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The Ponto-Caspian and native amphipod life history in the Daugava River, Latvia

by

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Abstract

Population structure, reproductive parameters and other life history traits are among the main preconditions for alien amphipods' successful invasion. In the freshwaters of Northern Europe, i.e. Latvia, the overall life history of alien Ponto-Caspian amphipods is little known. Furthermore, the population structure and reproductivity of native *Gammarus pulex* have not been studied in Latvian freshwaters. The aim of the study was to describe the life history of *Gammarus varsoviensis*, *Pontogammarus robustoides* and the coexistent *G. pulex*. Their population structure, reproductive period and fecundity in the Daugava River were evaluated as part of this study from 2017 to 2019. The results revealed that the reproductive period of *G. varsoviensis* and *P. robustoides* lasted from four to five months, with up to three generations per year and a high proportion of juveniles. The average number of eggs for *G. varsoviensis* was 31 (maximum: 69) and for *P. robustoides* 28 (maximum: 81), with ovigerous females of both species being an average of 11.3 mm. *Gammarus pulex* had one generation per year with a high proportion of juveniles. The average number of eggs per brood was 27 (maximum: 41) with the average size of ovigerous females being 10.7 mm.

Key words: *Gammarus varsoviensis*, *Pontogammarus robustoides*, *Gammarus pulex*, life history, Daugava River

1. Introduction

Understanding the life history of species and their populations is a fundamental requirement, since life history traits are adaptations which have a significant impact on population dynamics and the survival of a species (San Vicente 2018; Braendle et al. 2011). Life history traits, i.e. population structure and reproductive parameters, are among the main preconditions for successful invasion by an alien species, including amphipods. For example, juveniles' dominance indicates rapid growth of the population (Dobrzycka-Krahel et al. 2019). The reproductive potential of amphipods is related to body size, the number and size of eggs and embryos, the length of the reproductive period, the time of maturation and voltinism (San Vicente 2018; Bacela et al. 2009; Grabowski et al. 2007a; Bacela, Konopacka 2005; Sainte-Marie 1991). Life history traits are also dependent on other biological (competition and predation) and environmental factors (temperature, food, habitat, water quality and geographical location) (Poznańska-Kakareko et al. 2021; Grabowski et al. 2007a; 2007b; Pöckl 2007; Kley, Maier 2006; Panov, McQueen 1998; Sutcliffe 1993; Sainte-Marie 1991; Welton, Clarke 1980; Nilsson 1977; Hynes 1955).

Until recently *Gammarus varsoviensis* (Jazdzewski 1975) was considered a native species in Poland, Germany, Lithuania and Belarus. However, its occurrence in the Dnieper River in Ukraine and recent haplotype-based genetic analysis indicate that the species originates from the Ponto-Caspian region. *Gammarus varsoviensis* is grouped into two clades: one is found in the Lower Dnieper River, while the other is in the Upper Dnieper River and the Baltic Sea basin (Grabowski et al. 2012a; Grabowski et al. 2012b). *Gammarus varsoviensis* has been known in the Daugava River since 2006 (Arbačiauskas 2008). The life history of *G. varsoviensis* has been little studied, mainly in the Polish freshwaters by Jażdżewski (1975) and Konopacka (1988). According to these studies, *G. varsoviensis* produce one or two generations per year, the first in spring and the second in late summer and autumn, when the spring generation breeds.

The Ponto-Caspian *Pontogammarus robustoides* (Sars, 1894) has been an invader in large European rivers, canals, dam reservoirs and lakes since the second half of the twentieth century (Arbačiauskas et al. 2017; Arbačiauskas, Gumuliauskaitė 2007; Grabowski et al. 2007b; Bij de Vaate et al. 2002). *Pontogammarus robustoides* is the most common alien amphipod in the inland waters of Latvia. The species occurs in both the seaside lakes (Lake Liepāja and Lake Ķīšezers) and the estuaries of the large (Daugava, Lielupe and Gauja) and small rivers (Salaca, Saka and Venta) flowing into the Baltic Sea (Grudule et al. 2007). According to our recent investigations in the Daugava River, the species occurs in the Lower Daugava River, mainly in the Daugava River reservoirs (Riga, Ķegums and Pļaviņas) (Paidere et al. 2019; Paidere et al. 2016). The species was intentionally introduced into Latvian waters – those nearest to Riga, Lake Lielais Baltezers and the Lower Daugava River (Ķegums Reservoir) – in the 1960s as a valuable fish food (Bodniece 1976; Kachalova, Lagzdin 1968).

The life history of the Ponto-Caspian *P. robustoides* has been studied quite extensively, mainly in Central Europe (i.e. Poland) and at the northern end of the population invasion (the Gulf of Finland in the Northern Baltic Sea) and the eastern part of Russia (the middle and lower flow of the Volga) (Dobrzycka-Krahel et al. 2019; Kurina 2017; Berezina 2016; Arbačiauskas, Gumuliauskaitė 2007; Bacela, Konopacka 2005; Wawrzyniak-Wydrowska, Gruszka 2005). Among the Baltic states, studies of life history traits have been conducted only in the Curonian Lagoon in Lithuania (Jankauskiené 2002). According to these studies, *P. robustoides* is characterised by high reproductive potential (high fecundity, early maturity and three or more generations per year). However, these results can also differ depending on annual weather conditions. For example, depending on the average summer water temperatures, *P. robustoides* forms two or three generations per year in the Gulf of Finland (Berezina 2016).

Gammarus pulex (Linnaeus, 1758) is a well-known and widespread native species in the running waters of Europe (Hou et al. 2011; Karaman, Pinkster 1977). Although *G. pulex* occurs in Latvian freshwaters, its distribution, population structure and life history traits are unknown. According to our previous investigations, *G. pulex* occurs in the Daugava River, mainly in its middle flow, together with the alien species *G. varsoviensis* and *P. robustoides* (Paidere et al. 2019).

The species is characterised by having one or two generations per year. Females form two to four or more broods, which under optimal thermal conditions can breed almost throughout the year, with peaks of juveniles in spring and summer (Maazouzi et al. 2011; Graça et al. 1994; Sutcliffe 1993; Ward 1986; Sutcliffe et al. 1981; Welton, Clarke 1980; Karaman, Pinkster 1977; Nilsson 1977; Hynes 1955).

