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A CONTINUED STUDY OF AMPHIPOD LIFE HISTORIES IN THE DAUGAVA RIVER UNDER VARYING METEOROLOGICAL CONDITIONS

Jana Paidere*, Aija Brakovska

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Abstract
The Amphipoda *Gammarus varsoviensis* (Jazdzewski 1975) and *Pontogammarus robustoides* (Sars, 1894) are dominant amphipod species in the Daugava River. The study aims to describe the structure and fecundity of these populations continuing the previous investigations of 2017–2019 (Paidere & Brakovska 2022). To do this, we surveyed the Daugava River at four sites from April to September 2020. The meteorological conditions of spring and summer of this year were more typical for Latvian conditions than in 2018 and 2019. The population of *G. varsoviensis* had a univoltine life cycle with one generation per year. The average fecundity was 33 eggs per female, and the average size of ovigerous females was 10.6 mm. The population of *P. robustoides* had a bivoltine life cycle with two generations per year. The average fecundity was 51 eggs per female, and the average size of ovigerous females was 11.8 mm. The study confirmed that spring temperatures are an influential environmental factor for amphipod reproduction. Low spring temperatures are related to the release of juveniles approximately two weeks later than in 2018 and 2019 as particularly observed in the case of *G. varsoviensis*. Temperature rising and prolonged summer season allows higher reproductive success, which can also be expected accordingly to climate change. Evidently, alien *P. robustoides* has a more successful life cycle than *G. varsoviensis* and native *G. pulex*.

Keywords: *Gammarus varsoviensis*, *Pontogammarus robustoides*, population structure, reproduction traits, Daugava River

*Corresponding author: *Jana Paidere. Laboratory of Hydroecology, Department of Ecology, Institute of Life Sciences and Technologies, Daugavpils University, Daugavpils, Parādes Str. 1a, Latvia, E-mail: jana.paidere@du.lv*

Aija Brakovska. Laboratory of Hydroecology, Department of Ecology, Institute of Life Sciences and Technologies, Daugavpils University, Daugavpils, Parādes Str. 1a, Latvia, E-mail: aija.brakovska@inbox.lv

INTRODUCTION

Invasion of alien species, including crustaceans, is considered a threat to native species and biodiversity because invaders are often superior competitors and thus can replace natives or decrease biodiversity and affect aquatic food webs (Arbačiauskas et al. 2017, Bacela-Spychalska et al. 2013, Keller et al. 2011). The Ponto-Caspian amphipods are one of the most successful invaders in fresh and brackish European waters, mainly due to created cascades of reservoirs, canalisation and navigable waterways, and due to the intentional introduction of alien species (Copilaş-Ciocianu & Šidagytė-Copilas 2022, Arbačiauskas et al. 2017, Semenchenko et al. 2015, Leuven et al. 2009, Grabowski et al. 2007a, Bij de Vaate et al. 2002).

The Ponto-Caspian *Pontogammarus robustoides* (Sars, 1894) is the most common alien amphipod in the inland waters of Latvia (Paidere et al. 2019, Paidere et al. 2016, Grudule et al. 2007). *Pontogammarus robustoides* distribution in the Daugava River is mainly explained by the species intentional introduction into the Ķegums Reservoir located on the Lower Daugava River as valuable fish fodder in the 1960s (Bodniece 1976) and now occurring in the lower reaches of the river (Paidere et al. 2019, Paidere et al. 2016). The amphipod *Gammarus varsoviensis* (Jazdzewski 1975) that origin also is related to the Caspian region (Grabowski et al. 2012a, Grabowski et al. 2012b) occurs in the upper course of the Daugava River to the Pļaviņas Reservoir (Paidere et al. 2019a). Both species occur together at a stretch from Veczeļķi to Gostiņi upstream of the Pļaviņas Reservoir and are dominant amphipods in the Daugava River (Paidere & Brakovska 2022, Paidere et al. 2019a, Paidere et al. 2016).

