Environment. Technology. Resources, Rezekne, Latvia
Proceedings of the 11th International Scientific and Practical Conference. Volume I, 259-264

Distribution and Population Structure of the Invasive Amphipod *Gmelinoides fasciatus* (Stebbing) in Lake Onego

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***Abstract.** Since the middle of the XX century, the rapid spread of exotic species and their successful penetration in natural and artificial ecosystems has led to significant environmental changes all over the world [1, 2]. As it was pointed out by many researchers, biological invasion by alien species is one of the main threats to biodiversity [3, 4, 5, 6, 7]. Gmelinoides fasciatus (Stebbing 1899) attracts special attention due to the fact that it is the most successful alien species among other invaders in aquatic ecosystems in Eurasia. This invasive amphipod of Baikalian origin was first recorded in Lake Onego in 2001 by Berezina and Panov [8]. The results of the present study indicate that the invader significantly expanded its areal in Lake Onego during the last 15 years. At present amphipod G. fasciatus is dominant on the biomass among macrozoobenthos community in littoral biotopes of some islands and east part of the Lake. In Lake Onego the invader has a one-year life cycle with the generations of the previous and current year. Seasonal dynamics of the amphipod abundance in Lake Onego has two peaks during the vegetation period. According to our data G. fasciatus successfully reproduces in the new environment and shows stable sexual structure with sex ratio of approximately 1:1. Female fecundity of the amphipod in the Lake varied from 3 to 22 eggs per female, the average variation of fertility is 9 eggs per female. Revealed data of G. fasciatus abundance and biomass in Lake Onego are comparable with those for other water bodies where this amphipod species was successfully established earlier.*

***Keywords:** age structure, distribution, Gmelinoides fasciatus, Lake Onego.*

I. INTRODUCTION

Since the middle of the XX century, the rapid spread of exotic species and their successful penetration in natural and artificial ecosystems has led to significant environmental changes all over the world [1, 2, 9, 10, 11]. As it was pointed out by many researchers, biological invasion by alien species is one of the main threats to biodiversity [3, 4, 5, 6, 7, 12, 13].

Range extensions of aquatic macroinvertebrate species in Europe have mainly been facilitated by the interconnection of river basins through man-made canals and intentional introductions [14, 15]. Four water corridors which have been traced between the southern and the northern European seas [14, 16], made possible the migration of alien species to new habitats. The largest corridor, comprising 6.500 km of main waterways and 21 inland ports of international importance, is the “northern corridor”. This corridor route includes the Volga River → Lake Beloye → Lake Onego → Lake Ladoga → the Neva River → the Baltic Sea [14]. Among the species which are thought to have penetrated new environments through the northern corridor, many have reached high abundance and biomass and at present play a significant role in the functioning of recipient ecosystems [16, 17].

Gmelinoides fasciatus (Stebbing 1899) attracts special attention due to the fact that it is the most successful alien species among other invaders in aquatic ecosystems in Eurasia. In the 1960-70s, it has been intentionally introduced from Siberia into lakes and reservoirs in the former USSR with the purpose of enhancing fish production. During the 1960s – 2000s this species colonized the coastal zone of some large and small lakes and artificial reservoirs of European Russia [17, 18, 19, 20, 21, 22, 23].

This amphipod of Baikalian origin was first recorded in Lake Onego in 2001 by Berezina and Panov [8]. Their research was carried out on the southwestern shore of the Lake and showed that *G. fasciatus* population was characterized by high abundance (1.7-8.3 thous. ind. m^{-2}) and biomass (3.9-40.3 g m^{-2}). Further investigations showed that till 2006 the northern border of amphipod areal in Lake Onego was expanded and reached 63º N [24]. According to new estimations *G. fasciatus* abundance and biomass values ranged from 1.16 to 12.38 thous. ind. m^{-2} and 0.64-9.34 g m^{-2}, correspondently [24]. Previous studies [8, 24] were devoted to description of abundance and biomass values of *G. fasciatus* populations in the different parts of Lake Onego, however population characteristics such as seasonal