The population structure and reproductive traits of the Ponto-Caspian amphipods *P. robustoides* and *G. varsoviensis*, as well as the coexistent native species *G. pulex*, in Latvia and the northern part of European freshwaters are not well known. The aim of the study was to describe the life history of the aliens

G. varsoviensis and *P. robustoides* and the coexistent native *G. pulex* by evaluating their population structure, reproductive period and fecundity in the Daugava River. The results were compared to data available for populations from other geographic ranges in order to reveal the role of life history traits in promoting species invasion in the European freshwaters.

2. Materials and methods

2.1. Study site and sampling

The Daugava River is one of the largest rivers in Eastern Europe. Starting in the Valday Highlands in Russia, the river flows through the East European Plain, crosses Belarus and Latvia and flows into the Gulf of Riga. The catchment area of the Daugava River is around 87 900 km^2 and its total length is 1005 km, of which 342 km are located in Latvia. The cascade of three large hydroelectric power plants along the Lower Daugava at Pļaviņas, Ķegums and Riga forms the largest artificial reservoirs in Latvia (Anosova et al. 2006). Among the Daugava reservoirs, the Pļaviņas Reservoir is the deepest (average depth: 14.5 m, maximum depth: 47 m) and the largest (volume: 509.5 million m^3, area: 35 km^2) with an average annual discharge of 567 m^3 s^{-1} (Tidriķis 1997, Environmental impact assessment of wastewater of new projected cellulose factory 1998).

The physicochemical parameters of water were measured and amphipods were sampled within the Pļaviņas Reservoir at Gostiņi and upstream of the Pļaviņas Reservoir at Veczeļķi, Jēkabpils and Daugavpils. This was done once or twice a month from April/May to September/October from 2017 through 2019 (except Veczeļķi in 2018) (Figure 1, Table 1). Qualitative samples of amphipods were collected in the wadeable depths (up to 0.5 m) using a Hidrobios hand net with a mouth opening of 25 x 25 cm (500 µm mesh size). Two replicates of samples were collected by hitting and sweeping the net along the substrate. The final sample consisted of 10 to 12 sweep units; it was preserved in 75% ethanol. The substratum of the study sites consisted of sand, silty sand, detritus,