Life history traits (population structure and fecundity) are a few of the main preconditions in invasion success for alien species, including amphipods (San Vicente 2018, Grabowski et al. 2007b). According to our previous life history investigations of the species from 2017 to 2019, the two amphipods in the Daugava River have a reproductive period of four to five months, with up to three generations per year. The population of *G. varsoviensis* is characterized by a univoltine/bivoltine life cycle. In 2017, under more typical meteorological conditions for Latvia, *G. varsoviensis* produced one generation per year, but in 2019, with twice as long the meteorological summer, two generations were observed. The population of *P. robustoides* is characterized by a multivoltine life cycle. *Pontogammarus robustoides* population structure and reproduction traits in 2017 could not assessment unlike *G. varsoviensis* because, in the summer and autumn months, specimens were not obtained at the study sampling sites, it can be explained by the meteorological and hydrological conditions of the study period. In 2019, three generations of *P. robustoides* were observed (Tab. 2) (Paidere & Brakovska 2022).

Continuing these investigations, the study aims to further describe the population structure and fecundity in 2020. Overall, 2020 also was warming (winter and autumn), but the spring and summer were cool weather and more typical for Latvia's meteorological conditions. Only June of all summer months was the hottest (Fig. 2, Tab. 2) (Latvian Environment, Geology and Meteorology Centre 2020). It has been shown that the life history traits of various species of amphipod (induction of reproduction, size of body, number of generations per year, number of eggs, maturation time, and choice or migration of habitat) depend on the water temperature and food (Berezina 2016, Bacela et al. 2009, Bacela & Konopacka 2005, Pöckl et al. 2003, Panov & McQueen 1998, Sutcliffe 1993, Sainte-Marie 1991).

MATERIAL AND METHODS

The Daugava River (the Western Dvina) is one of the largest rivers in Eastern Europe. Starting in the Valday Highlands in Russia, the river flows through the East-European Plain and crosses Belarus and Latvia before draining into the Gulf of Riga (Volchak & Lyakmund 2006). The samples of amphipods were obtained within the stretch of the Daugava River at sites "Daugavpils", "Jēkabpils", "Veczeļķi", and "Gostiņi" (Pļaviņas Reservoir) (Fig. 1, Tab.1) in 2020, as during 2017–2019 (Paidere & Brakovska 2022). Water physicochemical parameters were measured and amphipods were sampled once a month, from April until September. In June, to not miss the beginning of the reproductive period, amphipods were sampled twice a month. Semiquantitative samples were obtained in the wadeable (up to 0.5 m) depths using a *Hydrobios* hand net with a mouth opening of 25x25 cm (500 µm mesh). The study sites' substratum mainly consisted of sand, silty sand, detritus, pebbles, some boulders, and macrophytes. The water physicochemical parameters (temperature, pH, conductivity, dissolved oxygen, and chlorophyll a) were measured using a *Hydrolab DS5* multiprobe and are presented in Tab 1.

