Research Article

Experimental evidence that the invasive snail *Potamopyrgus antipodarum* (Gray, 1843) survives passage through the digestive tract of common riverine fish

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Abstract

Potamopyrgus antipodarum is one of the most widespread invasive species worldwide and its expansion is ongoing. Although the snail has already been documented as surviving the digestive tract of various fish, there is insufficient data on potential riverine fish predators of *P. antipodarum* and of the ability of the snail to survive digestion by these fish. Lotic ecosystems are unfavourable for the upstream spread of this species by active movement and thus it is suspected that benthivorous riverine fish facilitate such upstream dispersal. In general, the results of this study indicated that *P. antipodarum* is not a preferable food object for the studied riverine fish. The study did indicate, however, that the invasive snail is capable of surviving the digestive tract of all the studied fish. As accidental consumption of abundant *P. antipodarum* with other food objects has already been documented, this study suggests that riverine fish can act as potential secondary dispersion vectors, facilitating the upstream dispersion of the snail.

Introduction

Throughout many parts of the world, lotic or running water ecosystems have been invaded by a variety of non-indigenous plant and animal taxa. Due to their connections with other aquatic habitats, such as lakes, streams and lagoons, these ecosystems are susceptible to non-native species. However, running waters are generally unfavourable for the active spread for most of these organisms, particularly in the upstream direction. Accelerating the dispersion of the various aquatic invaders, a variety of human- and non-human-mediated vectors have been documented in such ecosystems (Holmlund 2014; Green 2016; Coughlan et al. 2017 and others).

Potamopyrgus antipodarum (Gray, 1843) is a prosobranch snail native to New Zealand (Winterbourn 1970). In recent years, it has become one of the most widespread invasive aquatic species in the world and further rapid expansion is still ongoing (Radea et al. 2008; Son et al. 2008; Butkus et al. 2014 and others). The snail has been introduced and has established

in a wide range of aquatic ecosystems, including running waters (Ponder 1988; Bowler 1991; Alonso and Castro-Diez 2008; Davidson et al. 2008). Among the lotic habitats in which it has been recorded are streams flowing out from lakes, stream riffles, drainage ditches, high-elevation temperate streams, coastal waterways, Mediterranean-climate streams and cold water springs (Schreiber et al. 2002; Hall et al. 2003; Brown et al. 2008; Brenneis et al. 2011; Son et al. 2008; Butkus et al. 2014 and others). In these ecosystems, snail densities vary from scattered individuals in streams flowing out from lakes to extremely high densities of up to 500,000 ind. m^{-2} observed in productive streams (Hall et al. 2006; Butkus *personal observation*). Dispersion in lotic waters is frequently mediated by both active and a number of passive dispersion vectors. Due to their small individual size (shell length up to 6–7 mm), the active spread of invading snails is slow in running waters. A study by Haynes et al. (1985) showed that *P. antipodarum* demonstrate positive rheotactic behaviour, while Zaranko et al. (1997) found that the snail can move upstream by up to 60 m over a period of three months. However, with current distribution patterns showing that the species is frequently recorded in a very short timespan at considerable distances from initial introduction points (Butkus et al. 2014, Butkus and Vaitonis 2019), it is likely that secondary dispersion vectors facilitate the spread of the invaders. According to previous studies, the transfer of *P. antipodarum* by human carriers, such as during water recreation, is one of the most significant agents in the dispersal of this invader in some areas (Richards et al. 2004; Holmlund 2014; Butkus and Vaitonis 2019). As previous studies indicated, *P. antipodarum* can survive desiccation for several days (Gaino et al. 2008) and thus the possibility of transport while attached to boats or on waterfowl feathers is high (Crozet et al. 1980). More importantly, several studies have also found that the invader can survive the digestive tract of marine and lake benthivorous fish or waterbirds (Aarnio and Bonsdorff 1997; Bruce and Moffitt 2009; Brenneis et al. 2011; Rakauskas et al. 2016). It has been shown that, to some degree, *P. antipodarum* is consumed by marine or brackish water benthivorous fish species in the field (Azour 2011; Brenneis et al. 2011; Rakauskas et al. 2013). In this way, fish may act as potential dispersion vectors and thus reduce colonization time in a particular ecosystem or even between different ecosystems. Most of the evaluated studies that analysed the ability of *P. antipodarum* to survive digestion focused mostly on fish common in still water ecosystems. By contrast, relatively few studies sought to identify riverine fish species that were capable of consuming the invader effectively (Cada 2004; Bersine et al. 2008; Brenneis et al. 2011). Furthermore, most of these studies focused on salmonid fish, these not being common or benthivorous in temperate running waters. Nevertheless, given that active dispersion of *P. antipodarum* is generally limited in lotic ecosystems, it can be assumed that riverine benthivorous fish species are potential dispersion vectors for the snail.

