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CURRENT STATUS OF AN INTRODUCED BAIKALIAN AMPHIPOD, *Gmelinoides fasciatus* (Stebbing), IN THE LITTORAL COMMUNITIES OF LAKE PEIPSI

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Abstract. *Gmelinoides fasciatus*, an incidentally introduced gammarid of Baikalian origin, has been known from Lake Peipsi since 1972. It was common and abundant in the shallow stony littoral and in some rivers connected with the lake in 1987–98. However, at open-water stations, the species has become rare in recent years compared with its peak in the early 1990s. Native gammarids have been virtually superseded by *Gmelinoides* in this lake.

Key words: gammarids, introduced species, lakes, zoobenthos.

INTRODUCTION

Like other large lakes of the world, Lake Peipsi (= Chudskoe) on the border of Russia and Estonia has its own history of human-mediated biological invasions and introductions. Establishment of the zebra mussel *Dreissena polymorpha* Pallas in the 1930s and introduction of the Baikalian gammaridean amphipod *Gmelinoides fasciatus* (Stebbing) in the early 1970s can be considered the most important events in its bottom macroinvertebrate communities, according to Timm et al. (1996). Timm & Timm (1993) documented the colonization process of the coastal zone of L. Peipsi with *G. fasciatus*, using an available long-term data series on the zoobenthos of this lake. This exotic amphipod was introduced

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accidentally in L. Peipsi during headlong attempts to acclimatize *Gammarus lacustris* Sars from a Siberian population. It was found first in 1972, and established itself successfully in the littoral zone of L. Peipsi by 1990, replacing completely the native population of *G. lacustris* (along with possible successors of Siberian specimens) in this lake. Abundance of *Gmelinoides* in both L. Peipsi *s.s.* and L. Pihkva in 1988–92 was also noticed by Antipova (1995). Later on, according to data of yearly monitoring of zoobenthos on the western, i.e. Estonian, side of L. Peipsi, the abundance of *G. fasciatus* has declined, as suggested earlier by Timm & Timm (1993). In 1996, the first author conducted a survey of the eastern, i.e. Russian, side of the lake with the goal to assess the current status of the *Gmelinoides* population in the coastal zone. This amphipod was also discovered in several rivers connected with L. Peipsi. The paper summarizes recent data on the status of *G. fasciatus* in the drainage system of L. Peipsi *s.s.* The southern parts of the complex of L. Peipsi (lakes Pihkva or Pskovskoe and Lämmijärv or Teploe) are generally excluded from this survey.

METHODS

Quantitative samples of macroinvertebrates from eight locations in the littoral at the eastern shore of L. Peipsi were collected by the first author on 18 October 1996. On 5 August 1996, two more locations were sampled in the Narva (Narova) R. The description and location of the stations are given in Table 1. Samples were taken with an original plastic tube sampler (diameter 0.2 m, height 0.5 m). The tube sampler was placed on bottom, inserted in sediments, and samples containing stones, aquatic plants, detritus, and animals were gently removed with a small hand net (mesh size $250 \,\mu$ m). Stones were washed up in a

| Site | Latitude, N | Longitude, E | Depth, m | Substrate | Abundance, ind. m ⁻² | Biomass, g m ⁻² |
|------|----------------|-----------------|-------------|---------------------------|------------------------------------|-------------------------------|
| 1 | 58°57.5' | 27°43.5′ | 0.25 | Gravel, stones | 9 600 | 32.7 |
| 2 | 58°51.0′ | 27°48.0′ | 0.3 | Gravel, stones | 14 400 | 57.1 |
| 3 | 58°40.3' | 27°45.5′ | 0.3 | Sand, Potamogeton | 9 460 | 39.6 |
| 4 | 58°37.0' | 27°47.6' | 0.25 | Sand, gravel | 7 600 | 28.6 |
| 5 | 58°34.5' | 27°49.2′ | 0.25 | Gravel, sand | 17 300 | 64.3 |
| 6 | 58°30.0' | 27°50.0′ | 0.4 | Silt, Potamogeton | 50 | 0.1 |
| 7 | 58°28.0' | 27°49.8′ | 0.3 | Sand, Potamogeton | 5 060 | 8.8 |
| 8 | 58°46.0′ | 27°46.5′ | 0.4 | Gravel, sand | 15 260 | 64.4 |
| 9 | 58°04.0' | 27°47.5' | 0.3 | Gravel, sand, Potamogeton | 17 100 | 102.0 |
| 10 | 58°04.0' | 27°47.5′ | 0.25 | Gravel, stones | 13 200 | 53.6 |