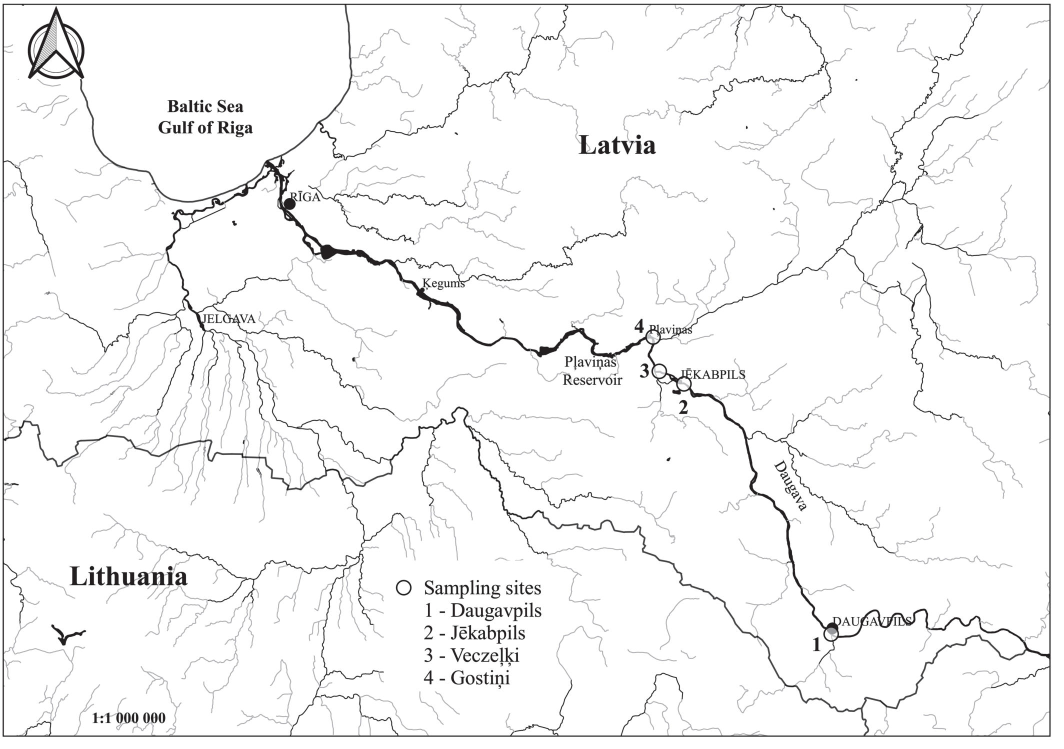

Figure 1. Sampling sites of amphipods along the Daugava River (2017–2020).

Table 1. Background characteristics of the sampling sites during the study.

Characteristics	"Daugavpils"	"Jēkabpils"	"Veczeļķi"	"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
Amphipoda	*G. varsoviensis* n=336 Obtained April–September	*G. varsoviensis* n=35 Obtained May–September	*G. varsoviensis* n=7 Obtained April and September *P. robustoides* n=48 Obtained June–August	*G. varsoviensis* n=3 Obtained September *P. robustoides* n=118 Obtained June–September
	average (range)	average (range)	average (range)	average (range)
T (°C)	15.93 (7.79–21.37)	16.03 (8.26–21.49)	16.20 (8.54–22.01)	16.90 (8.43–23.47)
Cond. ($\mu S\ cm^{-1}$)	313 (261–380)	312 (287–364)	312 (286–349)	348 (296–389)
DO ($mg\ L^{-1}$)	8.67 (6.80–11.91)	8.64 (6.91–11.23)	9.09 (7.45–11.54)	10.05 (7.61–12.70)
pH	7.82 (7.60–7.99)	7.93 (7.73–8.11)	8.04 (7.83–8.35)	8.14 (7.86–8.63)
CHL ($\mu g\ L^{-1}$)	2.94 (2.40–3.69)	3.64 (2.57–4.91)	3.30 (2.13–5.08)	3.70 (2.01–4.81)

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

The study year of 2020 was warmer (annual average air temperature 8.8°C) than the previous study period in 2018 and 2019 (annual average air temperature 8.2°C in 2019, which was the warmest previous study year). However, unlike the previous study years, the warm weather in 2020 was associated with the warm winter and autumn, instead of the spring and summer as in 2018 and 2019 (Fig. 2). The average air temperature in the study months April and May of 2020 was below the norm (0.5 and 1.9°C respectively). The average air temperature in the summer months was to close the more typical summer temperature of 17.2°C (Latvian norm 16.2°C), only June was warmer with 18.1°C. September, with 14.4°C, was the warmest autumn month (Fig. 2) (Klimata portāls. Gads, 2020. Latvian Environment, Geology and Meteorology Centre). Thereby, the average water temperature in the spring ranged from 8.2°C in April to 11.5°C in May, in the summer ranged from 18.4°C in June (only in the second decade of June it was 21.5°C) to 21.7°C in August. In comparison, the average water temperature in the spring and summer of 2018–2019 was higher. In May, it was already 18.5°C, and in all three summer months was above 20°C (Fig. 2). In turn, the weather of spring and summer in 2017 and 2020 were more typical of Latvian meteorological conditions (Tab. 2).