This paper investigates riverine fish species as a potential secondary dispersion vectors for *P. antipodarum* in lotic ecosystems. As some of the riverine benthivorous fish species are common and relatively abundant, there is a high probability that they act as secondary dispersion vectors and facilitate both downstream and upstream spread of *P. antipodarum*. However, due to a lack of data, the actual role of riverine fish in the secondary dispersion of the invasive snail is unclear. To plug this gap in current knowledge, we performed laboratory analysis of the consumption of *P. antipodarum* by the main local riverine benthivorous fish species. In the laboratory experiments, we tested whether these fish species consumed *P. antipodarum* in experimental aquariums in which the snails were the only available prey, and whether the snail survived passage through the digestive tract of these fish. In general, we predicted that *P. antipodarum* could survive passage through the digestive tract of most benthivorous riverine fish species, and thus these species could act as secondary dispersion vectors in river ecosystems.

Materials and methods

Individuals of *P. antipodarum* were collected in Lake Vilkokšnis using a standard dip net and sieving out the sand. The snails were transported to the laboratory and maintained in two 10 L plastic buckets at a temperature of 17 °C with part of the water changed every second day for a week before the experiments. Stones with epilythic algae collected in Lake Vilkokšnis were added as a food source for the snails. Snails with a shell length larger than 3 mm were selected and used in all experiments. Benthivorous fish species such as *Barbatula barbatula* (Linnaeus, 1758), *Barbus barbus* (Linnaeus, 1758), *Cottus gobio* Linnaeus, 1758, *Gobio gobio* (Linnaeus, 1758) and the long-distance migrant *Vimba vimba* (Linnaeus, 1758) were selected for the experiments. All of these are common benthivorous fish in running waters of central Europe, including Lithuania (Virbickas 2013, 2014). All fish specimens, except *V. vimba*, were collected in the River Neris (54°43′19.13″N; 25°02′56.33″E), using battery-powered electric fishing gear. Specimens of *V. vimba* were caught in the reservoir of Kaunas Hydroelectric Power Plant (54°53′54.15″N; 24°05′01.28″E) using multi-mesh benthic gillnets. It is worthy of note to mention that the invasive snail has not been recorded in either of the sampling sites. All fish specimens were acclimated in 92 L tanks filled with tap water circulating through ammonia filters for a week. During this period, frozen midge larvae were used as food. During the acclimation period and during the experiments, a natural photoperiod (18 h daylight, 6 h dark) and a temperature of 17 °C were maintained. The fish were not fed for 48 h prior to the experiments.

Two experiments were conducted in eight 9.5 L tanks connected to an ammonia filter forming a closed recirculating system – experiment 1 evaluated which of the riverine benthivorous fish consumed *P. antipodarum*, while

experiment 2 assessed snail survival on passing through the digestive tract of the fish. Following the methods described in Rakauskas et al. 2016, no substrate was added to the experimental tanks. In the feeding experiment, 100 living snails were presented for each tested fish specimen, allowing the fish to forage for 18 h. After this, they were removed and live snail specimens were carefully pumped out and counted, thereby allowing an estimate of the exact number of ingested snails. As the feeding experiments showed a low propensity among the study fish species to consume *P. antipodarum*, snails were inserted in earthworms *Lumbricus terrestris* (Linnaeus, 1758) for the survivorship experiments following Rakauskas et al. (2016). In total, 15 snails were served in 2–3 earthworms for each fish. As smaller fish specimens were unable to consume two large earthworms, the snails were served in three smaller earthworms. As the probability of accidental consumption of the snail together with preferable food objects by benthivorous fish is relatively high in the wild, this method of snail presentation in the current experiment imitates this process. After foraging for 18 h, the fish were placed individually into further experimental aquariums with a net (5 mm mesh) fastened about 3 cm above the bottom, this restricting the ability of the fish to reconsume the faecal pellets. Fish were left to defecate for 48 h at 17 °C and the faecal material from each aquarium was siphoned and sieved (50 μm mesh) every 8 h. All snails with intact shells were put into separate petri dishes filled with tap water for 12 h to recover from the digestion processes. The number and condition of the snails were assessed using a dissecting microscope. Assessment of condition was based on snail appearance and movement – dead snails either remained deep within their shells or, if their body was exposed outside of the shell, exhibited no movement when probed. Generally, surviving snails crawled around in the petri dishes.