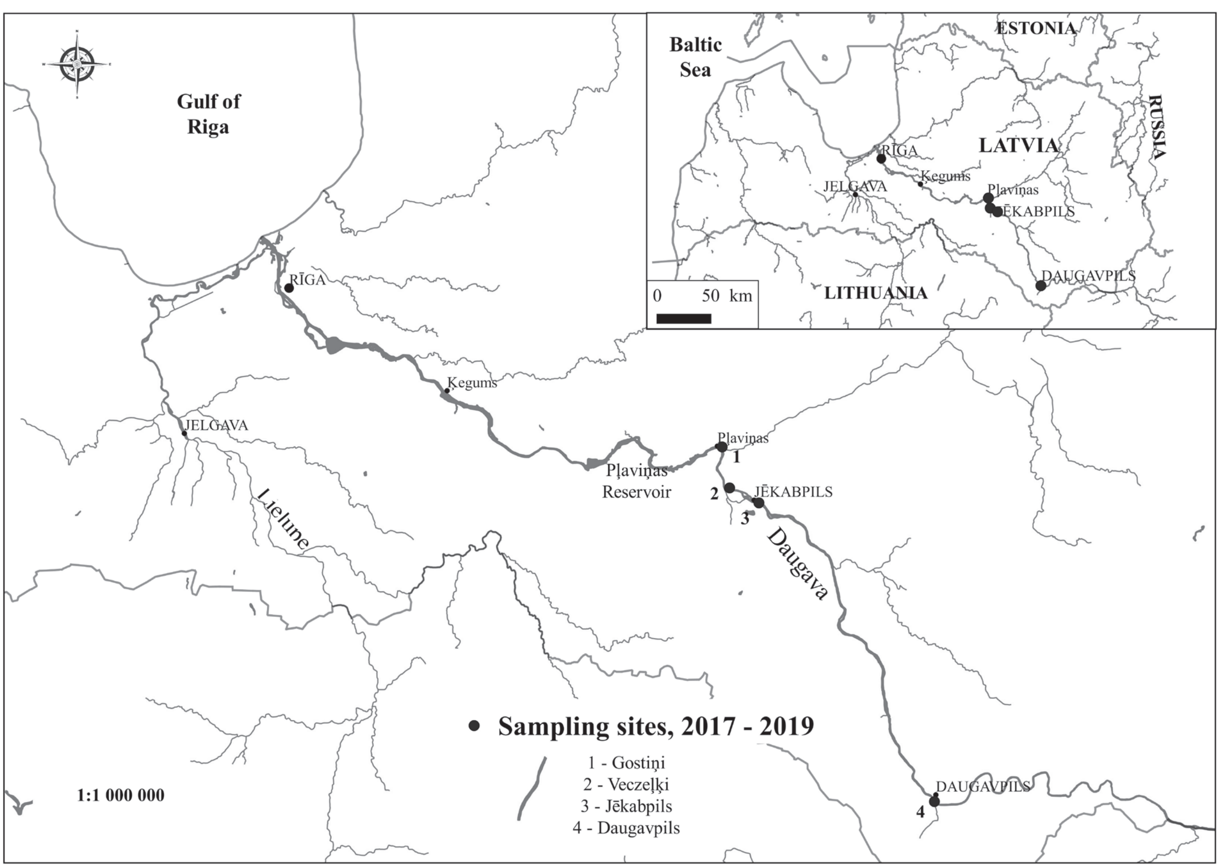

Figure 1

Sampling sites of amphipods along the Daugava River

Table 1

Background characteristics of the sampling sites during the study

Characteristics	"Daugavpils"	"Jēkabpils"	"Veczeļki"	"Gostiņi"
Position	55°52'04"N 26°30'32"E	56°29'52"N 25°53'30"E	56°31'50"N 25°47'01"E	56°36'56"N 25°45'31"E
Gammarids	*G. varsoviensis* 2017, n 342 2018, n 389 2019, n 299	*G. varsoviensis* 2017, n 437 2018, n 91 2019, n 87 *G. pulex* 2017, n 67 2018, n 36 2019, n 15	*G. varsoviensis* 2017, n 7 *G. pulex* 2017, n 20 2019, n 3 *P. robustoides* 2019, n 174 2018 no sampled	*P. robustoides* 2017, n 42 2018, n 286 2019, n 352
Substrate	sand, silty sand covered by detritus, some pebble and boulders, emergent and submerged macrophytes	sand, silty sand covered by detritus, emergent and submerged macrophytes	sand, fine gravel, pebble and some boulders covered by detritus, emergent macrophytes	sand, silty sand covered by detritus, some pebble and boulders, emergent and submerged macrophytes
2017, month	V-X	V-IX	V-IX	V-IX
	average (range)			
T (°C)	16.03 (9.76-20.45)	18.14 (15.75-20.47)	17.86 (15.38-20.25)	17.42 (14.14-20.52)
Cond. (µS cm^{-1})	306 (251-335)	313 (280-337)	311 (274-334)	317 (274-375)
DO (mg l^{-1})	7.67 (6.09-9.19)	7.45 (6.31-8.83)	8.20 (9.57-7.19)	7.74 (5.11-9.94)
pH	7.96 (7.72-8.24)	8.05 (7.84-8.14)	8.16 (7.98-8.47)	8.12 (7.51-8.60)
CHL (µg l^{-1})	3.89 (2.84-5.45)	4.98 (3.38-8.30)	3.23 (2.97-3.65)	4.68 (3.20-5.61)
2018, month	V-X	V-X		V-X
	average (range)			
T (°C)	18.62 (11.79-21.97)	17.16 (6.42-23.01)	2018 no measured	17.86 (6.56-23.62)
Cond. (µS cm^{-1})	382 (233-467)	367 (280-404)		404 (390-427)
DO (mg l^{-1})	9.60 (7.51-13.75)	8.48 (6.19-11.16)		9.63 (6.62-11.71)
pH	8.73 (8.16-9.22)	8.81 (8.45-9.06)		9.00 (8.92-9.41)
CHL (µg l^{-1})	3.26 (1.77-6.69)	3.99 (3.06-5.19)		4.56 (3.96-5.30)
2019, month	IV-IX	IV-IX	VI-IX	VI-IX
	average (range)			
T (°C)	18.13 (11.42-22.18)	18.28 (13.05-22.68)	19.68 (13.27-23.22)	20.79 (14.61-23.12)
Cond. (µS cm^{-1})	354 (216-512)	316 (227-378)	341 (289-374)	342 (288-377)
DO (mg l^{-1})	8.13 (6.39-10.64)	7.83 (5.91-9.94)	8.20 (6.33-10.19)	10.18 (8.00-13.67)
pH	7.73 (7.38-8.20)	7.80 (7.41-8.19)	8.09 (7.77-8.29)	8.40 (8.06-8.95)
CHL (µg l^{-1})	4.39 (3.03-8.26)	4.39 (2.16-6.89)	2.96 (2.11-4.29)	4.21 (2.95-6.60)

Abbreviations: T – temperature, Cond. – conductivity, DO – dissolved oxygen, CHL – chlorophyll *a*

pebbles, some boulders and macrophytes (Table 1). Simultaneously, the physicochemical parameters of the water (temperature, pH, conductivity and dissolved oxygen and chlorophyll *a* levels) were measured *in situ* using a HACH Hydrolab DS5 multiprobe. The physicochemical parameters of the study sites are presented in Table 1. The water quality of the study sites conforms to moderate ecological status according to the Latvian Environment, Geology and Meteorology Centre monitoring data of surface waters (Overview of the status of surface and groundwater in 2017, 2018).

2.2. Weather condition

In general, the average annual air temperature in Latvia gradually increased during the study period (Table 2). In 2017, the study season from May to October was more characteristic of Latvian climatic conditions. The duration of meteorological summer was typical of Latvian summer (60 days, June–August). In contrast, the duration of meteorological summer in 2018 and 2019 was twice as long (May–September). The spring (April and May) and the latter half of summer (the end of July and August) were hot in 2018; in fact, it was one of the warmest years. 2019 was the warmest year during the study period. The temperatures in June and August were +18.6°C and +17.0°C. The precipitation also varied within the study period. The summer and autumn of 2017 were rich in rainfall (Table 2), raising the water level in the Daugava River (Latvian Environment, Geology and Meteorology Centre 2017, 2018, 2019).

Table 2

Air temperature and precipitation in Latvia during the study*

	2017	2018	2019	Latvian norm
Annual mean air temperature, °C	+6.9	+7.6	+8.2	+6.4
Annual total precipitation (mean in Latvia), mm	809.8	472.7	629.2	685.6
Spring				
Average air temperature, °C	+5.6	+6.9	+7.2	+5.6
Precipitation, mm	116.3	80.7	100.5	122.7
Summer				
Average air temperature, °C	+15.4	+18.1	+17.2	+16.2
Precipitation, mm	237.0	162.4	176.7	225.7
Autumn				
Average air temperature, °C	+7.6	+8.6	+8.3	+6.7
Precipitation, mm	313.5	124.3	236.7	201.0

* Latvian Environment, Geology and Meteorology Centre, 2017, 2018, 2019

2.3. Analysis of samples and data

The specimens were identified using sources from the literature (Eggers, Martens 2004; Eggers, Martens 2001; Karaman, Pinkster 1977; Jażdżewski 1975; Pinkster 1970; Guide for Identification of the Fauna of the Black and Azov Seas 1969). A ZEISS Stemi 508doc stereomicroscope fitted with an ocular micrometer (10:100) was used to identify and measure the length of the specimens, taken as the distance from the anterior margin of the head to the telson base (Bacela, Konopacka 2005).

Based on the literature on the subject (Berezina 2016; Copilaş-Ciocianu, Boroş 2016; Bacela, Konopacka 2005; Sainte-Marie 1991), the population structure was divided into small specimens or juveniles (<5 mm), medium specimens or subadults (5–8 mm) and large specimens or adults (>8 mm). Adult specimens were further divided into males, females without eggs and ovigerous females. The following life history traits were recorded: body size, number of eggs per brood, length of reproductive period (indicated by the presence of ovigerous females in a population, in months) and generations per year.

The differences in the breakdown of population by size for each species population were compared with the Kruskal–Wallis test among all years at each site separately. The Mann–Whitney test was used to estimate differences in the adult size of amphipod species between seasons in all years and sites of the study, as well as to investigate differences in the size and number of eggs of ovigerous females between species in all years and sites. Spearman's rank correlation was used to determine the relationships between the size of ovigerous females and the number of eggs per brood in each species population in all years and sites, as well as relationships between water temperature and the size of ovigerous females and the number of eggs per brood in each species population in each study year for all study sites. Data manipulation and analysis were done using IBM SPSS Statistics 20.