Identification of specimens was done using the literature: Eggers & Martens 2004, Eggers & Martens 2001, Karaman & Pinkster 1977, Jażdżewski 1975. Specimen identification and length measurements were done with a *ZEISS Stemi 508doc* stereomicroscope fitted with an ocular micrometer (10:100). The length of the extended amphipods was measured as the distance from the anterior margin of the head to the base of the telson (Bacela & Konopacka 2005). Based on literature data (Berezina 2016, Copilaş-Ciocianu & Boroş 2016, Bacela & Konopacka 2005, Sainte-Marie 1991), the population structure was split by development into small size specimens, or juveniles,

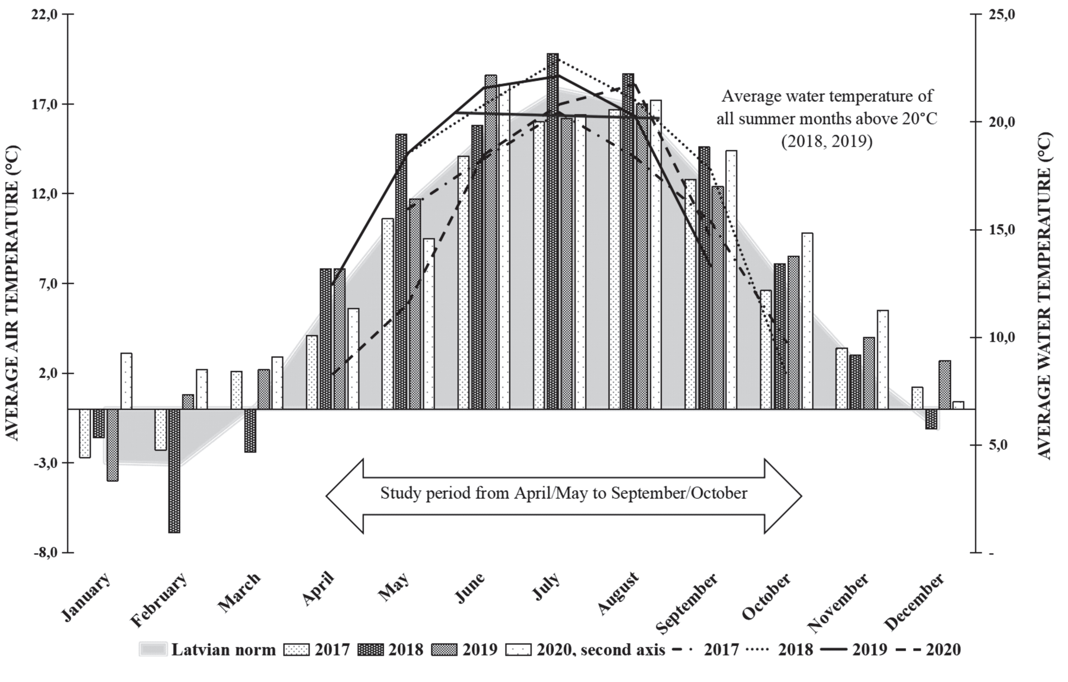

Figure 2. Average air temperature and average water temperature of the study sites in the Daugava River during the study (2017–2020) in Latvia. Air temperature prepared according to data from Latvian Environment, Geology and Meteorology Centre, 2017, 2018, 2019, 2020

(< 5 mm), medium size, or immature, (from 5 to 8 mm) and large, or adults, (> 8 mm). Within the latter group, males, females, and females with eggs (ovigerous females) among the latter were counted separately. Gender of *P. robustoides* was identified by the second pair of gnathopods. The second pair of gnathopods is generally larger for males of *P. robustoides*. Gender of *G. varsoviensis* was identified by the second antenna which in females is less than 1/3 and in males more than 1/3 of the body length, by the presence of the calceoli on the second antenna of males, and by the smaller gnathopod propodus of females. The following life history traits were recorded: size of ovigerous females, 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.

Data manipulation was done using *IBM SPSS Statistics 21*. The data were pooled across the study sites for analysis, including the data for 2017–2020 from our previous study.