ISSN 1691-5402

http://dx.doi.org/10.17770/etr2017vol1.2546

dynamics of abundance and biomass, reproduction and life cycle specifics of this species in the Lake were poorly studied. Taking into consideration that at present the Lake is the northern border of the invader areal in the European part of Russia and this species inhabits the littoral zone of almost whole Lake Onego, there is a pressing need to study biological and ecological characteristics of *G. fasciatus* in this environment. The aim of the study is: 1) to determine spatial distribution of this alien amphipod in littoral zone of the east part of the Lake and littoral zone of some islands; 2) to characterize reproduction and life cycle and investigate the dynamics of the size-age and sexual structure of *G. fasciatus* during the vegetation period.

II. MATERIALS AND METHODS

Study area. Lake Onego is one of the great lakes of the world and the second-largest European water body. With the exception of several bays, the water body still preserves its natural state and high water quality [25]. The Lake is invaluable ecological resources and very important for aquatic biodiversity in the region.

To investigate the current borders of *G. fasciatus* areal in Lake Onego, in 2014 samples were collected in the littoral zone of the east part of the Lake and littoral zone of some islands (Fig. 1). To study the life cycle of the crustacean, samplings were carried out in the northernmost point of invader areal in European part of Russia – the Povenets Bay of Lake Onego. The Bay is 64 km long and 21 km wide with 36% of shoreline marked by many indentations and shallow harbors [26]. Three sampling sites which represent a range of environmental conditions were selected in the Kumsa area of Povenets Bay (KB1, KB2, KB3) for detailed seasonal dynamics analysis. Samplings were collected in open-type slime bottom littoral biotopes with macrophyte beds from late May to early October 2011 at 10-day intervals in duplicate. Each studied site had some distinct characteristics, thus KB1 is known to be under the influence of strong wind-induced waves; KB2 is located in still water area; and KB3 can be considered as anthropogenically modified area, contaminated by waste water discharges from the Pindushi village and colophony-extraction plant.

Methods. Benthos samples were taken at each station by a plastic tube with working area 0.07 m^2 of modified Panov-Pavlov sampler [27]. Sampling and analysis was carried out in accordance with standard guidelines for the collection of freshwater benthos [28] at a depth of 0.4 m, where the abundance of amphipods was the highest [29]. The length of the individuals was measured under binocular microscope using and eyepiece micrometer with 0.1 mm precision. According to the size, 6 groups were distinguished: (1) ≤1.5 mm, (2) 1.6–3.0 mm, (3) 3.1–5.0 mm, (4) 5.1–7.0 mm, (5) 7.1–9.0 mm and (6) ≥9.1 mm. For ovigerous females, the reproductive capacity was measured (eggs per female). Statistical analysis was performed using the STATISTICA program. Data on abundance, biomass, specimen length and female frequency are presented as means, medians ± standard deviation (SD). χ^2-test was used to compare frequency distribution between the sites and analysis of sex ratio ($p<0.05$).

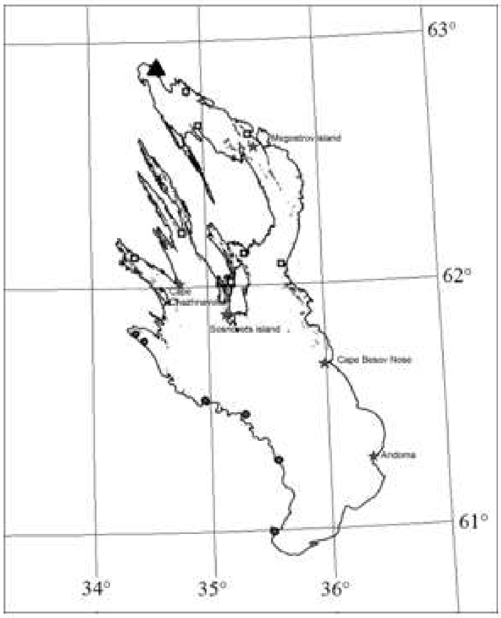

Fig. 1. Distribution of *G. fasciatus* in Lake Onego. Circles indicate presence of *G. fasciatus* in 2001 [8]; squares indicate presence of *G. fasciatus* in 2006 [24]; stars – new data. Black triangle - the location of the monitoring stations in the Povenets Bay of Lake Onego

