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The Colonization of a Cold Spring Ecosystem by the Invasive Species *Potamopyrgus antipodarum* (Gray, 1843) (Gastropoda: Tateidae) (Southern Poland)

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Abstract: Springs are unique aquatic environments that support specific biota, including endemic species and rare species listed in Red Lists. Due to their usually small size, springs are highly sensitive to disturbance. Many of them are threatened by aquifer depletion, contamination, surface-water diversion, livestock trampling, recreation, and invasive species. The aim of this study was to assess the colonization success of the invasive New Zealand mud snail (*Potamopyrgus antipodarum*) in a cold spring ecosystem in southern Poland. In Europe, this species has recently been added to the top "hundred worst" alien species due to its impact on invaded ecosystems. The study was carried out in two areas of the spring ecosystem—in the springhead and the springbrook—over a four-year period. *Potamopyrus antipodarum* dominated the benthic macroinvertebrate communities in both areas of the spring ecosystem. Nevertheless, its abundance in the springbrook was significantly greater, and increased noticeably during subsequent years compared to that in the springhead. The populations of *P. antipodarum* were exclusively composed of females. Smaller-sized New Zealand mudsnails were more abundant near the spring's source than at the second site. The females at the springhead became fecund at sizes as small as 3.7 mm (the number of embryos was between 0 and 37), while at the springbrook, embryos were found in snails as small as 3.4 mm (the number of embryos was between 0 and 42). Our results suggest that the lower water temperature at the springhead may limit the population size of *P. antipodarum*, thus making its density too low to be able to affect the community structure of benthic macroinvertebrates, including the spring snail *Bythinella* cf. *austriaca*.

Keywords: invasive alien species; cold spring ecosystem; spring fauna; spring threats

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1. Introduction

Springs are unique and usually isolated ecosystems that are at the interface between groundwater and surface water. They can be considered ecotones that link terrestrial and aquatic ecosystems and groundwater and surface water [1–3]. Springs are often described as ecosystems with relatively constant conditions, both physical and chemical [1], changing rapidly with distance from the crop out [4].

Springs are usually very small in size, but occur in large numbers [3]. Due to their specific conditions, they are inhabited by well-defined biocoenoses [5–7]. Some species are found only in springs (crenobionts) [1,8], while others inhabit springs and other comparable aquatic habitats (crenophiles) [9,10]. As a result of isolation, gene flow between springs is limited, which can lead to their considerable biodiversity and high levels of endemism [11]. They are often inhabited by relict species [12,13]. Examples of endemic fauna that have evolved and diversified using unique spring habitats include high numbers of pupfish species inhabiting North American desert springs [14], or snail species associated with springs in Australia [15].

The mosaic of microhabitat and high degree of individuality make springs significant contributors to local and regional biodiversity [3,13,16,17]. As they can be headwater stream, they can contribute to the biodiversity of entire river networks [18]. Springs and spring-fed habitats are recognized as biodiversity hotspots that support unique aquatic species communities around the world [2,9,19]. The waters of many springs are of high quality and thus provide suitable habitats for rare species due to their sensitivity to anthropogenic influences. Springs are often species-rich and contain a greater number of Red List taxa than other aquatic habitats [7]. In protected areas in the European Alps, Red List diatom species typically account for 40–50% of crenic species [7,20–22]. In Finland, Ilmonen et al. [9] found a high number of red-listed bryophyte and macroinvertebrate species in undisturbed springs compared to springs influenced by forest management and melioration.

Due to their small size, springs are highly sensitive to disturbance, and many of them are threatened by, among other things, aquifer depletion, contamination, surface-water diversion, livestock trampling, recreation, invasive species and results from surrounding landscape disruptions [23–26]. Alien species can have significant effects on the biodiversity and ecological functions of springs. Exotic plants can reduce overall plant and animal diversity and alter site hydrology, while alien animals can reduce or even destroy native aquatic species [27–29]. Invasive species can compete with endemic spring biota as a result of habitat alteration (e.g., non-native plant species) [30], competition and predation [31,32]. Colonization of a spring complex in central western Queensland, Australia, by the invasive mosquito fish *Gambusia holbrooki* has led to population declines and local extinctions of the endemic and critically endangered fish *Scaturiginichthys vermeilipinnis* [33,34]. As a result, this species was included on the list of the 100 most endangered species in the world [35]. The native flora and fauna of springs in California and Nevada suffered from stocking with sportfish and bait [36,37] and introduced aquarium fish, mostly cichlids, and invertebrates among other Melanoides snails, frequent occurred in springs of Nevada and Mexico [38,39]. The risk of invasion by exotic species increases in springs with greater human disturbance [40,41]. For example, livestock farming can facilitate the colonization of non-native plants by both removing native species and supporting vectors that provide propagules of exotic plants [42].

Potamopyrgus antipodarum (Gray, 1843; Gastropoda, Tateidae), native to New Zealand, is a snail that has successfully invaded fresh and brackish waters throughout the world. To date, it has been found in Europe, Asia, North America and Australia [43]. In recent years, *P. antipodarum* has also been found in South America [44] and Africa [45]. To date, only in Antarctica are there no data on its occurrence. In Europe, *P. antipodarum* has recently been added to the top “hundred worst” alien species, among which it is the third “worst alien” mollusc, after *Dreissena polymorpha* and *Pomacea canaliculata* [46].