Statistical analysis

As the data did not meet the normality assumption of parametric methods (Shapiro-Wilk's W tests, $P < 0.05$), non-parametric statistics were used. Kruskal-Wallis ANOVA tests were applied to test for species effect on the number of *P. antipodarum* ingested by different fish species and on the number of snails that survived passing through the gastrointestinal tracts of different predators. If necessary, multiple comparison of mean ranks was applied. Calculations were performed using Statistica 10.

Results

All studied fish species consumed the presented snails, though the ingestion rate varied among the species (Kruskal-Wallis ANOVA test: $H_{4, 45} = 28.92$, $P < 0.001$; Table 1). *Barbus barbus* showed the greatest prevalence for feeding on the invasive snail: every *B. barbus* individual used in the experiment

Table 1. Experimental ingestion of *P. antipodarum* by five main riverine benthivorous fish species: the number of investigated fish individuals of each particular species (n); the number of investigated fish individuals that consumed *P. antipodarum* served in earthworms (n_c); the total body length of fish (TL); the percentage of fish individuals that ingested *P. antipodarum* (P); the percentage of ingested *P. antipodarum* individuals (C); the number of ingested *P. antipodarum* individuals per fish (I). Values are mean ± standard deviation.

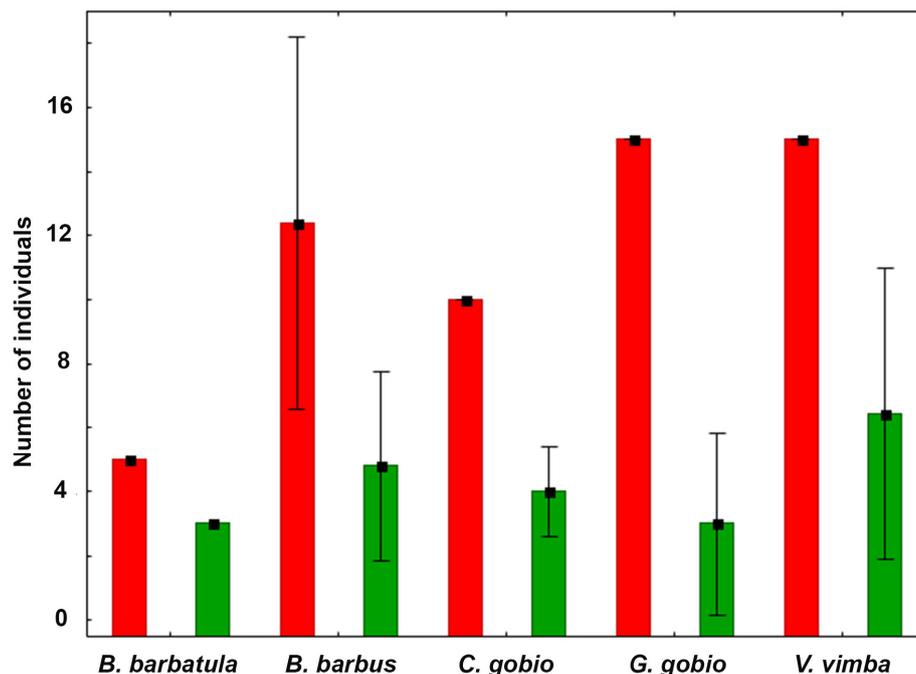| Species		Consumption experiment				Survivorship experiment		
	n	TL (cm)	P (%)	C (%)	I (ind.)	TL (cm)	n	n_c
B. barbatula	15	10.1 ± 0.9	13.3	0.2 ± 0.6	1.5 ± 0.7	11.3	5	1
B. barbus	8	23.6 ± 1.0	100.0	10.3 ± 6.1	10.3 ± 6.1	23.6 ± 1.1	5	5
C. gobio	5	6.5 ± 2.2	80.0	3.0 ± 2.5	3.8 ± 2.2	7.2 ± 1.4	5	2
G. gobio	8	10.2 ± 0.6	37.5	0.8 ± 1.2	2.0 ± 1.0	10.2 ± 0.9	5	2
V. vimba	10	21.0 ± 1.1	80.0	2.2 ± 1.9	2.8 ± 1.7	21.0 ± 1.2	7	7

Figure 1. The Number of ingested *P. antipodarum* individuals per fish (red bars) and the number of snails that survived passing through the digestive tract (green bars). Values are mean ± standard deviation.

ingested them. However, on average, they ate only 10.3% of the snails available in the aquariums (Table 1). The applied multiple comparison on the number of consumed snails indicated significant (P = 0.009) differences only between *B. barbus* and *V. vimba* specimens. The prevalence of the other studied fish species for feeding on the invasive snail varied from 13.3% in *B. barbatula* to 80% in *C. gobio* and *V. vimba*. However, The ingestion rates by *B. barbatula*, *C. gobio*, *G. gobio* and *V. vimba* were low, these fish were eating less than 3% of the available snails and, on average, less than four snails per fish (Table 1).