RESULTS AND DISCUSSION

A total of 381 *G. varsoviensis*, and 166 *P. robustoides* specimens were collected in 2020. Native *Gammarus pulex* also was obtained at sites "Jēkabpils" and "Veczeļķi" (20 and only 1 specimen respectively), thereby *G. varsoviensis* and *P. robustoides* were the dominant amphipods at the study sites (Tab. 1). *Gammarus varsoviensis* was obtained during all study period but *P. robustoides* was found only from June – same as during 2017–2019 due to fluctuating water levels in spring (Paidere & Brakovska 2022) – and in a small number of specimens (Tab. 1).

The population structure of *G. varsoviensis* varied seasonally in 2020 (Fig. 3A, Fig. 4A). The population structure of *G. varsoviensis* consisted of adult specimens and few immatures in spring, which might suggest a longer reproductive period due to the previous warm period of autumn and winter (Fig. 2). The specimen size of males and females continued to increase until the beginning of summer. In this period, the males showed their maximum size of 13.8–16.5 mm. The females reached their maximum size of 12.4–13.0 mm in the beginning of summer and most of them consisted of ovigerous females (Fig. 3A, Fig. 4A). Although the ovigerous females were observed already from April, their highest proportion was observed at the beginning of June (44 %) followed by the peak of juveniles (89 %) at the second week of June. Thereby, the summer population structure mostly consisted from juveniles in the second part of June to immatures in July, and August. The adult males and females in the population again appeared in August and September, reached the maximum size of specimens of 11.0–12.0 mm and 9.5–10.1 mm respectively (Fig. 3A, Fig. 4A). The ovigerous females (6 %) were also observed in August but a high peak of juveniles did not follow. Our results showed that the breeding period of the population of *G. varsoviensis* lasted 5 months from April to August, when the ovigerous females were observed (Fig. 4A) and had a univoltine life cycle in 2020 with one generation per year in the middle stretch of the Daugava River. Similar results were also obtained in the previous study, 2017–2019 (Paidere & Brakovska 2022) when in the population, ovigerous females were observed from April or May to August, but the peak of juveniles was different (Tab. 2). In 2020 and 2017, the maximum of juveniles was reached in the second part or at the end of June when from April to May average water temperatures was 8.2°C to 11.5°C respectively in 2020, but in May 2017 was 15.9°C. It is approximately two weeks later than in 2018 and 2019 when already in May the average water temperature was above 18°C. Moreover, in September 2019, the second release of *G. varsoviensis* juveniles was observed (Tab. 2). The population structure of *G. varsoviensis* in 2020 appears to be similar to the native *G. pulex* population in 2017 (Paidere & Brakovska 2022). This also corresponds to investigations of *G. varsoviensis* population in the Central Poland waters, where the breeding period lasted from April to July/August, but unlike our study, the appearance of juveniles in the population occurred in May (Konopacka 1988). Our results confirm that the population structure and breeding of *G. varsoviensis* during the study can be explained by the water temperature, thereby, availability of food what is also noted other studies of temperate freshwater gammarid. At low temperatures, with poor availability of food, growth is slow and the probability of survival decreases, as well as release of the first brood are dependent on water temperature (Pöckl et al. 2003, Sutcliffe 1993, Konopacka 1988).