The high tolerance to a wide range of physical and chemical conditions, high reproductive rate [43,47], high tolerance to air exposure [48], ability to survive in non-aquatic media for example attach to sediment and clay which allows overland translocation and spreading [49], capacity to spread via various mechanisms and lack of natural predators and parasites within new ecosystems [43,47] are considered to be the reasons for the invasive success of the New Zealand mud snail. It also has a variety of ways of dealing with potential enemies and parasites and is weakly affected by parasites [50–52]. In the invaded range of *P. antipodarum*, no infected snails were found in Belgium, Germany and the Netherlands [53,54], and only very low percentages in Poland [55,56], the USA [57,58], France [50,59,60], the United Kingdom (UK) [61] and Australia [62]. Verhaegen et al. [54] suggest adding early sexual maturity and the adaptation of size at sexual maturity to the list of functional traits explaining the invasive success of *P. antipodarum*.

The impact of the New Zealand mud snail in established ecosystems varies across habitats, which can be explained by the different densities the snail can achieve [43]. For example, in Australia, a positive relationship has been noted between *P. antipodarum* abundance and native benthic fauna [63], while in the USA and Chile, a negative impact on endemic macroinvertebrate communities has been indicated [64], as well as on gastropods [65–68]. Despite the fact that *P. antipodarum* can dominate mollusc assemblages in

Europe, only a low impact on macroinvertebrate communities has been documented to daste [69,70]. In very high abundance, *P. antipodarum* can modify the structure of native communities and change the functioning of entire ecosystems, including controlling the carbon and nitrogen cycles, alga and invertebrate communities [71–73]. Additionally, it is rarely eaten by most benthivorous fishes, and can even survive passing through their digestive tracts, and therefore, there is a justified concern that its invasion may limit the flow of primary production towards a higher trophic level [52,74–76]. In other cases, it can integrate into the host assembly and cause no obvious harmful effect [46,69,77].

Outside its natural range, *P. antipodarum* has been reported in various types of freshwater ecosystems (streams, rivers, lakes, ponds, artificial lakes, reservoirs etc.) and saltwater ecosystems (estuaries, polder-marshes etc.) [47]. It has also colonized very peculiar habitats such as a sulfidic spring and a sulfidic phreatic pool near the entrance to the Grotta del Fiume in Italy [78], an underground water pipe in Grummount Road, Peckham, South London and the thresholds of some caves and mines around Morecambe Bay, England and the Isle of Man [79]. In general, the New Zealand mud snail can likely establish itself successfully at sites around the world that have similar conditions to that in its native area [77]. As a general rule, human-disturbed ecosystems are more vulnerable to a *P. antipodarum* invasion because they open new niches for invaders that are more adaptable compared to pristine ecosystems [50,77,80–83].

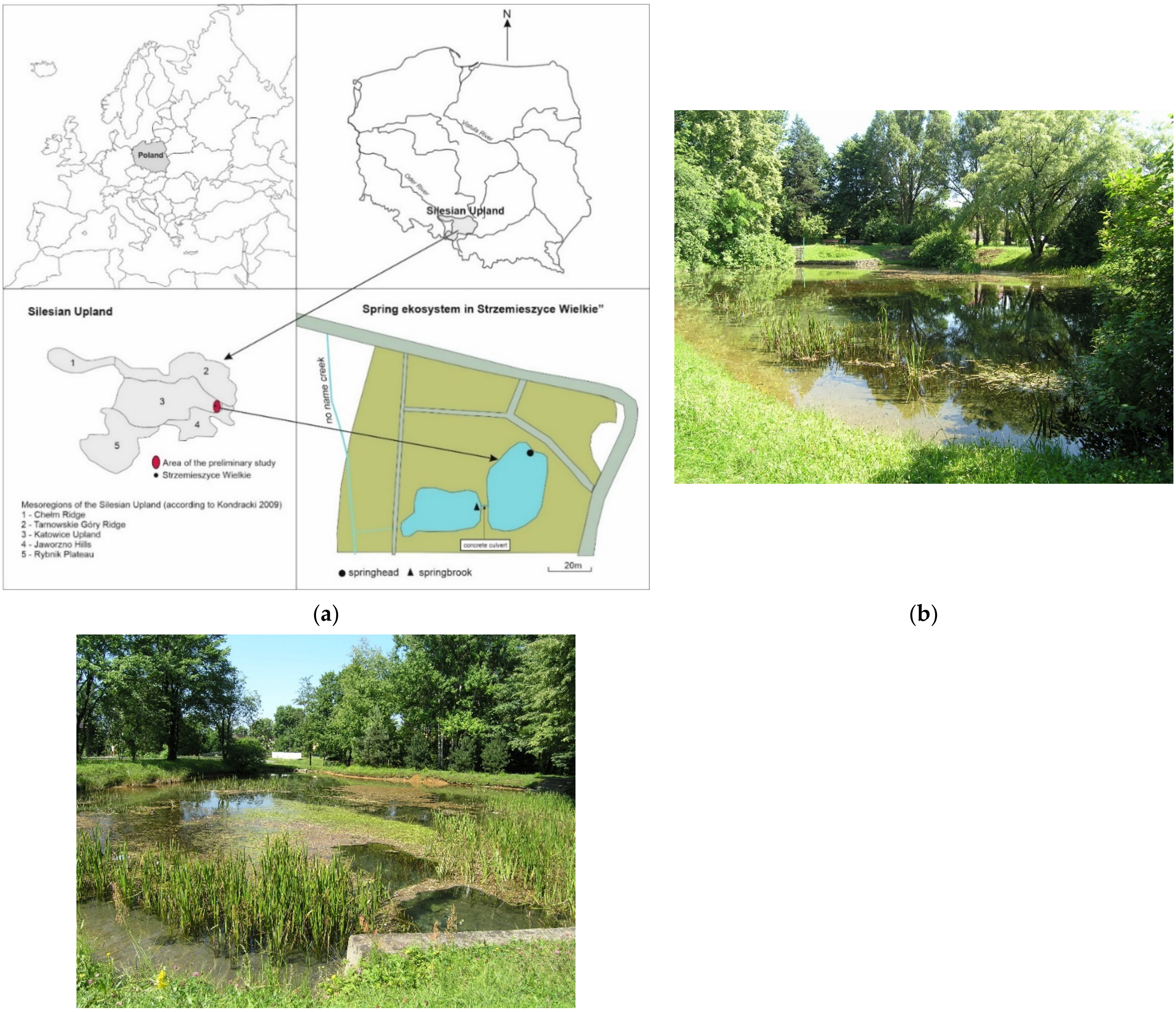
Beyond its native range, *P. antipodarum* is generally less frequently established in springs. It has previously been observed in springs in the Spanish province of Cuenca [84], in springs in the British Isles [85] and in Banbury Springs (a tributary of the Snake River) near Hagerman, ID, USA [86]. According to Hinz et al. [84], it inhabits brooks and rivers more often than springs.

