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THE RECENT APPEARANCE OF A BAIKALIAN CRUSTACEAN, *Gmelinoides fasciatus* (Stebbing, 1899) (Amphipoda, Gammaridae) in Lake Peipsi

Abstract. *Gmelinoides fasciatus* was first found in Lake Peipsi in 1972, and consistently since 1980. In 1990, it proved to be common and abundant anywhere in the littoral and sublittoral, particularly at the water edge and on a stony bottom. It has almost superseded *Rivulogammarus lacustris* in this ecological niche while the other aboriginal species, *Pallasea quadrispinosa*, inhabiting sandy bottoms, has maintained its state. In all probability, *G. fasciatus* was unintentionally introduced here in 1970—1975 when a fruitless attempt of acclimatizing a Siberian population of *R. lacustris* was made, by bringing amphipods from the Selenga Delta at Lake Baikal. The rapid increase of the number and biomass of gammarids in Lake Peipsi due to the unwanted acclimatization of *G. fasciatus* can be provisionally evaluated as beneficial for fishery.

Introduction

Lake Peipsi, or Lake Peipsi-Pihkva is a large (3560 km², maximum depth 15 m) tripartite eutrophic water-body on the border of Estonia and Russia. Its zoobenthos is species-rich, the average abundance in June measuring 2,770 ind./m², biomass about 12 g/m², without considering big clams (Тимм et al., 1982).

The local *Amphipoda* were first noticed by C. Joffe (Июффе, 1939, 1948). According to her data, *Pallasea quadrispinosa* inhabited sandy bottoms both in Lake Peipsi proper and Lake Pihkva in the 1930s, accompanied by *Gammarus pulex* [= *Rivulogammarus pulex* (L.)] in the phytal of the first lake. The latter identification, repeated also by O. Tõlp (Тыльп, 1966), seems to be doubtful since *R. pulex* is characteristic only of hard-water rivers, streams, and springs in Estonia. N. Minina (Минина, 1975, 1982) has mentioned, probably joining together her own and literature evidence, two species of *Rivulogammarus*: *R. lacustris* (Sars) and *R. pulex*. We have identified, both in Lake Peipsi and in many other Estonian lakes, only *R. lacustris* (also a personal communication by A. Järvekülg), together with *P. quadrispinosa* (Тимм et al., 1982).

R. lacustris lives in huge masses in many Siberian and Uralian lakes, poor in fish due to periodical winter-kills or drying up (Дексбах, 1952; Зыбин, 1958; Юффе, 1973). Presuming the abundance of the population in different parts of the distribution range can be genetically determined, the All-Union Institute of Lake and River Fishery (GosNIORH) in Leningrad recommended that feeding conditions for fish in Lake Peipsi and other north-western Russian lakes should be improved by acclimatizing there *R. lacustris* from Siberia (Июффе, 1963; Юффе et al., 1966, 1976).

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During 1970—1975, altogether 20,875,000 amphipods, allegedly *R. lacustris*, caught in the Selenga Delta (at Lake Baikal), were brought into Lake Peipsi by the East Siberian Acclimatization Station. The crustaceans were released near the eastern shore of Lake Peipsi proper in the vicinity of Gdov and in the Raskopel Bay. The sharp increase in the abundance of the gammarids by 1980 (8.5-fold in comparison with 1970), particularly near the eastern shore, was associated, although with some hesitation, with the above-mentioned introduction (Тимм et al., 1985).

In May 1985 and 1986, the staff of the Fish Protection Inspection notified that there was a mass invasion of amphipods into the mouth of the Mustvee River. It was apparently a seasonal migration never observed so far among local gammarids. An examination of the problematical animals proved them to be *Gmelinoides fasciatus*, a Baikalian species rather similar to *R. lacustris* by its external appearance but belonging to another genus (Тимм, Тимм, 1988). This provoked us to revise the gammarids collected earlier from Lake Peipsi and maintained at the Vörtsjärvi Limnological Station. So, we could specify the process of the distribution of this exotic species in Lake Peipsi.