3. Results and discussion

The occurrence of the three species – *G. varsoviensis*, *P. robustoides* and *G. pulex* – in the middle flow of the Daugava River differed from 2017 to 2019. It was rare for all three species to be found in one place together in the Daugava (Paidere et al. 2019). *Gammarus varsoviensis* were observed at Daugavpils and Jēkabpils in all years of the study, and at Veczeļki in 2017. *Pontogammarus robustoides* were found at Gostiņi in all years of the study and at Veczeļki in 2019. *Gammarus pulex* co-occurred with Ponto-Caspian amphipods at Jēkabpils from 2017 to 2019 and at Veczeļki in 2017 and 2019. *Gammarus varsoviensis* and *P. robustoides* were the dominant amphipods at the study sites. A total of 786 *G. varsoviensis*, 42 *P. robustoides* and 87 *G. pulex* specimens were collected in 2017. In 2018, there were 480, 286 and 36 specimens, respectively, and in 2019 386, 526 and 18 specimens, respectively (Table 1). It should be noted that in 2017 the samples of *P. robustoides* were collected only in May and June. Due to a high water level in the Daugava River, specimens of *P. robustoides* were not collected after that at the study sampling sites Veczeļki or Gostiņi. In turn, in 2018 and 2019, specimens of *P. robustoides* were not collected in April or May (Figure 2). *Pontogammarus robustoides* inhabit shallow nearshore areas with different types of microbiotopes (Poznańska-Kakareko 2021; Żytkowicz et al. 2008). Changes in the hydrological regime due to heavy rainfall in 2017 and higher water levels in spring could have affected

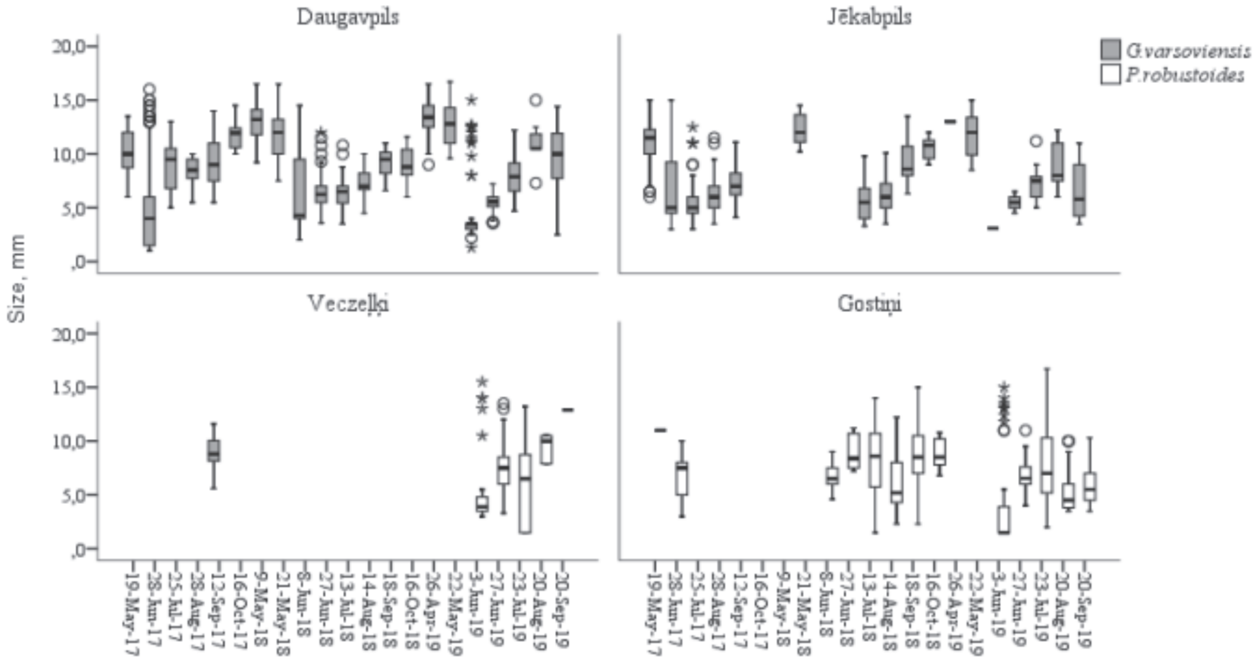

Figure 2

Population structure of *Gammarus varsoviensis* and *Pontogammarus robustoides* in the Daugava River during the study, by size

the species at the nearshore. The variability in the temporal and spatial occurrence of *P. robustoides* coinciding with changes in the hydrological regime also has been reported in estuary studies on the Odra (Wawrzyniak-Wydrowska, Gruszka 2005).

3.1. Population structure, breeding period and generations per year

The breakdown of the population of all amphipods by size varied seasonally and differed from year to year at the study sites (Figure 2, 3) (Kruskal–Wallis test for *G. varsoviensis* at Daugavpils: chi square 52.55, $p < 0.001$; at Jēkabpils: chi square 23.05, $p < 0.001$; for *P. robustoides* at Gostiņi: chi square 128.15, $p < 0.001$; for *G. pulex* at Jēkabpils: chi square 11.05, $p < 0.004$). The reproductive period of all three species begins in early spring, as evidenced by the presence of ovigerous females in the population (Figure 4, 6, 8).

The breeding period of *G. varsoviensis* (when ovigerous females are among the population) was mainly observed from April/May to August (4–5 months), with a peak in May and June; however, in 2019 a large number of ovigerous females was also observed in August (80%) (Figure 4). Similar observations were made in Polish waters, where ovigerous females of *G. varsoviensis* were observed for 4 to 5 months from April to July/August (Konopacka 1988; Jażdżewski 1975). Ovigerous females were also observed in August in the Nemunas River in Lithuania (Arbačiauskas 2008). Juveniles were found from June to September, but their peak was mainly in early June (Figure 5), ranging from 60% in 2017, 67% in 2018, to 81% in 2019; in September 2019, though, the proportion of juveniles was 21%. According to our studies, it can be assumed that the population of *G. varsoviensis* in the middle flow of the Daugava River likely has a univoltine/bivoltine life cycle. In 2017, *G. varsoviensis* produced one generation per year; in 2019 there apparently were two generations (Figure 4, 5). According to similar studies, in European freshwaters (Jażdżewski 1975; Konopacka 1988; Arbačiauskas 2008), *G. varsoviensis* also produce one or two generations per year – the first in spring and the second in late summer and autumn, when the spring generation breeds.