III. RESULTS AND DISCUSSION

Invasion success is related to both abundance and distribution of alien species in the new environment. The results of the present study revealed that *G. fasciatus* significantly expanded its areal in Lake Onego during the last 15 years. Surveys carried out in 2014 indicate that *G. fasciatus* established permanent population in the east part of Lake Onego and some islands and was the only species of amphipod in littoral zone. The invader abundance varied between 14 and 2264 ind. m^{-2}, biomass – from 0.021 to 3.86 g m^{-2} (Table 1). In relation to biomass, the amphipod was dominant among other groups of macrozoobenthos (51-94%) in all studied locations, with the exception of Cape Chazhnavolok biotope, where the species prevalence reached only 34%.

The data on the population characteristics of *G. fasciatus* in the Povenets bay of Lake Onego revealed that mean values of invader abundance varied among the studied sites from 1202 to 2970 ind. m^{-2}, while mean values of biomass ranged from 1.9 to 5.6 g m^{-2} (Table 2).

Table I
Abundance (ind. M^{-2}) and Biomass (G M^{-2}) of Macrozoobenthos

Location site	Cape Chazhnavolok		Megostrov island		Sosnovets island		Besov Nose		Andoma	
Group	N, ind. m^{-2}	B, g m^{-2}	N, ind. m^{-2}	B, g m^{-2}	N, ind. m^{-2}	B, g m^{-2}	N, ind. m^{-2}	B, g m^{-2}	N, ind. m^{-2}	B, g m^{-2}
Oligochaeta	155.7	0.03	2151.5	0.57	3411.2	0.24	14.2	0.002	84.9	0.024
Chironomidae	226.5	0.01	594.5	0.10	580.3	0.05	-	-	141.5	0.003
Bivalvia	42.5	0.10	-	-	-	-	-	-	-	-
Gastropoda	14.2	0.24	14.2	0.00	127.4	0.20	-	-	-	-
Hydracarina	-	-	113.2	0.02	141.5	0.08	-	-	28.3	0.003
Amphipoda	863.4	1.73	835.1	1.17	2264.7	3.86	14.2	0.021	877.6	2.190
Ephemeroptera	410.5	0.10	99.1	0.02	750.2	0.30	-	-	113.2	0.058
Trichoptera	42.5	0.11	212.3	0.22	1075.7	0.42	-	-	42.5	0.014
Coleoptera	-	-	70.8	0.01	28.3	0.07	-	-	-	-
Diptera	-	-	42.5	0.06	28.3	0.00	-	-	-	-
Hirudinea	56.6	2.46	-	-	-	-	-	-	-	-
Plecoptera	42.5	0.15	169.9	0.02	14.2	0.00	-	-	14.2	0.020
Heteroptera	-	-	127.4	0.01	-	-	-	-	-	-
Isopoda	70.8	0.13	-	-	-	-	-	-	-	-
Total	1925.0	5.06	4430.3	2.22	8421.8	5.22	28.3	0.03	1302.2	2.31

Table II
Abundance, Biomass, Fecundity and Body Sizes of G. Fasciatus in Three Monitoring Stations of the Povenets Bay of Lake Onego

