Potamopyrgus antipodarum as a potential defender against swimmer’s itch in European recreational water bodies—experimental study

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ABSTRACT

Swimmer’s itch is a re-emerging human disease caused by bird schistosome cercariae, which can infect bathing or working people in water bodies. Even if cercariae fail after penetrating the human skin, they can cause dangerous symptoms in atypical mammal hosts. One of the natural methods to reduce the presence of cercariae in the environment could lie in the introduction of non–host snail species to the ecosystem, which is known as the “dilution” or “decoy” effect. The caenogastropod Potamopyrgus antipodarum—an alien in Europe—could be a good candidate against swimmer’s itch because of its apparent resistance to invasion by European bird schistosome species and its high population density. As a pilot study on this topic, we have carried out a laboratory experiment on how P. antipodarum influences the infestation of the intermediate host Radix balthica (a native lymnaeid) by the bird schistosome Trichobilharzia regenti. We found that the co–exposure of 200 P. antipodarum individuals per one R. balthica to the T. regenti miracidia under experimental conditions makes the infestation ineffective. Our results show that a non–host snail population has the potential to interfere with the transmission of a trematode via suitable snail hosts.

INTRODUCTION

Biodiversity loss and disease emergence have become two of the most challenging issues confronting science and society (Johnson et al., 2009). Different authors indicate the strong correlation between parasite success in ecosystems and the biodiversity of ecological communities (Johnson et al., 2012; Lagrué & Poulin, 2015). Mitchell et al. (2003), Begon (2008), Allan et al. (2009) as well as many others underlined that rapid loss of populations significantly increase disease emergence. Studies concerning the causal relationship between biodiversity and disease emergence in an environment are focused on testing the “dilution effect”, which parasitologists refer to as a “decoy-effect” hypothesis (Combes & Moné, 1987; Johnson & Thieltges, 2010). According to these authors, the “decoy effect”
mechanisms, observed in the case of high biodiversity of ecological communities, concern:
(i) degeneration of invasive parasite stages penetrating the non-target host, (ii) exhausting
of these stages by trying to penetrate the non-target host and (iii) stimulation of defense
mechanisms of the non-target host against invasive stages of parasite. Regardless of the
mechanism, the non-target host becomes the dead-end host, that is the real factor reducing
the parasitic disease emergence (Mehlhorn, 2008).

One of the re-emerging worldwide medical problems connected to parasites of complex
life cycle is cercarial dermatitis, also known as swimmer’s itch (Cort, 1936; Hunter et al.,
1949; Jarcho & Van Burkalow, 1952; Macy, 1952; Hoefler, 1974; Leedom & Short, 1981;
Eklu-Natey et al., 1985; Blankespoor & Reimink, 1991; Loken, Spencer & Granath Jr, 1995;
Pilz, Eisels & Disko, 1995; Lindblade, 1998; Kolářová, Skírnisson & Horák, 1999; Horák
et al., 2015). Marszewska et al. (2016) observed this medical problem in many bathing
localities in Polish Lowland Lakes during the last two years. The dermatitis appears as
an itchy, lumpy rash on the skin that persists for several weeks (Zbikowska, Wójcik &
Grygon-Frankiewicz, 2002). The skin lesions resemble the early stage of chickenpox, and
are a result of penetration by cercariae of bird schistosomes (Zbikowska, 2003). Normally,
cercariae of bird schistosomes develop inside the host snail for six to seven weeks (Amen
& Meuleman, 1992). Cercariae then abandon the mollusk, swim in the water environment
seeking to penetrate the skin of an avian final host; once in the skin they transform to
schistosomulae, then they migrate through the blood or nervous pathway, mature, and
reproduce sexually (Soldánová et al., 2013). If a human becomes the accidental target of
a cercariae attack, an allergic skin reaction may follow, but the worms do not mature in
humans (Kolářová, Horák & Skírnisson, 2010; Horák et al., 2015).