The adult specimens of *G. varsoviensis* (ranging in average size from 10.7 mm ± 1.9 SD, with a maximum of 16.0 mm in 2017 to an average of 11.3 mm ± 2.2 SD, with a maximum of 16.7 mm in 2019) were observed from April/May to September/October, predominantly in spring or autumn (Figure 5), but significantly smaller than those occurring in spring (Mann–Whitney Z: -11.0, $p < 0.001$). The largest specimens were observed in spring 2019 (average: 13.3 mm ± 1.5 SD in April). To compare, in the Central European freshwaters

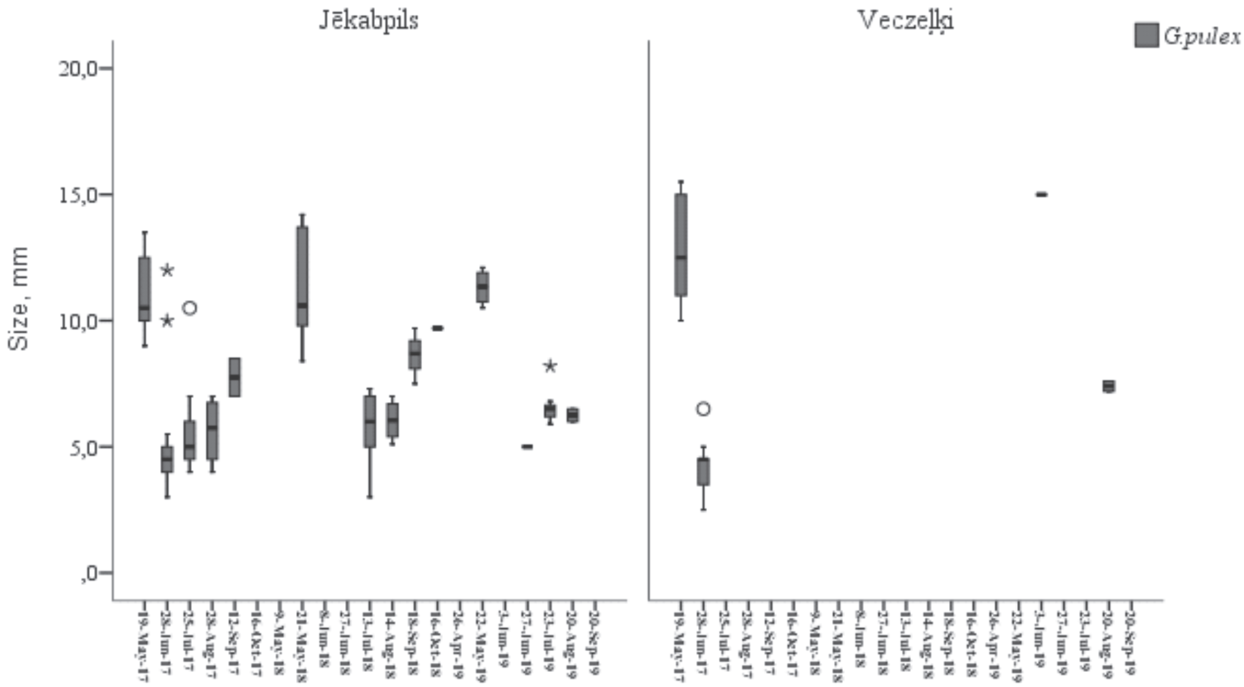

Figure 3

Population structure of *Gammarus pulex* in the Daugava River during the study, by size

of Poland and Germany, *G. varsoviensis* had a larger maximum size and varied from 14 to 20 mm for females and up to 21 mm for males (Rudolph, Zettler 1999; Karaman, Pinkster 1977; Jażdżewski 1975); the specimens were also larger in May/June. These differences in specimen size could be explained by temperature and food supply in a favourable growing season (Sutcliffe 1993; Panov, McQueen 1998). For example, according to long-term observations in the Daugava River, in the period of May to October only in July is the average monthly water temperature 20°C; in September it ranged from 13.6 to 14.1°C and in October from 7.6 to 8.0°C (observation period: 1945–2000) (Latkovska 2015). In turn, during the same

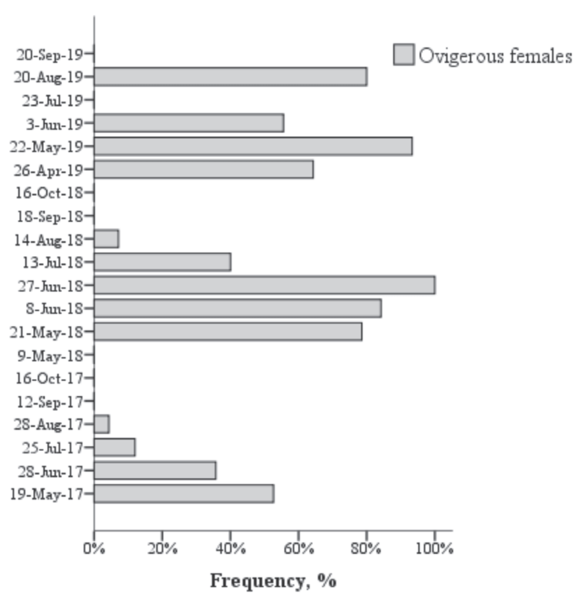

Figure 4

Ovigerous females of *Gammarus varsoviensis* in the Daugava River during the study

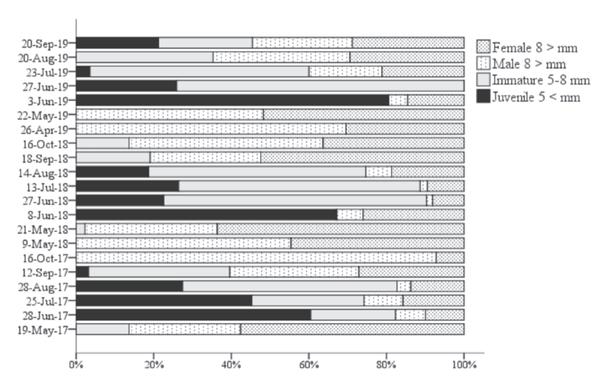

Figure 5

Proportions of adults, immature specimens and juveniles of *Gammarus varsoviensis* in the Daugava River during the study period, in the rivers of Central Poland in July and August the average monthly water temperatures are over 20°C, in September it ranges from 15 to 16°C and in October from 10 to 11°C (observation period: 1971–2015) (Graf, Wrzesiński 2020). Thus, food is more available and energy investment in growth, development and reproduction increases (Jourdan et al. 2019; Sutcliffe 1993).

