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Research Article

Structure and dynamics of gastropod communities in highly transformed aquatic environments colonized and uncolonized by globally invasive *Potamopyrgus antipodarum* (Gray, 1843)

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Abstract

We examined the association between habitat parameters and gastropod communities across a number of freshwater ecosystems, whose biodiversity has been affected by increased mining activities over decades. Reservoirs inhabited by the New Zealand mud snail (*Potamopyrgus antipodarum* (Gray, 1843)) exhibited different abiotic conditions than waterbodies that were not, such as higher salinity indicators (max. conductivity 13400 µS/cm, TDS 7700 mg/l and chlorides 7200 mg/l), and degraded water quality. In such water bodies *P. antipodarum* density was high (max. 23686/m^2). Further, invaded waters were inhabited by less diverse gastropod communities than reservoirs without *P. antipodarum*. The invader has established reproducing populations and were the dominant species (D 87.53%), or formed mono-specific assemblages, in the reservoirs. Our results indicate that *P. antipodarum* occurred in habitats whose conditions are unfavorable or less preferred by other species, such as those with high conductivity, and high concentrations of chlorides and calcium. Since this snail is known to inhabit water bodies with degraded water quality, we assumed that along with the progressing development of industries worldwide, this species will continue to spread to industrial areas and will inhabit increasing numbers of anthropogenically affected water environments. Our study contributes to the global understanding of the mechanisms involved in successful establishment in waters by *P. antipodarum*, and is especially novel in addressing its occurrence in anthropogenically created ecosystems. Our results showed that human impact is the cause of the trend in *P. antipodarum* populations, and compared habitats from the perspective of both abiotic parameters and community structure. Human activities can have a significant impact on water quality that can result in the permanent establishment of *P. antipodarum* populations, especially when the environment is not favorable for the native species.

Key words: aquatic invasions, global anthropopressure, aquatic snails, freshwater environments, alien species, industry development

Introduction

In recent years, there has been an increasing occurrence of invasive molluscs in aquatic environments as a result of extensive human activities. Globally, this phenomenon significantly affects the structure and composition of various ecosystems and poses a serious threat to the diversity of native flora and fauna (Łabęcka and Czarnołęski 2019; Emery-Butcher et al. 2020).

The New Zealand mud snail *Potamopyrgus antipodarum* (Gray, 1843) (Caenogastropda: Tateidae) is a small gastropod species that is globally known as an invasive aquatic snail. Presently, it is found in North and South America, Australia, Africa, and Asian countries, such as Iraq, Turkey, and Japan. This species is also predominantly found in Europe, and the British Isles (Gérard et al. 2003; Radea et al. 2008; Riley et al. 2008; Thomsen et al. 2009; Collado 2016; EPPO 2020; Son et al. 2020; Taybi et al. 2021). The selection of this research object is related to the fact that the presence of invasive species in aquatic habitats is considered to be one of the greatest threats to biodiversity of snails, similar to the disappearance or fragmentation of habitats (Simberloff et al. 2013; Tickner et al. 2020).

Generally, aquatic snails, such as *P. antipodarum*, rely on several vectors for their dispersal (Alonso and Castro-Diez 2008). They can be carried by water birds and can also be dispersed between the habitats when they are attached to large mammals. In nature, they are often dispersed passively and show an intermittent occurrence pattern (Jarne and Delay 1991). Human activities (e.g., boating and water sports, aquarium trade, use of water equipment, and transport of macrophytes), can significantly affect their dispersal and population structure and, consequently, their evolutionary dynamics (Albrecht et al. 2009). Various dispersal vectors can also contribute to the overall occurrence of the *P. antipodarum* population (Van Leeuwen et al. 2013). Its ability to disseminate via different passive dispersal vectors could result in the cosmopolitan distribution of *P. antipodarum* and its successful establishment as an invasive species. According to Figuerola and Green (2002), both endozoochory and ectozoochory transport mechanisms are essential for the effective dispersal of an alien species. The survival rate of *P. antipodarum* after passing through the digestive system of predatory fish is relatively high (Vinson and Baker 2008; Butkus and Rakauskas 2020). Successful invasive species also show high potential for dispersal by adopting different strategies that facilitate their survival even in adverse conditions (Statzner et al. 2008). Their ability to easily adapt to the changing environmental conditions and wide ecological tolerance to desiccation and pollution enhance the invasive potential of *P. antipodarum* (Alonso and Camargo 2003; Romero-Blanco and Alonso 2019).

Although *P. antipodarum* is a frequently studied species (Ramskov et al. 2015; Geiß et al. 2016; Imhof and Laforsch 2016; Marszewska et al. 2018; Blasco-Costa et al. 2020; Gething et al. 2020), studies on its population ecology have been mainly conducted in lotic waters and through laboratory experiments (Mazza et al. 2011; Gérard et al. 2018; Bankers et al. 2020; Butkus and Višinskienė 2020; Mulero et al. 2020; Zorina-Sakharova and Lyashenko 2020). There are several recent studies analyzing the correlation between environmental factors and *P. antipodarum*. However, these have been carried out mainly in rivers and streams or as experimental studies on, for example, the impact of conductivity or temperature on fecundity or

growth of this species (Hoy et al. 2012; Verhaegen et al. 2021; Larson et al. 2020). Study on environmental factors such as ammonia, cooper and urban effluent on *P. antipodarum* have been carried out in the context of its mortality and tolerance (Alonso and Camargo 2003; Zounkova et al. 2014). Data regarding the occurrence of *P. antipodarum* in anthropogenically transformed areas is lacking. As such, our research is novel, as it aims to determine the occurrence of *P. antipodarum* in subsidence water bodies and analyzes the effect of various environmental factors on snail communities of lentic habitats that are vulnerable to increasing pressure from human activities. This species is listed as the worst invasive species in several regions of the world and is known to significantly affect the biodiversity of the invaded habitats. Therefore, it is essential to study its colonization pattern in heavily transformed aquatic habitats and its possible negative effects on the native snail fauna.

A few of our previous studies have highlighted the role of anthropogenic reservoirs in the dispersion of alien species (Spyra and Strzelec 2014; Cieplok and Spyra 2020). The current study was performed in water bodies that were formed as a consequence of industrial development, which has increased rapidly over the last two centuries. Human activities, particularly coal mining and construction of iron and steel industries, have not only led to the disappearance of natural lakes and ponds but also resulted in the creation of new water bodies (Wójcik 2018). The exploitation of underground coal resources continues to be the primary cause of the Earth's surface transformations, which subsequently result in the formation of various types of water bodies (Dulias 2016). These transformations have been extensively observed in many regions of the world. We conducted research in the water bodies that had been formed due to land subsidence, and they showed differences in depth, surface area, water source, fluctuation, and water chemistry parameters.

This study attempts to determine the spatial and environmental factors (types of substratum, physicochemical parameters of water, age of water body, depth, surface area, and drainage system) that can effectively predict the distribution patterns of *P. antipodarum*, to understand the mechanisms underlying its successful invasion, and study the influence of *P. antipodarum* on native snail communities of the aquatic ecosystems. We also aim to characterize the ecological parameters in the surrounding areas, to determine the role of anthropogenic habitats in the establishment of *P. antipodarum* in industrial areas, and intend to provide an answer to the question as to why *P. antipodarum* inhabits some anthropogenic water bodies and does not colonize others. In addition, we hypothesize that human activities would facilitate the establishment of *P. antipodarum* in the disturbed areas and that its density would be positively associated with high conductivity and water hardness values.