Stations	Characteristics	Mean ± SD	Median ± SD	min	max
KB1	N, ind. m^{-2}	2970±196	1819±204^{ab}	859	4885
	B, g m^{-2}	5.6±0.6	3.1±0.5^{b}	1.2	14.0
	L_{males},mm	6.0±0.2	6.2±0.2 ^{b}	3.1	11.5
	$L_{females}$, mm	4.8±0.1	4.6±0.1^{a}	3.1	10
	E, eggs per female	8.8±0.4	8±0.6	4	19
KB2	N, ind. m^{-2}	2236±251	2864±268^{a}	842	6468
	B, g m^{-2}	3.5±0.4	5.3±0.6	465	7.6
	L_{males},mm	6.3±0.2	6.3±0.2	3.1	15
	$L_{females}$, mm	5.0±0.1	5±0.1^{a}	3.1	11
	E, eggs per female	9.2±0.4	8±0.3	3	22
KB3	N, ind. m^{-2}	1202±155	1044±136 ^{b}	320	3234
	B, g m^{-2}	1.9±0.2	1.6±0.2^{b}	0.4	4.2
	L_{males},mm	5.3±0.1	5.5±0.1 ^{b}	3.1	9.6
	$L_{females}$, mm	4.8±0.1	4.9±0.1	3.1	9.3
	E, eggs per female	9.0±0.4	8±0.9	4	19

Note: N– Abundance; B – Biomass; L – Body size; E – Fecundity; a - Represent Significant Differences Between KB1 and KB2; b - Represent Significant Differences Between KB1 and KB3

Revealed data of the invader abundance and biomass in Lake Onego are comparable with those for other water bodies where this amphipod species were successfully established earlier (Table 3). The closest values of *G. fasciatus* abundance and biomass observed in the Lake were detected in Gulf of Finland Baltic Sea (Table 3).

At present *G. fasciatus* wildly distributed on the littoral zone of Lake Onego [30, 31], however the invader abundance in the different biotopes significantly varied from 1.22 to 18.79 thous. ind. m^{-2} [24]. The reasons of high variability of the amphipod abundance in the Lake were unknown. According to the results of the present study in the Povents Bay, median values of abundance and biomass was about 2 times higher in KB2 compared to KB1 (Table 2). Observed differences can be explained by contrast in relation to wind conditions, which probably led to concentration of individuals in areas with the absence of wind-induced waves. Similar tendencies were detected by Bekman [32] in *G. fasciatus* native area – Lake Baikal. The absence of significant differences in relation to individuals length and female fecundity between two stations also allows us to conclude that the feeding conditions do not limit the development of *G. fasciatus* population at KB1 station. Thus, higher values of biomass and abundance medians of the amphipod in KB2 are probably related to its horizontal migration to more favorable environmental conditions. In littoral biotope of KB3 station values of *G. fasciatus* abundance and biomass were significantly lower compared to KB1 station. At this station significant decrease in male length was observed compared to KB1, however similar tendency in relation to female length and fecundity was not found. Presented data indicate that among 3 studied sites, assemblage associated with contaminated area (KB3 biotope) was characterized by lowest values of biomass and abundance.

Table III
Population Characteristics of G. Fasciatus in Different Water Bodies

Water bodies		Abundance, ind. m^{-2}	Biomass, g m^{-2}	Fecundity, eggs per female	References
Posolsk Sor Bay of Baikal Lake		10000–20000	63–100	3–32	32
Lake Pepsi		50–17300	0.1–102	–	19
Lake Otradnoe		26–692	–	3–34	33
Lake Ladoga	1988-1990	8–53800	0.02–158.60	–	34
	1992	6000-7000	80-100	-	35
	2004-2005	936–3141	4.2–10.3	3–35	17
	2006	9090±2024	18.65±3.61	-	36
	2009	8–7160	0.024–15.3	–	37
Gulf of Finland Baltic Sea		300–3000	0.4–8.8	3–46	38
Rybinsk Reservoir		6800	19.8	3-20	39
Gorky Reservoir		15000	66	–	21
Western shore of Lake Onego (2001)		1696–8256	3.9–40.3	8–18	8
Petrozavodsk Bay of Lake Onego (2005)		132–462	0.2–6.2	4–15	30
Northern part of Lake Onego (2006)		310–18740	0.2–12.2	–	24