The breeding period of *P. robustoides* (when ovigerous females are among the population) lasted four months, from June to September. The highest proportion of ovigerous females was observed in June and July (respectively, 50% and 28% in 2018, and 71% and 48% in 2019) and in September (33% in 2019) (Figure 6). Juveniles were obsderved from June to September, with peaks in June (81% at the beginning of June 2019) and in July/August (44% in August 2018, and 61% in August 2019). In September 2019, the proportion of juveniles was up to 38% (Figure 7). The breeding period of the *P. robustoides* population appears to last at least 5 months, as evidenced by the high proportion of juveniles in the population in early June, although no samples were obtained in April/May. In previous studies, we also observed ovigerous females of *P. robustoides* in May (Paidere et al. 2016). In a warmer climate (Polish waters) ovigerous females were observed for 7 months, from April to October (Bacela, Konopacka 2005). A seven-month-long breeding period was also observed in the Saratov and Kuybyshev reservoirs in the middle and lower flows of the Volga (Kurina 2017). However, in Northwestern Russia (the Gulf of Finland and the Neva estuary), ovigerous females were observed for 4 to 5 months: in warmer years from May to September, and in colder years from June to September (Berezina 2016). Our studies show that the *P. robustoides* population has a multivoltine life cycle, and that there can be three generations per year. In 2019, the proportion of ovigerous females peaked in June, July and September. Consequently, the first juveniles peaked in June, a second peak of juveniles was observed in August – forming the summer generation – and a large proportion of juveniles (38%) was observed in September, suggesting that *P. robustoides* might have a third winter generation (Figure 6, 7). This finding is consistent with investigations in the Neva estuary, where *P. robustoides* formed two or three generations per year, depending on the average summer water temperatures; in the warmest years there were three generations, while in the coldest years there were two (Berezina 2016).

Adult specimens of *P. robustoides* (2018 average size: 10.3 mm ± 1.7 SD, maximum: 15.0 mm; 2019 average: 10.0 mm ± 1.8 SD, maximum: 16.7 mm) were observed from June to September/October, predominantly in early summer or autumn (Figure 7), though the differences were not statistically significant (Mann–Whitney Z: -0.05, $p > 0.96$). In comparison, the size of adult specimens in the Daugava River did not reach the sizes found in the waters of Central and South-eastern Europe (Russia). In different Polish waters, the maximum size of specimens varied from 11.5 to 21.4 mm, while in the lower and middle Volga reservoirs they ranged from 19.2 to 20 mm (Dobrzycka-Krahel et al. 2019; *Jażdżewska*, Jażdżewski 2008; Kurina 2017; Bacela, Konopacka 2005; Wawrzyniak-Wydrowska, Gruszka 2005). As in the case of *G. varsoviensis*, the differences in specimen size could be explained by a longer favourable growing season. For example, in the Kuybyshev Reservoir, in July and August the average monthly water temperature (0.5 m) ranged from 20.6 to 21.9°C, in September it ranged from 15.3 to 17.5°C and in October from 11.4 to 8.0°C (observation period: 1967–1980) (Kujbyshevskoe Reservoir, World Lake Database).

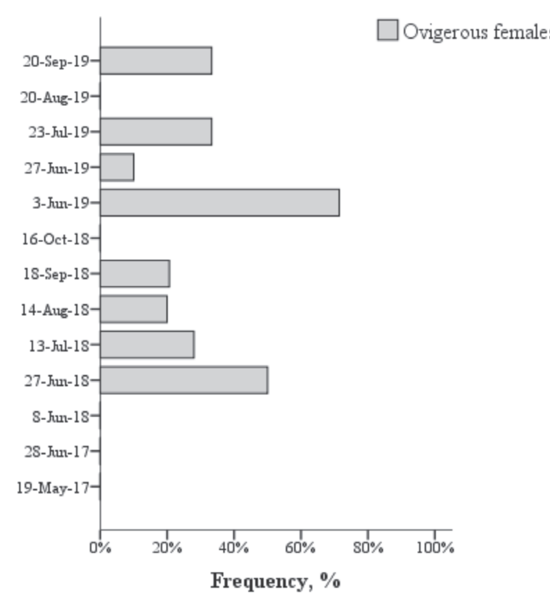

Figure 6

Ovigerous females of *Pontogammarus robustoides* in the Daugava River during the study

In the middle flow of the Daugava River, ovigerous females of native *G. pulex* were observed from May to July (3 months). The highest proportion of *G. pulex* ovigerous females was observed in June/July 2017 (Figure 8). Juveniles were observed from June to August, but their occurrence and predominance were mainly in June (86% in 2017 and 100% in 2018) (Figure 9). Studies on *G. pulex* in the rivers of England,

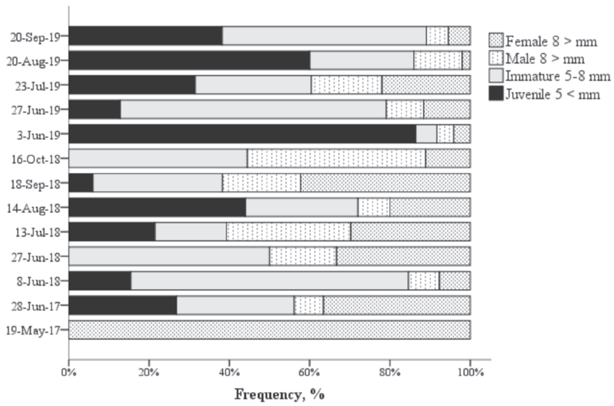

Figure 7

Proportion of adults, immature specimens and juveniles of *Pontogammarus robustoides* in the Daugava River during the study

in contrast, reported ovigerous females among the population almost throughout the year, with a predominance of ovigerous females from April to June and of juveniles from June to July (Graça 1994; Hynes 1955). The population structure suggests that *G. pulex* has a univoltine life cycle in the middle flow of the Daugava River. Females carry eggs and juveniles are found from May/June to August, with a noticeable peak in June. Then, small and medium-sized specimens prevail until they increase in size by September/October (Figure 8, 9). According to other research on *G. pulex*, ovigerous females were observed throughout the year (from two to four broods for females and one generation per year), and there was a significant peak in spring and early summer (Goedmakers 1981; Welton, Clarke 1980; Nilsson 1977; Hynes 1955).