In the summer of 2011, during a routine sampling for macroinvertebrates in the springs in the eastern part of the Silesian Upland (the Katowice Upland, southern Poland) a small population of New Zealand mud snails was detected in one of the springs. Unfortunately, previous studies on the composition of benthic fauna in this spring [87,88] were only carried out at the family or subfamily level, which made it impossible to determine whether *P. antipodarum* (this species was previously classified in the family Hydrobiidae, but it was recently included in the family Tateidae see Wilke et al. [89]) had become established at that time. This finding (to the best of our knowledge, the first locality record in springs in Poland) provides the opportunity (1) to assess the colonization of a spring ecosystem by this invasive snail species; (2) to evaluate its abundance, the population structure and the fecundity; and (3) to examine the change in the structure of benthic macroinvertebrate communities.

2. Material and Methods

2.1. Study Area

The spring in which the New Zealand mud snails were found is situated in the middle of a small park in Strzemieszcze Wielkie, a district of the city of Dąbrowa Górnicza (the Katowice Upland, southern Poland) (Figure 1a). It flows with a discharge of about 50 l s^{-1} from the bottom of a small pond (surface area: 972 m^2) with banks partially physically modified by concrete structures (see Figure 1b). The water next flows through a concrete culvert into another small pond (surface area: 664 m^2) (Figure 1c) and then empties into a creek of the Rakówka Stream (a right-bank side tributary of the Bobrek Stream, a tributary of the Biała Przemsza River).



(**a**) (**b**)

(**c**)

Figure 1. (**a**) Location of the study area; (**b**) spring in the bottom of a pond in Strzemieszyce Wielkie; (**c**) pond into which waters from the spring flow.

According to the ecomorphological classification of springs based on current velocity conditions [90,91], it is a rheocrenic spring (springs with rapid currents such as those in streams). It is located on a Triassic limestone and dolomite bedrock in a valley of the Biała Przemsza River [92].

In the 19th century, during the period of the development of the mining industry, the spring water was used in the processes of washing lead ore and iron ore. Since 1996, the spring has been protected by Polish law as the natural monument "Wywierzyska in Strzemieszyce Wielkie" due to its unique spring biota (the permit for sample collection was provided by the Dąbrowa Górnicza City Hall—WER. 6121.6.2012. MW (Dąbrowa Górnicza, Poland).

2.2. Sampling Procedure

The study was carried out in two areas of the spring ecosystem: in the springhead (eucrenal), and in the springbrook, which forms an encased pond (hypocrenal). For the research, the spring area was divided into two sections with the boundary of the springhead at the point at which the water temperature varies from the temperature at the source by 2 °C [93] or at 5 m downstream from the source [94]. The first sampling area was situated in the immediate vicinity of the spring's source (within 1 m of the source) and the other was located at a distance of about 40 m from the source (Table 1; Figure 1a).

Table 1. Characteristics of the spring and the sampling sites.

Characteristic	Description	
Type of a spring	valley, rheocrene, in the bottom of the pond	
Discharge (l s^{-1})	50	
Drainage basin of a river	Przemsza	
Altitude	290 m a.s.l.	
Geographical location	Katowice Upland	
Geographical coordinates	N 50°18.399′ E 19°19.422′	
Management	natural monument named "Wywierzyska in Strzemieszyce Wielkie"	
Range of water temperature (°C)	9.0–11.0	
	springhead	springbrook
Location	within 1 m of the spring's source	within 40 m of the source
Dominant type of substrate	loamy sand	loamy sand
Aquatic macrophytes	none	*Sparganium erectum* L., 1753

The number of samples had to be restricted to one per year due to the protection of the spring by Polish law, its small surface area, and the possibility of destroying the spring environment. At each sampling area, macroinvertebrates were collected in June from 2012 to 2015 using a cuboid metal frame with Plexiglass sides (frame dimensions: W 25 cm × D 25 cm × H 50 cm). The frame was placed into the substratum by hand and the topmost 5 cm of sediment was moved into a labeled plastic container using a shovel. At each sampling area, sediments from five randomly placed frames were pooled together in the container and constituted one composite sample. In the laboratory, the sediments were sieved using a 0.5 mm mesh sieve. The macroinvertebrates that remained on the sieve were sorted under a dissecting microscope and then preserved in an 80% ethanol solution.

