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Research Article

THE DISTRIBUTION AND LOCAL DISPERSAL OF PONTO-CASPIAN PERACARIDA IN LITHUANIAN FRESH WATERS WITH NOTES ON *PONTOGAMMARUS ROBUSTOIDES* POPULATION ESTABLISHMENT, ABUNDANCE AND IMPACT

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Abstract

Recently, the introduced Ponto-Caspian mysids and amphipods live in three water reservoirs (WR) and fifteen lakes of Lithuania. *Hemimysis anomala* inhabits only Kaunas WR, whereas other mysids, *Paramysis lacustris* and *Limnomysis benedeni*, occur in three and two WRs, and in eleven and two lakes, respectively. The alien amphipods *Pontogammarus robustoides*, *Chaetogammarus warpachowskyi*, and *Obesogammarus crassus* inhabit three, two, and two WRs, and nine, seven, and three lakes, correspondingly. The ability of the mysid *P. lacustris* to disperse upstream is higher than that of the introduced amphipods. Of the introduced peracaridan species, the mysid *P. lacustris* and the amphipod *P. robustoides* are best adapted to stagnant water environments. They can only establish viable populations in large, open lakes, or in lakes with high water turnover. The probability of *P. robustoides* establishing a sustainable population is higher in mesotrophic lakes than it is in eutrophic lakes. In lakes that provide sufficient oxygen conditions for *P. robustoides*, the process of the development of populations might be mediated by water ion content. The abundance of the amphipod *P. robustoides* in stagnant water bodies is

positively correlated with their area. In habitats that are favorable for *P. robustoides*, this alien amphipod species out-competes the native amphipod species *Gammarus lacustris* and has a negative impact on the native isopod *Asellus aquaticus*.

INTRODUCTION

Ponto-Caspian amphipods and mysids are among the most successful invaders of new aquatic environments and might have a significant impact on indigenous peracaridan species (Dick and Platvoet 2000, Jazdzewski *et al.* 2004). In the fresh waters of Lithuania, native species of amphipods are represented by *Gammarus pulex*, *G. lacustris*, and *Pallasiola quadrispinosa* (Gasiūnas 1963, 1972b). The glacial relict mysid species *Mysis relicta* still inhabits the large, deep lakes of Lithuania (Grigelis and Arbačiauskas 1996). The most common native freshwater peracaridan species, obviously, is the isopod *Asellus aquaticus* (Gasiūnas 1972b).

Extensions of the range of Ponto-Caspian amphipods and mysids in Europe have been greatly facilitated by the junction of river basins through man-made canals and intentional introductions (Bij de Vaate *et al.* 2002). The first Ponto-Caspian peracaridan invader was most probably the amphipod *Chelicorophium curvispinum*, which reached Lithuanian waters via the Oginskij Canal from the Dniepr River basin and was first recorded in the Nemunas River near the town of Tilžė (Sovietsk) in 1921 (Schidat 1926, cit. by Gasiūnas 1956). *Chaetogammarus ischnus* was found in the lower reaches of the Nemunas River in the 1960s (Gasiūnas 1963). Although Gasiūnas (1972a) later recognized this amphipod as an introduced Ponto-Caspian species, it most likely invaded the inland waters of Lithuania through natural spreading. Other alien amphipods (*Pontogammarus robustoides*, *Obesogammarus crassus*, *Chaetogammarus warpachowskyi*) and mysids (*Paramysis lacustris*, *Limnomysis benedeni*, *Hemimysis anomala*) were introduced into the Kaunas WR located on the Nemunas River, during 1960-1961 (Gasiūnas 1963, 1965, 1968). These peracaridans have established sustainable populations in this water reservoir and dispersed downstream to the Curonian Lagoon, where all of them, excluding *H. anomala*, have established permanent populations (Arbačiauskas 2002). The amphipods *P. robustoides* and *O. crassus* were recently noted in Polish waters (Gruszka 1999, Konopacka and Jazdzewski 2002) and are considered to be invaders from the Nemunas River drainage system (Jazdzewski and Konopacka 2000, 2002, Jazdzewski *et al.* 2002). The Ponto-Caspian amphipod *P. robustoides* has also invaded the eastern Gulf of Finland (Berezina and Panov 2003) probably from adjacent inland waters, where it was transferred from the Kaunas WR, but never checked for acclimatization (Gasiūnas 1972, Berezina 2004).

Within Lithuania, attempts were made to transfer Ponto-Caspian peracaridan species from the Kaunas WR into two other water reservoirs and over 100 lakes; however, these species have survived only in a few locations. Information on introduced crustaceans collected until 2000 was summarized in Arbačiauskas (2002). Since then, new data have become available. Thus, the purpose of the present work was to present the recent distribution of Ponto-Caspian mysids and amphipods in the inland waters of Lithuania and to compare the ability of introduced peracaridan species to spread naturally in flowing waters. The author also analyzed factors that might affect the establishment of a population and the long-term survival and abundance of the alien amphipod *P. robustoides* in stagnant waters and its impact on native peracaridans.

