In July, the maximum water temperature can reach +36°C. Zone 2 of moderate heating partly includes the area of circulation flow of cooling water. Ice cover is completely absent here, or can form for a short period. Zone 3 of minimum heating is situated in the upper reach and near to the dam. The thermal regime here is close to natural conditions.

The maximum difference in temperature in these zones usually occurs within a cold season. The reservoir can be classified as a water body with a moderate thermal regime, where the mean annual heating of the discharged water does not exceed +5°C (Yanygina et al., 2010).

Benthic macroinvertebrates were sampled in different locations of the reservoir and the Inya River in April, June, August and September 2002 and April 2008. The periods that reflected the main phases of the *G. fasciatus* life cycle in Siberian reservoirs were studied, i.e. the onset of the breeding of overwintered females (April), the emergence of juveniles (June), the beginning of breeding of the first generation of the current year (August) and the termination of reproduction (September). In April, we collected subglacial samples in the zone of minimal heating. Sampling from silted soils was performed using a 0.025 m² Petersen dredge. Quantitative washouts were taken from rocky substrates, and the rock’s area was subsequently determined by projecting it onto a plane. In macrophyte thickets, sampling was performed by a scoop net and by weed wash-off. Additionally, artificial substrates (i.e. claydite) were exposed to the water of the littoral site for 2–3 days. The benthic samples were washed through a capron mesh (350 × 350-µm mesh size), sorted and fixed in 70% ethanol. Most organisms were identified to the lowest taxonomic level (generally species or group of species), except for the coelenterates (determined to genus) and nematodes (determined to class).

Each of 857 collected individuals of *G. fasciatus* was measured from the anterior margin of the head to the posterior margin of the telson using a microscope equipped with an ocular micrometer. The number of eggs in a brood pouch was counted, to determine female fecundity. A breeding period was identified by the presence of breeding females in the population.

The Spearman’s rank correlations were calculated to test the mean length dependence of female fecundity. Multi-way analysis of variance (ANOVA) was used to assess the effect of various environmental
factors (depth, bottom type, temperature) on the relative density of *G. fasciatus* in the benthic communities. When results were statistically significant, pairwise multiple comparisons were performed using Tukey’s test. To estimate the statistical significance of differences in the species richness, density and biomass of the benthos in littoral areas that were populated and unpopulated by *G. fasciatus*, the Mann-Whitney test (U) was applied. A significance of *p* < 0.05 was assumed for all tests.

**RESULTS & DISCUSSION**

In the reservoir, *G. fasciatus* was more abundant on solid substrates represented by boulders, gravel and crushed stone in the littoral zone of the reservoir, except for silts in deep sites. *Gmelinoides fasciatus* was also found on stones and sand of the Inya River, both upstream and downstream from the reservoir. In macrophytes, *G. fasciatus* was met sporadically. During the whole study period, peak values of density (24.4 thousand ind./m$^2$) and biomass (36.1 g/m$^2$) were observed in September in the littoral zone of minimal heating. Generally, these indicators were similar to those in other water bodies with the introduced species (Yanygina, 2011b).

In some sites of the reservoir, different habitat conditions for hydrobionts resulted in a number of quantitative indicators for the total zoobenthos and *G. fasciatus*. The distribution of *G. fasciatus* in different areas of the reservoir depended on abiotic factors such as depth, substrate type and temperature. Amphipods preferred the sandy and rocky bottom of the littoral, thus making up the bulk of the density and biomass of the zoobenthos. In deep sites of the reservoir, only few individuals were found on silted soils. Basically, crustaceans inhabited a narrow coastal strip: the population density averaged 2.1 thousand ind./m$^2$ above 0.5 m, 0.54 thousand ind./m$^2$ deeper than 0.5–0.8 m and less than 0.01 thousand ind./m$^2$ in other parts of the reservoir. The peak density and biomass of *G. fasciatus* was registered in zones 2 and 3 at different times. In zone 1 (discharge channel), crustaceans were found only in the cold period. The maximum water temperature where *G. fasciatus* was discovered was +25.7°C. Multivariate analysis revealed that the combined effect of depth, bottom type and temperature accounted for 39% of the relative density dispersion and 48% of the relative biomass dispersion of *G. fasciatus* in benthic communities of the reservoir (Table 1).