The majority of faunal groups were identified to the family level with the exception of gastropods and crustaceans, which were identified to the species level using the keys of Glöer [95] for Gastropoda and Eggers and Martens [96] for Amphipoda.

Water temperature, conductivity, pH, concentration of total dissolved solids (TDS) and dissolved oxygen were measured in situ using Hanna Instruments portable meters at the same time as the macroinvertebrates were collected. Furthermore, water samples were collected in plastic bottles for the analyses of other parameters. Nitrates, ammonium, phosphates, chlorides, total hardness, alkalinity, calcium, magnesium and iron were analyzed in the laboratory according to the standard methods of Hermanowicz et al. [97].

From both sampling sites, the shell length (measured from the apex of the shell to the anterior edge of the aperture) of all of the collected specimens was measured to the nearest 0.1 mm using a stereoscopic microscope equipped with a camera and cellSens Standard 1.4 software to determine the size structure of the *P. antipodarum* populations. The entire size range of shell lengths was divided into five (1mm-distanced) classes.

The fecundity of *P. antipodarum*, which was based on the number of embryos in a brood pouch, was assessed for 30 specimens from each sampling site in each year of the study. In total, 240 snails were analyzed. For this study, we selected snails whose shell length was no less than 3.0 mm, because *P. antipodarum* reaches sexual maturity at a length of 3.0 mm [98,99].

2.3. Data Analysis

The taxonomic composition of the macroinvertebrate communities was assessed using the non-metric multidimensional scaling (NMDS) ordination method. The macroinvertebrate abundance data were log (x + 1) transformed and rare taxa (those that occurred in only one sample) were removed from the analysis in order to reduce the noise in the data set [100]. In the NMDS method, the Bray–Curtis was applied as the distance measure to calculate any dissimilarity among the samples. The strength of the ordination was assessed by stress value. The importance of the environmental variables in explaining the structure of the macroinvertebrate communities was tested by Pearson correlation (r) with the sample scores of NMDS dimension. CANOCO for Windows version 5.0 was used for the NMDS [101].

The mean shell length of *P. antipodarum* and the mean number of embryos in a brood pouch were compared between the sampling areas using the t-test. A one-way analysis of variance (ANOVA) was performed for the shell length and the number of embryos in a brood pouch between the years of the study period for each sampling site. The relationships between the shell length of *P. antipodarum* and the number of embryos in a brood pouch was explored using the Pearson correlation coefficient. All of these statistical analyses were performed using Statistica version 13.1. Factors with a $p < 0.05$ were considered to be significant.

3. Results

3.1. Water Chemistry

Most of the water properties were similar at the sampling sites. At both areas of the spring ecosystem, the water was hard, rich in magnesium (calcium-magnesium waters), and well oxygenated, with pH close to neutral values (ca. pH 7) (Table 2). The sampling sites only varied with respect to water temperature. The water was approximately 4 °C colder at the springhead compared to that at the springbrook (Table 2).

Table 2. Water parameters of the sampling sites in the spring ecosystem.

Parameter	Site	Year			
		2012	2013	2014	2015
Temperature (°C)	SH	10.1	9.9	10.0	10.1
	SB	14.1	13.9	14.0	14.2
Dissolved oxygen (mg L $^{-1}$)	SH	7.7	7.8	7.9	7.7
	SB	7.6	7.6	7.8	7.3
pH	SH	7.2	7.3	7.6	7.3
	SB	7.3	7.7	7.7	7.4
Conductivity (μS cm^{-1})	SH	720	799	760	830
	SB	770	798	740	810
Total dissolved solids (mg L $^{-1}$)	SH	460	520	370	410
	SB	380	518	360	400
Chlorides (mg L $^{-1}$)	SH	60	40	42	46
	SB	60	46	44	40
Nitrate nitrogen (mg L $^{-1}$)	SH	2.1	4.6	7.2	5
	SB	4.2	4.4	5.2	8.4
Ammonium nitrogen (mg L $^{-1}$)	SH	0.16	0.09	0.5	0.1
	SB	0.17	0.1	0.05	0.21
Phosphates (mg L $^{-1}$)	SH	0.14	0.11	0.08	0.08
	SB	0.14	0.13	0.07	0.1
Total hardness (mgCaCO$_3$ L $^{-1}$)	SH	435	501.9	405	355
	SB	435	494.7	325	355
Calcium (mg L $^{-1}$)	SH	86.0	104.0	102.0	100.0
	SB	86.0	108.0	92.0	120.0
Magnesium (mg L $^{-1}$)	SH	53.5	58.8	46.5	45.6
	SH	53.5	54.7	53.1	53.4
Alkalinity (mgCaCO$_3$ L $^{-1}$)	SB	285	250	235	290
	SH	240	240	215	285
Iron (mg L $^{-1}$)	SB	0.02	0.05	0.02	0.01
	SB	0.02	0.05	0.18	0.03

Abbreviations: SH—springhead, SB—springbrook.