MATERIAL AND METHODS

This paper is based on studies performed during 2002-2004 but also includes some data collected in 1998-2000 and 2005. Lakes and WRs were studied for the presence of Ponto-Caspian species and the abundance of the alien amphipod *P. robustoides*. The Nemunas River and selected sites in its basin downstream and upstream from potential source populations were investigated to compare the ability of the introduced crustaceans to spread naturally. Sampling was performed using sledge nets and dredges, or by analyzing various substrates that were collected manually from the littoral or riverbeds. The abundance of the Ponto-Caspian amphipod *P. robustoides* (or native amphipod *G. lacustris*, if necessary) was estimated using the relative abundance index (*RAI*), which was calculated as $RAI = 10 \times N / (t - (t_h \times N))$, where N is the number of individually collected and counted specimens; t is the total time of sample collection and analysis, t_h is the mean handling time of one individual (for details see Arbačiauskas 2002). This measure of abundance indicates the number of amphipod specimens counted during a 10 min search in substrates where amphipods should live, and correlates well with absolute density (Arbačiauskas and Gumuliauskaitė, unpubl. results). The *RAI* values presented are means of all the estimates for a given water body, or means of estimates for a certain sampling date when expressing the dynamics of abundance of the native amphipod *G. lacustris* and the Ponto-Caspian amphipod *P. robustoides* after its introduction into Lake Asveja. The absolute density of amphipods in the littoral of Lake Dusia was assessed using a cylinder with a cross-section area of 0.1 m^2.

Table 1

Lakes and water reservoirs recently inhabited by Ponto-Caspian mysids and amphipods including all those mentioned by Gasiūnas. Species: PL (*P. lacustris*); LB (*L. benedeni*); PR (*P. robustoides*); OC (*O. crassus*); CW (*C. warpachowskyi*). Status (Kavaliauskienė 1996): M (mesotrophic); ME (mesotrophic with eutrophic traits); E (eutrophic). Occurrence: (+) (before 1970, Gasiūnas 1970, 1972a,b); [+] (1989-1992, Lazauskienė 1997); + (present) or 0 (absent) (this study, 2002-2004).

	Water body	Mysids		Amphipods			Area, ha	Status
		PL	LB	PR	OC	CW		
1	Dysnai	**(+) +**		**(+) 0**	**[+] 0**	**[+] 0**	**2439**	**E**
2	Dusia	**(+) +**		**(+) +**	**(+) +**	**(+) +**	**2334**	**ME**
3	Antalieptė WR	**(+) +**		**(+) +**	**(+) 0**	**(+) 0**	**1911**	**M**
4	Sartai	**(+) +**		**(+) 0**			**1332**	**E**
5	Metelys	**(+) +**		**(+) +**	**[+] +**	**[+] +**	**1286**	**ME**
6	Elektrėnai WR	**(+) +**	**(+) +**	**(+) +**	**(+) +**	**(+) +**	**1250**	**ME**
7	Plateliai			**(+) +**	**[+] 0**	**(+) 0**	**1204**	**ME**
8	Asveja			**+**			**1015**	**ME**
9	Daugai	**(+) +**	**+**	**(+) +**	**(+) +**	**+**	**954**	**ME**
10	Kretuonas	**(+) 0**					**880**	**E**
11	Obelija	**(+) +**		**(+) +**		**+**	**584**	**E**
12	Dysnykštis	**[+] +**		**[+] 0**			**538**	**E**
13	Ančia			**+**			**504**	**ME**
14	Seirijis			**+**		**+**	**501**	**M**
15	Žeimenys	**[+] +**				**[+] +**	**455**	**ME**
16	Lūšiai	**+**					**391**	**ME**
17	Arinas	**(+) +**		**(+) 0**			**375**	**E**
18	Simnas	**(+) +**	**(+) +**	**(+) +**	**(+) 0**	**(+) +**	**243**	**E**

RESULTS

Distribution in stagnant waters

All of the introduced Ponto-Caspian mysids (*P. lacustris*, *L. benedeni*, *H. anomala*) and amphipods (*P. robustoides*, *O. crassus*, *C. warpachowskyi*) still inhabit the Kaunas WR. Information on alien peracaridan species in other WRs and lakes and their locations are presented in Table 1 and Figure 1. Gasiūnas (1970, 1972a, b) reported the acclimatization of the introduced crustaceans in two WRs and nine lakes. In these water bodies, the same species composition was found only in the Elektrėnai WR (two mysids and three amphipods) and Lake Dusia (one mysid and three amphipods). It is noteworthy that the mysid *H. anomala* was also transferred into the Elektrėnai WR, but its survival was not studied earlier. Recent extensive sampling for this species

indicated that it was absent. More species were recorded in lakes Metelys, Daugai, and Obelija. In addition to the previously established *P. robustoides*, Lake Metelys is inhabited by *O. crassus* and *C. warpachowskyi*, which were also found by Lazauskienė (1997). In Lake Daugai, the presence of *P. lacustris* and the two new species *L. benedeni* and *C. warpachowskyi*, which were detected during 1998-2000 (Arbačiauskas 2002), was recently confirmed. A study of Lake Obelija showed that in addition to the previously recorded *P. lacustris* and *P. robustoides*, the amphipod *C. warpachowskyi* has also established a viable population here.