The current increase in the number of swimmer’s itch cases in temperate climate
might be a consequence of both: (i) climate change accompanied by the extension of the
period of active vegetation in freshwater ecosystems, linked with abundant populations
of host snails releasing bird schistosome cercariae, and (ii) people spending more time
in recreational activities (Angilletta Jr, 2006; Rempfer et al., 2010). Biomass of cercariae of
the bird schistosome Trichobilharzia szidati can even reach 4.65 tons per year for a small
eutrophic reservoir (Soldánová, Selbach & Sures, 2016).

The above factors limit safe water recreation (Chamot, Toscani & Rougemont, 1998;
Lévesque et al., 2002; Farahnak & Essalat, 2003; Skírnisson & Kolárová, 2005; Jouet et al.,
2008). Efforts to reduce human cercarial dermatitis have been made by using some
trematode species or by lowering the density of first intermediate host snail populations;
however, such efforts were not always successful (Chapter 1; Loker & Hofkin, 2015). The
mechanical removal of potential intermediate hosts of bird schistosomes brings only
limited positive effects (Dubois, 2003), and the use of molluscicides, however successful
for a short period, has a clear limitation (see as review: King & Bertsch, 2015) or even a
negative impact on local fauna (McCullough, 1992).

The increasing number of cases of human cercarial dermatitis together with our
knowledge on migration of bird schistosomes in mammalian hosts (Horák & Kolárová,
2001; Horák et al., 2008; Horák et al., 2015) foster research on natural methods that may
decrease the risk. As for human schistosomes, biological control has been tested in some
areas (see review: Pointier, David & Jarne, 2011) and promising results have been obtained for the use of applied alien or even invasive snail species for reduction of parasite prevalence in the snail hosts. The “decoy effect” described by Combes & Moné (1987) can be another mode of resolving the problem. Combes & Moné (1987) indicate that Schistosoma mansoni miracidia can fail to actively penetrate non-host snails. We suspect that the same variant of biological control can be useful in the case of bird schistosomes, especially when using the planned alien species for human cercarial dermatitis control—Potamopyrgus antipodarum, which has been present in European waters for years (Boycott, 1936; Walter, 1980; Dorgelo, 1987; Ponder, 1988; Simoes, 1988; Hinz, Boeters & Guenther, 1994; Berg et al., 1997; Carlsson, 2000; Wagner, 2000; Mouthon & Dubois, 2001). The presence of this New Zealand native species has been recorded in several European countries (Gérard & Le Lannic, 2003; Zettler & Richard, 2006; Sousa, Guilhermino & Antunes, 2005; Alonso, 2006; Lewin & Smolinski, 2006; Soler, 2006; Cianfanelli, Lori & Bodon, 2007; Múrria, Bonada & Prat, 2008; Son, Nabozhenko & Shokhin, 2008; Zieritz & Waringer, 2008; Radea, Louvrou & Economou-Amilli, 2008; Arle & Wagner, 2013), but only a few reports have given it the status of invasive species (Brzeziński & Kołodzieczyk, 2001; Gaino et al., 2008; Thomsen et al., 2009). P. antipodarum spreads easily thanks to its wide tolerance to environmental factors and its parthenogenetic reproduction, so a population can start from a single female. In some non–native regions even up to six generations per year can develop (Piechocki & Wawrzyniak-Wydrowska, 2016). P. antipodarum can create populations with densities reaching thousands of individuals per square meter under favorable conditions (Richards, Cazier & Lester, 2001; Hall Jr, Tank & Dybdahl, 2003), but densities may undergo a drastic collapse in a few months (Extence, 1981; Moffitt & James, 2012) or in a longer term (Moore et al., 2012; Gérard, Hervé & Hechinger, 2017). These top-down and bottom-up changes in invaded ecosystems can be extremely temporally dynamic and connected to environmental factors (Moore et al., 2012). Among the reasons for a collapse, an impact of acquired parasites was postulated. Even if parasites cannot complete the life cycle in P. antipodarum due to host–parasite incompatibility (Żbikowski & Żbikowska, 2009), the penetration of miracidia or cercariae through the tegument can be devastating for snails. The expansion of P. antipodarum in European waters and scarce cases of its stable association with a trematode species (Gérard & Le Lannic, 2003; Morley, 2008; Gérard, Hervé & Hechinger, 2017; Żbikowska & Nowak, 2009) resulted in the hypothesis that the introduction of P. antipodarum to the European bathing localities may help eliminate the risk of dermatitis in a safe way.