Material and methods

Quantitative zoobenthos samples with Borutski and Zabolotski bottom grabs (225 cm²) were taken at 22—24 stations yearly in June from 1964 to 1991, and also in the midsummer (July—August) of 1970 and 1980. In July—August of 1970, 1980, and 1990 the near-shore zone at a depth of 0—4 m was studied on 50 profiles at 219—221 stations. In annual collections each sample consisted of three hauls with the grab, while in 1970, 1980 and 1990 only one haul was taken at every near-shore station. The animals were picked out alive, preserved in 70% ethanol and weighed in wet condition. About 21,000 individuals of gammarids were found and counted.

G. fasciatus was identified, using the guide by A. Bazikalova (Базикалова, 1945). As it seems to be somewhat intermediate between *P. quadrispinosa* and *R. lacustris* by its macroscopical characters (it is often transversally striped like *P. quadrispinosa* but never bearing the four dorsal spines typical of the latter), we had to use the following microscopical characters for distinguishing three gammarid taxa in Lake Peipsi (Fig. 1).

The relative length of the antennula. In *P. quadrispinosa* and *R. lacustris* much longer than the antenna; in *G. fasciatus* only slightly longer.

The relative length of the 1st—3rd segments of the antennula. In *P. quadrispinosa*, bigger than the length of the respective segments of the antenna; in *R. lacustris* and *G. fasciatus*, much smaller.

The number of segments in the appendix of the antennula. In *P. quadrispinosa*, 2; in *R. lacustris*, more than 3; in *G. fasciatus*, 1.

The number of segments in the funiculus of the antennula. In *P. quadrispinosa*, about 26; in *R. lacustris*, about 22; in *G. fasciatus*, 10—13.

The number of segments in the funiculus of the antenna. In *P. quadrispinosa* and *G. fasciatus*, about 6; in *R. lacustris*, about 11.

Eyes are large, goggle, oval or reniform in *P. quadrispinosa*; in *R. lacustris* they are smaller, reniform or oval; in *G. fasciatus* they are small, reniform.

Telson. In *P. quadrispinosa* it is with a low rounded notch; in *R. lacustris* it is cleft to the middle; in *G. fasciatus* it is cleft to the basis, with sharpened halves.