Adult specimens of *G. pulex* (2017 average size: 11.4 mm ± 1.8 SD, maximum: 15.5 mm; 2018 average size: 10.8 mm ± 2.0 SD, maximum: 14.2 mm) were observed from May to September/October (Figure 9), but were smaller than those in spring (Mann–Whitney Z: -3.8, $p < 0.001$). The size of *G. pulex* specimens concurs with the population structure reported in a study from Great Britain (Gee 1988). According to the extensive material published by Karaman and Pinkster (1977), *G. pulex* varies in size from a maximum of 23 mm for males to a maximum of 15 mm for females.

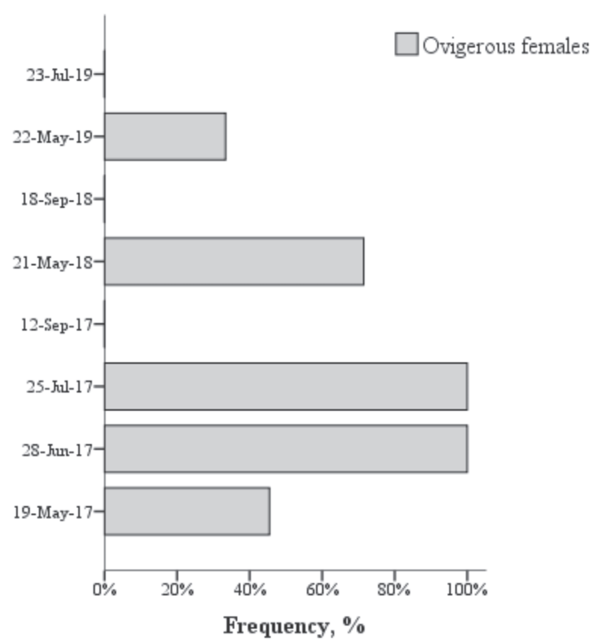

Figure 8

Ovigerous females of *Gammarus pulex* in the Daugava River during the study

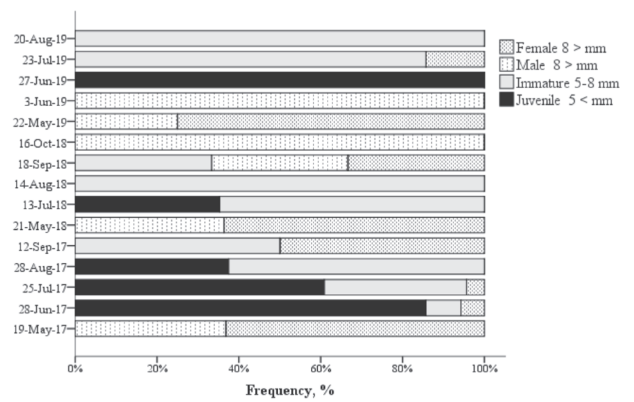

Figure 9

Proportion of adults, immature specimens and juveniles of *Gammarus pulex* in the Daugava River during the study

The population structure of *G. pulex* in the middle flow of the Daugava River, the breeding period (spring to autumn) and the number of generations per year can be explained to a certain extent by the weather and hydrological conditions of the study period (Table 2). The study season May to October 2017 was more characteristic of Latvian climatic conditions. Only in July did the average water temperature of the study sites reach 20.5°C (Figure 10). In addition, in the second half of the summer, the water level in the Daugava River increased due to heavy rainfall (Latvian Environment, Geology and Meteorology Centre 2017). In 2018 and 2019, the meteorological summer was twice as long, with average water temperatures at the study sites of over 20°C in all three summer months

(Figure 10). This could explain why in the middle flow of the Daugava River, the 2017 season was favourable for the development of the native population of *G. pulex*. In turn, in the summer months of 2018 and 2019, the constant water temperature above 20°C was favourable for the alien amphipods *P. robustoides* and *G. varsoviensis*.

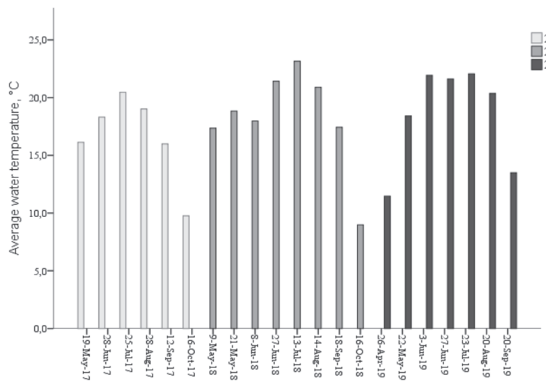

Figure 10

The average water temperature of the study sites in the Daugava River during the study

A shorter life span, faster juvenile development and a tendency to produce more broods are usually associated with a higher average water temperature (Pöckl et al. 2003; Panov, McQueen 1998). For example, in the Eastern Gulf of Finland, the development of *P. robustoides* eggs was observed at 21°C to 25°C for 10 to 15 days in summer (Berezina 2016). In turn, in the population of native *G. pulex*, such prolonged higher temperatures may affect the reproductive process. Studying the native species of the Austrian rivers, *G. roeseli* and *G. fossarum*, Pöckl et al. (2003) reported that water temperatures above 20°C in summer-warm rivers has adverse effects on the gammarus reproduction process. According to experimental studies, the optimal growth temperature among temperate populations of *G. pulex* is 17°C (Moenickes et al. 2011). Also, studies on other amphipods showed that temperature had a significant effect on their life cycle (Panov, McQueen 1998; Sainte-Marie 1991; Welton, Clarke 1980). The life cycle and low occurrence of *G. pulex* can also be explained by competition and predation of macroinvertebrates and alien amphipods (Arbačiauskas et al. 2017; Bacela-Spychalska, Van der Velde 2013; Maazouzi et al. 2011; Orlova et al. 2006; MacNeil, Platvoet 2005). For example, in the sympatric population of *Assellus aqaticus* and *G. pulex*, the latter had a shorter recruitment period and ovigerous females and juveniles were observed earlier than in allopatric populations (Graça et al. 1994).