3.2. Macroinvertebrate Communities

At the springhead, the benthic macroinvertebrate community was composed of nine higher taxonomical groups (Gastropoda, Bivalvia, Crustacea, Oligochaeta, Plecoptera, Trichoptera, Coleoptera, Diptera, Turbellaria), among which gastropods and crustaceans dominated (more than 80% of the total benthic fauna) (Table 3). At the springhead, the gastropods were represented by two species—native *Bythinella* cf. *austriaca* and exotic *Potamopyrgus antipodarum*—while *Gammarus fossarum* and *Asellus aquaticus* represented crustaceans. The density of *P.antipodarum* changed slightly throughout the period of the study and was no greater than 4700 specimens per m^2 (Figure 2), and its share in the assemblage was no greater than 20% (Table 3). The abundance and share of other macroinvertebrates in the benthic macroinvertebrate community did not change significantly (Table 3, Figure 2).

Table 3. Macroinvertebrate taxa at the sampling sites (n—number of individuals, %—percentage share).

Higher Taxa	Family	Species	Springhead								Springbrook							
			2012		2013		2014		2015		2012		2013		2014		2015	
			n	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
Gastropoda	Tateidae	*Potamopyrgus antipodarum* (Gray, 1843)	468	20.0	398	19.1	419	18.8	589	19.9	579	64.0	706	69.5	828	69.0	2303	86.1
	Bythinellidae	*Bythinella* cf. *austriaca* (v. Frauenfeld 1857)	478	20.5	410	19.7	435	19.6	625	21.1	19	2.1	14	1.4	9	0.8	4	0.1
	Lymnaeidae	*Radix balthica* (Linnaeus, 1758)													5	0.4		
		Stagnicola palustris (O. F. Müller, 1774)													9	0.8	6	0.2
	Planorbidae	*Anisus spirorbis* (Linnaeus, 1758)									2	0.2	4	0.4	2	0.2	13	0.5
Bivalvia	Sphaeriidae		24	1.0	28	1.3	33	1.5	37	1.2	35	3.9	29	2.9	63	5.3	52	1.9
Crustacea	Gammaridae	*Gammarus fossarum* Koch, 1836	1123	48.1	943	45.3	1073	48.3	1358	45.8	51	5.6	58	5.7	67	5.6	65	2.4
	Asellidae	*Asellus aquaticus* (Linnaeus, 1758)	5	0.2	6	0.3	4	0,2	7	0.2	3	0.3	4	0.4	2	0.2	3	0.1
Oligochaeta			7	0.3	8	0.4	10	0.4	12	0.4	16	1.8	18	1.8	13	1.1	15	0.6
Hirudinea	Erpobdellidae												1	0.1			1	0.04
Plecoptera	Nemouridae		3	0.1	2	0.1	2	0.1	2	0.1							1	0.04
Trichoptera	Limnephilidae		186	8.0	240	11.5	203	9.1	284	9.6	23	2.5	24	2.4	23	1.9	25	0.9
	Hydroptilidae																12	0.4
Coleoptera	Haliplidae										3	0.3	4	0.4	4	0.3	2	0.1
	Elmidae		3	0.1	2	0.1	3	0.1	2	0.1	5	0.6	3	0.3	4	0.3	4	0.1
Odonata	Coenagrionidae																1	0.04
Megaloptera	Sialidae																1	0.04
Diptera	Chironomidae		25	1.1	27	1.3	29	1.3	28	0.9	169	18.7	151	14.9	171	14.3	164	6.1
	Ceratopogonidae																1	0.04
	Stratiomyidae																1	0.04
Turbellaria			15	0.6	16	0.8	12	0.5	18	0.6								
Number of macroinvertebrates			2337		2080		2223		2962		905		1016		1200		2674	
Density of macroinvertebrates (ind m^{-2})			18,696		16,640		17,784		23,696		7240		8128		9600		21,392	

At the springbrook, seventeen families and one higher taxa (Oligochaeta) were found. Gastropods were the most dominant group and comprised from 66.3% to 87% of all of the benthic macroinvertebrates, and among them, *P. antipodarum* prevailed (Table 3). There was a noticeable increase in the density of this alien species in the fourth year of the study. It increased from 4632 to 18,424 individuals per m^2 between 2012 and 2015 (Figure 2). The share of *P. antipodarum* in the community increased from 64.0% in 2012 to more than 86.1% in 2015 (Table 3). On the contrary, during the four year study period, the density of *B.* cf. *austriaca* decreased from 152 individuals per square meter in 2012 to 32 individuals per square meter in 2015, respectively. On the other hand, the density of other invertebrates did not change noticeably (Figure 2).