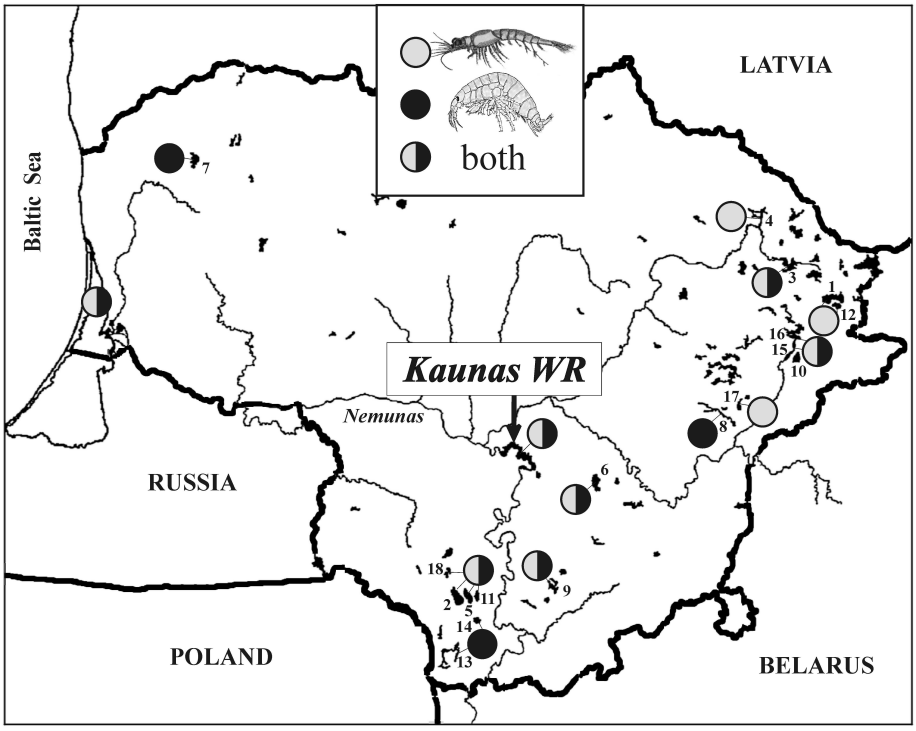

Fig. 1. Lithuanian lakes and water reservoirs currently inhabited by Ponto-Caspian mysids and amphipods. The names of the water bodies correspond to the numbered names in Table 1.

In other water bodies that Gasiūnas (1970, 1972a, b) identified as habitats for introduced peracaridans, fewer species were detected (Table 1). In Lake Simnas, in addition to *L. benedeni* and *P. robustoides* recorded during 1998-2000 (Arbačiauskas 2002), *P. lacustris* and *C. warpachowskyi* were also found. Thus, this lake lacks only the amphipod *O. crassus*. The Antalieptė WR is inhabited by *P. lacustris* and *P. robustoides*, but the other two species of

amphipods were recently absent. Despite a large sampling effort, the mysid *P. lacustris* was not found in Lake Kretuonas. This was the only lake in which the extinction of a Ponto-Caspian mysid was identified. The mysid *P. lacustris* still inhabits lakes Dysnai, Sartai, and Arinas, from which the Ponto-Caspian amphipods referred to previously are absent. Finally, these amphipods have recently been represented only by *P. robustoides* in Lake Plateliai.

In lakes Dysnykštis and Žeimenys, the establishment of populations of Ponto-Caspian peracaridan species was recorded during 1989-1992 (Lazauskienė 1997), and both lakes have recently been inhabited by the mysid *P. lacustris*. Lake Žeimenys is also inhabited by the amphipod *C. warpachowkyi*. Lake Asveja, into which Ponto-Caspian amphipods were transferred during 1998 (Arbačiauskas 2002), still contains *P. robustoides*. Ponto-Caspian peracaridans were noted for the first time in the other three lakes. The mysid *P. lacustris* was detected in Lake Lūšiai. It was determined that another two lakes in southwestern Lithuania contained alien amphipods. *P. robustoides* was found in lakes Seirijis and Ančia, and *C. warpachowskyi* was recorded in Lake Seirijis (Table 1, Figure 1).