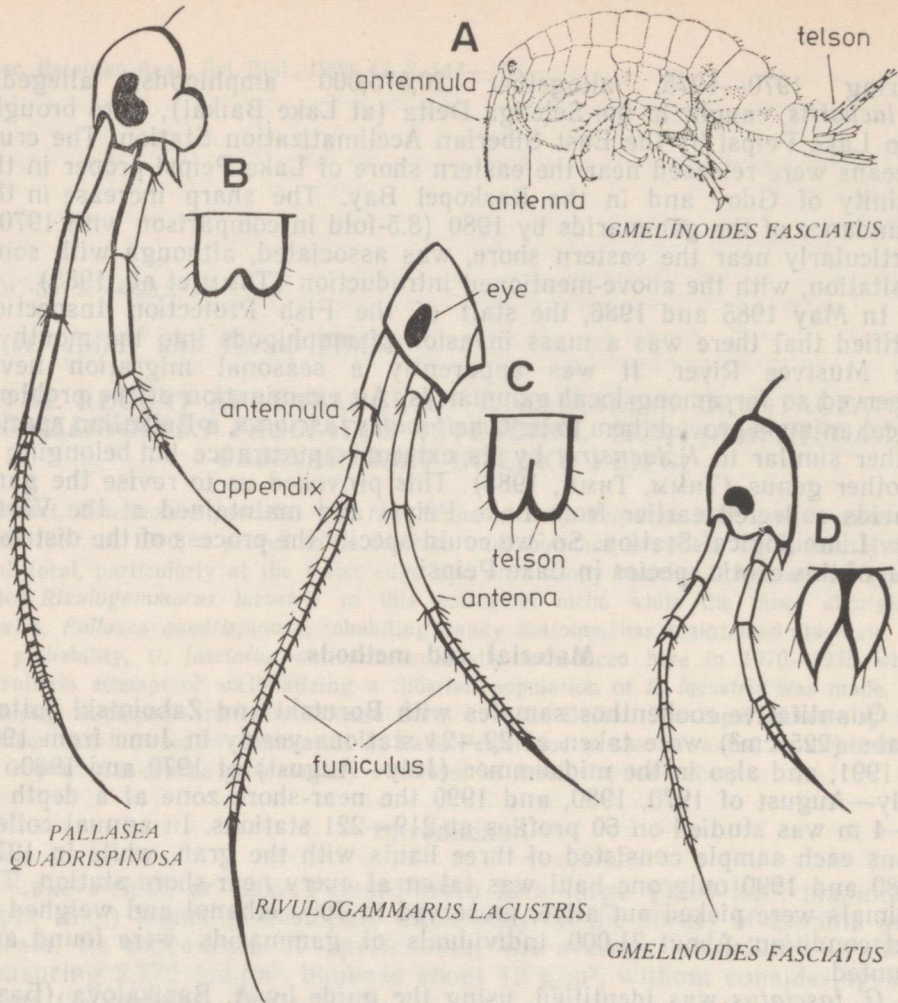


Fig. 1. Schematic depiction of the main characters suitable for the discrimination of gammarid taxa living in Lake Peipsi. A — general view of *Gmelinoides fasciatus* (after Мордухай-Болтовской, Чиркова, 1971); B—D — heads and telsons of *Pallasea quadrispinosa*, *Rivulogammarus lacustris*, and *Gmelinoides fasciatus* (original drawings).

Results

During 1964—1971, only two aboriginal gammarid species, *P. quadrispinosa* and *R. lacustris*, occurred in samples from Lake Peipsi, both in small numbers (Tables 1 and 2, Fig. 2). The first species inhabited mostly the sublittoral and littoral sands, with some single specimens also in the upper profundal mud. The latter was found mainly on stony bottoms both at the water edge and deeper.

The first occurrence of *G. fasciatus* in our samples was fixed in June 1972. More than 30 young individuals (<1 mg wet weight) were found at a station in the north-eastern corner of the lake on a stony bottom, at a depth of 2 m. Then a considerable interval followed. The species was met with again in 1980, now at many spots, most abundantly near the eastern shore of Lake Peipsi proper (Tables 1 and 2, Fig. 3). At one spot at the water edge they numbered as many as 20,000 ind./m², with the biomass 80 g/m². As the frequency and abundance of the aboriginal species remained continuously low, *G. fasciatus* formed an overwhelming majority of gammarids caught in 1980: 88% of specimens and 83% of their biomass at near-shore profiles, and over 90% at annual sampling spots.

Table 1

Average abundance and biomass of gammarids in the annual samples from 22—24 stations

Time	<i>P. quadrispinosa</i>		<i>R. lacustris</i>		<i>G. fasciatus</i>		Total	
	ind./m ²	g/m ²	ind./m ²	g/m ²	ind./m ²	g/m ²	ind./m ²	g/m ²
June 1964	2	0.002	—	—	—	—	2	0.002
June 1965	2	0.002	—	—	—	—	2	0.002
June 1966	—	—	1	0.001	—	—	1	0.001
June 1967	2	0.001	—	—	—	—	2	0.001
June 1968	—	—	—	—	—	—	—	—
June 1969	—	—	3	—	—	—	3	—
June 1970	—	—	—	—	—	—	—	—
July 1970	—	—	12	0.046	—	—	12	0.046
June 1971	—	—	—	—	—	—	—	—
June 1972	4	0.008	—	—	19	0.017	23	0.025
June 1973	4	0.005	—	—	—	—	4	0.005
June 1974	5	0.059	—	—	—	—	5	0.059
June 1975	1	0.004	—	—	—	—	1	0.004
June 1976	3	0.013	—	—	—	—	3	0.013
June 1977	16	0.015	—	—	—	—	16	0.015
June 1978	5	0.102	—	—	—	—	5	0.102
June 1979	6	0.005	1	0.001	—	—	7	0.006
June 1980	2	0.003	—	—	30	0.265	32	0.268
July 1980	—	—	—	—	69	0.239	69	0.239
June 1981	3	0.003	1	0.001	4	0.006	8	0.010
June 1982	4	0.002	—	—	—	—	4	0.002
June 1983	10	0.007	14	0.056	64	0.230	88	0.293
June 1984	1	0.043	—	—	10	0.027	11	0.070
June 1985	5	0.002	—	—	126	0.636	131	0.638
June 1986	1	0.001	—	—	63	0.340	64	0.341
June 1987	7	0.046	—	—	24	0.182	31	0.228
June 1988	2	0.001	—	—	25	0.211	27	0.212
June 1989	4	0.002	—	—	86	0.100	90	0.102
June 1990	3	0.001	—	—	212	0.715	215	0.716
June 1991	20	0.023	—	—	130	1.523	150	1.546