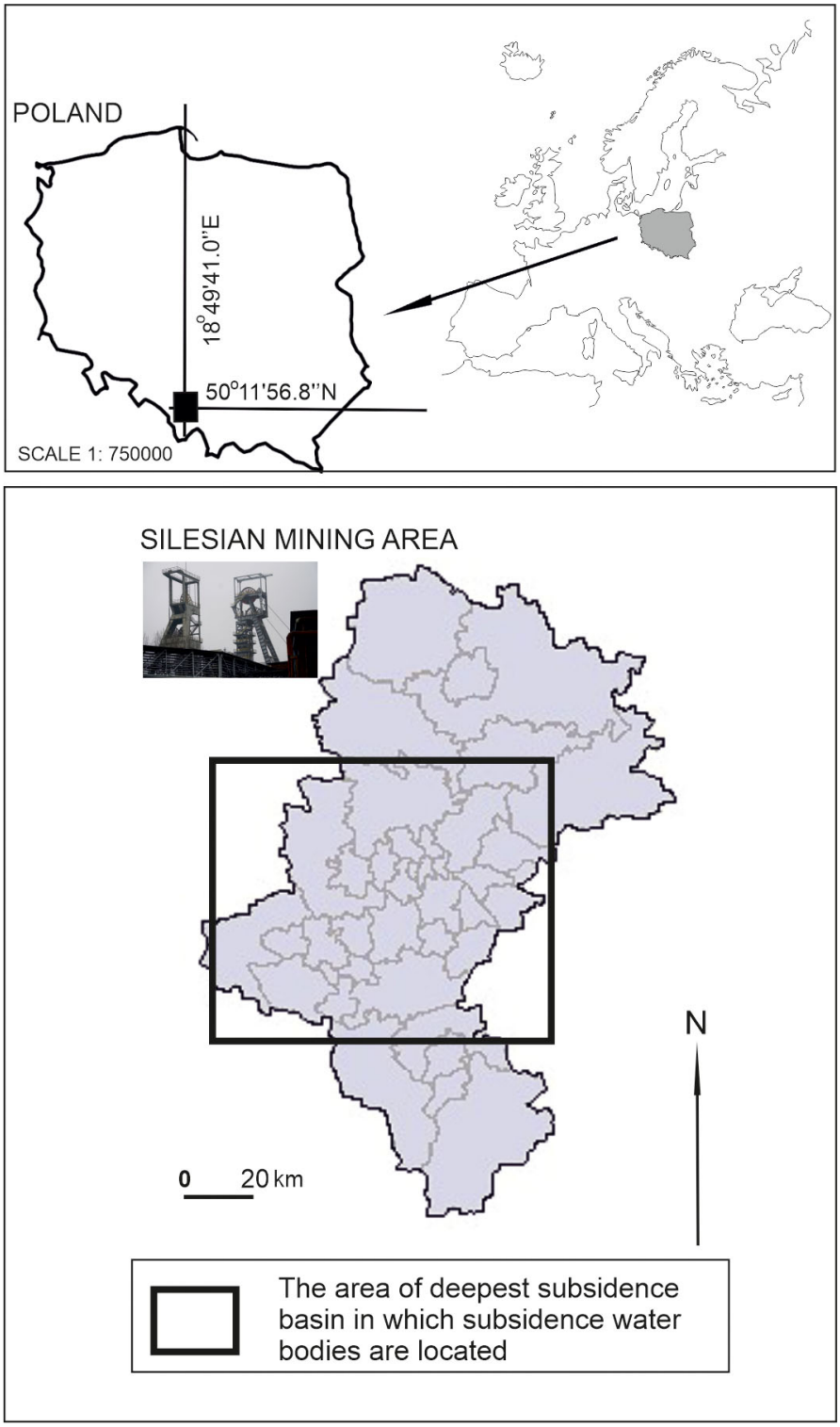

Figure 1. Location of the subsidence water bodies, formed in the anthropogenic land depressions in southern Poland.

Materials and methods

Study area and ecosystem

The study was conducted in water bodies that have been formed in subsidence depressions, which are abundantly found in Southern Poland (Figure 1). They remain under the influence of human activity and increased

anthropopressure, which further impacts the physical and chemical properties of their waters. Despite the advances in technical knowledge, environmentally friendly methods for the extraction of raw materials have not yet been developed and implemented in either the global or Polish mining industries (Pietrzyk-Sokulska et al. 2015; Wójcik 2018). The pressure due to anthropogenical activities is particularly evidenced in urbanized and industrialized areas due to large-scale human interference in all elements of the environment. Among the various industries that have developed in our study area, mining activities have been known to significantly affect the quality of water and pollute the subsidence water bodies, which consequently influence the aquatic fauna and flora in the region. Undoubtedly, hard coal mines show the most significant impact on these changes. In this region, the aquatic communities are particularly susceptible to heavy metal pollution.

To determine how *P. antipodarum* inhabits subsidence water bodies, 70 were selected in Southern Poland (Figure 1). Our study was carried out in subsidence water bodies which are formed in land depressions as a result of intensive activity from the coal mining industry. Depths of water bodies vary depending on the size of the subsidence basin. They were located in urban localities, which were usually surrounded by slag heaps and mining dumps. The subsidence water bodies differed in the parameters such as depth, surface area, age, management practices and recreational use, type of bottom sediments, and water chemistry, but the source of water supply was similar (atmospheric precipitation and surface run-off) (Tables 1 and 2). From the initial 90 water bodies, 70 were finally selected (35 colonized by *P. antipodarum* and 35 uncolonized by *P. antipodarum*) for the study because no freshwater snails were found in the other water bodies. Plants in each reservoir were identified.

Gastropod survey methods

The distribution of freshwater gastropods and characteristics of their habitats were studied in the water bodies from spring to autumn from 2014 to 2020 (to standardize the data for subsequent analysis, the average values of five samples taken in this period of time were used). The water body area (which ranged from 1.1 to 780 ha), depth (from 1.2 to 6 m), and degree of shading (exposed to sun – completely exposed shoreline; shaded – water surface shaded by riparian trees and shrubs) were determined for each of reservoirs. The water regime (permanent versus temporary) of the reservoirs was also assessed. The sampling was conducted at sites that were less than 100 cm in depth. The mollusks were sampled within a quadrat (50 × 50 cm) using a dip-net (0.4 mm mesh size) of diameter 20 cm. The snails were collected using the same standard methodology of hydrobiological studies from all the sites. The snails were then transferred to plastic vials containing

Table 1. Subsidence water bodies colonized and uncolonized by *P. antipodarum*- characteristic features.