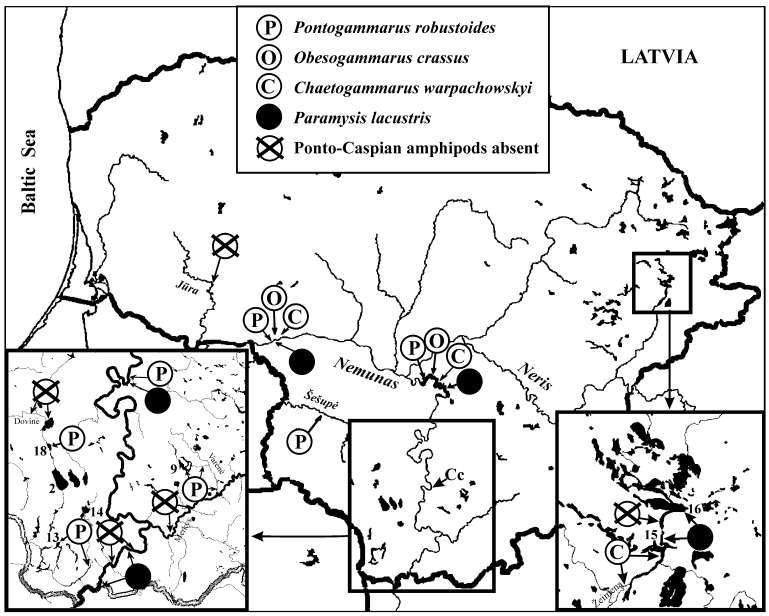

Fig. 2. Distribution of introduced Ponto-Caspian amphipods and the mysid *Paramysis lacustris* in the Nemunas River basin. Sampling places indicated by arrows; numbers correspond to the lake names in Table 1. The occurrence of *Chelicorophium cursvispinum* is indicated by (Cc).

Distribution in the Nemunas River basin

During 2002-2004, selected sites in the Nemunas River basin were monitored for local dispersal, *i.e.*, the ability of introduced Ponto-Caspian peracaridans to spread naturally (Figure 2). All amphipod species (*P. robustoides*, *O. crassus*, *C. warpachowskyi*) and the mysid *P. lacustris* were found in the Nemunas River near the town of Jurbarkas, downstream from the Kaunas WR. Upstream, this mysid species and the amphipod *P. robustoides* were present at the town of Birštonas, where the Kaunas WR actually begins. However, further upstream (near the towns of Liškiava and Druskininkai), *P. robustoides* was absent while *P. lacustris* still occurred, even in the Nemunas River at the boarder with Belarus.

Two medium-sized tributaries of the Nemunas River downstream from the Kaunas WR were monitored. The Ponto-Caspian amphipods were not detected in the Jūra River, although *P. robustoides* was recorded in the middle reach of the Šesupė River (Figure 2). To determine if this alien species might have invaded the Šešupė River from lakes Dusia and Simnas that are directly connected with this river, sampling was performed downstream from Lake Simnas. Ponto-Caspian amphipods were not found in the eutrophic Lake Žuvintas or in its outflow, the Dovinė Stream. In reference to recently discovered populations of alien amphipods in lakes Seirijis and Ančia, migration between them is possible since the outflows from these lakes are connected and *P. robustoides* was found at their confluence (Figure 2).

The study of the natural dispersal of alien amphipods from Lake Daugai showed that at least *P. robustoides* is migrating downstream. This species was abundant in the outflowing stream and present downstream in the Varėnė River, even at its fall into the Merkys River. However, this amphipod was not recorded further downstream in the Merkys River (Figure 2). The ability to disperse downstream was also demonstrated by another alien amphipod, *C. warpachowskyi*. This amphipod inhabits Lake Žeimenys and was also found at the outlet of the Žeimena River, whose source is this lake (Figure 2). It was not investigated how far downstream *C. warpachowskyi* occurs in the Žeimena River, but Ponto-Caspian amphipods were absent in its middle reach.

A narrow canal with strong flow velocity connects lakes Žeimenys and Šakarvai; the latter, in turn, has a wide connection with Lake Lūšiai. These lakes comprise the downstream lakes of the whole Ignalina lake system (Figure 2). Thus, Lake Šakarvai was sampled to determine if Ponto-Caspian peracaridans inhabiting Lake Žeimenys might have expanded upstream. The amphipod *C. warpachowskyi* and the mysid *P. lacustris* were not found in Lake Šakarvai; however, this mysid was caught in Lake Lūšiai during dredging for glacial relict crustaceans at depths between 5 and 15 m. This discovery suggests

that the Ponto-Caspian mysid *P. lacustris* has managed to cross the junction canal between lakes Žeimenys and Šakarvai, and likely will be dispersing further upstream.

Information on other non-native amphipods that have reached Lithuanian inland waters through natural spread is also relevant. *Chaetogammarus ischnus* was not recorded in recently available samples, but *Chelicorophium curvispinum* was found in abundance in the Nemunas River near the town of Alytus (Figure 2).

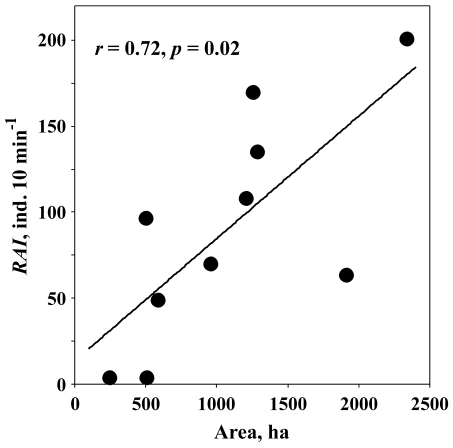

Fig. 3. Correlation between relative abundance (*RAI*) of *Pontogammarus robustoides* and the surface area of a lake or water reservoir.

