Aquatic Invasions (2012) Volume 7, Issue 2: 211–218
doi: http://dx.doi.org/10.3391/ai.2012.7.2.007

Research Article

Two morphotypes of the New Zealand mud snail *Potamopyrgus antipodarum* (J.E. Gray, 1843) (Mollusca: Hydrobiidae) invade Lithuanian lakes

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Received: 8 August 2011 / Accepted: 21 December 2011 / Published online: 28 December 2011

Abstract

The New Zealand mud snail, *Potamopyrgus antipodarum*, was found in four lakes and one medium-sized river located in the southern part of Lithuania during 2010. These are the first records of *P. antipodarum* from Lithuanian freshwaters, a considerable distance from the Curonian Lagoon wherein the species was reported during the 1950s. Available information shows that the species has invaded quite recently. Two morphotypes of the species, the regular and carinatus (keeled) forms, were observed in three lakes. The presence of separate morphotypes and variation in shell morphometry suggest multiple (at least two) independent invasion events, and species expansion on a local scale. The most abundant population of the invasive snail was recorded in Lake Dusia which is an inland lake of exceptional importance for staging and moulting of migratory waterfowl. Thus, the most probable vector of the invasion and local dispersal is ornithochory, while translocation with fish stocking material may also be operating. Further rapid expansion of the species in Lithuanian lakes and rivers seems very possible.

Key words: *Potamopyrgus antipodarum*, morphotypes, morphometry, invasion, freshwaters, Lithuania

Introduction

The mud snail, *Potamopyrgus antipodarum* (J.E. Gray, 1843), is a prosobranch gastropod with a small conical shell of height up to 7 mm originating from New Zealand (Cianfanelli et al. 2007). Recently *P. antipodarum* has become among the most widespread non-indigenous aquatic invertebrates in the world, and now occurs in Europe, Asia, North America, and Australia. In the 19th century, it was transferred from New Zealand to European waters by shipping, probably in tanks with fresh or ballast waters (Ponder 1988). In Europe, only Iceland and a few countries in Southern Europe (Albania, Bulgaria, and former Yugoslavia) have no records of its presence (Cianfanelli et al. 2007 and references therein; Radea et al. 2008; Son 2008).

Many native *P. antipodarum* populations contain both obligately sexual dioecious individuals and obligately parthenogenetic females (Nelson et al. 2011). However, non-indigenous populations mainly consist of parthenogenetic females, and males are very rare or even absent. Due to reproduction mode, invasive populations can build rapidly to extremely large sizes, up to 800,000 ind. m^{-2} (Kerans et al. 2005), consisting of one or a few parthenogentic lineages (Dybdahl and Drown 2011).

For the first time *P. antipodarum* was detected in the Baltic Sea during 1887 (Nikolaev 1951). In Lithuanian inland waters, the species was first recorded in the Curonian Lagoon in 1954 (Gasiūnas 1959). Later it was recorded to occur in the outskirts of the lagoon and the Baltic Sea (Šivickis 1960a, 1960b) and more recently has been reported again to be present in the Curonian Lagoon and to occur in the Nemunas River Delta (Zettler et al. 2005; Zettler and Daunys 2007).

P. antipodarum inhabits various freshwater bodies in Poland and Belarus (Strzelec et al. 2005; Zbikowski and Zbikowska 2009 and references therein; Semenchenko et al. 2009), therefore, its occurrence in Lithuanian freshwaters at a location distant from the Baltic Sea and the Curonian Lagoon has been expected (Arbačiauskas et al. 2011). This prediction was confirmed by the current study. Moreover, two morphotypes of the mud snail, with and without a haired keel on shell whorls (referred below as the carinatus and regular morphotypes, respectively), were observed in lakes. In this work, we provide information on new *P. antipodarum* localities and species abundance, collate characteristics of invaded and non-invaded studied lakes testing if species establishment is associated with lake attributes, compare morphometry of detected morphotypes, and analyse possible vectors of the species invasion.