Table 1. Selected characteristics of sampling locations in the eastern L. Peipsi littoral (sites 1–8) and the Narva R. (9, 10), 1996, including the abundance and biomass of *Gmelinoides fasciatus*

bucket and the remaining portion of the sample was placed in a plastic bag and preserved with 4% formalin. Two replications were taken from each location. In laboratory, the samples were washed through standard soil sieves. Animals were removed under a dissecting microscope, sorted, counted, and weighed on the electrobalance to the nearest 0.01 mg (wet weight).

Yearly monitoring samples were collected by the Võrtsjärv Limnological Station at 11–12 stationary points over the whole Estonian part of L. Peipsi, mostly in the sublittoral and profundal, in May or June. The exact location of the stations, as referred to by Timm & Timm (1993), was changed in 1992. Borutskij or Zabolotskij type box samplers with a grasp area of 225 cm² were used for taking three replications at each station. Animals were sorted when alive, fixed in 70% ethanol, and weighed on the torsion balance to the nearest 1 mg. The station most regularly and abundantly inhabited by *G. fasciatus* was located at 58°50′45″ N, 26°57′28″ E, near the mouth of the Mustvee R. on stony bottom at a depth of roughly 3 m.

A few Estonian rivers were sampled by the third author in 1987–98, using different hand nets. The upper reaches of the Narva R. were sampled at three stations, its western tributary, the Mustajõgi, at one station $(59^{\circ}15'39'' \text{ N}, 27^{\circ}53'18'' \text{ E})$, and the Emajõgi R. along its whole course of 100 km (from $58^{\circ}23'12'' \text{ N}, 26^{\circ}08'41'' \text{ E}$ to $58^{\circ}26'44'' \text{ N}, 27^{\circ}14'00'' \text{ E})$, covering the mouths of its main tributaries, at up to 31 stations (three times); several other, smaller rivers flowing into the lake were sampled near their mouths only. The presence of the species was registered without any quantitative estimations.

RESULTS

Gmelinoides fasciatus was found in all samples collected in the shallow littoral of the eastern side of L. Peipsi and near the bank of the Narva R. in 1996 (Table 1). The lowest abundance (50 ind. m^{-2}) was recorded at station 6 in sheltered Lahta Bay on silt bottom with *Potamogeton* stands. At station 7 in the the adjacent, more open Raskopel Bay with a similar type of substrate the species appeared much more abundantly (5060 ind. m^{-2}). *G. fasciatus* had the highest densities on hard bottom, where amphipods concentrated under stones and gravel, attaining abundances and biomasses of 14 000–17 000 ind. m^{-2} and 57–64 gm⁻², respectively. The density of *Gmelinoides* in the Narva R. was also very high, up to 17 100 ind. m^{-2} and 102 gm⁻². Similarly high densities of this amphipod were registered earlier in L. Peipsi only twice: about 20 000 ind. m^{-2} and 80 gm⁻² in 1980 at a shallow stony station near Zigoska, at about 58°41' N on the eastern shore (Timm & Timm, 1993), and 24 420 ind. m^{-2} and 71.34 gm⁻² in 1992 in the mouth of the Nimolovka R., L. Pihkva (Antipova, 1995).

The contribution of *Gmelinoides* to the total biomass of macroinvertebrates in most studied locations in the eastern littoral of L. Peipsi and in the Narva R. was

considerable (Fig. 1): on average 58.5% for L. Peipsi (without large snails and clams), and 82.5% for the Narva R. Its role in the overall abundance of macro-invertebrates was also significant, averaging 37.9% and 72% for locations in L. Peipsi and the Narva R., respectively.

The highest densities of *Gmelinoides* and the lowest densities of other macroinvertebrates were noted on small stones and gravel in both L. Peipsi and the Narva R. Such a substrate apparently provides good shelter. Low abundance of other taxonomic groups is most likely the result of both competition and predation by this omnivorous amphipod.

Gammarus lacustris, a native amphipod for L. Peipsi, was not found in the eastern littoral of the lake in 1996. According to Timm & Timm (1993), it was almost completely replaced by *Gmelinoides* in L. Peipsi by 1990. The last known finding of *G. lacustris* on the Estonian side was in an open-water station in



Fig. 1. Proportion of *Gmelinoides fasciatus* in the biomass of macrozoobenthos (without large molluscs) in the eastern shallow littoral of L. Peipsi and in the Narva R., 1996.