The results of the NMDS analysis, which was based on the taxonomic composition of benthic fauna, showed differences between the samples that were collected at the springhead and the samples that were collected at the springbrook. The stress value of the ordination was 0.000413. The first strong axis (eigenvalue 0.9194) grouped the samples from the springhead on the left side, whereas the samples from the springbrook were located on the right side (Figure 3). The first axis was positively correlated with water temperature (Table 4). *Bythinella* cf. *austriaca*, Gammaridae (*Gammarus fossarum* Koch, 1836), Asellidae (*Asellus aquaticus* (Linnaeus, 1758)), Nemouridae, Limnephilidae and Turbellaria were negatively correlated with axis 1 (Table 4), thus demonstrating their preference for colder water. The other axes were distinctly weaker (eigenvalue of axis 2 0.0536, eigenvalue of axis 3 0.0270).

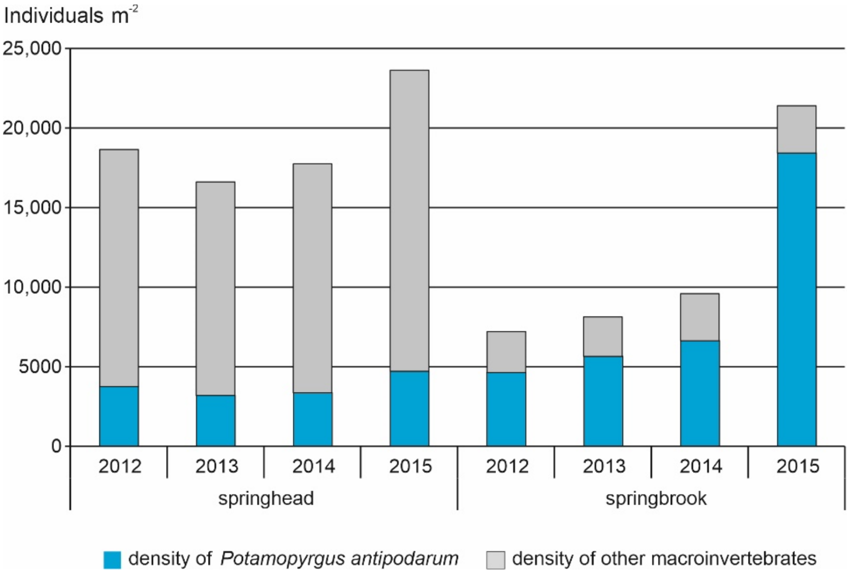


Figure 2. Density of *Potamopyrgus antipodarum* and other macroinvertebrates at the sampling areas during the study period.

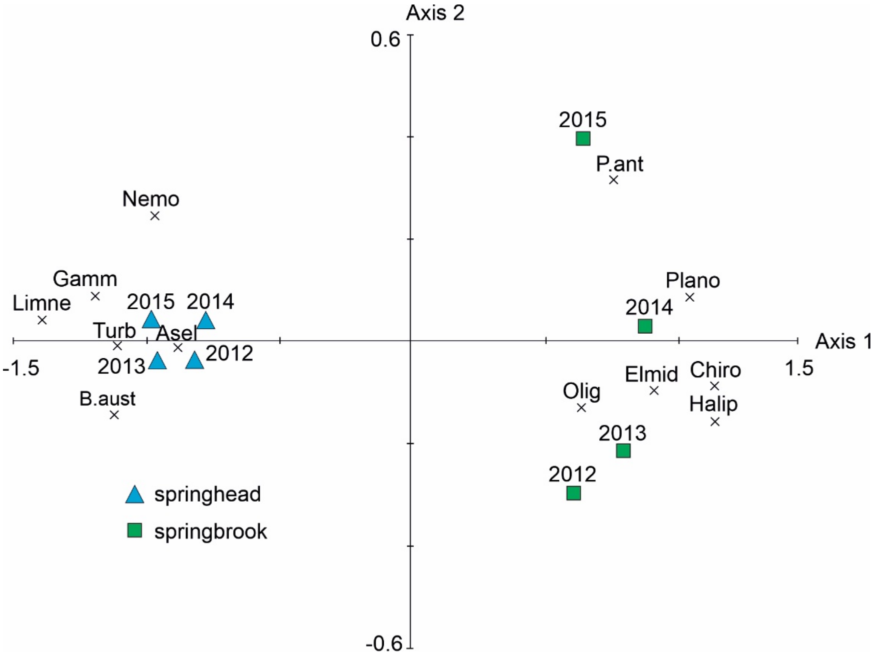


Figure 3. Non-metric multidimensional scaling (NMDS) ordination of the macroinvertebrate taxa at the studied spring ecosystem. Taxa codes: Asel—Asellidae, B.aust—*Bythinella* cf. *austriaca*, Chiro—Chironomidae, Elmid—Elmidae, Gamm—Gammaridae, Halip—Haliplidae, Limne—Limnephilidae, Nemo—Nemouridae, Olig—Oligochaeta, Plano—Planorbidae, P.ant—*Potamopyrgus antipodarum*, Turb—Turbellaria.

Table 4. Statistically significant correlation coefficients between the macroinvertebrate taxa, environmental variable and the NMDS axis 1.

Taxa	Axis 1
Potamopyrgus antipodarum	0.8491 **
Bythinella cf. *austriaca*	−0.9898 ***
Planorbidae	0.9643 ***
Gammaridae	−0.9853 ***
Asellidae	−0.8287 *
Oligochaeta	0.8230 *
Nemouridae	−0.8361 **
Limnephilidae	−0.9882 ***
Haliplidae	0.9851 ***
Elmidae	0.7649 *
Chironomidae	0.9938 ***
Turbellaria	−0.9937 ***
Water temperature	0.9460 ***

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

3.3. Characteristic of the Potamopyrgus Antipodarum Populations

3.3.1. Size-Class Distribution

The shell length ranged from 0.6 mm to 4.7 mm at the springhead and from 0.6 mm to 5.1 mm at the springbrook, respectively. The mean shell length of *P. antipodarum* was significantly smaller at the first site compared to that at the second in each year of the research period (Table 5). The results of one-way ANOVAs indicated no significant difference in the mean shell length between the years of the study period in both sampling areas (Table 5).