Pontogammarus robustoides

Among the studied lakes and WRs (excluding Kaunas), the most favorable environment for Ponto-Caspian amphipods is probably in Lake Dusia, which is a large (area 2334 ha, maximal depth 32.4 m, mean depth 14.7 m), open mesotrophic lake with a wide, shallow littoral zone. The mean estimated relative abundance (*RAI*) of *P. robustoides* in Lake Dusia was highest among the investigated stagnant water bodies at 200 ind. per 10 min. The absolute density of this amphipod in the littoral was estimated to be up to 2700 ind. m^{-2}. In this study, estimates of the relative abundance of amphipod *P. robustoides* were obtained for two WRs and eight lakes (Lake Asveja was excluded as this species occurs there only locally), which permitted analyzing the relation between water body characteristics and amphipods. The abundance of *P. robustoides* was correlated with lake/WR area (Figure 3), while the effect of maximal depth, mean depth, water retention time, or total ion content of the water was not significant.

In Lake Asveja, the Ponto-Caspian amphipod *P. robustoides*, which was transferred to here in 1998, is not expanding across the lake. It co-occurred with the native amphipod *Gammarus lacustris* in the place of its introduction, *i.e.*, an open littoral area 50 m wide, but was not found in adjacent parts of the lake. The abundance of *P. robustoides* in the year following introduction was rather high (Figure 4). Alien and native amphipods were actually found in the same place, but in different substrates. *P. robustoides* occupied the flooded roots of

terrestrial grasses, which were inhabited by native amphipods the previous year, while *G. lacustris* was collected from submerged macrophytes and detritus. Later, the abundance of Ponto-Caspian species decreased, but *P. robustoides* survived, and usually appeared with *G. lacustris* in substrates of the same type (Figure 4).

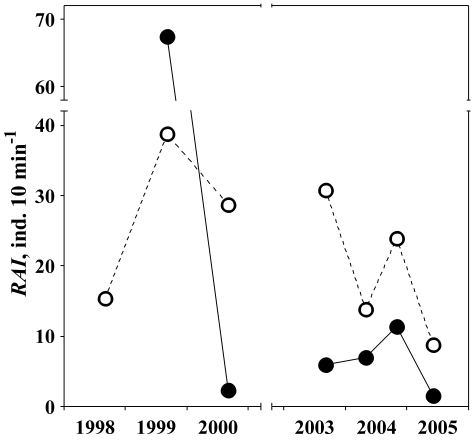

Fig. 4. Relative abundance of native amphipod *Gammarus lacustris* (open circles) and Ponto-Caspian amphipod *Pontogammarus robustoides* (closed circles) in the seven years since its introduction into Lake Asveja. Estimates indicate the abundance at the introduction site where *P. robustoides* occurs locally.

Among the other water bodies listed in Table 1, the native amphipod *G. lacustris* was noted in lakes Dysnai, Sartai, Kretuonas, Dysnykštis, Žeimenys, and Arinas (no study of littoral amphipods was conducted in Lake Lūšiai), whereas the Ponto-Caspian species *P. robustoides* was absent. The co-occurrence of these two amphipod species at the same sampling site was observed in the closed bay in southern Lake Plateliai and in the bays in the middle of the Antalieptė WR. The relative abundance of alien and native amphipods at these sites in Lake Plateliai and the Antalieptė WR was estimated at 11 vs. 4 ind. 10 min^{-1} and 4 vs. 5 ind. 10 min^{-1}, correspondingly. However, the open parts of these water bodies, where *P. robustoides* was numerous, were devoid of the native species *G. lacustris*. The abundance of the Ponto-Caspian amphipod across the open part of Lake Plateliai varied from 36 to 156 ind. 10 min^{-1}, at a mean of 70 ind. 10 min^{-1}. The range at sampling sites in the Antalieptė WR was from 50 to 87 ind. 10 min^{-1} at a mean of 64 ind. 10 min^{-1}.

DISCUSSION

Thus far, the introduced Ponto-Caspian amphipods and mysids have inhabited the Kaunas, Elektrėnai, and Antalieptė WRs and fifteen lakes (Table 1). The mysid *H. anomala* only inhabits the Kaunas WR, where it was

introduced in the 1960s and has established a viable population (Gasiūnas 1968). The mysid *P. lacustris*, which, of the introduced peracaridan crustacean species, is probably best adapted to stagnant aquatic environments, inhabits three WRs and eleven lakes, while *L. benedeni*, another mysid species, was noted in only two WRs and two lakes. Of the introduced amphipods, *P. robustoides* had the widest distribution across stagnant waters, which suggests that this species is better adapted to lacustrine environments than other non-native amphipods. *P. robustoides* was noted in three WRs and nine lakes. The amphipods *C. warpachowskyi* and *O. crassus* inhabit the Kaunas and Elektrėnai WRs and were found in seven and three lakes, respectively. Since *C. warpachowskyi* inhabits a considerable number of lakes in comparison with *P. robustoides*, it seems that it might also be well adapted to stagnant fresh waters, or at least it is better adapted than *O. crassus*.