L. Lämmijärv, a narrow southern appendix of L. Peipsi *s.s.*, in October 1992. Analysis of available long-term data series on the average densities of amphipods in the near-shore zone showed that both the trend of increase in the *Gmelinoides* population and the corresponding decrease in the *Gammarus* population fit in well with an exponential model (Fig. 2). Another native amphipod, *Pallasea quadrispinosa* Sars, inhabiting sandy bottom in the open region of the lake, did not suffer seriously in 1990. Its last reliable records also originate from October 1992, when the species was found at 4 stations out of 11 on the Estonian side.

A decrease in the abundance of *Gmelinoides fasciatus*, followed by stabilization, was predicted by Timm & Timm (1993). Now, this assumption can be verified on the basis of the monitoring of zoobenthos carried out in the 1990s on the Estonian side of the lake. Figure 3a demonstrates fluctuations of the density and biomass of this species at the station near Mustvee in 1987–98. *Gmelinoides* appeared here in 1988 and reached its maximum during 1990–92. After empty samples in 1993, the species was again abundant in 1994. In 1995–98, only single individuals occurred.

The same trend was observed when data were summarized for all other monitoring stations (from the sublittoral and profundal) on the Estonian side of the lake, very sparsely inhabited by *Gmelinoides*, as shown in Fig. 3b. Although common near the water's edge, the species was virtually lacking at these openwater stations until 1991. It became more frequent (found at 4–7 stations out of 10–11) and abundant here in 1992–94, but decreased again both in frequency (0–3 stations) and abundance in 1995–98. The maximum observed in October 1992 may have been caused by the peak of general abundance that year, as well as by the spreading of amphipods into deeper zones during autumnal overturn when the whole water column became well oxygenated.



Fig. 2. Long-term trends in the mean abundance of *Gammarus lacustris* and *Gmelinoides fasciatus* in the shallowest littoral zone (depth < 1 m) of L. Peipsi according to the data of Timm & Timm (1993) and new samples from the eastern side, 1996. Abundance is given as the logarithm of ind. m⁻² on the vertical axis.



Fig. 3. Fluctuations in the abundance and biomass of *Gmelinoides fasciatus* at the Mustvee station, per 225 cm² (a), and at the other 10–11 stations of the Estonian part of L. Peipsi jointly, per 6750–7425 cm² (b). Left-hand columns in every pair: number of individuals; right-hand columns: absolute biomass, mg.

The abundant occurrence of *G. fasciatus* in the outflow of L. Peipsi, the Narva R., was observed also by the third author. Its upstream migration (active or passive?) was apparent in the Emajõgi R., where the species was found up to the central part of Tartu ($58^{\circ}23'00''$ N, $26^{\circ}43'00''$ E), 46 km from the river mouth, both in 1996 and 1998. No tendency was noted for *G. fasciatus* to invade the mouths of the tributaries of this large navigable river. It was also found in the lowest reaches of the Rannapungerja R., falling into L. Peipsi from the north, and the Mustajõgi R. (Fig. 4). Unidentified gammarids have been recorded in many smaller watercourses connected with the lake.



Fig. 4. Records of Gmelinoides fasciatus in Estonia, 1991-98.

DISCUSSION

A peak in the abundance of *G. fasciatus* in L. Peipsi passed in the 1990s, more than twenty years after its assumed introduction. Possibly, balance between the invader and the environment has been reached by now. A large, well-naturalized population inhabits the shallow stony littoral only, while occasional individuals invade deeper zones now and again. To draw more definite conclusions, additional efforts, including organization of monitoring of the littoral fauna on the Russian side of L. Peipsi, are needed.