Size and age structure dynamics. Analysis of seasonal abundance dynamics of *G. fasciatus* revealed similar tendency in all studied stations of the Povenets Bay of Lake Onego (Fig. 2a). In the beginning of the vegetation period (the end of May) *G. fasciatus* population was represented by individuals of overwintered generation (Fig. 2b). The appearance of first occasional juveniles (body length less than 1.5 mm) was registered in early June. Females released high number of juveniles in the last decade of June and early July. During that period the number of the juvenile amphipods reached 4 thousand ind. m^{-2} and significantly contribute (85%) to the first peak of abundance. In July and August newborn specimens (less than 1.5 mm) demonstrated decrease in prevalence (from 65% to 15%) whereas individuals with body size 1.6-3 mm showed the opposite tendency (from 15% to 50 %). In the first half of September specimens of all size groups (1.2-9 mm) were found but at the end of the month crustaceans with a body length less than 1.5 mm were not detected. Therefore, seasonal dynamics of *G. fasciatus* abundance in Lake Onego has two peaks in July and August (Fig. 2a), which were formed by individuals of different size groups. Observed seasonal changes in size structure of population can be related to juvenile recruitment and old individuals elimination as well as horizontal migration of individuals [38].

There are 4 different types of *G. fasciatus* life cycles in relation to the amphipod life duration and number of generations per season [21]. According to presented data, in Lake Onego Baikalian invader has a one-year life cycle with the generations of the previous and current year, i.e. similar to those found in Lake Ladoga, Lake Otradnoe and the Neva Bay [17, 39, 40]. The appearance of first occasional juveniles in early June indicates that the reproduction of invader in Lake Onego begins in May while absence of specimens with a body length less than 1.5 mm at the end of September indicates the termination of amphipod reproduction.

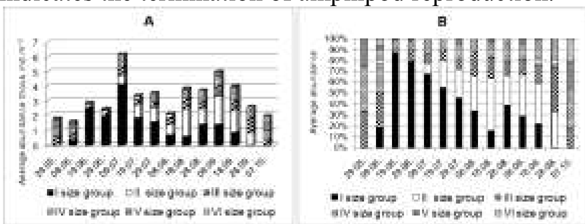

Fig. 2. Abundance (A. thous. ind. m^{-2}; B - %) of different size groups of *G. fasciatus* in the Povenets Bay of Lake Onego. Body length, mm: (1) ≤1.5; (2) 1.6–3.0; (3) 3.1–5.0; (4) 5.1–7.0; (5) 7.1–9.0 and (6) ≥9.1

Sexual structure. It is well known, that amphipod population often shows seasonal fluctuations in the sex ratio and generally, female outnumber males [41, 42, 43]. The sexual structure of *G. fasciatus* population was stable and during the vegetation period sex ratio rarely deviated from approximately 1:1 ratio. On several occasions during the investigation period, there was a significant imbalance in the sex ratios: in the third decade of July and the first decade of August prevalence of female individuals reached 80 and 90%. However, in the end of May and the begging of October the dominance of males was observed. Thus, in the Lake the domination of females in sexual structure of population was observed during the reproduction period (so called “harem” formation) and promoted fast increasing of population abundance [22]. Similar cases of female domination in *G. fasciatus* populations were observed in other freshwater (e.g. Ladoga Lake) and brackish water (e.g. the Neva Bay) ecosystems [38, 17].

The length of females in the Povenets Bay varied between 4.8 and 5.0 mm and 5.3-6.3 mm for males, while the maximum values of the female individuals length reached 11 mm, male – 15 mm (Table 2).