In June 1981, *G. fasciatus* occurred only in one of the annual samples, in 1982, in none. Since 1983 it has appeared again, at first in the north-western corner and in the Raskopel Bay, becoming ever more numerous from year to year (Tables 1 and 2). In seasonal samples collected by H. Timm in 1984—1986 at 4 stations, it was regularly found on a sandy bottom of the shallow sublittoral (in 1984, on the average 35 ind./m² with the biomass 0.12 g/m², and in 1985, 112 ind./m², 0.33 g/m²). Only a few single specimens were caught at the station located in the deeper sublittoral, and none in the profundal (Тимм, 1990).

The near-shore samples of 1990 demonstrated the presence of an abundant *G. fasciatus* population in the littoral and sublittoral of the whole lake (Table 2, Fig. 4), which made up over 99% of all the gammarids collected.

The explosive reproduction of *G. fasciatus* caused a drastic increase in the share of gammarids in the zoobenthos. While it constituted only 0.2% of the annual samples in 1964—1978 and slightly over 1% of the near-shore samples in 1970 (Тимм et al., 1982), it reached 5.7% in abundance and 9.5% in biomass in the annual samples in 1991, and at the near-shore profiles in 1990, 37.8 and 37.7%, respectively.

Average abundance and biomass of gammarids in the near-shore samples from 50 profiles, 0–4 m depth

Year	Species	0 m	1 m	2 m	3 m	4 m	Average
Abundance, ind./m ²							
1970	<i>P. quadrispinosa</i>	—	2	9	17	4	7
	<i>R. lacustris</i>	74	4	10	4	47	25
	<i>G. fasciatus</i>	—	—	—	—	—	—
	Total	74	6	19	21	51	32
1980	<i>P. quadrispinosa</i>	1	3	10	27	57	15
	<i>R. lacustris</i>	40	3	6	4	23	14
	<i>G. fasciatus</i>	810	6	44	29	90	210
	Total	851	12	60	60	170	239
1990	<i>P. quadrispinosa</i>	—	7	3	11	4	5
	<i>R. lacustris</i>	6	—	—	—	—	1
	<i>G. fasciatus</i>	2565	1110	627	176	433	1044
	Total	2571	1117	630	187	437	1050
Biomass, g/m ²							
1970	<i>P. quadrispinosa</i>	—	—	0.015	0.039	0.010	0.013
	<i>R. lacustris</i>	0.297	0.013	0.036	0.014	0.339	0.115
	<i>G. fasciatus</i>	—	—	—	—	—	—
	Total	0.297	0.013	0.051	0.053	0.349	0.128
1980	<i>P. quadrispinosa</i>	0.005	0.003	0.029	0.054	0.164	0.036
	<i>R. lacustris</i>	0.287	0.008	0.054	0.034	0.290	0.114
	<i>G. fasciatus</i>	2.812	0.012	0.161	0.095	0.366	0.732
	Total	3.104	0.023	0.244	0.183	0.820	0.882
1990	<i>P. quadrispinosa</i>	—	0.015	0.003	0.046	0.014	0.016
	<i>R. lacustris</i>	0.017	—	—	—	—	0.004
	<i>G. fasciatus</i>	6.645	2.731	2.208	0.586	2.260	2.950
	Total	6.662	2.746	2.211	0.632	2.274	2.970

No essential changes were found in the distribution or abundance of *P. quadrispinosa* during the whole observation period. As a matter of fact, *R. lacustris* seems to have been vanishing in the last decade. It was last found in annual samples of 1983 (Table 1). Among the 220 samples collected in the near-shore zone in 1990, *G. fasciatus* occurred in 145 samples, *P. quadrispinosa* in 12, *R. lacustris* only in 2 samples taken in the shallow, vegetation-rich inner part of the Värška Bay, devoid of *G. fasciatus* so far (Fig. 4).