The population structure of *P. robustoides* was difficult to assess in 2020 because the specimens were not obtained in spring (Fig. 3B, Fig. 4B). The males were observed only in summer and showed their maximum size of 18.0 mm in July. The females were observed in the summer with a maximum size of 14.5–13.4 mm at the beginning of June, and July, and September with a maximum size of 9.0 mm (Fig. 3B). The ovigerous females were observed in June and July (Fig. 4B). Simultaneously at the beginning of June, both ovigerous females (20 %) and a high proportion of juveniles (40 %) were observed. In the second week of June and July, the population mostly consisted of juveniles (24 % and 11 % respectively) and immature (67 % and 31 % respectively) specimens and of females (41 % in July). The second peak of juveniles (74 %) was observed in August although the proportion of observed ovigerous females in July was small (11 %) (Fig. 4B). Results showed that the breeding period of *P. robustoides* lasted two months, from June to July in 2020. However, considering that no samples were obtained in April/May, the breeding period of *P. robustoides* appear to last at lasted three months and had a bivoltine life cycle in 2020 with two generation per year in the middle stretch of the Daugava River. Because, in previous studies, we also observed females and ovigerous females of *P. robustoides* in May (Paidere et al. 2016, Paidere & Brakovska 2022). In 2017, similar to *G. varsoviensis*, 26 % of *P. robustoides* juveniles in the population were observed at the end of June (Tab. 2) (Paidere & Brakovska 2022). As similar to *G. varsoviensis* the population structure and breeding of *P. robustoides* during the study can explain by the water temperature. For example, in the population of alien amphipod *Dikerogammarus haemobaphes* in the Vistula River, from egg fertilization to release of juveniles took around three weeks from 10°C to 13°C in April (Bacela et al. 2009). But in our study, the average water temperature was from 8.2°C in April to 11.5°C in May, and only at the beginning of June it was 14.4°C. The laboratory studies of

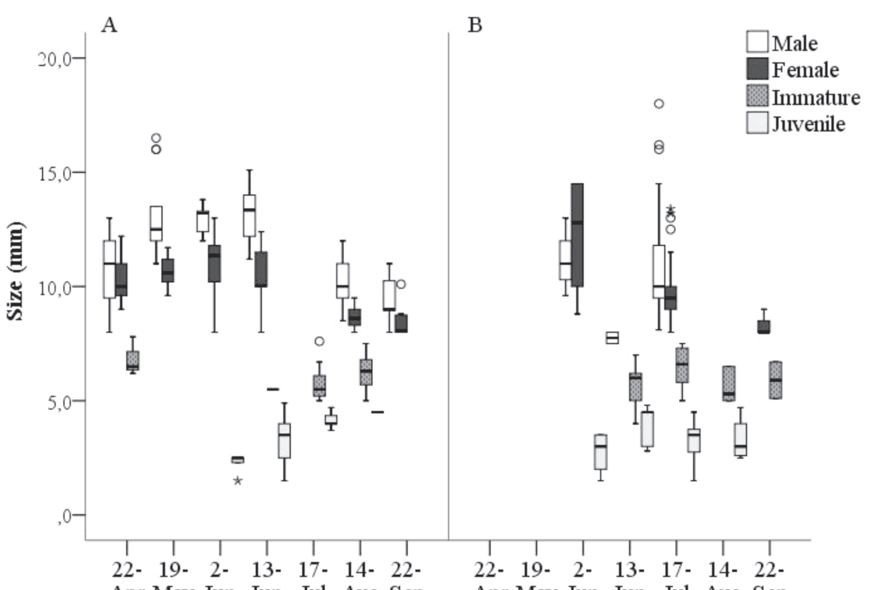

Figure 3. Seasonal population structure of A – *Gammarus varsoviensis* and B – *Pontogammarus robustoides* by size (mm) in 2020.

the relationship between brood development time and water temperature of the other alien amphipod *Dikerogammarus villosus* showed that at 16°C, mean brood development time was 14 days, compared with about three weeks for the indigenous species *G. fossarum*, *G. roeseli* and at 10°C, mean brood development time of *D. villosus* was 24 days (Pöckl, 2007). Our results correspond to investigations in the Neva estuary, where the northernmost population of *P. robustoides* formed two or three generations per year; in the warmest years, there were three generations (reproduction period May–September), while in the coldest years there were two generations (reproduction period June–September) (Berezina 2016).