Table 5. Shell length (range and mean) and number of embryos per female of *P.antipodarum* (range and mean) in the sampling areas and the results of the statistical tests for the effects of the year (one-way ANOVA tests) and localization of site (t-tests).

Variable	Site	Year				One-Way Anova	
		2012	**2013**	**2014**	**2015**	**F Ratio**	**P**
Shell length (mm)	springhead	0.8–4.7 3.3 ± 0.8	0.6–4.7 3.2 ± 0.9	0.7–4.7 3.2 ± 0.9	0.6–4.7 3.3 ± 0.9	1.741	0.157
	springbrook	0.7–4.9 4.2 ± 0.6	0.6–4.9 4.2 ± 0.4	0.6–5.1 4.1 ± 0.6	0.6–5.1 4.1 ± 0.7	2.315	0.074
	t-test	19.757	25.539	18.848	24.682		
	p	<0.001	<0.001	<0.001	<0.001		
Fecundity (number of embryos per female)	springhead	0–36 15.4 ± 12.5	0–34 14.5 ± 11.9	0–37 14.9 ± 12.2	0–37 15.2 ± 12.5	2.087	0.106
	springbrook	0–41 19.4 ± 12.7	0–42 21.4 ± 12.3	0–39 20.3 ± 10.3	0–42 19.8 ± 12.1	1.775	0.156
	t-test	2.377	2.585	2.159	2.025		
	p	<0.01	<0.01	<0.01	<0.01		

During the period of the field surveys, individuals from tree classes (classes 3, 4 and 5) prevailed in the population of *P. antipodarum* at the springhead and from one class (class 5, shell length >4 mm) at the springbrook, respectively (Figure 4).

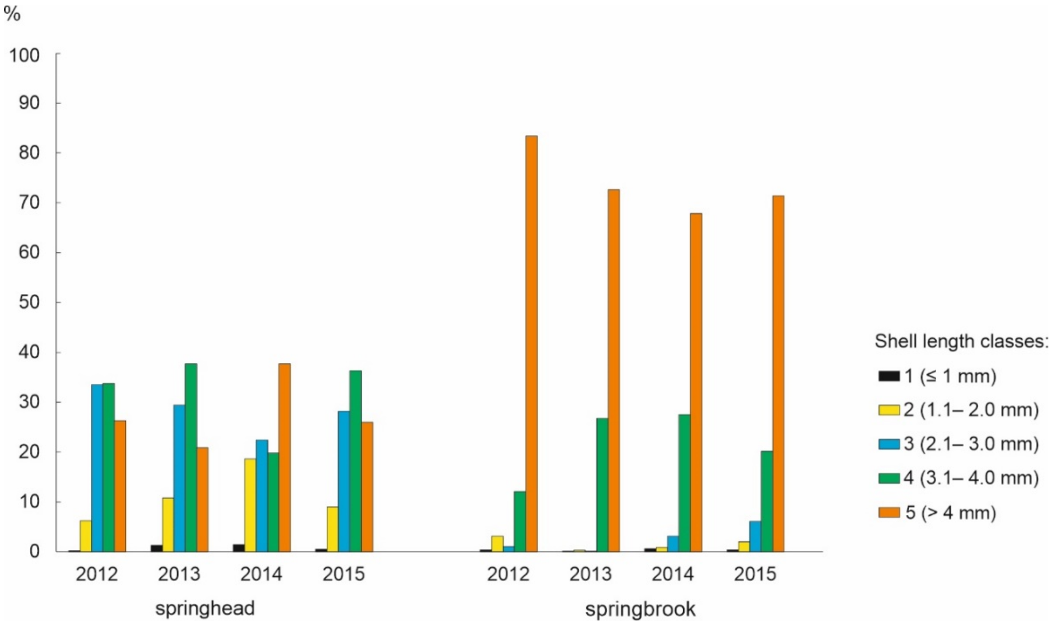


Figure 4. Size (shell length) class distribution of *Potamopyrgus antipodarum* at the sampling areas during the study period.

3.3.2. Fecundity of Potamopyrgus Antipodarum

The population of *P. antipodarum* that was investigated in our study only consisted of females. They became fecund at a size of more than 3.0 mm at both sampling sites. At the springhead, embryos were found in snails as small as 3.7 mm, while at the springbrook, embryos were found in snails as small as 3.4 mm. The number of embryos that were carried ranged from 0 to 37 at the springhead and from 0 to 42 at the springbrook, respectively. In the springbrook, the mean number of embryos in a brood pouch was significantly greater compared to that at the springhead in each year of the study period (Table 5). The results of one-way ANOVA showed no significant difference in the mean number of embryos between the years of the research period in both sampling areas (Table 5). The number of embryos in a brood pouch indicated a significant positive correlation with shell length in the Pearson correlation (the springhead: $n = 30$, R = 0.974, $p < 0.001$; the springbrook: $n = 30$, R = 0.980, $p < 0.001$)

4. Discussion

The discovery of the invasive species *P. antipodarum* in the spring in southern Poland made it possible to follow the colonization process of cold-water spring ecosystems by this species. For this purpose, we monitored two life history traits, i.e., shell size and fecundity, in two areas of the spring ecosystem. We also analyzed whether there were changes in the structure of the benthic communities following the arrival of New Zealand mud snails.