Our pilot laboratory experiments aimed at evaluating the potential impact of P. antipodarum on the effectiveness of T. regenti (an avian schistosome) miracidia to infect the natural, native host snail Radix balthica.

**MATERIALS AND METHODS**

**Snails**

*Radix balthica* (Linnaeus, 1758) (Pulmonata: Basommatophora: Lymnaeidae) is one of the most common pond snails in Poland (Piechocki & Wawrzyniak-Wydrowska, 2016).
Based on external morphology, these snails are similar to *R. labiata* (Rossmassler, 1835). Therefore, the species-level taxonomy within the *Radix* genus was verified on the basis of anatomical features of the reproductive system (*Schniebs et al.*, 2011). *R. balthica* is the intermediate host for many digenean species, such as bird schistosomes, including *T. regenti* (*Horák, Kolářová & Dvořák, 1998; Cichy, Faltynkova & Żbikowska, 2011*). In the experiment, 40 *R. balthica* individuals with shell height of 8–10 mm (mean size: 9.0 ± 0.1) and shell width of 4–6 mm (mean size: 5.1 ± 0.1) (very susceptible to parasitic invasion) were used. All *R. balthica* individuals came from laboratory breeding cultures of the Department of Invertebrate Zoology at Nicolaus Copernicus University in Toruń, Poland.

*Potamopyrgus antipodarum* (Gray, 1843) (Caenogastropoda, Hydrobioidea, Tateidae) is a mud snail species introduced from New Zealand to Europe in the mid 1850s (*Hubendick, 1950*). In Poland it was first found in Lake Trląg (*Urbański, 1938*). Nowadays it is common in Pomerania, Greater Poland, Masurian Lakeland and Upper Silesia (*Cichy, Faltynkova & Żbikowska, 2011*). In the experiment, parthenogenetic females with shell height of 4 mm (most prevalent during summer season in Poland) were used. The snails were collected from Sosno Lake (53°20′15″N, 19°20′55″E) in May 2016.

**Bird schistosome**

*Trichobilharzia regenti* (Schistosomatidae, Bilharziellinae) was described by *Horák, Kolářová & Dvořák* (1998). As for the maintenance of parasites in the laboratory, the intermediate host snails of *Radix lagotis* were kept in aquaria with sponge filters, fed on lettuce leaves, and repeatedly collected and placed in glass beakers to stimulate release of cercariae after lighting. The definitive hosts, ducks (*Anas platyrhynchos* f. dom.), were kept in cages approved for this purpose (accreditation no. 13060/2014-MZE-17214). Their infection with cercariae was performed as described by *Meuleman, Huyer & Mooij* (1984). After 22 days, the ducks were sacrificed by decapitation to obtain eggs with developing miracidia, and adult trematodes living in the nasal mucosa. The maintenance care and sacrificing of experimental animals was carried out in accordance with European Directive 2010/63/EU and Czech law (246/1992 and 359/2012) for biomedical research involving animals. Experiments have been performed under legal consent of the Expert Committee of the Section of Biology, Faculty of Science, Charles University, Prague, Czech Republic, and the Ministry of Education, Youth and Sports of the Czech Republic under ref. no. MSMT-31114/2013-9.