The assessment of the invasive effect on native communities is an important part of the alien species research that invade new reservoirs. In the Belovo reservoir, a total of 139 species of benthic invertebrates were noted during the period of study. The greatest numbers of species were insects (91 species, of which 42 species belonged to the Chironomidae). The species richness, density and biomass of aboriginal zoobenthos varied greatly in different sites of the reservoir due to the strong variability in macroinvertebrate habitat in the littoral zone and aggregation in the distribution of organisms. The dynamics of species richness, density and biomass of zoobenthos in the parts of the reservoir that were inhabited by amphipods was analysed to assess the role of *G. fasciatus* in the formation of littoral benthic communities. The density and biomass of *G. fasciatus* in the areas of its mass development amounted to 95% of those for zoobenthos. The data analysis did not show a statistical difference among

<table>
<thead>
<tr>
<th>Factor</th>
<th>Index</th>
<th>$r^2$</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth</td>
<td>N</td>
<td>0.14</td>
<td>7.96</td>
<td>0.0069</td>
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<tr>
<td>Bottom type</td>
<td>B</td>
<td>0.19</td>
<td>11.47</td>
<td>0.0014</td>
</tr>
<tr>
<td>Thermal zone</td>
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<td>0.15</td>
<td>8.74</td>
<td>0.0048</td>
</tr>
<tr>
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<td>12.67</td>
<td>0.0008</td>
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<td>0.0579</td>
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<tr>
<td>Bottom type + thermal zone + depth</td>
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<td>6.71</td>
<td>0.0007</td>
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<tr>
<td>Bottom type + thermal zone + depth</td>
<td>B</td>
<td>0.37</td>
<td>9.13</td>
<td>0.0001</td>
</tr>
</tbody>
</table>

*F* - Fischer’s F-criterion, *p* - significance value, $r^2$ - Coefficient of Determination

Table 1. Statistical comparisons of relative density (N) and biomass (B) of *Gmelinoides fasciatus* (Stebbing, 1899) at sites with different depths, temperatures and bottom types.
species richness ($U = 63.5$, $p = 0.18$), density ($U = 65.0$, $p = 0.21$) and biomass ($U = 83.0$, $p = 0.70$) of zoobenthos in littoral areas of the reservoir populated and unpopulated by *G. fasciatus*, thus suggesting that this amphipod does not greatly modify the invaded habitat (Fig. 1).

Within new reservoirs, alien species occupy vacant ecological niches or begin to compete with native species. Some cases are known, where a reduction in density or the disappearance of other Gammaridae species (including *G. lacustris* Sars) caused by *G. fasciatus* invasion occurs. Previously, the displacement of *Gammarus* by *G. fasciatus* was observed in the reservoirs of the European part of Russia and in Siberia (Panov & Berezina, 2002). Experimentally (Timofeev et al., 2008), *G. fasciatus* and *G. lacustris* have a similar resistance to hypoxia and increased temperature, although *G. lacustris* is toxically less resistant. Furthermore, *G. fasciatus* is characterised by a higher thermal preference (17–18°C) than *G. lacustris* (15–16°C), which probably confers a major advantage on *G. fasciatus* in cooling reservoirs.

*Gmelinoides fasciatus* is the most numerous species in the Belovo reservoir, but is not the only species of amphipod present. In the zone of minimal heating (diversion channel), artificial substrates were massively colonised by *Gammarus lacustris*; here only a few individuals of *G. fasciatus* were found. In other parts of the reservoir (including discharge channel), *G. fasciatus* inhabited artificial substrates, while *G. lacustris* was not registered at all. When studying the Belovo reservoir in 1978 (prior to the establishment of the fish farm), *G. fasciatus* was not present at all. *G. lacustris* was also not observed in most parts of the reservoir. A high density of *G. lacustris* was observed only on artificial substrates (coal slag) in the littoral of the headrace (Stepanova, Bazhina, 1983). Thus, spatially isolated

**Fig. 1.** Species richness (A), density (B) and biomass (C) of zoobenthos in populated (I) and unpopulated (II) by *G. fasciatus* littoral areas of the reservoir (thermal zones: 1 – maximum, 2 – moderate, 3 – minimal heating)
populations of both species with a dominance of *G. fasciatus* in the littoral of the Belovo reservoir has probably coexisted for a long time.