The average individual weight of *G. fasciatus* was 2.8–3.5 mg in the majority of sample sets. Bigger specimens were found in several cases in June, up to the average of 16.5 mg (Raskopel Bay, June 1991). Seasonal migration was observed in the Mustvee River in May 1985 and 1986, but not any more in the high-water spring of 1987.

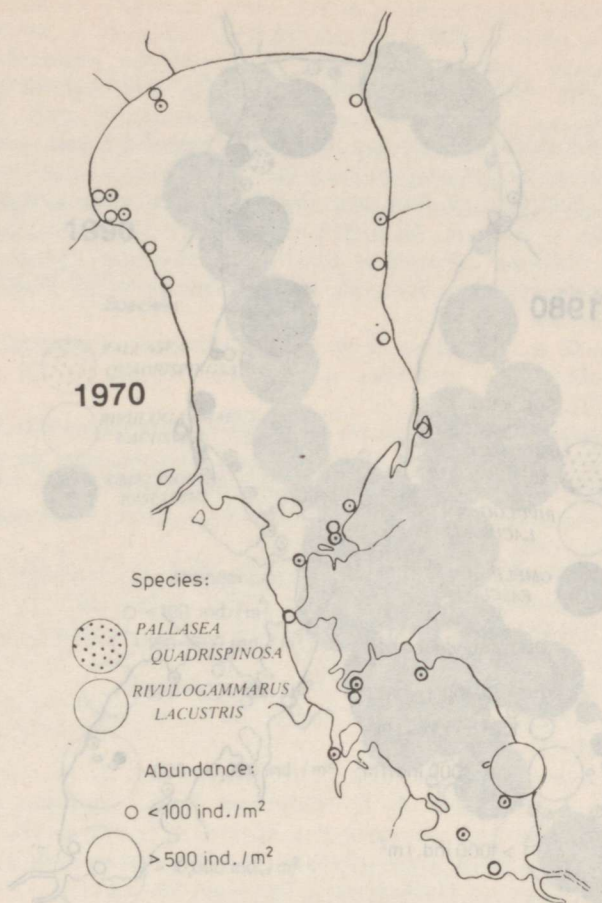


Fig. 2. Distribution of gammarids on the near-shore profiles in Lake Peipsi in 1970.

Discussion

There are more than 200 species of gammarids endemic in Lake Baikal but very few of them can survive outside this lake, under different hydrological conditions (Бекман, 1962). *G. fasciatus* is the single one of them which has successfully acclimatized in many Siberian and East European lakes and reservoirs. It has persisted in 25 new water-bodies (58% of the stocking attempts) and invaded independently into 3 further reservoirs (Задоевко et al., 1985). Among others, it is now common in the Gorki and Kuibyshev Reservoirs on the Middle Volga River (Мордухай-Болтовской, Чиркова, 1971; Бородич, 1979), it also occurs in the lakes Otradnoye on the Karelian Isthmus (Нилова, 1976) and Ilmen (Саватеева, 1985).

The latter lake is located near Lake Peipsi and is of a comparable size. It was stocked with *G. fasciatus* from the Possolskiy Sor (a bay of Lake Baikal) in 1973—1981, altogether 17,660,000 individuals. *G. fasciatus* was met with there again in 1979, in the sixth year after the first stocking (in the third and eleventh year after the first release of the alleged *R. lacustris* in Lake Peipsi). In 1981, about one tenth of the potential distribution range was occupied by *G. fasciatus* in Lake Ilmen; the average abundance in the inhabited area was 8 ind./m² (Саватеева, 1985). In