Material and methods

Two surveys, a study of littoral macro-invertebrate communities of 16 lakes and a study of molluscan assemblages in five rivers outflowing from lakes (including one lake, Lake Vilkokšnis), were performed during September and October in 2010. Both surveys included quantitative sampling by a stovepipe sampler (cross-sectional area 0.1 m^2) and a frame (area 1 m^2), respectively. Similar as possible littoral habitats in the lakes (sandy or stony bottom frag-mentally (≤10%) overgrown with macrophytes: *Potamogeton* sp., *Chara* sp. or *Phragmites australis* (Cav.) Trin. ex Steudel were sampled. In rivers, quantitative samples were collected from sandy or stony substrates occasionally with some macrophytes present. Three replicates were taken at each study site. This data was used to assess species absolute abundance. In the lake survey, macroinvertebrate biomass was also estimated.

An additional semi-quantitative sampling procedure, similar to that described by O'Hare et al. (2007), was applied in the lake study. Using a standard dip-net, two samples were collected from two core eulittoral mesohabitats of each lake: a bottom (preferably hard) kick sample and a vegetation (preferably submerged) sweep sample. Within a stand of each mesohabitat, a stretch of about 15-20 meters long was sampled while moving along the shore in a trajectory of a zigzag curve (from the shoreline to a depth of 1 m) within a period resulting in a 3 minute (actual) sampling time (O'Hare et al. 2007). In the river survey, a timed semi-quantitative sampling of major habitats was also applied. These data sets provided species relative abundance estimated as catch per timed sampling effort.

Integrated water samples, from the surface and depths of half, one and double Secchi depths, were taken in each lake to assess concentrations of chlorophyll *a*, and total nitrogen and phosphorus. Similar characteristics for Lake Vilkokšnis during early autumn were measured in 2009 (data from Environment Protection Agency, Lithuania). Morphometric features of *P. antipodarum*, such as shell height and width, as well as height and width of an aperture were measured to the nearest 0.1 mm for all sampled specimens of the carinatus morphotype, and thirty random specimens of the regular morphotype in all invaded water bodies. Shell width to height (SW/SH) and aperture height to shell height (AH/SH) ratios were utilised as characteristics of shell shape.

A logistic regression was applied for a multiple test of proportions of morphotypes between invaded water bodies (Sokal and Rohlf 1995) using the *glm* function in R (R Develop-ment Core Team 2011). Lake characteristics were compared using non-parametric Kruskal-Wallis test. Since shell morphometry data were normally distributed, ANOVA tests, planned comparison and post-hoc Tukey HSD and Unequal N HSD tests, were applied with analysis performed with StatSoft's Statistica 8.0 software.

Results

Localities and abundance

In the study of lake littoral macroinvertebrate communities, *P. antipodarum* was detected in three of 16 lakes, lakes Daugai, Dusia and Metelys (Figure 1). Among investigated rivers, the species was recorded in the Verknė River, at two of five study sites, which were the closest to the source-lake. Further investigation also revealed the presence of *P. antipodarum* in the source-lake Vilkokšnis (Figure 1). The major features of invaded lakes are provided in Table 1. The Verknė River (similarly to three of four other studied rivers) is characterised as a medium-sized warm-water river with 77.1 km length, 5.05 m^3s^{-1} annual discharge, and 728 km^2 drainage area (Gailiušis et al. 2001). If a comparison is made between the main characteristics of the invaded lakes and the uninvaded ones, differences are absent. For example, surface area, mean depth and chlorophyll *a* concentration (mean ± SD) of invades and uninvaded lakes were 1218.8 ± 841