Four ducks in the patent period (22 days post infection) were sacrificed, and their heads immediately (within 10 h) transported to the Polish laboratory at the temperature of 8 °C. In the laboratory nasal conchae were removed from the duck beaks and torn apart in Petri dish with conditioned tap water to release eggs and hatched miracidia, which were then placed in a dark flask with conditioned tap water at 20 °C. The flask was placed under artificial light. After a few minutes, hatched miracidia were concentrated under illuminated water surface. The larvae were then individually collected with a micropipette.
Experiment I: the infection of *P. antipodarum* snails with miracidia of *T. regenti*

*P. antipodarum* individuals were experimentally infected in Petri dishes (50 mm in diameter) with conditioned tap water at 20 °C. In the experiment two variants were applied—one miracidium per one snail, and five miracidia per one snail. The experiment was performed in 25 replicates. The time of exposure was 20 h, and was adjusted to the duration of the miracidia life span (*Horák et al., 2015*). Then snails were carefully placed into beakers with conditioned tap water at 20 °C, and water in Petri dishes was checked under a stereomicroscope for presence of living or dead miracidia.

Twice a week, the water in incubation beakers was changed, and the *P. antipodarum* individuals were fed. Every day the activity of snails was tested. Dead individuals were immediately checked for parasite infestation. After 60 days all surviving snails were killed and autopsied.

**Experiment II: the infection of *R. balthica* in the presence of *P. antipodarum* with miracidia of *T. regenti***

During this experiment snails were exposed to miracidia in Petri dishes (50 mm in diameter) filled with conditioned tap water at 20 °C. In the experiment, three variants of non–host snail density were applied: 50, 100 and 200 individuals of *P. antipodarum* per one individual of *R. balthica*. The size of experimental *P. antipodarum* groups was determined according to the ratio of number specimens of both snail species per square meter in different Polish water bodies (*Żbikowski & Żbikowska, 2009; Strzelec, Krodkiewska & Królczyk, 2014*). *R. balthica* were placed individually in the central part of the dish, whereas *P. antipodarum* specimens were arranged around them. For each dish with snails, three newly hatched miracidia of *T. regenti* were added, according to a common laboratory procedure (*Lichtenbergová et al., 2011*). The dishes were covered and placed in the incubator (SANYO, Osaka, Japan) at 20 °C and natural photoperiod for 24 h (adjusting the time to the maximum survival of larvae). The experiment was performed in 10 replicates. The three control groups of snails constituted (i) separately placed individual of *R. balthica* with three miracidia (without *P. antipodarum*), and (ii) separately placed individual of *P. antipodarum* with three miracidia (without *R. balthica*)—both in 10 replicates. The additional, third control consisted of only one Petri dish with fifty *P. antipodarum* snails incubated together with fifty miracidia (*Table 1*). After 24 h, the control snails were rinsed with water and placed separately in beakers with conditioned tap water at 20 °C. Similarly to experiment I, the water was changed and the snails were fed twice a week. Every day their activity was observed. Dead individuals were immediately checked for parasite infestation. After 60 days all remaining (living) snails were killed and autopsied.

**Statistical analysis**

The prevalence of *T. regenti* in both snail species populations was counted as percent of specimens of *R. balthica* or *P. antipodarum* with bird schistosome larvae (sporocysts and/or cercariae). In order to verify if the density of *P. antipodarum* accompanying *R. balthica* can affect *T. regenti* miracidia infectivity, logistic regression was used, with the *Potamopyrgus antipodarum* abundance as a predictor variable and infection status of *Radix balthica* as
Table 1  The exposure of host and/or non-host snails on Trichobilharzia regenti miracidia at 20 °C—
Experiment II.

| Number of snails exposed to parasitic larvae* | Number of miracidia | Number of replicates | Experimental condition |
|---------------------------------------------|---------------------|----------------------|------------------------|
| 1 R. balthica + 50 P. antipodarum           | 3                   | 10                   | Experimental          |
| 1 R. balthica + 100 P. antipodarum          | 3                   | 10                   | Experimental          |
| 1 R. balthica + 200 P. antipodarum          | 3                   | 10                   | Experimental          |
| 1 R. balthica                               | 3                   | 10                   | Control               |
| 1 P. antipodarum                            | 3                   | 10                   | Control               |
| 50 P. antipodarum                           | 50                  | 1                    | Control               |

Notes.