Ponto-Caspian amphipods were introduced into all of the lakes that had been recently inhabited (Table 1), excluding lakes Seirijis and Ančia (Arbačiauskas 2002). These two lakes have no connection with lakes Dusia, Metelys, or Obelija, which are the closest lakes inhabited by non-native amphipods (Figure 2). Invasion from the Nemunas River seems unlikely as outflowing from lakes Seirijis and Ančia waters above the fall are dammed. Furthermore, these alien amphipods were not detected in the adjacent part of the Nemunas River. Therefore, Ponto-Caspian amphipods were probably intentionally transferred to at least one of these two lakes during the 1960s although no official records regarding this exist (Lazauskienė 1997).

Current research on local dispersal showed clearly that the introduced Ponto-Caspian peracaridan species are extending their ranges downstream, as was noted as early as in the first years following the establishment of their populations in the Kaunas WR (Gasiūnas 1963, 1972a). They have probably colonized the larger part of the Nemunas River below Kaunas WR. Ponto-Caspian amphipods could also disperse downstream via small rivers and streams, but the long-term survival of these crustaceans in parts of drainage systems below the source population might be restricted due to hostile environmental conditions (Figure 2). Meanwhile, the ability of the mysid *P. lacustris* to disperse upstream is certainly higher than that of the introduced amphipods. Recently, this alien mysid has occurred in the Nemunas River, at least up to the border with Belarus. It has also invaded the Ignalina lake system. In contrast, the introduced Ponto-Caspian amphipods were not recorded in the Nemunas River above the Kaunas WR (Figure 2). It should not, however, be ruled out that these amphipods may have also dispersed upstream, but were not noted due to insufficient environmental conditions for the establishment of permanent populations.

Based on previous research of the distribution of introduced Ponto-Caspian peracaridans across Lithuanian lakes, it was concluded that they can only establish viable populations in large, open lakes or in those with high water turnover rate (Arbačiauskas 2002). Gasiūnas (1970, 1972a, b) reported the acclimatization of introduced Ponto-Caspian amphipods in nine lakes. Two additional lakes were later added to the list (Lazauskienė 1997). The present author's pervious study confirmed by the current results indicated that alien amphipods had vanished from the lakes Dysnai, Sartai, Dysnykštis and Arinas (Table 1). All these are eutrophic lakes, while the most of lakes inhabited by Ponto-Caspian amphipods are described as mesotrophic. Therefore, it was also concluded that the long-term survival of Ponto-Caspian amphipods might be possible only in mesotrophic or well-drained lakes such as the eutrophic Lake Simnas with water retention time 0.6 year (Arbačiauskas 2002). Recently, alien amphipods were found in Lake Obelija, which is characterized as an eutrophic lake, but has a rather high water retention (2.8 years). The other two lakes, Seirijis and Ančia, where populations of these peracaridans were detected for the first time, are categorized as mesotrophic lakes (Table 1). Thus, it appears that the previous conclusion is still valid: the probability of Ponto-Caspian amphipods surviving long-term in mesotrophic lakes is higher than in lakes of high trophy, especially in those with low water renewal.

In eutrophic lakes, the temporary occurrence of adverse oxygen conditions in the littoral, especially during winter under ice cover, is much more probable than in mesotrophic lakes. Therefore, it was hypothesized that oxygen concentration might be the principal factor determining the survival and sustainability of populations of Ponto-Caspian amphipods in Lithuanian lakes (Arbačiauskas 2002). As is the case with most amphipods, the introduced species are considered to have high oxygen demands. According to the lethal oxygen concentrations reported by Dedyu (1980), of the Ponto-Caspian amphipods currently occurring in the inland waters of Lithuania the amphipod *P. robustoides* is the most tolerant to oxygen decreases. This corresponds well with the fact that *P. robustoides* has the widest distribution across stagnant Lithuanian waters of all the alien amphipods. This amphipod succeeded in establishing sustainable populations in only eight lakes (Table 1, Lake Asveja is discussed below) despite attempts to transfer it into a large number of lakes. The native amphipod species *G. lacustris* is widely distributed throughout Lithuanian lakes and lives in most of the lakes in which *P. robustoides* did not survive after being transferred (Arbačiauskas 2002, unpubl. results). The native amphipod is common in eutrophic lakes and occurs in low numbers even in lakes overgrown with macrophytes such as Lake Kretuonas, where drastic drops in oxygen concentration occur, especially during winter. Consequently,

G. lacustris should be more tolerant to low oxygen concentrations than *P. robustoides*. According to Dedyu (1980), *G. lacustris* is less tolerant to low oxygen than *P. robustoides* (lethal oxygen concentrations 0.330 vs. 0.209 mg O_2 L^{-1}, respectively) and even less so than all other Ponto-Caspian amphipods occurring in Lithuanian waters. However, this must not be true of the *G. lacustris* from Lithuanian waters. This amphipod species is distributed widely across the Palearctics and has also been reported to be highly resistant to oxygen deficiency and a common inhabitant of winterkill water bodies (Safronov and Erbajeva 1993). Pennak and Rosine (1976) measured the oxygen death point of *G. lacustris* to be 0.08 and 0.12 mg O_2 L^{-1} at 3 and 28°C, respectively, and interpreted these as an ecological advantage, especially during periods of ice and snow cover when dissolved oxygen drops drastically.