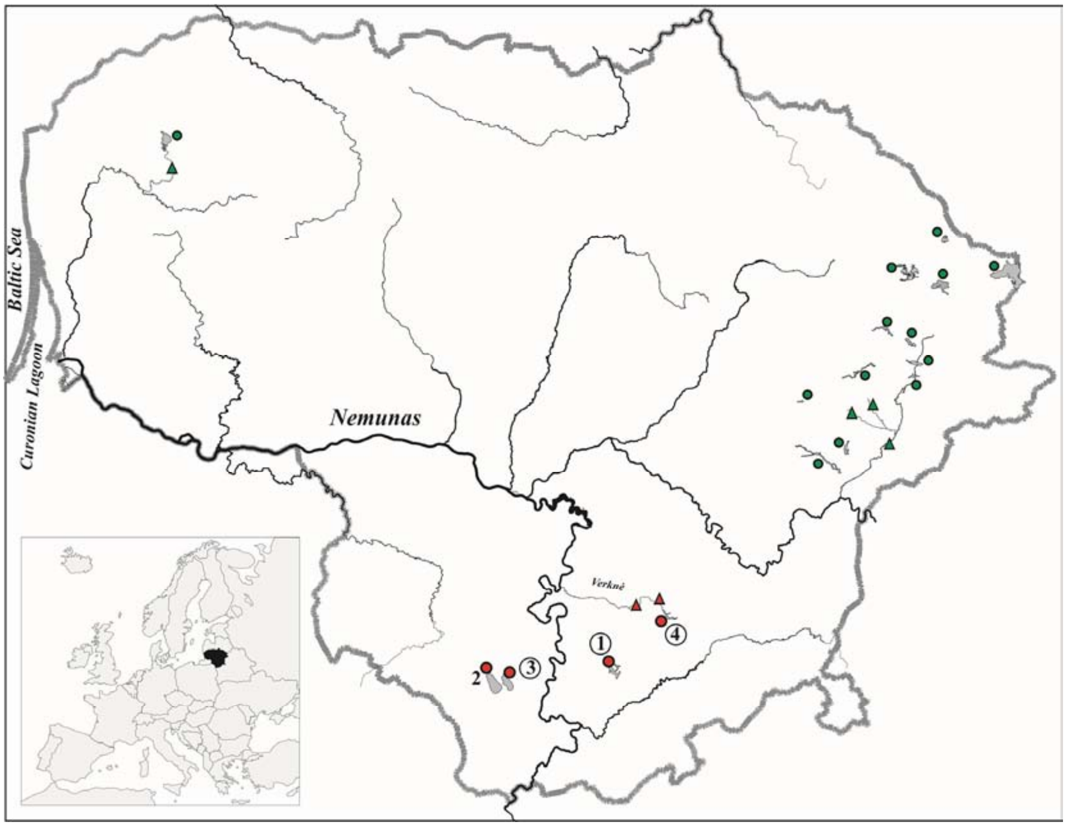

Figure 1. Location of studied lakes (circles) and rivers (triangles) inhabited by the New Zealand mud snail *Potamopyrgus antipodarum* (red) and devoid of the species (green). *P. antipodarum* was recorded in lakes Daugai (1), Dusia (2), Metelys (3) and Vilkokšnis (4), and two study sites in the Verknė River. NB Encircled numbers indicate localities with two species morphotypes.

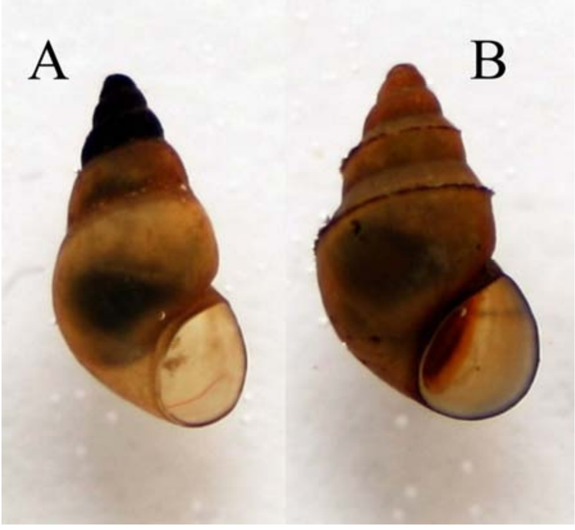

Figure 2. Regular (**A**) and carinatus (**B**) morphotypes of *Potamopyrgus antipodarum* from Lake Vilkokšnis.

vs. 871 ± 947 ha, 10.6 ± 4.3 *vs*. 11.3 ± 3.6 m, 6.6 ± 3.8 *vs*. 5.4 ± 3.4 µg L^{-1}, correspondingly, with no significant difference between lake groups (Kruskal-Wallis tests, KW-H(1,17) ≤ 1.04, P ≥ 0.31). Thus, in terms of the lake parameters, water bodies invaded by *P. antipodarum* only differ from the others in their geographical location: they are situated in the southern part of the country whilst uninvaded water bodies are located in other Lithuanian parts (Figure 1).