	Colonized	Uncolonized
Water body locality	urban, surrounded by heaps and mining dumps	meadow, forest
Area [ha]	1.1–780	1.7–72
Maximal depth [m]	1.8–6	1.2–4
Year of origin	1951–1993	1945–1991
Substratum inhabited by snails	macrophyte, anthropogenic wastes, bottom sediments	Bottom sediments covered with macrophytes, tree leaves, detritus
Bottom sediments	sand- muddy, muddy, muddy covered with algae, stones, or branches, muddy-gravel	sandy, sand- muddy, bottom sediments covered with detritus, plants and tree leaves
Fluctuation in water level and permanency	small permanent	from small to large permanent, temporary
Water body usage and management	intense or moderate fish stocking, recreational angling, swimming, wildfowl feeding, kayaks, water bikes, motorboats	wildfowl feeding, recreational angling
Water supply	surface runoff, precipitation, meadow ditches, forest ditches, groundwater,	
Macrophytes	water bodies with no plants in other: *Acorus calamus* (L.), *Alisma plantago-aquatica* (L.), *Calystegia sepium* (L.) R.Br., *Ceratophyllum demersum* (L.), *Elodea canadensis* (Michx.), *Eleocharis palustris* (L.) Roem.Schult., *Epilobium palustre* (L.), *Glyceria fluitans* (L.) R. Br., *Glyceria maxima* (Hartm.) Holmb., Juncus sp., *Lemna minor* (L.), *Lycopus europaeus* (L.), *Lysimachia vulgaris* (L.), *Myriophyllum spicatum* (L.), *Najas marina* (L.), *Phragmites australis* (Cav.) Trin. Ex Steud., *Polygonum amphibium* (L.) Delarbre, *Potamnogeton crispus* (L.), *Potamogeton natans* (L.), *Schoenoplectus lacustris* (L.) PALLA, *Senecio paluster* (L.), *Sparganium erectum* (L. em. Rchb. s.s.), *Typha latifolia* (L.)	*Acorus calamus* (L.), *Alisma plantago-aquatica* (L.), *Bidens tripartitus* (L.), Carex sp., *Ceratophyllum demersum* (L.), *Cirsium palustre* (L.) Scop., *Eleocharis palustris* (L.) Roem&Schult., *Elodea canadensis* (Michx.), *Equisetum fluiatile* (L.), *Galium palustre* (L.), *Glyceria maxima* (Hartm.) Holmb., *Hottonia palustris* (L.), *Irys pseudacorus* (L.), Juncus sp., *Lemna minor* (L.), *Lisimachia thyrsiflora* (L.), *Lycopus europaeus* (L.), *Lysimachia vulgaris* (L.), *Mentha aquatic* (L.), *Myriophyllum spicatum* (L.), *Oennthe aquatica* (L.), *Peucedanum palustre* (L.) Moench, *Phalaris arundinacea* (L.), *Phragmites australis* (Cav.) Trin. Ex Steud., *Polygonum amphibium* (L.) Delarbre , *Potamogenton lucens* (L.), *Potamogeton natans* (L.), *Ranunculus sceleratus* (L.), *Schoenoplectus lacustris* (L.) PALLA , *Scutellaria galericulata* (L.), *Sparganium erectum* (L. em. Rchb. s.s.), Sphagnum sp., *Typha angustifolia* (L.), *Typha latifolia* (L.), *Utricularia vulgaris* (L.)

water and transported to the laboratory of the Institute of Biology, Biotechnology and Environmental Protection (University of Silesia, Katowice). After separating the coarser components of the material (small stones, pieces of wood, leaves, and fragments of plants) and rinsing using sieves (0.4-mm mesh size), the samples were preserved in 80% ethanol. Snails were identified to species level in the laboratory using a stereoscopic microscope (Olympus SZX16) and specific keys (Glöer 2002) with supplemental information provided by Piechocki and Wawrzyniak-Wydrowska (2016). The density of each species was expressed as the number of individuals per square meter of the bottom sediment.

Physicochemical parameters of the water were obtained by collecting surface water samples (at a depth of 0.5 m). The samples were stored in cold conditions during their transport to the laboratory at the Institute of Biology, Biotechnology and Environmental Protection (University of Silesia, Katowice), where they were further analyzed for alkalinity, Cl ions,

Table 2. Environmental properties that have been reported for the records of *P. antipodarum* in Southern Poland; Mean values and standard deviation (SD) are presented for each environmental parameter. Z – values of Mann-Whitney U test. *p* – level of significance.

Parameter	Colonized		Uncolonized		Mann-Whitney U test	
	mean	SD	mean	SD	Z	*P*
pH	7.6	0.5	7.1	0.7	−3.14795	0.001644
Conductivity µS/cm	3644	3391.3	400.5	351.4	−5.77320	0.000000
TDS mg mg/l	2321	1695.5	197.6	175.3	−5.79670	0.000000
Chlorides mg/l	906.2	1147.9	11.7	8.0	−2.06731	0.038706
N-NO_3 mg/l	1.4	2.4	1.3	0.75	2.97720	0.003500
Nitrates mg/l	6.1	1.8	3.9	3.3	2.91890	0.003513
N-NO_2 mg/l	0.02	0.04	0.01	0.01	2.27287	0.023035
Nitrites mg/l	0.06	0.1	0.02	0.03	2.22001	0.026419
N-NH_4 mg/l	0.4	0.8	0.2	0.1	2.26112	0.020000
Ammonia mg/l	0.5	1.0	0.3	0.2	2.26112	0.023752
Phosphates mg/l	0.27	0.33	0.4	0.7	1.77953	0.075153
Hardness mg $CaCO_3$/l	218.2	252.0	87.9	55.8	−0.52857	0.597101
Calcium mg/l	71.5	77.5	41.2	16.8	−0.24079	0.809714
Iron mg/l	0.132	0.218	0.022	0.08	−2,47843	0,013190
Temperature °C	19.80	2.35	18.03	2.35	−2,12017	0,033993

PO_4^{3-}, NO_2^-, NO_3^-, NH_4^+, water hardness, magnesium ions according to the International (ISO) or European (EN) standard guidelines (Hermanowicz et al. 1999; Wilander et al. 2003). Conductivity, TDS, temperature and pH were measured directly at each site.

The dominance index (D) and the constancy index (C) were determined for snail communities (Górny and Grüm 1981). Populations were categorized into five groups based on the D values: supereudominant species (D > 44%), eudominant species (10.1%–44%), dominant species (5.1%–10%), subdominant species (2.1%–5%), and recedent species (D < 2.0%). Populations were divided into four groups based on the C values: constant species (100%–70.1%), common species (70%–50.1%), rare species (50%–25.1%), and accidental species (C ≤ 25%). The diversity of snail communities were compared between the water bodies using the Shannon diversity index (H') and the Simpson diversity index (S). We used Pielou's evenness index (J) as the measure of evenness: J = H'/ln(S), where H' = Shannon index and S = number of taxa observed (MVSP 3.13.p software; Kovach Computing Services) (Clarke et al. 2014).