The current study also indicated that the mysid *P. lacustris* had disappeared from Lake Kretuonas. This certainly occurred due to the dramatically increasing eutrophication that has caused the macrophyte overgrowth in this lake and the consequent deterioration of oxygen conditions. Thus, progressing eutrophication in a lake might be disastrous even for the mysid *P. lacustris*, which is more tolerant to decreased oxygen than Ponto-Caspian amphipods (Komarova 1991).

The established correlation between the area of a water body and the abundance of the amphipod *P. robustoides* (Figure 3) suggests that, in general, for introduced Ponto-Caspian amphipods the quality of the environment improves as the area of the lake increases. This favors higher population densities. The importance of lake size for alien amphipods is most probably mediated by oxygen. Due to wind-drifted water motion, the littoral waters of large lakes, especially open ones with a wide, shallow littoral, contain high concentrations of dissolved oxygen that must favor Ponto-Caspian amphipods. Lake Dusia, where the highest abundance of *P. robustoides* was observed, is one such water body.

The establishment of a population of *P. robustoides* in Lake Asveja is progressing with difficulty, and the fate of this alien species seven years following its introduction remains uncertain. It still only occurs locally at low abundance (Figure 4). In contrast, Gasiūnas (1970, 1975) declared the establishment of Ponto-Caspian amphipods in Lake Dusia as fully successful three years following introduction. However, he has also indicated that the duration of the establishment of populations of introduced peracaridans may vary among lakes.

According to official records, large batches of *P. robustoides* were transferred into Lake Asveja during 1995-1998, but only the last batch taken from Kaunas WR during the late season was effective. Lake Asveja is the

product of glacial scouring that created a large basin that is long and deep with a water retention time 2.2 years. It still harbors an abundant population of the glacial relict mysid *Mysis relicta* (Arbačiauskas, unpubl. results), which means that oxygen conditions in Lake Asveja should be sufficient for the Ponto-Caspian amphipod *P. robustoides*. Chemical analysis has indicated that the total ion and calcium-ion contents of the water in Lake Asveja are even higher than those in Lake Dusia and Lake Daugai, which are inhabited by numerous populations of the introduced Ponto-Caspian amphipods (Table 2). In contrast to these lakes, the concentration of kalium, natrium, sulphate, and chloride ions in Lake Asveja is substantially lower by about twofold. The values of the content of these ions in the water of Lake Asveja are close to those in Lake Plateliai (Table 2), which was recently also abundantly populated by the alien amphipod *P. robustoides*.

Table 2

Ion content of water (mg L^{-1}) in lakes Asveja, Plateliai, Dusia, and Daugai. The ranges of total ion content from Kavaliauskienė (1996) are in brackets.

Lakes	K^+	Na^+	Mg^{2+}	Ca^{2+}	SO_4^{2-}	Cl^-	Total ion content
Asveja	1.9	4.5	16.6	57.6	11.4	5.5	338
Plateliai	1.6	3.4	5.0	40.1	9.0	6.0	185 (160-202)
Dusia	3.0	7.7	17.7	44.8	28.3	13.9	296 (216-331)
Daugai	2.8	9.6	13.2	54.0	25.4	15.0	310 (249-322)

Although the establishment and expansion of a population of *P. robustoides* in Lake Plateliai was not documented in detail, it seems that this process was difficult and slow. The transfer of Ponto-Caspian amphipods into this lake in 1964 was repeated in 1968 (Lazauskienė 1997). During 1989, *i.e.*, 25 years following the introduction of *P. robustoides*, Grigelis (unpubl. results) still found an abundant population of the native amphipod *G. lacustris* in the open part of Lake Plateliai. The density of it near the island located some 400 m offshore was estimated at 120 ind. m^{-2} and 7.2 g m^{-2}. During 1998, however, the native amphipod species was absent from the open part of that lake, although it still survived in the closed bay, where recently it was noted to co-occur with the alien species. In conclusion, the conquest of Lake Plateliai by the Ponto-Caspian amphipod *P. robustoides* was slow; the ion content of the water might have been responsible for this. The difficulty *P. robustoides* is having establishing a population in Lake Asveja under pressure from native amphipod species might also be related to the same reason. The ion content and other physicochemical characteristics of the water have been found to be important

for the competitive ability of amphipod species (MacNeil *et al*. 2000, Vijnhoven *et al*. 2003). Furthermore, it has been suggested that for amphipods not only are the absolute values of different ion contents significant, the ratio between metal ions might also be important (Dedyu 1980). Nevertheless, the Ponto-Caspian amphipod *P. robustoides* has successfully adapted to the water properties of Lake Plateliai, where the natrium-ion concentration in the water is fivefold lower in comparison to the lower natrium-ion threshold concentration suggested for this species in the eastern Gulf of Finland (Berezina and Panov 2003). For the other introduced Ponto-Caspian amphipod species, however, survival in lacustrine environments may be determined by low-oxygen resistance as well as by physiological tolerance to low levels of certain ions in the lake water.