Our study revealed a small population of *P. antipodarum* in the springhead, with no increase in abundance during the four-year study period (see Figure 2). Conversely, in the springbrook, the population increased almost fourfold in the fourth year of the study compared to the first three years (see Figure 2). Given that the study areas differed with respect to water temperature (the water temperature was about 10 °C in the springhead and about 14 °C in the springbrook), we suggest that low temperature may be an important factor limiting the population size of *P. antipodarum*. Although *P. antipodarum* tolerates a wide range of temperature from near 0 °C to 31 °C and is unable to survive for long periods only at temperatures below freezing, temperature can affect the size of its population [102–104]. Our results are consistent with findings by Hall et al. [105], who found that New Zealand mud snail abundance in the colder Gibbon River, Greater Yellowstone Area, USA, was lower compared with warmer streams. In a stream in southern California, the population density of *P. antipodarum* peaked between 15 °C and 20 °C and declined when temperatures exceeded 20 °C [73].

In our survey, temperature had a positive effect on shell size and fecundity of *P. antipodarum*. Larger and more fecund snails occurred in the warmer springbrook compared to the colder springhead. Larger snails also brooded significantly more embryos. Our observed positive impact of temperature was consistent with earlier surveys on size [54,106] and fecundity [58,106–108]. As shown by experimental studies [73,109], the positive effect of temperature on life history has an upper limit. The temperature in the studied spring ecosystem was within the tolerance range [73,110,111] and below the upper limit for fecundity [109]. Our study showed that snail shell size was positively correlated with the number of embryos they brooded, as found previously [53,58,106,112,113].

In this study, the populations of *P. antipodarum* were exclusively composed of females. It should be stressed that beyond its native range, males occur very rarely. In Europe, for example, the share of males in populations did not exceed 10% [114,115]; in many countries, no males were found at all [53], and in Poland, only one male has been detected so far [116]. As shown previously [117], invaders that reproduce parthenogenetically have an advantage, as they are not limited by the difficulty of finding a mate, allowing them to establish a viable population during the early stages of colonization.

Our study showed that the abundance of non-native *P. antipodarum* in the springhead is too low to affect the macroinvertebrates, including native gastropods so far. It is thought that when invader densities are lower than or the same as natives, the negative impact on indigenous species is low [118]. At the springhead, the number of native fauna has not changed significantly. We also did not find any adverse effect on the abundance of native *Bythinella* cf. *austriaca* in this place (see Table 3). This Central European snail species [119] lives in high-quality waters that have a constant temperature of around 10 °C [120]. It has also been observed in small biotopes fed by fresh water with temperatures not exceeding 15 °C, e.g., small ponds, streams and lakes [121]. *B. austriaca*, like other species of the genus *Bythinella*, is considered to be a cold-stenothermic species that prefers well-oxygenated environments [122]. Conversely, the research of Klockmann et al. [123] showed that the occurrence and abundance of *Bythinella dunkeri* was not influenced by temperature, and laboratory experiments revealed its high tolerance toward both high and fluctuating temperatures; therefore, this parameter may not be the critical factor limiting its distribution. This finding may also refer to other species of the genus *Bythinella*, including *B. austriaca*, that are ecologically very similar. Although *B. austriaca* is not nowadays threatened with extinction—it is classified as being of Least Concern (LC), according to the European Red List of Nonmarine Molluscs [119]—threats to springs may directly or indirectly contribute to a decrease in its population. Given that *P. antipodarum* has inhabited the spring for a relatively short time, we cannot draw conclusions with respect to its impact on benthic fauna. It is difficult to assess whether, with increasing density of the invasive snail, the population size of the spring snail *B.* cf. *austriaca* will decrease; thus, further research is required.

Nevertheless, it is important to highlight that the presence of many species, especially endangered or endemic species, in springs is endangered after invasive species settlement, as was the case, for example, of critically endangered red-finned blue-eye in Australian springs [124]. The impact of alien species is magnified in isolated aquatic ecosystems, especially in arid areas devoid of water [125], and they are most harmful in areas with high endemicity of local biota [126]. Once an invasive species is established in a given water body, it can more easily spread to other nearby systems, and the chance of colonization is much greater for nearby populations than those far away [118]. There is a strong need to implement effective management so that promising sites for relocation of endangered species combined with the eradication of invasive species can be identified [124]. According to Davis et al. [25], spring management and removal of alien aquatic species may be more feasible and cost-effective in small springs than for larger aquatic ecosystems. Therefore, their monitoring is very important, which is also confirmed by our research. Taking into consideration the above-mentioned threat to springs, monitoring and management measures should be undertaken to preserve and protect these unique environments [1,7]. Our study constitutes an important contribution to general knowledge of spring ecology, as well as invasive species, since conservation concern for imperiled invertebrates is growing, but action is stalled by data deficiency, according to Rossini et al. [127].

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