Statistical approach to study environmental variables and community structure

The data regarding the distribution of snail communities and environmental factors that potentially influence their distribution were determined based on 350 sampling events. Habitat characteristics of the subsidence ponds were analyzed, and their association with the snail distribution patterns were evaluated. Twenty-two environmental variables were initially considered for investigation; however, their number was reduced to avoid multicollinearity. The indirect (correspondence analysis (CA)) and direct (Canonical Correspondence Analysis (CCA)) techniques were used to assess the

relationship between the snail community composition and environmental variables. The data used in the analyses were log-transformed [ln (x + 1)]. The collected samples were initially analyzed through gradient length calculations via Detrended Canonical Correspondence Analysis (DCA, 3.5 SD). The relationship between environmental factors and freshwater snails was assessed using a CCA to identify the habitat variables that play a crucial role in determining the structure of the snail assemblages. During the CCA analysis, forward selection was performed to assess the role of different environmental variables in the development of the snail groupings. The environmental variables with a high inflation factor were excluded from the final CCA analysis. The statistical significance of both the environmental variables and the canonical axes was analyzed by applying the Monte Carlo permutation test for 499 replicates. The results of the CA and CCA analyses were computed using the CANOCO 4.5 software (Ter Braak and Smilauer 2002).

Prior to the statistical analysis, the data were initially tested for normality using the Kolmogorov-Smirnov test. Since the data did not meet the assumptions of the normality distribution tests, then a non-parametric alternative was used to estimate the differences in snail density among colonized and uncolonized water bodies. In addition, the physicochemical parameters of the water bodies and differences in the values of the diversity indices and density of snails were statistically analyzed by performing Mann-Whitney U test (Statistica version 13.1, Dell version).

The hierarchical clustering method (MVSP 3.13.p Software; Kovach Computing Services) was adopted to classify the water bodies according to the similarities in faunal composition. The clusters were divided using the average linkage (WPGMA) method based on the Euclidean distance metric which measures the similarity between two clusters.

Results

Potamopyrgus antipodarum inhabited permanent water bodies in which only slight fluctuations were observed in their water levels (Table 1; Supplementary material Figures S1, S2). The maximal values of the surface area (1.1–780 ha), and depth (1.8–6.0 m) of the water bodies colonized and uncolonized by *P. antipodarum* were found to be different. The mud snail was found to inhabit water bodies that were extensively or moderately stocked with fish and were used for different forms of recreation. This species was predominantly found in muddy bottom sediments that were layered with algal biofilms or stones. Twenty-three species of aquatic plants were commonly found in the aquatic systems inhabited by *P. antipodarum*; however, no plant species were found in almost half of the studied water bodies (Table 1). Significantly fewer plant species were observed in water bodies colonized by *P. antipodarum* when compared to those uncolonized by *P. antipodarum*. Many macrophyte species were observed in only one water body.

Table 3. Density (ind./m^2) and diversity of freshwater snails in the water bodies colonized and uncolonized by *Potamopyrgus antipodarum*; statistical significane: Mann Whitney U test.

	Colonized	Uncolonized
Mean density of all snail species per water bodies	4592	1623
Density of all snails per water body (min.–max)	27–23788	4–24056
Density of per water body	2–23686	–
Density of native snails per water body	0–4094	4–24056
Mean number of species	6	7
Number of species per water body	1–12	2–11
Mean value of Shannon-Wiener index	0.841	1.242
Shannon-Wiener index per water body	0–1.876	0.393–1.854
Mean value of Simpson index	0.410	0.615
Simpson index per water body	0–0.822	0.231–0.816
Mean value of Pielou index	0.491	0.755
Pielou index per water body	0–0.925	0.335–0.964
Number of collected specimens	160703	56799
Number of water bodies studied	35	35

The water bodies that were formed in the subsidence land depressions and colonized by *P. antipodarum* had high conductivity values (maximum, 13400 µS/cm), TDS (maximum, 7700 mg/dm^3), and chloride ion concentrations (maximum, 7200 mg/dm^3). In water bodies high values of these parameters, the density of *P. antipodarum* was high. The maximal values of these parameters in the water bodies not colonized by *P. antipodarum* were found to be 1859 µS/cm, 978 mg/dm^3, and 38 mg/dm^3, respectively.

The results of the Mann-Whitney U analysis revealed significant differences in the values of most of the studied parameters, such as pH, conductivity, TDS, the concentration of chloride, and ammonium ions (Table 2) between water bodies colonized and uncolonized by *P. antipodarum*. The values of all of the studied parameters except the concentration of phosphates were found to be higher in the reservoirs occupied by *P. antipodarum*. These observations indicate that this species predominantly colonized water bodies with deteriorated water quality conditions compared to the other water bodies of the same origin and the same location. In addition, water hardness values were much higher in the water bodies that had been colonized by *P. antipodarum*; however, this difference was not found to be significant (Table 2).

In the water bodies colonized by *P. antipodarum*, the mean and median density of all snails was significantly higher compared to the density observed in the uncolonized water bodies (Mann Whitney U test: $Z = -0.35884$, $P = 0.00033$) (Table 3, Figure 2). The densities of native species of snails was higher in the water bodies uncolonized by *P. antipodarum* (maximum value 19 202 ind./m^2) compared to the colonized water bodies (maximum value 4 094 ind./m^2); however, the difference in mean density in both groups of water bodies was not statistically significant (Mann-Whitney U test: $Z = 0.340$, $p = 0.73300$). In both types of water bodies, the mean number of species and their corresponding range values were found to be similar in each water body (Table 3, Table S1). The study results showed

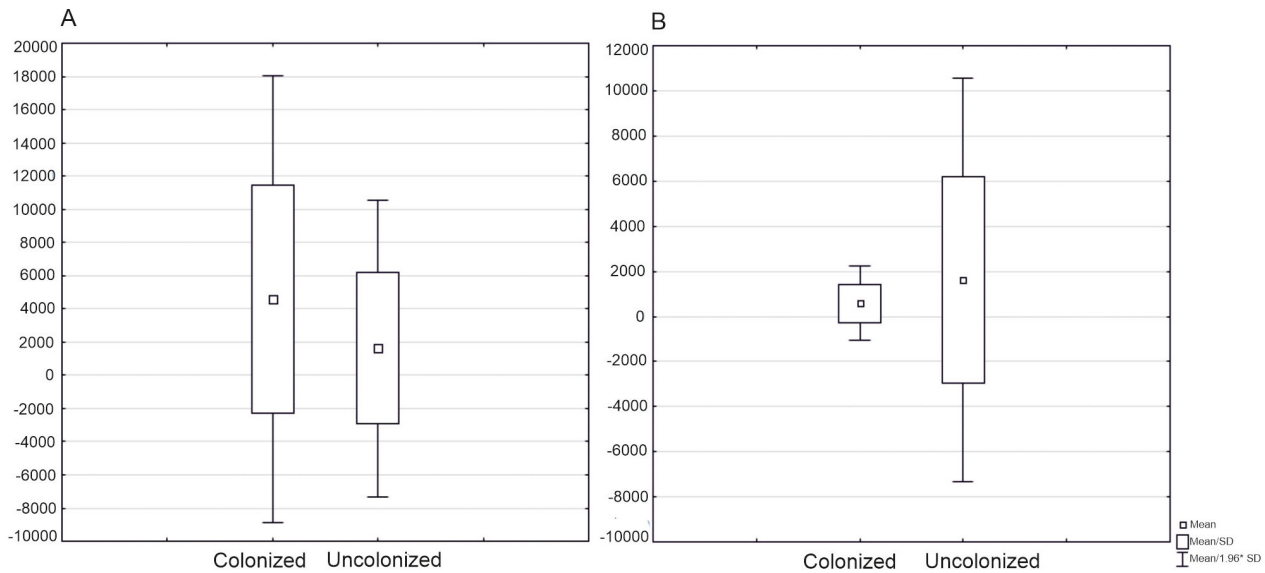

Figure 2. The density of freshwater snails in the water bodies that were colonized and uncolonized by *P. antipodarum;* A – density of all snails, B – density of snails after excluding *P. antipodarum.* Unit measure on axis – density individuals/m^2.

that the mean diversity values, measured using various indices, were always higher in the water bodies not colonized by *P. antipodarum* (Table 3), and these differences were statistically significant (Mann-Whitney U test: Shannon-Wiener diversity index Z = 3.0657 *P* = 0.0021; Pielou's index: Z = 3.7881 *P* = 0.0001; Simpson diversity index: Z = 3.0481 *P* = 0.0023). Some water bodies (with the highest values of conductivity, TDS and chlorides) were characterized by the presence of only *P. antipodarum* (density ranged from 10 712 ind./m^2 to 19 927 ind./m^2) and the absence of other species, and in these systems, the values of diversity indices were found to be 0 (Table S2).