The body length of *G. fasciatus* individuals ranged from 1.2 to 10.2 mm. The largest size (10.2 mm for males and 9.2 mm for females) was registered in April. The maximum size of *G. fasciatus* is relatively small (Table 2). The small size of the Gammaridae is usually associated with an insufficient food supply. Apparently, the small size of *G. fasciatus* in the eutrophic Belovo reservoir results from the increased water temperature, which accelerates amphipod development but is not limited by the trophic resources.

Unlike other Siberian reservoirs (Novosibirsk Reservoir, Lake Arakhlei) that are populated by *G. fasciatus*, *G. fasciatus* newborns appeared earlier in the Belovo reservoir (Table 2). In the first days of April, when Siberian reservoirs are covered with ice and few females begin to lay eggs, the first juvenile of *G. fasciatus* was already noted in the Belovo reservoir in the zone of maximum heating. In April, the majority (~90%) of females in the ice-free part of the Belovo reservoir carried eggs at +6–8°C; the remaining females had oostegites with setae. During this period, the upper part of the reservoir was covered with ice, and only one-third of the females laid eggs (Fig. 2). In the discharge channel, where the water temperature during this period reached 15°C, we detected females (6.3–9.0 mm long) with eggs and juveniles recently released from eggs (1.2 mm in length). In April, *G. fasciatus* juveniles were also sporadically observed at sites where heated waters inflow to the reservoir. All these observations show that in the zone of maximum heating, gammarid reproduction starts before than other part of reservoir.

In summer, *G. fasciatus* was not found in the zone of maximum heating. In other sites of the reservoir, the population was mainly composed of individuals with size of 2.0–5.0 mm. There were juveniles hatched in the current year (Fig. 3). During this period, the reproduction of juveniles of the spring generation started in zones 1 and 2.

### Table 2. Biological features of *Gmelinoides fasciatus* (Stebbing, 1899) from different water bodies

<table>
<thead>
<tr>
<th>Water body</th>
<th>Maximum length, mm</th>
<th>Breeding period</th>
<th>Minimal size of breeding females</th>
<th>Maximum number of eggs per 1 female, pcs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lake Baikal, Posolsky sor</td>
<td>11.2</td>
<td>May - June</td>
<td>3.5</td>
<td>32</td>
</tr>
<tr>
<td>Novosibirsk reservoir</td>
<td>12.8</td>
<td>May - August</td>
<td>3.9</td>
<td>54</td>
</tr>
<tr>
<td>Belovo reservoir, zone of minimal and moderate heating</td>
<td>10.1</td>
<td>April - August</td>
<td>3.7</td>
<td>33</td>
</tr>
<tr>
<td>Belovo reservoir, zone of maximal heating</td>
<td>10.2</td>
<td>April</td>
<td>6.3</td>
<td>46</td>
</tr>
<tr>
<td>Rybinsk reservoir</td>
<td>10.0</td>
<td>May - September</td>
<td>3.5</td>
<td>23</td>
</tr>
<tr>
<td>Lake Arakhlei</td>
<td>9.9</td>
<td>May - August</td>
<td>3.6</td>
<td>27</td>
</tr>
<tr>
<td>Lake Ladoga</td>
<td>11.8</td>
<td>May - September</td>
<td>3.8</td>
<td>35</td>
</tr>
<tr>
<td>Lake Otradnoye</td>
<td>12.7</td>
<td>May - September</td>
<td>4.4</td>
<td>45</td>
</tr>
</tbody>
</table>

In summer, *G. fasciatus* was not found in the zone of maximum heating. In other sites of the reservoir, the population was mainly composed of individuals with size of 2.0–5.0 mm. There were juveniles hatched in the current year (Fig. 3). During this period, the reproduction of juveniles of the spring generation started in zones 1 and 2.

Fig. 2. Sexual structure (% of density) and the proportion of breeding females (% of total females) of the *Gmelinoides fasciatus* (Stebbing, 1899) population at various sites of the Belovo Reservoir (thermal zones: 1 – maximum, 2 – moderate, 3 – minimal heating)
Fig. 3. Population structure (% of density) of *Gmelinoides fasciatus* (Stebbing, 1899) in the Belovo reservoir

In September, the basis of *G. fasciatus* density (68%) in the Belovo reservoir and Inya River mainly consisted of grown juveniles (4–6 mm) from the summer generation; newborns and females with eggs were absent, which is evidence of the termination of amphipod reproduction in the reservoir. Considering the time of breeding termination (August), the period of Gammaridae reproduction in the Belovo reservoir lasted one-month longer than in other Siberian water bodies. The breeding duration for the *G. fasciatus* population from the Belovo reservoir and the reservoirs of the European part of Russia was five months.