Fecundity. Fecundity of organisms should be considered as the most significant factor that determines the dynamics of species population abundance [44]. Thus, in order to reveal potential reproductive capacity of the organisms, information concerning reproductive parameters of species is required. According to our estimations, during vegetation season female fecundity ranged from 3 to

22 eggs per female and usually reached 9 eggs per female (Table 4). Females with maximum fecundity (10.2 eggs per female) were predominant in the begging of June and belonged to the generation of the previous year (Table 4). From the end of July and till September females of new generation progressively started to reproduce. This fact was confirmed by significant decline of female individuals length: at the end of May it reached 5.4±0.2 mm; in August the length decreased to 4.6±0.2 mm due to the gradual substitution of previous year generation by females of new generation.

Table IV
Seasonal Changes in Length and Fecundity of Ovigerous Females of G. Fasciatus During Vegetation Period in the Povenets Bay of Lake Onego

Month	Number of samples	Mean body length, mm (mean ± SD)	Fecundity, eggs per female (mean ± SD)	Fecundity, eggs per female	
				min	max
May	167	5.4±0.2	8.0±0.7	4	16
June	95	5.4±0.2	10.2±0.8	4	19
July	50	5.2±0.1	8.8±0.8	4	15
August	65	4.6±0.2	9.2±1.1	3	22
September	43	5.1±0.2	8.4±1.2	4	14

Our data correspond to the results of the previous studies carried out in Lake Onego southwestern shore: in 2001 the values ranged from 8 to 18 eggs per female [8]. On the whole, observed in Lake Onego parameters of *G. fasciatus* fecundity are close to those detected in other recipient areas. It should be noted, that in native area (Lake Baikal) the fecundity was higher compared to Lake Onego and reached 32 eggs per female [32], however maximal fecundity was observed in the Neva Bay of the Gulf of Finland and reached 46 eggs per female [38].

Detected changes in mean length of reproducing females were also revealed in other water bodies. Due to the gradual substitution of previous year generation by females of new generation, significant decline of female individuals length was detected during vegetation season. Similar changes were shown for the Rybinsk Reservoir (ovigerous female length in spring varied from 5 to 9 mm, in summer was about 4 mm, and reached 5-6.5 mm in autumn) and the Neva Bay of the Gulf of Finland (mean length was about 7 mm in May, 6 mm in August and increased to 7 mm till the end of September) [38, 39]. This data confirm the connection revealed by Alimov [44] between the water temperature and individuals maturation period and sexual maturity.

IV. CONCLUSIONS

The results of the present study clearly demonstrate that the Baikal invader successfully established in the new conditions on the northern border area of the European part of Russia. At present amphipod *G. fasciatus* is dominant on the biomass among macrozoobenthos community in littoral biotopes of some islands and east part of Lake Onego. *G. fasciatus* of the Lake has a one-year life cycle with the generations of the previous and current year. According to our data the invader successfully reproduces in new environment and shows stable sexual structure with sex ratio of approximately 1:1. Female fecundity of the amphipod in the Lake varied from 3 to 22 eggs per female, the average variation of fertility is 9 eggs per female. Revealed data of it abundance and biomass in Lake Onego are comparable with those for other water bodies where this amphipod species was successfully established earlier. It should be noted that *G. fasciatus* continues to expand its areal and according to some estimations has ability to enter in Great Lakes in Northern America from the Gulf of Finland in Baltic Sea [21] and inland Finland lakes through the Saimma channel [45] due to the intensive shipping. Moreover, some researchers pointed out, that the amphipod from Lake Onego is capable to enter the White Sea through the second branch of invasive corridor (Lake Onego → the White Sea – Baltic Sea Channel → the White Sea) [10].

V. ACKNOWLEDGMENTS

The part (50%) of the study has been financially supported by the Russian Science Foundation (№14-17-00766). We also thank Natalia Kalinkina and Tatyana Polyakova for their assistance during preliminary work and statistical analysis of data.

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