The analysis of the dominance structure of snail communities revealed large differences between the water bodies. Although a greater number of species was found in the water bodies colonized by the invasive *P. antipodarum* (23 species), the dominance index value of 17 species was found to be well below 1%. For four species, *Lymnaea stagnalis* (Linnaeus, 1758), *Radix balthica* (Linnaeus, 1758), *Planorbis planorbis* (Linnaeus, 1758), and *Gyraulus albus* (Müller, 1774), dominance index values were found to be in range between 1.32 and 3.93 (Table 4). The dominant species in the water bodies not inhabited by *P. antipodarum* were very rare (*Gyraulus cristata* and *Ferrissia fragilis*) or not found (*Hippeutis complanatus*) in water bodies colonized by *P. antipodarum*. *Potamopyrgus antipodarum* was the dominant species in colonized water bodies. The structure of the snail communities in water bodies uncolonized by *Potamopyrgus antipodarum* exhibited noticeable differences. The Dominance index values was found to be more than 10% for three species, between 1 to 10% for eight species, and below 1% for seven species (Table 4).

The structure of the snail communities was reflected in the results of the analysis of faunistic similarities between the water bodies. The cluster analysis

Table 4. Dominance (D%) and Constancy (C%) patterns in water bodies colonized and uncolonized by *P. antipodarum*.

Snail species	Colonized		Uncolonized	
	D%	C%	D %	C %
Potamopyrgus antipodarum (Gray, 1843)	87.53	100.00	–	–
Radix baltica (Linnaeus, 1758)	3.93	75.68	1.63	57.14
Planorbis planorbis (Linnaeus, 1758)	2.21	45.95	6.78	37.14
Gyraulus albus (O.F.Müller, 1774)	1.37	59.46	4.47	91.43
Lymnaea stagnalis (Linnaeus, 1758)	1.32	48.65	2.65	40.00
Bithynia tentaculata (Linnaeus, 1758)	1.01	10.81	–	–
Planorbarius corneus (Linnaeus, 1758)	0.48	29.73	5.22	71.43
Physa acuta (Draparnaud, 1805)	0.43	21.62	1.26	34.29
Gyraulus crista (Linnaeus, 1758)	0.42	32.43	18.99	51.43
Bathyomphalus contortus (Linnaeus, 1758)	0.28	10.81	2.42	22.86
Viviparus contectus (Millet, 1813)	0.22	16.22	–	–
Radix auricularia (Linnaeus, 1758)	0.20	29.73	7.34	34.29
Stagnicola palustris (O.F.Müller, 1774)	0.14	16.22	0.06	14.29
Anisus lacustris (Linnaeus, 1758)	0.11	2.70	–	–
Anisus spirorbis (Linnaeus, 1758)	0.10	10.81	0.03	8.57
Segmentina nitida (O.F.Müller, 1774)	0.08	13.51	–	–
Valvata piscinalis (O.F.Müller, 1774)	0.07	21.62	–	–
Galba truncatula (O.F.Müller, 1774)	0.04	8.11	0.01	8.57
Anisus vortex (Linnaeus, 1758)	0.04	5.41	0.54	14.29
Physa fontinalis(Linnaeus, 1758)	0.01	10.81	0.07	11.43
Stagnicola turricula (Held, 1836)	0.01	8.11	–	–
Ferrissia fragilis (Tryon, 1863)	0.01	5.41	12.15	65.71
Stagnicola corvus (Gmelin, 1778)	0.01	2.70	0.07	14.29
Hippeutis complanatus (Linnaeus, 1758)	–	–	36.31	62.86
Valvata cristata (O.F.Müller, 1774)	–	–	0.01	2.86

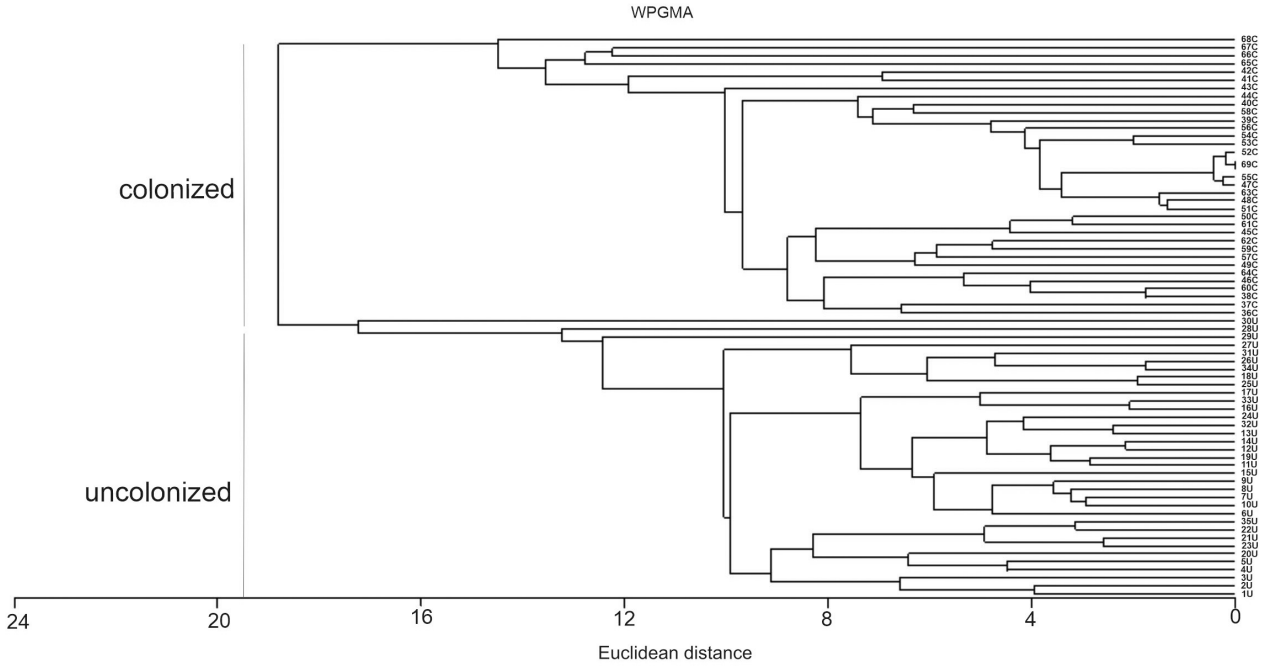

Figure 3. Diagram of the faunistic similarities of gastropods using hierarchical cluster analysis. In the upper part of the diagram is a cluster of water bodies colonized by *P. antipodarum*; in the lower part of the diagram, a cluster of water bodies is found that are uncolonized by *P. antipodarum*.