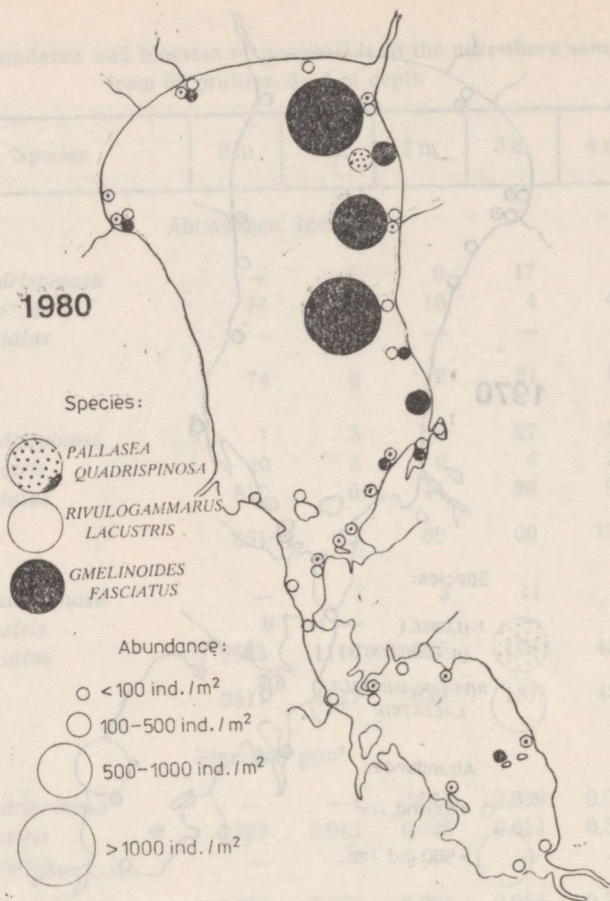


Fig. 3. Distribution of gammarids on the near-shore profiles in Lake Peipsi in 1980.

Lake Otradnoye *G. fasciatus* gathers at shallows for copulation and egg-laying at the end of April, at the water temperature 4–5°C; embryonal development takes 220–250 degree-days (Нилова, 1976), maturation 1035–1230 more degree-days (Мицкевич, 1980). The respective number of degree-days accumulates in Lake Ilmen by the end of July. As very small egg-bearing females, only 4.4 mm long and weighing 2.5 mg were found in August (at least 5 mm and 3.4–10.4 mg in July, respectively), the occurrence of two generations a year was assumed in Lake Ilmen (Саватеева, 1985). In all probability, the same is true for Lake Peipsi, too.

How did *G. fasciatus* appear in Lake Peipsi where it was never deliberately introduced? Apparently, with shipments of *R. lacustris* brought from the Selenga Delta. Since both species are quite similar in appearance, no one can discover any addition of one species among millions of individuals of the other species. Moreover, even the mixing-up of whole consignments cannot be excluded. We ourselves mistook the amphipods, numerous in Lake Peipsi in 1980, for the representatives of an introduced or mixed population of *R. lacustris* (Тимм et al., 1985).

It should be mentioned that an attempt to acclimatize the Siberian *R. lacustris* in Lake Peipsi failed as a consequence of wrong presumptions.