There is little evidence that decline in the population density of a successful invader following its explosive reproduction is a general rule for freshwater ecosystems (Gollasch & Leppäkoski, 1999, p. 53). The zebra mussel, *Dreissena polymorpha*, recorded in Estonian L. Võrtsjärv for the first time in 1958, reached its maximum abundance there in the 1970s (Timm, 1984). Later on, the mussel has become rare in the lake, while its larvae have virtually disappeared from its zooplankton (Haberman, 1998). However, shallow turbid L. Võrtsjärv cannot be regarded as a favourable habitat for this mussel. In deeper and cleaner L. Peipsi, *D. polymorpha* has flourished already more than 60 years (Timm et al., 1996). Analysis of some other available long-term data series on *Dreissena* populations demonstrated that within a certain lake its population densities varied in the range of several orders of magnitude over several decades (Stanczykowska & Lewandowski, 1993). On the other hand, model based estimations allow

researchers to predict that the population densities of *Dreissena* in the North American Great Lakes will be constant for a long period (Ramcharan et al., 1992). Evidently, accurate monitoring of successful invaders in freshwater ecosystems will help cast light on this issue.

Grigelis (1999, Fig. 2.4.4) demonstrated successive phases in the acclimatization of the Ponto-Caspian mysid crustacean, *Paramysis lacustris*, in the Kaunas Reservoir, Lithuania, during 1960–95. Maximum abundance (about 900 ind. m^{-2}) was reached in 1969, followed by several drastic fluctuations. Stable low abundance (about 100 ind. m^{-2}) was observed from 1978 on and interpreted as naturalization of the species in the local biocenosis. This process is very similar to changes taking place in the abundance of *Gmelinoides* in L. Peipsi.

Recent invasion of the Lower Rhine by another, Ponto-Caspian amphipod, *Corophium curvispinum*, is one of the most drastic examples of the explosive development of newly introduced species. In four years following the first record of this crustacean from the Lower Rhine in 1987, its density increased from initial 2 ind. m^{-2} up to 200 000 ind. m^{-2} , with a maximum of 750 000 ind. m^{-2} in one location. Explosive development of this invader resulted in a decrease in other benthic animals, including the previously established non-indigenous amphipod *Gammarus tigrinus* and the zebra mussel, *Dreissena polymorpha* (Van den Brink et al., 1993).

Negative impact of successful invaders, resulting in a significant decrease in native species or even their complete replacement, on benthic, planktonic, and fish communities has been reported from several freshwater ecosystems. Invasion of *Dreissena* in the North American Great Lakes in the late 1980s caused a drastic decline in unionids in L. St. Clair (Nalepa et al., 1996) and in the upper St. Lawrence R. (Ricciardi et al., 1996). Establishment of the Eurasian predatory cladoceran *Bythotrephes cederstroemi* in a Canadian inland lake has led to significant changes in its zooplankton community, including disappearance of several native species of filtering cladocerans (Yan & Pawson, 1997). Decline in native fish species was registered following the establishment of Amur sleeper (*Perccottus glehni*) in the delta of the Selenga R. (L. Baikal) as well as following the invasion of the European ruffe (*Gymnocephalus cernuus*) in L. Superior (Pronin et al., 1998).

Replacement of native gammaridean amphipods by *Gmelinoides*, which occurred in L. Peipsi, has been observed also in L. Ladoga (Panov, 1996), in Siberian freshwater ecosystems (Safronov, 1993), and in Volga R. reservoirs (Borodich, 1979). The exact mechanism of such replacement is not known and requires further study.

The ability of *Gmelinoides* to migrate will most likely result in gradual colonization of rivers and smaller lakes in the drainage basin of L. Peipsi. This may lead to drastic changes in the biological diversity of the area. A special survey of freshwater ecosystems of the Peipsi basin, accompanied with experimental studies on the biology of *Gmelinoides*, would serve as a basis for accurate assessment and prognostication of the possible effects of such invasion.

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BAIKALIST SISSE TOODUD KIRPVÄHILISE Gmelinoides fasciatus (Stebbing) PRAEGUNE OLUKORD PEIPSI LITORAALI KOOSLUSTES

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1970. aastate algul kogemata Peipsisse sisse toodud kirpvähiline *Gmelinoides* fasciatus oli 1990. aastate esimeseks pooleks ohter nii litoraalis kui ka sügavamal kõval põhjal (sublitoraalis). Alates 1995. aastast on ta sublitoraalist taas peaaegu kadunud (iga-aastased andmed Eesti poolelt), aga litoraalis kivisel põhjal endiselt väga arvukas (andmed Vene poolelt, 1996). Ta on Peipsist välja tõrjunud kaks kohalikku kirpvähiliste liiki. Tulnukliiki on juba leitud ka Narva jõest koos Mustajõega, Rannapungerja jõe suudmest ja Emajõest kuni Tartuni.