categorized 70 water bodies into the two main groups (Figure 3). The water bodies colonized by *P. antipodarum* comprised one group, while those uncolonized by *P. antipodarum* constituted the other group. The group of

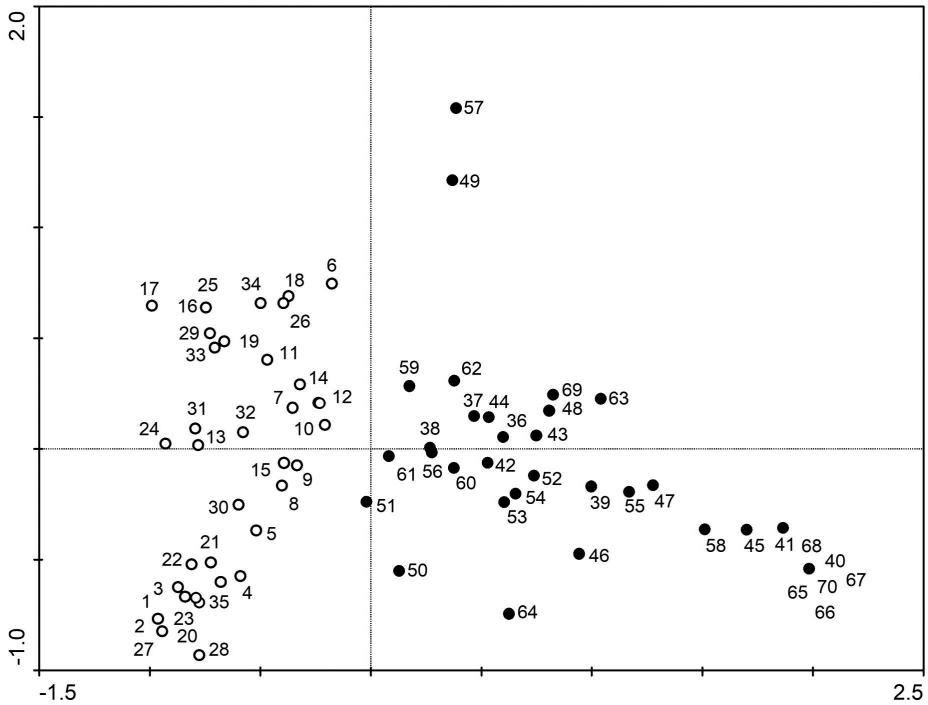

Figure 4. Correspondence analysis (CA) ordination diagram of the subsidence water bodies showing the distribution of the water bodies in the ordination space based on the species of freshwater snails; 1–35 water bodies uncolonized by *P. antipodarum*, 36–70 water bodies colonized by *P. antipodarum*.

water bodies populated by this species could be subdivided into two groups based on whether or not *P. antipodarum* was the only species found in the reservoir (Figure 3). In the CA the first axis explained 21.6%, while the second axis explained 10.8% of the overall variability in the occurrence of the snail species. The first ordination axis, which had an eigenvalue of λ = 0.531, significantly differentiated the water bodies. The gradient represented by the first ordination axis can be considered as a conductivity gradient. The gradient represented by the second ordination axis, with the eigenvalue λ = 0.266, was the factor that caused the internal differentiation within the snail communities. It clearly separated the water bodies colonized by *P. antipodarum* from the uncolonized water bodies (Figure 4).

The CCA model used to determine the structure and composition of the snail communities in the studied water bodies presented statistically significant results (Table S3). A forward selection of environmental variables was performed in order to select those variables that were crucial for the species diversification of the samples. Simultaneous with the forward selection of variables, the statistical significance of each variable was tested using the Monte Carlo permutation test. The Monte Carlo permutation test showed statistical significance for both the first canonical axis (F = 10.156, p = 0.002) and for all canonical axes (F = 2.579, p = 0.002). The results of forward selection and the Monte Carlo permutation test showed that conductivity is statistically significantly ($p \leq 0.05$) responsible for 8.9% of the overall variability in the occurrence of snails in the analyzed data, which

Table 5. Results of forward selection and Monte Carlo permutation tests from canonical correspondence analysis (CCA) of subsidence water bodies and snail communities.

Parameter	λ-1	λ-A	*p*
Conductivity	0.22	0.22	0.042
Shannon div. ind.	0.19	0.11	0.002
pH	0.18	0.15	0.002
Hardness	0.11	0.09	0.002
Nitrates	0.09	0.06	0.034
Temperature	0.09	0.06	0.006
Calcium	0.06	0.04	0.022

indicates that this parameter contributes to the major proportion of variability in the species composition (λ − A = 0.22, p = 0.042). The other key factor that contributed to significant variation in the data was the pH (λ − A = 0.15, p = 0.002). The contribution of other variables to species variability was found to have a lower effect (Table 5).

Potamopyrgus antipodarum was positively associated with axis I, which indicates a strong relationship with the high values of conductivity. Species located in the left part of the ordination space (including *Anisus vortex*, *Radix auricularia,* and *Valvata cristata*) were negatively associated with axis I, which suggests that they occur in the waters with low conductivity values. Species occurrence was also associated with the lower pH, total hardness, and water temperature. The occurrence of *P. antipodarum* was associated with a low diversity of the snails measured using the Shannon-Wiener diversity index (Figure 5).

Discussion

Our study analyzes the role of environmental variables (water quality and habitat characteristics) in determining the structure and composition of native snail communities as well as on the occurrence of globally invasive *P. antipodarum*. The study aimed to determine the extent to which *P. antipodarum* invade the human-created lentic habitats, which are subjected to constant pressure by anthropogenic activities, and evaluate the relationship between the density of the *P. antipodarum* population and the physicochemical characteristics of water. These observations indicate that this species predominantly colonized water bodies with deteriorated water quality conditions compared to the other water bodies of the same origin and the same location. We observed that *P. antipodarum* colonizes habitats with conditions that are not suitable or less preferred by the other species, such as high conductivity values and high chloride and calcium ion concentrations. High conductivity values favor the growth and survival of the invasive *P. antipodarum* because it can easily adapt to acute high salinity stress conditions (Hoy et al. 2012) and can occur in estuaries in invaded regions (conductivity 10 000 µS/cm). Such a tendency was found by Larson et al. (2020) in experimental studies and showed that its growth increases with an increase in conductivity values. In some cases, the water