Of the eight lakes that have been inhabited by the Ponto-Caspian amphipod *P. robustoides* since the 1960s (Table 1), the native amphipod species *G. lacustris* was only noted in Lake Plateliai. It was also found in the Antalieptė WR, which was formed after the flooding of a few lakes. In both these water bodies native and non-native amphipods recently co-occurred only in bays where the abundance of *P. robustoides* was low, while the open parts of Lake Plateliai and the Antalieptė WR, which are abundantly populated by alien species, were devoid of *G. lacustris*. A drastic decrease in the abundance of native amphipods following the introduction of Ponto-Caspian amphipods was noted previously in Lake Dusia (Gasiūnas 1975). All of these data definitely suggest the competitive exclusion of the native amphipod *G. lacustris* by the alien species *P. robustoides* in habitats which sustain abundant populations of the newcomers (Arbačiauskas 2002). Intraguild predation, which is often a biotic interaction among amphipod species when they clash over a habitat (Dick 1996, Dick and Platvoet 2000, Berezina and Panov 2003), seems to be responsible for the competitive replacement of native species. The coexistence of the Ponto-Caspian amphipod *P. robustoides* and the native species *G. lacustris* could possibly occur only in an environment which suppresses, at least spatially or temporarily, increases in the number of alien species. The environment in the closed bays of lakes, where adverse oxygen conditions for *P. robustoides* regularly occur, especially in winter, might favor the survival of both native and non-native amphipods.

The introduced Ponto-Caspian amphipods and mysids most certainly also interact with other native peracaridan species. The isopod *Asellus aquaticus* occurs in all the lakes which the introduced crustaceans have recently inhabited (Table 1). Among these water bodies, lakes Lūšiai, Žeimenys, Dusia and Asveja were still inhabited until 2003 by the glacial relict species *M. relicta* and *Pallasiola quadrispinosa* (Arbačiauskas, unpubl. results). Due to the lack of

available data, comparing the state of native Peracarida before and after the invasion of aliens is possible only for lakes Plateliai and Dusia.

Prior to the introduction of Ponto-Caspian amphipods, Gasiūnas (1958) wrote that of the fifty commercial lakes of Lithuania known to him, Lake Plateliai harbored the most abundant population of the isopod *A. aquaticus*. He estimated its density in the littoral among macrophytes (*Elodea* sp. and *Fontinalis* sp.) at 1466 ind. m^{-2}. This, however, is not the case today. Native isopods occur in abundance only in the closed bay of Lake Plateliai, where, during 2004, its density in the littoral was at a mean of 792 ind. m^{-2}, although it was absent in quantitative samples from the open part of that lake (Gumuliauskaitė, unpubl. data). The specimens of *A. aquaticus*, however, occurred in littoral catches made with drags. In Lake Dusia, *A. aquaticus* was common in the shallow waters of the littoral (Gasiūnas 1957), but about ten years after the introduction of non-native species it was often only in the bay overgrown with macrophytes (Gasiūnas 1975). During 1999-2004, this native isopod was absent in the shallow waters of the littoral, or at least from samples collected in the open part of the lake. It appeared in low numbers only in samples collected with drags from depths of 3 -10 m that usually contained *Chara aspera*. At these depths, the abundance of *P. robustoides* was substantially lower than that from the higher littoral zone. Thus, recent data in comparison to previous observations unambiguously suggest the negative effect the Ponto-Caspian amphipod *P. robustoides* has on the native isopod *A. aquaticus*, which is probably related to direct predation by the former.

The relict mysid *M. relicta* was abundant in Lake Dusia even after the introduction and establishment of a population of the Ponto-Caspian mysid *P. lacustris*. In the early season during isothermy, both mysid species occurred in similar numbers from depths of 2 to 17 m. During the summer thermal stratification, the glacial relict mysid was numerous at depths below 17 m, while the alien mysid inhabited shallower waters (Gasiūnas 1975). Recently, however, the abundance of *M. relicta* fell drastically, and single specimens of relict mysid occurred rarely in samples collected with sledge nets or drags from depths of 12 to 15 m during the summer. When compared with previous data (Gasiūnas 1975), the abundance of the amphipod *P. quadrispinosa* has also recently decreased in relation to that of the Ponto-Caspian amphipod C. *warpachowskyi*, which prefers the lower littoral of Lake Dusia and has overlapped spatially with the glacial relict amphipod (Arbačiauskas, unpubl. results). Although the increasing trophy of Lake Dusia is probably involved, the negative impact of alien species on native species seems very probable. Interactions between Ponto-Caspian and glacial relict peracaridan species certainly warrant additional research and analysis. A study that addresses this has recently been undertaken.

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