3.2. Fecundity

Males and females of the alien species occurred among the population during all study seasons. Females prevailed, especially in the reproductive period (Figure 5, 7, 9), thus indicating a high potential to increase the population in a short time, as has been observed in studies on alien species. For example, in the aggressive alien species *Dikerogammarus villosus* in the Moselle River, France, *D. haemobaphes* in the Vistula River, Poland and *P. robustoides* in the Gulf of Finland (Neva estuary) in north-western Russia, females were more prevalent during the reproductive period, making a significant contribution to the development of the population with a large number of eggs and juveniles in the spring generation (Berezina 2016; Bacela et al. 2009; Devin et al. 2004).

In order to measure the reproductive potential of an amphipod, the average number of eggs per brood and the average size of ovigerous females were used. In the *G. varsoviensis* population, the size of ovigerous females and the number of eggs per brood gradually increased from 2017 to 2019 (Table 3), the average size of ovigerous females was 11.3 mm and the average number of eggs was 31 (maximum: 69). A similar trend was observed in the populations from Polish waters. Ovigerous females were found in the average range of 10 to 14 mm with an average of 28 to 35 eggs, or from 5 eggs (females 10 mm long) to 53 eggs (females 16 mm long) (Konopacka 1988; Jażdżewski 1975).

In the population of *P. robustoides*, the average size of ovigerous females was 11.3 mm, and the average number of eggs was 28 (maximum: 81) (Table 3). The traits were similar to *G. varsoviensis* (Mann–Whitney test for the size of ovigerous females: $Z = -0.8$, $p > 0.37$; for number of eggs: $Z = -0.7$, $p > 0.45$).

These results are no higher than those from the Central European (in the Wloclawek Reservoir of the Middle Vistula, Poland) and the Eastern European freshwaters (Kuybyshev Reservoir and Saratov reservoirs in the middle and lower flows of the Volga, Russia), but were closer to the *P. robustoides* populations in the Gulf of Finland (the Neva estuary). In the Wloclawek Reservoir, the average size of ovigerous females was 11.7 mm, the average number of eggs was 64 and there was a maximum of 185 eggs (Bacela, Konopacka 2005). These figures were relatively high in the Kuybyshev and Saratov reservoirs, as well. The average size of ovigerous females was 12.6 mm, the average number of eggs was 33 and there was a maximum of 122 eggs (Kurina 2017). In the Gulf of Finland, the average size of ovigerous females was from 11.2 to 12.2 mm, the average number of eggs was from 33.4 to 43.0 and the maximum number of eggs

Table 3

Reproductive parameters of amphipod species during the study

	2017	2018	2019
G. varsoviensis			
n	34	68	32
Average size of ovigerous females, mm	11.2 ± 1.1 SD min. 9.0 max. 13.0	11.3 ± 1.2 SD min. 9.0 max. 13.5	11.4 ± 1.3 SD min. 9.6 max. 14.5
Average number of eggs per brood	26 ± 11 SD min. 9 max. 50	30 ± 13 SD min. 9 max. 60	37 ± 14 SD min. 9 max. 69
P. robustoides			
n	ovigerous females were not obtained	22	17
Average size of ovigerous females, mm	-	11.6 ± 1.3 SD min. 9.4 max. 15.0	10.9 ± 1.5 SD min. 9.0 max. 15.0
Average number of eggs per brood	-	25 ± 16 SD min. 8 max. 57	31 ± 22 SD min. 13 max. 81
G. pulex			
n	8	only two ovigerous females were obtained	only one ovigerous female was obtained
Average size of ovigerous females, mm	10.7 ± 0.5 SD min. 9.0 max. 12.0	-	-
Average number of eggs per brood	27 ± 5 SD min. 11 max. 41	-	-

was 75 (Berezina 2016). Other invasive alien species in freshwaters are also characterized by a high number of eggs per brood. The size and number of eggs will also depend on the life strategy of the species (Kurina 2017; Bacela et al. 2009; Grabowski et al. 2007a; Kley, Maier 2006; Pöckl 2007; Nelson 1980).

In the native *G. pulex* population, ovigerous females were collected mainly in 2017 and a low number. The average number of eggs per brood was 27 eggs (maximum: 41) with a mean female size of 10.7 mm (Table 3). It has been reported that the average number of eggs in a female up to 11 mm long is about 24 (Hynes 1955).

For all species, fecundity is also associated with female size. The number of eggs significantly and positively correlated with the size of ovigerous females (for *G. varsoviensis*: r = 0.73, $p < 0.0001$; for *P. robustoides*: r = 0.46, $p < 0.02$; for *G. pulex*: r = 0.72, $p < 0.04$). In the populations of *G. varsoviensis* and *G. pulex*, the largest females and the maximum number of eggs were observed in spring or early summer. In the *P. robustoides* population, it was observed in June, but it should be noted that no *P. robustoides* specimens were collected in May. Also, in the population of *P. robustoides* in the middle of summer (July/August), larger females and more eggs were observed. This explains the significant positive correlation between the size of ovigerous females, the number of eggs and the water temperature (for 2019: r = 0.53, $p < 0.03$; for 2018: r = 0.50, $p < 0.04$). Similar observations have also been made for *P. robustoides* and other alien amphipod species – *Dikerogammarus haemobaphes* and *D. villosus*. However, females are commonly larger in spring, and a relatively higher fecundity of females has been observed. The large number of juveniles in the spring is associated with readily available food and rising water temperature (Berezina 2016; Bacela et al. 2009; Pöckl 2007; Bacela, Konopacka 2005). The positive, significant relationship between the size of ovigerous females and the number of eggs indicates that larger females are more fecund than smaller females. The resources that females invest in their offspring also reveal the fitness of the females themselves (Glazier 2018).

4. Conclusions

If the environmental conditions are favourable, alien gammarids in the Daugava River have a successful reproductive period. They produce several consecutive broods in a shorter time within the breeding season, as evidenced by the bivoltine and multivoltine life cycle. The length of the favourable seasons in 2018 and 2019 influenced the size of adult specimens and the number of eggs, as particularly observed in the case of *G. varsoviensis*. The reproductive rates of the *P. robustoides* population (brooding period, generations per year, mean ovigerous female size and mean/maximum number of eggs) were similar to the *P. robustoides* populations in the Gulf of Finland (Neva estuary). In order to obtain more reliable results and a clearer picture of the population structure and productivity of the native species, *G. pulex*, such studies in the Daugava River must be continued.

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