The number of eggs in the brood pouch correlated well with female size ($r^2 = 0.89$ for the zone of maximum heating, and $r^2 = 0.98$ for the zones of moderate and minimum heating). In April, when crustaceans inhabited the whole reservoir (including the site of maximum heating), female fecundity was different in various thermal zones. A particularly significant difference was observed in large females, whose fecundity in the zone of maximum heating was higher than in other sites of the reservoir (Fig. 4). The maximum fecundity of crustaceans in zone 1 (46 eggs per female) also exceeded that in zones 2 and 3 (33 eggs). In the zone of minimal heating, maximum female fecundity corresponded with or was slightly higher than in most other water bodies where the species was introduced; this index tends to be the highest in the zone of maximum heating (zone 1) (Table 2). In thermal zone 3, the proportion of males in different seasons was slightly less than that of females. In zone 1, *G. fasciatus* was detected only in April. Notably, males were three-times rarer than females.

The minimum length of breeding females in the summer significantly decreased. Breeding females reached 6.3 mm in size in April, 5.0 mm in June, 4.7 mm in July and 3.7 mm in August. This might indicative a continuation of active reproduction of *G. fasciatus* in the summer. The reduction in the minimal body size of breeding females (from 6.3 to 3.7 mm) also contributes to the productivity of the population, because early maturation leads to an increase in progeny number and general generative production that is typical of other amphipod species (Sutcliffe, 1993). The minimum size of breeding females was the same in all reservoirs (Table 2). An increase in *G. fasciatus* productivity in the cooling reservoir also occurred due to an acceleration of growth and...
embryonic development when heated within the tolerance values. At higher temperatures that were recorded solely in the summer in the zone of maximum heating, crustaceans migrated into the area with better thermal conditions. Based on the known dependency of the duration of embryonic and post-embryonic (before maturity) on the development of *G. fasciatus* (Panov & Berezina, 2002), it can be suggested that the growth of one generation in the cooling Belovo reservoir in summer takes about 40 days. Early sexual maturity, a high fecundity and the short development time of Gammaridae invasive species explain their rapid spread and high density in invasion locations (Bacela *et al.*., 2009).

**CONCLUSIONS**

The invasion of alien species often occurs rapidly as they enter new reservoirs with favorable conditions (Bohonak & Jenkins, 2003; Boltovskoy *et al.*, 2006; Yakovleva & Yakovlev, 2010). The colonisation of the cooling reservoir of the Belovo power plant by *G. fasciatus* was also very rapid. Previous studies performed in 1989 do not report on this species. In 2002, it already dominated most of the littoral zone in terms of species density and biomass.

The rapid spread of *G. fasciatus* in the cooling reservoir might be caused by its reproduction ability in the heating zone during early spring. Moreover, the proportion of breeding females in the zone of minimal heating in the sites covered with ice was significantly less than in the heated ice-free part of the reservoir for the same period. A high absolute fecundity rate is characteristic for *G. fasciatus* from the Belovo reservoir, which is indicative of its active invasion of the reservoir. The peak fecundity of females in the zone of maximum heating was also higher than that in other sites of the reservoir. This study suggests that the thermal regime is significant to *G. fasciatus* expansion. This species has potential to populate the thermally polluted water and we expect its invasion in other cooling reservoirs. Despite the significant contribution of *G. fasciatus* to the density and biomass of the benthos, the structural characteristics of aboriginal communities (species richness, density and biomass) of the reservoir parts unpopulated and populated by crustaceans were not statistically different. Apparently, successful invasion of *G. fasciatus* occurred due to the incomplete use of the trophic resources of this eutrophic reservoir by the indigenous zoobenthos, thus, invasion did not aggravate the competitive interactions in the benthic communities.

**ACKNOWLEDGEMENTS**

The author is grateful to E.N. Krylova and M.I. Koveshnikov for their help in collecting the material.

**REFERENCES**


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