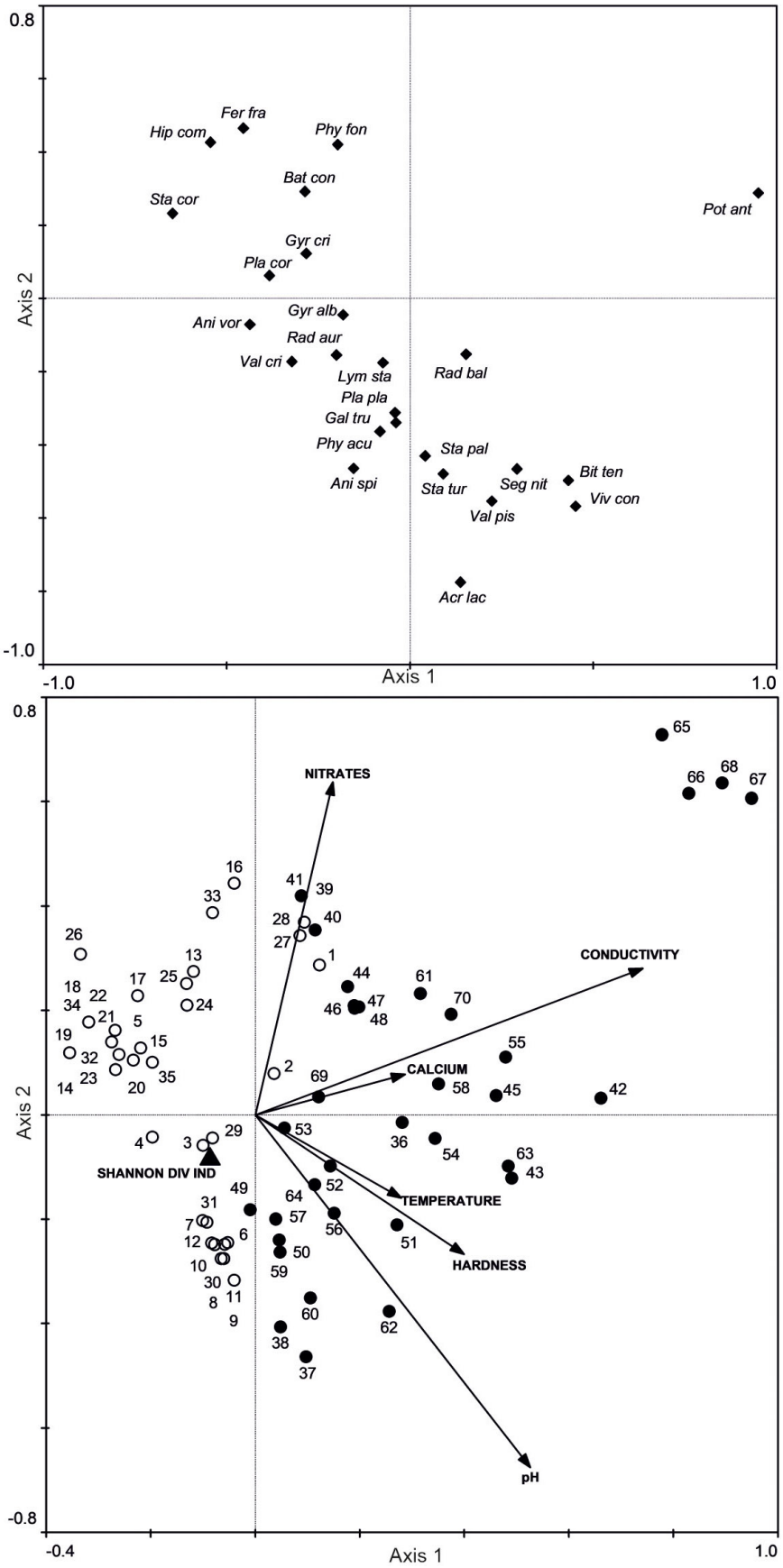

Figure 5. Ordination diagram based on Canonical Correspondence Analysis (CCA) showing the distribution of the freshwater snail species and *P. antipodarum* in ordination space in relation to statistically significant environmental variables. Species names are coded with the first three letters of the genus and species (see Table 4); Shannon div. ind. – Shannon-Wiener Diversity index.

chemistry may inhibit the spread of *P. antipodarum*. In laboratory experiments, *P. antipodarum* showed high mortality rates at higher salinity values (Paolucci and Thuesen 2020). At a conductivity of 200 µS/cm, adult *P. antipodarum* can survive for more than four months irrespective of the calcium concentration (maximum 17.5 mg/L) (Vazquez et al. 2016). Subsidence water bodies showing high values of these parameters may create new habitats that are favorable for its existence, and thereby free niches that are not always available for native species. The density of *P. antipodarum* was found to be high, in the hypohaline anthropogenic ponds (Sowa et al. 2019). Savić et al. (2020) reported that this species was also tolerant to a wide range of temperature, oxygen concentration, and pH values. In the Iberian Peninsula in different habitats (mostly lotic ones) *P. antipodarum* occurs in a pH range of 6.4–9.2, primarily at 8.16, and with conductivity in the range of 63.5 to 11 450 µS/cm; however, mean conductivity was found to be relatively low (847.8 µS/cm) (Alonso et al. 2019). In Pennsylvania the abundance of *P. antipodarum* populations was positively related to pH and conductivity values (Levri et al. 2020). However, it is difficult to relate this with its density since substantial data to establish this association were not obtained.

According to the studies of Gallardo et al. (2020), habitats with high temperature, increased human interference, and elevated nitrate concentrations are usually preferred by *P. antipodarum*. This species also benefits from wastewater inputs (Sánchez-Morales et al. 2018) and achieved higher densities in intermediate impaired conditions in a pollution gradient (Múrria et al. 2008). From our study, we can conclude that highly transformed water bodies are likely to constitute habitats that favor its establishment. Some invasive species are known to inhabit systems with multiple stressors, such as those located in urbanized areas (Emery-Butcher et al. 2020). Freshwater ecosystems appear to be particularly threatened by human activities, which further leads to the extinction of local species (Blettler et al. 2018), and on the other hand, are impacted by the colonization of invasive non-native species. Human disturbances are responsible for the majority of changes in species structure and composition globally, thus facilitating the spread of invaders and creating new habitats more susceptible to invasions (Sala et al. 2000). Therefore, the water reservoirs created by human activities constitute the main habitats for their settlement. In several Australian streams, their abundance was positively correlated with human land use and flow disturbance (Schreiber et al. 2003); thus, it is likely that their success might be facilitated by human disturbances. Subsidence water bodies are found to be highly susceptible to invasion by *P. antipodarum* since increased density of this snail community was observed in these habitats and therefore human impact is the cause of the trend in its populations.

In our study, the maximal density of *P. antipodarum* was found to be 23 686 ind./m^2. In some of the water bodies, it occurred as the only species.