Two morphotypes of the mud snail, the regular and carinatus forms (Figure 2) were observed in three lakes: Daugai, Metelys and Vilkokšnis (Figure 1). The proportion of the carinatus morphotype in lakes Daugai and Vilkokšnis was the same, but significantly larger than that in Lake Metelys (Table 2; logistic regression: Vilkokšnis vs. Daugai, z = –0.03, P = 0.98; Vilkokšnis vs. Metelys, z = 3.61, P < 0.001).

Table 1. Location of lakes and river study sites where *Potamopyrgus antipodarum* was recorded, and major lake characteristics: surface area (A, ha), maximum depth (H_m, m), average depth (H_a, m), chlorophyll *a* (Chl *a*, µg L^{-1}), total nitrogen (N_T, µg L^{-1}), and total phosphorus (P_T, µg L^{-1}).

Water body	Latitude, N	Longitude, E	A	H_m	H_a	Chl *a*	N_T	P_T
Lake Daugai	54°18'53.69"	24°22'51.61"	911	44	13.2	4.55	928	29
Lake Dusia	54°19'32.85"	23°40'36.75"	2334	33	15.4	2.86	718	22
Lake Metelys	54°18'18.00"	23°44'53.68"	1290	15	6.8	11.64	1009	36
Lake Vilkokšnis	54°30'17.19"	24°40'13.98"	336	24	7.1	7.40	352	24
Verknė River (1)	54°32'24.83"	24°38'23.50"						
Verknė River (2)	54°33'14.89"	24°30'56.99"						

Table 2. Abundance and composition of *Potamopyrgus antipodarum* populations: number of sampled specimens (N_S), proportion of carinatus form (Pro, %), absolute density (N, mean±SD, ind. m^{-2}), relative abundance (N_R, ind. min^{-1}), biomass (B, g m^{-2}) and its share in total macroinvertebrate biomass (Sh, %).

Water body	Date	N_S	Pro	N	N_R	B	Sh
Lake Daugai	09.09.10	48	23.08	3.3±5.8	7.8	0.034	0.28
Lake Dusia	09.10.10	2029	0	816.7±680.8	297.3	5.395	49.99
Lake Metelys	09.10.10	181	0.56	20.0±17.3	29.2	0.234	0.40
Lake Vilkokšnis	25.09.10	124	22.77	41.3±23.3	26.3		
Verknė River (1)	25.09.10	42	0	14.0±6.1	14.0		
Verknė River (2)	25.09.10	162	0	54.0±26.0	0		

Table 3. Shell morphometry (mean ± SD) of regular (Re) and carinatus (Ca) morphotypes of *Potamopyrgus antipodarum*: shell height (SH, mm) and width (SW, mm), aperture height (AH, mm) and width (AW, mm), and ratios SW/SH and AH/SH characterising shell shape. NB In Lake Metelys only one specimen of carinatus morphotype was detected (SH, SW, AH and AW were 3.6, 2.0, 1.5 and 1.3 mm, correspondingly).

Water body	Morphotype	SH	SW	AH	AW	SW/SH	AH/SH
Lake Daugai:	Re	3.44±0.74	1.92±0.34	1.49±0.26	1.12±0.20	0.56±0.04	0.44±0.03
	Ca	3.71±0.62	2.03±0.37	1.57±0.23	1.14±0.15	0.55±0.05	0.42±0.04
Lake Dusia:	Re	4.16±0.67	2.28±0.37	1.59±0.25	1.26±0.19	0.55±0.03	0.38±0.03
Lake Metelys:	Re	4.24±0.48	2.33±0.29	1.73±0.22	1.35±0.28	0.55±0.06	0.41±0.05
Lake Vilkokšnis:	Re	3.37±0.72	1.96±0.34	1.40±0.22	1.12±0.19	0.59±0.06	0.43±0.07
	Ca	4.25±0.44	2.44±0.24	1.91±0.15	1.33±0.13	0.57±0.04	0.45±0.05
Verknė River	Re	3.29±0.71	1.91±0.34	1.35±0.22	1.10±0.22	0.59±0.06	0.42±0.07