*Animals were placed in Petri dishes of 50 mm diameter.

a dependent variable. Snail life time since exposure to miracidia, expressed in number of days, was analyzed by one–way ANOVA, followed by post–hoc Tukey test. Significant differences in the survival rates between infected and uninfected R. balthica were tested using Mann–Whitney U test.

RESULTS

None of the P. antipodarum individuals exposed to T. regenti miracidia in Experiment I or Experiment II were found to be infected. During Experiment I, after 20 h of incubation we did not find parasitic larvae in the water of the Petri dishes, where P. antipodarum snails were individually exposed to three miracidia. Also, no patent infection (with fully developed cercariae) was found in R. balthica specimens experimentally exposed to T. regenti miracidia. Inside the infected snails only sporocysts or sporocysts with immature cercariae were noticed. The effective infestation of R. balthica by T. regenti (Table S1) depended on the number of accompanying P. antipodarum individuals during exposure to miracidia (Table S2). Abundance of Potamopyrgus antipodarum significantly decreased the probability of infection of Radix balthica (logistic regression: Wald statistic = 9.5, df = 1, p = 0.002) (Fig. 1). Almost all control R. balthica individuals (90%), and all R. balthica snails co-incubated with 50 specimens of P. antipodarum exposed to miracidia had parasite sporocysts. The infestation of R. balthica was completely ineffective in the density combination of 200 P. antipodarum per one R. balthica specimen (p < 0.0001). When 100 P. antipodarum individuals were co–exposed to miracidia, up to 40% R. balthica snails were non–infected, however, the difference was not statistically significant if compared with the P. antipodarum—absent control (p = 0.0867).

Experimental conditions had an impact on the life span of snails. All P. antipodarum individuals survived until the end of the experiment (60 days), whereas the life span for R. balthica varied (Table S3). The average survival of R. balthica ranged from 35 to 58 days, and depended on the presence of non–host P. antipodarum snails during exposure to miracidia (one–way ANOVA F₃,₃₆ = 16.85, p < 0.001). Post–hoc tests indicated that the longest survival rate occurred in the case of R. balthica exposed to miracidia in the presence of 200 individuals of P. antipodarum (Fig. 2). Additionally, the Mann–Whitney U test (p < 0.001) indicated that infected R. balthica lived shorter than non–infected ones.
regardless of experimental condition (avg. 34 ± 1 and 57 ± 1 days respectively) (Table S4, Fig. 2). Infected *R. balthica* survived for 18–40 days (range) after exposure to miracidia, while most non-infected *R. balthica* lived until the end of the 60 day experiment.

**DISCUSSION**

Our study indicates that *T. regenti* larvae cannot use *P. antipodarum* as an intermediate host successfully. This is not surprising because all known *Trichobilharzia* species use only Lymnaeidae and Physidae as intermediate hosts (*Horák et al., 2015*). On the other hand, the lack of miracidia in water after 20 h exposure to snails is extremely interesting. It could be the effect of parasitic larvae entering the snail shell or even possible attachment to non-host