The fecundity of *G. varsoviensis* averaged 33 eggs per female (n=36) with an average ovigerous female size 10.6 mm in 2020. The ovigerous females reached their maximum size 12.4–13.0 mm at the beginning of summer with a maximum number of eggs per brood 47–69. The smallest ovigerous females (only five) were an average size of 9.0 mm in August with a maximum number of eggs per brood 26. The fecundity of *P. robustoides* averaged 51 eggs per female (n=15) with the average ovigerous female size 11.7 mm in 2020. The maximum size (14.5 mm, n=4) of ovigerous females was observed at the beginning of June with a maximum number of eggs per brood 98. The smallest ovigerous females were observed a size of 10.0–13.4 mm in August with a maximum number of eggs per brood 25–63. Females of *G. varsoviensis* and *P. robustoides* can become ovigerous when they reach a size of about 8.0 and 10.0 mm respectively. The largest females and the maximum number of eggs were observed in spring and at the beginning of summer for both species (Fig. 5). Such decreases are quite general among amphipods. Decreasing of amphipod female size and fecundity in summer populations has been explained by three factors. It is temperature, the food supply decreasing and predation (Nelson 1980). In comparison, the fecundity of *P. robustoides* and *G. varsoviensis* are similar and correspond to our previous studies (Tab. 2), but these results are higher than for the native *G. pulex* in the Daugava River (in 2017, the average number of eggs per brood was 27 eggs, maximum 41, with a mean female size of 10.7 mm) and in our studies, *P. robustoides* has mainly reached the maximum number of eggs (Tab. 2) (Paidere & Brakovska 2022).

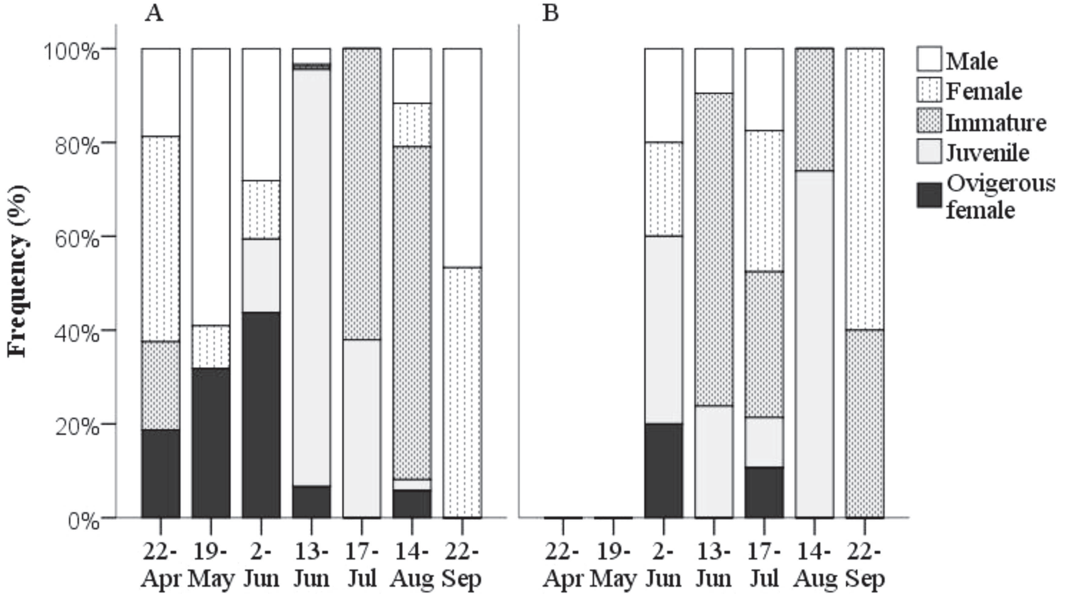

Figure 4. Seasonal occurrence (%) of females, ovigerous females, males, immature and juvenile, A – *Gammarus varsoviensis* and B – *Pontogammarus robustoides* in 2020.