The highest abundance of *P. antipodarum* was recorded in Lake Dusia, where its absolute density exceeded 800 ind. m^{-2} and relative abundance was at 300 ind. min^{-1}. In this lake, the mud snail constituted half of the macro-invertebrate biomass (Table 2). The lowest abundance, at 3 ind. m^{-2}, and proportion in biomass below 0.3%, were observed in Lake Daugai, whilst in other invaded localities, the absolute density varied between 14 and 54 ind. m^{-2}, and relative abundance was up to 30 ind. min^{-1} (Table 2).

Shell morphometry

The results of morphometric measurements of shells are shown in Table 3. When comparing the sizes of the two morphotypes, the carinatus form was larger in Lake Vilkokšnis while the difference was not observed in Lake Daugai (Figure 3). The shell shape did not differ between the morphotypes in these lakes (two-way ANOVAs: morphotype effect on ratios of shell width to height (SW/SH) and aperture height to shell height (AH/SH), $F_{1,88} \leq 1.58$, $P \geq$

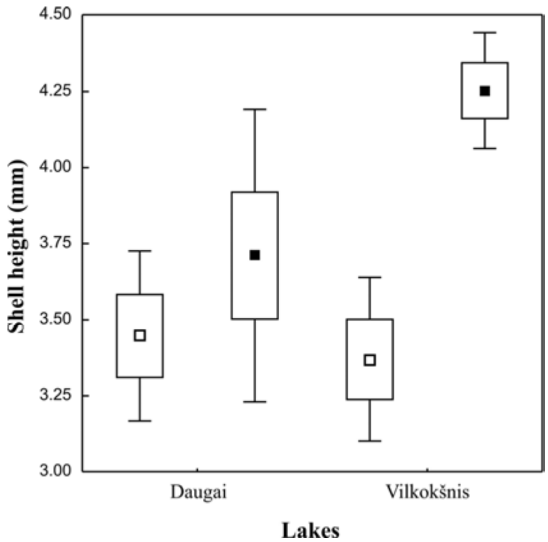

Figure 3. Shell height (mean, SE, 0.95 CI) of regular (open squares) and carinatus (closed squares) morphotypes of *Potamopyrgus antipodarum* in lakes Daugai and Vilkokšnis. Difference between morphotypes was significant in Lake Vilkokšnis (two-way ANOVA: morphotype effect, $F_{1,88}$ = 13.8, P < 0.001; difference for lakes Daugai and Vilkokšnis, Unequal N HSD post-hoc tests, P = 0.8 and P < 0.001, correspondingly).

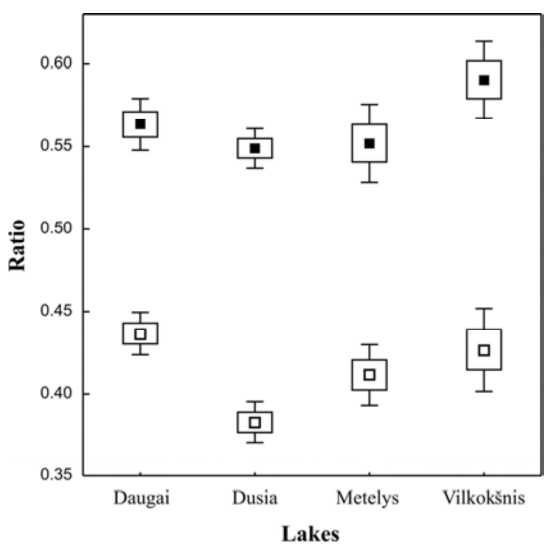

Figure 4. Ratio (mean, SE, 0.95 CI) of shell width to shell height (closed squares) and aperture height to shell height (open squares) for regular morphotype of *Potamopyrgus antipodarum* from studied lakes. The widest shell was observed in Lake Vilkokšnis (one-way ANOVA: lake effect, $F_{3,116}$ = 4.0, P = 0.009; difference from lakes Daugai, Dusia and Metelys, Tukey HSD post-hoc tests, P = 0.18, P = 0.012 and P = 0.024, correspondingly), while relatively small aperture was typical for Lake Dusia (lake effect, $F_{3,116}$ = 7.1, P < 0.001; difference from lakes Daugai, Metelys and Vilkokšnis, Tukey HSD post-hoc tests, P < 0.001, P = 0.10 and P = 0.003, correspondingly).