The density of native species was higher in water bodies uncolonized by *P. antipodarum* when compared to the colonized water bodies. Diversity of snails was lower in water bodies colonized by *P. antipodarum*. The density of alien species shifted from rare to dominant when disturbance opens up space for their settlement and becomes rare when competitive, late successional species become dominant (Halpern 1989). Their densities show a rapid increase in the growth rate which is followed by a rapid decline (Greenwood et al. 2020), which is also true in the case of *P. antipodarum*, although the potential mechanisms involved remain unclear (Simberloff and Gibbons 2004; Gérard et al. 2018). While *P. antipodarum* can occur at extremely high densities in rivers (Hall et al. 2006), its density varies considerably. For example, as observed in the Snake River Springs (USA), it can exceed 30 000 individuals/ m^2 (Richards et al. 2001), and 300 000 individuals/m^2 as observed in the Madison River in Yellowstone National Park (Kerans et al. 2005). Richards et al. (2001) reported a density of 500 000/m^2 in streams. In California streams, it ranged from 500 to 100 000 ind./m^2 (Moore et al. 2012), while in the Iberian Peninsula it ranged from 1 to 98 300 ind./m^2 (Alonso et al. 2019). In lentic habitats, populations of *P. antipodarum* are found in lower densities. In Lake Ontario, Zaranko et al. (1997) found *P. antipodarum* in at density 244–5653 ind/m^2 in 1995. However, a study by Levri et al. (2007) in this lake conducted in 2006 indicated densities only on the range of 0–158 /m^2. In Polish lakes this species had been found in different densities most frequently from a dozen to several hundred individuals, with a maximum density of 28 500 ind/m^2 (Brzeziński and Kołodziejczyk 2001). Carlsson (2000), in water with low values of conductivity, found few specimens of *P. antipodarum*. This suggests that the density of populations is diverse depending on the type of environment and most probably on salinity.

The migration of species from other geographical areas is one of the factors that can modify the native communities. The negative effects of invasive *P. antipodarum* on the macroinvertebrate community structure along the pollution gradient in a small Mediterranean stream at the Iberian Peninsula were assessed by Múrria et al. (2008). However, the sites dominated by *P. antipodarum* did not show a different community structure than the sites without the mud snails. A colonization experiment conducted in the Madison River (USA) revealed that an increasing abundance of *P. antipodarum* led to a decrease in the density of native invertebrates (Kerans et al. 2005). Furthermore, it can monopolize the benthic substrate, thereby interfering with the space that is required by some macroinvertebrates to feed (Greenwood et al. 2020). The dietary requirements of *P. antipodarum* suggest that it can probably compete with native snails because *P. antipodarum* is primarily a grazer on benthic periphyton (Winterbourn and Fegley 1989) and detritus (James et al. 2000). Its ability to reproduce asexually, combined with high densities, can cause a negative ecological impact in the affected

habitats (Richards et al. 2001). In the water bodies studied, *P. antipodarum* dominated the native snail assemblages. The results of our study showed that in colonized areas, *P. antipodarum* co-occurrence resulted in a decreased density and diversity of native snails, compared to water bodies not colonized by *P. antipodarum*. We also found substantial differences in the snail community structure between water bodies colonized and uncolonized by *P. antipodarum*. The Dominance index for four species, *L. stagnalis*, *R. balthica*, *P. planorbis*, and *G. albus,* ranged between 1.32 and 3.93. The structure of the snail communities in the water bodies uncolonized by *P. antipodarum* was visibly different.

Potamopyrgus antipodarum inhabits a variety of freshwater and brackish ecosystems and is also found to be present on mud, sand, gravel, aquatic plants, and rocks (Fretter and Graham 1994). In Poland, it occurs in different habitats and also in human-created ponds (Spyra and Strzelec 2014). We found this destructive snail in subsidence water bodies located in urban regions, where they were frequently surrounded by heaps of waste materials and mining dumps. This species also occurred in permanent water bodies that showed variety in surface area (1.1–780 ha) and depth (1.8–6.0 m), were extensively or moderately stocked with fish, were used for different forms of recreation, showed only small fluctuations in their water levels and had poor or no vegetation. This species predominantly inhabited muddy bottom sediments, which in some cases were covered with algae or stones. In the Iberian Peninsula, it occurred mainly in flowing waters, and in a few sites situated in small lentic habitats (Alonso et al. 2019). *Potamopyrgus antipodarum* was also found in springs, where it was the only mollusk species (Savić et al. 2020), and can potentially be found worldwide in sites with similar ecological characteristics (Schreiber et al. 2003).

Potamopyrgus antipodarum is included in the lists of invasive species in many countries (e.g., Poland, Spain). Hence, it is highly pertinent to monitor its distribution. There is an urgent need for a comprehensive framework to predict the effects of invasive species that remains incomplete (Emery-Butcher et al. 2020). Aquatic professionals, anglers, and aquatic recreationists are the most likely modes of transportation due to their association with different types of water bodies (Gates et al. 2009), and there is currently no effective method for removing *P. antipodarum* after its establishment in a water body (Stout et al. 2016). Although water bodies in this study were extensively used for recreational fishing and fish management, no preventive measures have been adopted to restore the structure of the native communities. Therefore, this species can continue to spread and colonize other ecosystems under the influence of extensive human activities. Our findings confirmed the hypothesis of Larson et al. (2020) that some of the abiotic parameters contribute to the successful invasion of *P. antipodarum*. Therefore, water bodies with high conductivity, chlorides, high water hardness, are at the greatest risk of invasion by this species and hence

require immediate management to prevent establishment by this snail. Since subsidence water bodies are constantly exposed to sewage discharges and saline mining waters, they constitute ideal habitats for the colonization of this species, and the increasing number of the water bodies in the industrial areas further enables the spread of *P. antipodarum*.

Aquatic invasions, which often lead to drastic changes in the entire ecosystems, are a global threat to biodiversity (Mollot et al. 2017). Freshwater ecosystems are particularly vulnerable to invasions because anthropogenic use increases the possibility of their spread. Nowadays, the progressive degradation of ecosystems is one of the most important global environmental problems. In this context, and in the context of global climate changes, our research is part of a global trend that reflects the urbanization process and anthropogenic land transformations such as mining activity which results in the formation of subsidence water bodies, as well as air and water pollution even many years after the mines are closed, which in turn can be attributed to the gradual progression of land subsidence. The extensive use of freshwater bodies by industries significantly affects the quality of surface water (Machowski et al. 2019), which consequently influences the water chemistry. These findings showed that anthropogenically transformed reservoirs are not always suitable for native species, but facilitate the colonization of alien species because of limited competition. Since *P. antipodarum* is a eurybiotic, euryoecious and ubiquist species, it can tolerate adverse conditions while natives cannot or are less prone to tolerate. Newly created reservoirs have various, unoccupied niches, which can probably be one of the factors that facilitate the introduction and settlement of a foreign species. The current study has identified a group of environmental factors that favour *P. antipodarum* colonization and building of sustainable populations. In conclusion human impact is the cause of the trend in *P. antipodarum* populations. Further research is also needed in anthropogenically transformed aquatic habitats to analyze how *P. antipodarum* influences the existence of other groups of benthic invertebrates.

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Authors' contributions

AS and AC Investigation and data collection; AS Writing – original draft, Writing – review and editing; figures design; AC Conceptualization, sample design, and methodology, data analysis and interpretation, statistical analysis, Writing – review and editing.

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Supplementary material

The following supplementary material is available for this article:

Figure S1. The photograph of *P. antipodarum* inhabited anthropogenically transformed water bodies.
Figure S2. *P. antipodarum* – view of the front and side of the shell.
Table S1. Total density alien and native snails in water bodies colonized and uncolonized *P. antipodarum*.
Table S2. The values of diversity indices in anthropogenic water bodies colonised and uncolonised by the invasive New Zealand Mud snail – *Potamopyrgus antipodarum*.
Table S3. Summary of Canonical Correspondence analysis (CCA).

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