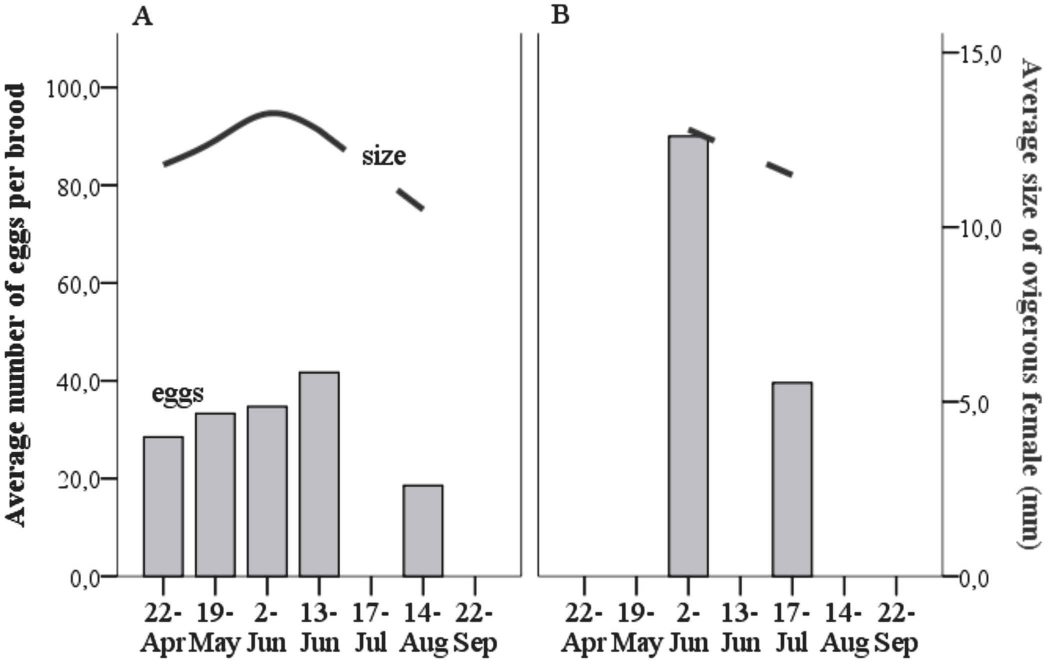

Figure 5. Seasonal variation of the average brood size and average size of ovigerous females (mm) of A – *Gammarus varsoviensis* and B – *Pontogammarus robustoides* in 2020.

Table 2. Main characteristics of the study environment and the life history of amphipods.

Parameter\Year	2017	2018	2019	2020
Average water temperature (°C)				
April, May	15.9 (V)	18.5 (V)	12.4, 18.5	8.3, 11.5
June, July, August	18.3, 20.5, 18.3	20.8, 22.9, 21.0	21.6, 22.1, 20.3	18.5, 20.8, 21.7
September, October	15.4, 9.7	17.8, 8.2	13.3 (IX)	14.6 (IX)
Meteorological summer (length in months)	VI–VIII (3)	VI–IX (5)	VI–IX (5)	VI–VIII (3)
Gammarus varsoviensis				
Breeding period (length in months)	V–VIII (4)	V–VIII (4)	IV–VIII (5)	IV–VIII (5)
Juvenile peaks	the end of VI	the first week of VI	the first week of VI and IX	the second week of VI
Number of generations	1	1	2	1
Average (min–max) size of ovigerous females (mm)	11.2 (9.0–13.0)	11.3 (9.0–13.5)	11.4 (9.6–14.5)	10.6 (8.0–13.0)
Average (min–max) eggs number per brood	26 (9–50)	30 (9–60)	37 (9–69)	33 (13–69)
Pontogammarus robustoides				
Breeding period (length in month)	–	V–IX (5)*	V–IX (5)*	V–VIII (4)*
Juvenile peaks in month	juveniles observed only in the end of VI	the first week of VI and VII/VIII	the first week of VI and VII/VIII, the end of IX	the second week of VI and VIII
Number of generations	–	2	3	2
Average (min–max) size of ovigerous females (mm)	–	11.6 (9.4–15.0)	10.9 (9.0– 15.0)	11.8 (10.0–14.5)
Average (min–max) number of eggs per brood	–	25 (8–57)	31 (13–81)	51 (25–98)

* due to missing samples estimated taking into account the juvenile appearance.

CONCLUSIONS

Temperature rising and prolonged summer season allows higher reproductive success of the amphipods, which can also be expected accordingly to climate change. Spring and summer water temperature is an influential environmental factor for species reproduction and growth. Evidently, alien *P. robustoides* has a more successful life cycle than *G. varsoviensis* and native *G. pulex*.

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