0.21). The shell height and shape of the regular morphotype in Lake Vilkokšnis and its outflow, the Verknė River, were the same (Table 3; one-way ANOVAs: water body effect, $F_{1,63} \leq 0.18$, P ≥ 0.67).

The comparison of the regular form between the lakes showed that mud snails in lakes Dusia and Metelys had a higher shell than those in lakes Daugai and Vilkokšnis (Table 3; one-way ANOVA: lake effect, $F_{3,116}$ = 14.6, P < 0.001, Tukey HSD post hoc tests, P < 0.001). Further we tested by the planned comparison if shell shapes differed between these lake groups. In lakes Daugai and Vilkokšnis, the mud snails were relatively wider ($F_{1,116}$ = 7.9, P = 0.006), and had a relatively larger aperture ($F_{1,116}$ = 15.4, P < 0.001). The widest shells were observed in Lake Vilkokšnis, while the smallest aperture was a characteristic of the mud snail from Lake Dusia (Figure 4).

Discussion

The invasive species, *Potamopyrgus antipodarum*, was found in four Lithuanian lakes and one medium-sized river for the first time. The estimated abundance of *P. antipodarum* in Lake Dusia indicates that the species is well-established, highly abundant and comprises almost half of the macroinvertebrate biomass, and that suggests that the invasion may have occurred a substantial time ago. However, investigations performed during 2003-2006 in the same lake applying the same sampling method did not detect the species (Gumuliauskaitė 2007). Moreover, the samples of littoral macroinvertebrates collected at the same study site in Lake Daugai during 2009 and 2010 showed that the species was absent in the first year (Šidagytė unpubl. results), but was recorded in considerable numbers in the second year, as an exponential growth of invasive species following its invasion is to be expected (Arim et al. 2006). Consequently, quite recent invasions of *P. antipodarum* can be anticipated.

Shell morphology of *P. antipodarum* has been reported to be extremely variable and dependent upon environmental variables (Haase 2003). It is known that parthenogenetic (clonal) populations of *P. antipodarum* undergo both sexual and clonal reproduction in their native range, and the genotypic diversity of such clonal populations is very high (Dybdahl and Lively 1995; Dybdahl and Drown 2011). However, bi-parental reproduction in invasive populations is very rare or even absent. For this reason, invasive clonal lineages are relatively stable. On the basis of shell shape and intensity of pigmentation, three main morphological strains have been described in the United Kingdom (Warwick 1969). Later molecular studies have revealed that these morphological strains represent three distinct clonal genotypes with low levels of genotypic diversity within these obligate parthenogenetic lineages (Hauser et al. 1992; Weetman et al. 2002).

In Lithuania, two morphotypes of *P. antipodarum* have been found in the Curonian Lagoon and in the outskirts of the Baltic Sea (Šivickis 1960a): the regular and carinatus forms. As these morphotypes depend upon genetic difference, at least two introductions of the species must have occurred. The same morphotypes have been recorded in Lithuanian lakes during this study. In comparison to shell metrics measured in the Curonian Lagoon and the Baltic Sea (shell height and width 4.8 and 2.2 mm, ratio of width to height 0.46; Šivickis 1960a), the specimens of *P. antipodarum* in lakes and a medium-sized river were smaller in size but relatively wider (Table 3). When collating the variation in shell morphometry of the regular morphotype between the invaded localities, we observed a considerable variance. Although there was no difference in shell size and shape between Lake Vilkokšnis and its outflow, the Verknė River, i.e. habitats with differing environmental variables which are probably invaded by the same parthenogentic strain of the regular morphotype, the variation was obvious over the invaded lakes. Such a variation in shell features can be the result of lake-specific environmental impacts, however, an invasion of different clonal lineages may not be discarded. If the latter is true, then multiple introductions of the mud snail from different source localities seem most probable.