Survival experiments indicated that some of the tested fish did not consume the earthworms with the inserted *P. antipodarum* (Figure 1). The experiments also yielded no significant differences in the number of *P. antipodarum* surviving after passing through the gastrointestinal tract of the different fish species (Kruskal-Wallis ANOVA test: $H_{4, 16} = 3.36$, P = 0.49). consumed snails were able to survive passing through the digestive tract of

all the studied fish species (Figure 1). the number of surviving snails ranged from 20% in *G. gobio* to 60% in *B. barbatula*. Additionally, none of the studied fish were able to crush the shell of *P. antipodarum*, thus resulting in the passage of all consumed snails undigested.

Discussion

Running water ecosystems do not favour the active spread of *P. antipodarum*. Secondary dispersion vectors, including fish, may facilitate species dispersion in such ecosystems. There is, however, limited current data on common riverine fish as potential vectors for the spread of this invasive species. In this study, Potential riverine fish predators of *P. antipodarum* were evaluated under laboratory experiments. Prior to our experiments, we assumed that the snail would be able to survive passing through the digestive tract of these fish and we also expected that *V. vimba*, *G. gobio* and *B. barbus* could be potential predators of *P. antipodarum* and would consume a significant quantity of the presented snails. Molluscs are common food objects for these fish species in the wild (Kennedy and Fitzmaurice 1972; Okgerman et al. 2013; Djikanović et al. 2015) and, more importantly, gastropods (mainly of the genus *Hydrobia*) predominate in the diet of large *G. gobio* individuals in some ecosystems (Kennedy and Fitzmaurice 1972). Meanwhile, we expected *Cottus gobio* and *Barbatula barbatula* to consume insignificant quantities of the *P. antipodarum* individuals, as molluscs are not common food objects in the diets of these species (Hyslop 1982; Rău et al. 2015). Overall, the results of this study indicated that most of the studied riverine fish fed to a very limited degree on the *P. antipodarum* under laboratory experiments. This corresponds with previous results on benthivorous lake fish, whereby most of the studied fish consumed an insignificant number of the snails during laboratory experiments (Rakauskas et al. 2016). Despite several studies indicating benthivorous fish avoid consuming *P. antipodarum* (Cada 2004; Bersine et al. 2008; Rakauskas et al. 2016), the role of these species in facilitating snail dispersion can still be assumed important. the accidental consumption of the snail together with preferable food objects is highly possible and this probability to consume accidentally increases with increasing snail density. In the study of Hall et al. (2003), an extremely high density of up to 500,000 *P. antipodarum* ind. m^{-2} were recorded in a river. In this case, the invasive snail dominated over other taxa and thus had a high probability to be consumed accidentally.

In this study, *P. antipodarum* was shown to survive digestion by riverine benthivorous fish under laboratory conditions, including by the migratory *V. vimba*. Such survival through the digestive tract, particularly in a migratory species, may lead to increased dispersion rates of the snail in river ecosystems. Currently, the translocation of aquatic invaders,

including *P. antipodarum*, both upstream and between river basins, has been widely attributed to anthropogenic activities (Alonso and Castro-Díez 2008; Kappes and Haase 2012; Banha et al. 2016). However, alternative natural vectors for passive dispersal remain under-researched (Kappes and Haase 2012; Banha et al. 2016; Coughlan et al. 2017). Zoochorous transport of one organism by another more mobile animal can facilitate dispersal of various taxa (Reynolds et al. 2015; Green 2016). Previous studies have indicated the ability of *P. antipodarum* to survive the gastrointestinal tract of various benthivorous fish under laboratory conditions (Aarnio and Bonsdorff 1997; Vinson and Baker 2008; Bruce and Moffitt 2009; Rakauskas et al. 2016). The results of this study correspond with these results. More importantly, previous studies have shown molluscs to be the predominant food source for the anadromous *V. vimba* (Bubinas and Vaitonis 2003; Ermolin and Shashulovskii 2006; Okgerman et al. 2013). In general, as *P. antipodarum* is capable of surviving the digestive tract of *V. vimba*, there is a high possibility of accelerated *P. antipodarum* dispersal. This has not, however, been directly documented yet.

Concluding remarks

The results of this study support the assumption that fish may have a potential role in the secondary dispersal of *P. antipodarum* in riverine ecosystems. However, this hypothesis needs additional investigation. Further research should be carried out to evaluate the proportion of the snail in riverine fish diet and the survival rates of the snail under natural conditions.

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