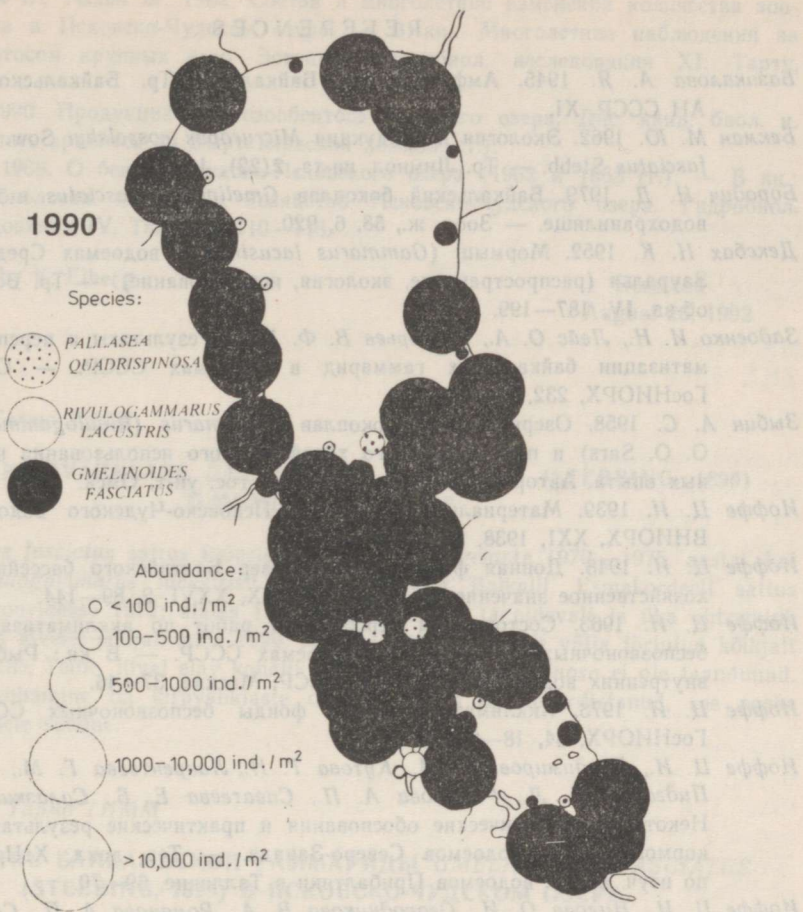


Fig. 4. Distribution of gammarids on the near-shore profiles in Lake Peipsi in 1990.

There are several winter-kill lakes (e.g. Kahala and Mäha) in Estonia, which are swarming with *R. lacustris* like the famous Siberian gammarid lakes. The scarcity of the species in Lake Peipsi (and many other lakes) can be explained simply by stronger predation by fish, without involving any genetical differences between separate populations. Moreover, *R. lacustris* has almost been superseded in Lake Peipsi by the new, more successful competitor, *G. fasciatus*. Whether this happens in the form of food competition, predation of young individuals of the other species, or in some other way, has not yet been established. A loss of various other gammarids after the acclimatization of *G. fasciatus* was earlier observed in the Gorki Reservoir, too (Мордохай-Болтовской, Чиркова, 1971).

Nevertheless, the miscarried acclimatization experience with *R. lacustris* can have some positive effect on the biota of Lake Peipsi. The increased total abundance of amphipods — omnivorous benthic invertebrates and excellent fish food — must be rather beneficial for fishery. The actual increase in the abundance of *G. fasciatus* can represent a stage in the early explosive development characteristic of successful newcomers. Later on it will be followed by a decrease, and then by a stable, balanced state. *R. lacustris* is probably already doomed in Lake Peipsi, while the population of *P. quadrispinosa*, having a different ecological niche, will survive.

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**BAIKALI KIRPVÄHKLASE GMELINOIDES FASCIATUS (STEBBING, 1899)
ILMUMINE PEIPSISSE**

Gmelinoides fasciatus sattus Peipsisse arvatavasti kogemata 1970.—1975. aastal, kui siia toodi *Rivulogammarus lacustris*'t Selenga deltast Baikaliil. Esmakordselt sattus *G. fasciatus* proovidesse 1972; alates 1980. aastast esineb ta pidevalt ja üha ohtramini, eriti veepiiril ja kivisel põhjal. Juba 1990. aastaks oli *R. lacustris* välja tõrjutud kõikjalt peale Värska lahe. Teine, liival elav kohalik liik *Pallasea quadrispinosa* ei ole taandunud. *G. fasciatus*'e vohamine on kirpvähklaste ohtrust järves mitmekordistanud, see peaks olema kalandusele soodne.

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**ПОЯВЛЕНИЕ БАЙКАЛЬСКОЙ ГАММАРИДЫ GMELINOIDES FASCIATUS
(STEBBING, 1899) В ПСКОВСКО-ЧУДСКОМ ОЗЕРЕ**

Gmelinoides fasciatus попал в Псковско-Чудское озеро, очевидно, в 1970—1975 гг., когда в это озеро были завезены *Rivulogammarus lacustris* из Селенгинской дельты на Байкале. Впервые он был обнаружен в пробах 1972 г., а с 1980 г. встречается постоянно и все обильнее, особенно около уреза воды и на каменистом грунте. *R. lacustris* был к 1990 г. вытеснен везде, кроме Вярскаского залива. Другой местный вид *Pallasea quadrispinosa*, обитающий на песке, пока не пострадал. Массовое развитие *G. fasciatus* многократно увеличило количество гаммарид в озере, что следует считать полезным для рыб.