Such an invasion pattern can be firstly associated with ornithochory, the long-distance translocation by birds. This supposition is confirmed by the fact that the most abundant population of *P. antipodarum* currently inhabits Lake Dusia. This lake is the most important Lithuanian inland lake for staging and moulting of waterfowl during seasonal migrations (Stanevičius et al. 2008). Although the major characteristics monitored between lakes invaded by *P. antipodarum* and devoid of the species did not differ in our study, the exceptional importance of Lake Dusia for migratory waterfowl is predicated by its wide littoral zone, which enables effective feeding (ibid.). Therefore, large shallow lakes, or large lakes with a wide littoral zone, that attract waterfowl during migrations, may be subjected to a larger propagule pressure of the mud snail. Specimens of *P. antipodarum* may be transferred with mud attached to bills or legs of birds, or even inside the guts of fish and birds (Aarnio and Bonsdorff 1997; Alonso and Castro-Diez 2008). Ornithochory was suggested to be primarily responsible for the species rapid expansion in Northern Europe and the Azov-Black Sea region (Lassen 1978; Son 2008). Translocation by birds may be indeed an effective way of *P. antipodarum* dispersal, as parthenogenetic reproduction is a characteristic of this species, and a single specimen can start a population at a new locality.

Concerning other invasion vectors, commercial fishing in lakes where *P. antipodarum* has been detected during this study is currently rather occasional or absent (information from Fishery Department under the Ministry of Agriculture, Lithuania), while accidental transference by recreational boats or other devices between these lakes is unlikely. Therefore, although another possible vector of invasion may be translocation with commercial fish stocking material, this does not seem of major importance.

It is of interest that *P. antipodarum* shell features were more similar between neighbouring lakes, and carinatus morphotype was actually abundant in only two lakes located closer to each other. Although our sample of invaded lakes is too small to draw a firm conclusion, such a pattern may suggest a primary invasion from a distant locality and a subsequent secondary expansion from established populations on a local scale, probably by means of ornithochory.

What impacts on resident ecosystems due to invasion of *P. antipodarum* may be predicted? With respect to feeding mode, *P. antipodarum* belongs to the scrapers/grazers group (Cummins and Klug 1979). It mainly consumes plant and animal detritus, and can graze on green algae and diatoms (Radea et al. 2008). These mud snails can attain extremely high density and biomass due to their ecological plasticity and high demographic potential associated with propensity to parthenogenetic reproduction (Kerans et al. 2005; Radea et al. 2008; Nelson and Neiman 2011). Although the establishment and abundance of the species depend upon water body-specific properties and environmental variables (Kolosovich et al. 2012; Moffitt and James 2012), in some places the density of *P. antipodarum* can reach hundreds of thousands of individuals per square metre (Kerans et al. 2005). The mud snail can comprise up to 80% of the macroinvertebrate biomass and consume up to 75% of the gross primary production (Hall et al. 2003; Hall et al. 2006; Bersine et al. 2008). Consequently, *P. antipodarum* may have a dramatic effect on community structure and ecosystem function in invaded waters.

In conclusion, the New Zealand mud snail, *P. antipodarum*, has invaded the freshwaters of the southern Lithuania quite recently. Multiple introductions of the species, at least independent introductions of the two morphotypes, by means of ornithochory seem most probable. Rapid expansion of this invasive mud snail over Lithuanian lakes and rivers due to possible further primary introductions from distant localities and secondary introductions on a local scale can be definitely expected in the nearest future. Because of the high demographic potential, the species may attain high densities at some new localities, and subsequently induce a significant change of resident macroinvertebrate assemblages and ecosystems. Future spread of *P. antipodarum* and its impacts on native biota will require further investigations.

Acknowledgements

This study was supported by the Research Council of Lithuania, Project No. LEK-18/2010. We are grateful to Michael L. Zettler for the confirmation of the species identification, and anonymous referees for valuable comments.

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