*P. antipodarum* body. *Sapp & Loker (2000)* observed miracidia which tended to adhere to incompatible snails, but these larvae could not develop inside a non-host mollusk. It should be noted that according to *King, Jokela & Lively (2011)* trematodes have only one chance when they attach to a snail body—successful infection or death. *Combes & Moné (1987)* described the impact of non-target hosts on parasite success as a “decoy effect” and suggested the “decoy effect” as potentially useful in schistosomiasis control. Unfortunately, the protocol of our experiment did not allow us to track the fate of *T. regenti* miracidia, because the snails were stored in the incubator during the exposure period. Observations after the end of exposure revealed the lack of invasive larvae on Petri dishes, which could be the result of them being swallowed by snails or the effect of the degeneration of the unsuccessful larvae that died during the experiment. The only certainty is that the presence of non-host snails (*P. antipodarum*) of bird schistosome (*T. regenti*) in the neighborhood of native host (*R. balthica*) can affect the parasite transmission success of miracidia. The hatched larvae respond to different environmental stimuli, such as light or gravity, and various chemical compounds released by potential host species (*Hertel et al., 2006*). *Smyth & Halton (1983)* when using the choice-chamber to study miracidial chemo-orientation indicated that nearly half of the tested larvae were attracted by chemical attractants other than those released by their specific host snail. *P. antipodarum* individuals co-exposed to miracidia may have successfully disturbed the access of parasitic larvae to the specific host. However, the lack of data on the chemical composition of *P. antipodarum* mucus does not allow a clear conclusion that the lack of miracidia in water after 20 h exposure to individuals of this species during Experiment I could support our hypothesis.

According to *Sullivan & Yeung (2011)*, miracidia that were experimentally injected into snails were encapsulated inside incompatible hosts, but survived and developed in the compatible ones only. The result shows that real recognition of the intruder by the immune system of the host depends on the internal milieu of the snail. This fact allows us to understand why the imprecise identification of the host by miracidia does not result in snail—Digenea compatibility (*Combes & Moné, 1987*). We suggest that the probable lack of precision in *T. regenti* miracidia orientation could be used for the biological control of this trematode invasion in the environment.

The introduction of an alien snail species into the environment, even to protect people against parasites, may raise doubts concerning long-term consequences of manipulation in the environment: (i) the influence on populations of native snail species, and (ii) the danger of a new parasite–snail association. As for the first consequence, data on the displacement of native European snail species by *P. antipodarum* seem to be exaggerated. Some statistical analysis has shown the coincidence between the appearance of *P. antipodarum* in water bodies and a drop in Simpson’s diversity index. Such an analysis was presented by *Strzelec, Spyr & Krodkiewska (2006)* who used number of individuals as currency in the Simpson’s diversity index. Such an analysis was presented by *Strzelec, Spyr & Krodkiewska (2006)* who used number of individuals as currency in the Simpson’s diversity index. It should be emphasized that the large numbers of the small *P. antipodarum* could easily drive down the Simpson index (or any other abundance-based diversity index) if numbers are used as currency. In our opinion the biomass would be more appropriate currency in such analysis.
The threat of new snail–parasite association seems to be more serious collateral damage to planned manipulation in the environment (Morley, 2008). However, it must be emphasized that P. antipodarum already occurs in European waters, and the possible introduction into recreational waters would only slightly increase its range (Städler et al., 2005). From New Zealand, where this mud snail plays the role of intermediate host for many avian parasite species, there are no reports of infection of P. antipodarum with Trichobilharzia species (Hechinger, 2012), even if Trichobilharzia quequedulae was noted in birds of the Southern Hemisphere (Ebbs et al., 2016). The facts above indicate potentially safe use of P. antipodarum against swimmer’s itch.

The absence of patent infection in R. balthica individuals after an experimental exposure is also of interest. Huňová et al. (2012) underlined that the intramolluscan development of T. regenti needs several weeks. In our experiments, none of the successfully infected R. balthica lived longer than 40 days. The increased mortality of snails experimentally infected with trematodes is widely known (Muñoz Antoli et al., 2007; Kalinda, Chimbari & Mukaratirwa, 2017), especially when juvenile snails are exposed to miracidia. In our experiments, the R. balthica snails that remained uninfected after exposure to T. regenti lived longer than the infected ones (Fig. 2). Many of them survived until the end of the 60 day experiment. As the limiting factor for parasite invasion of R. balthica seems to be the presence of P. antipodarum individuals, it can be concluded that the presence of non–host snails during exposure to miracidia indirectly increased the survival of R. balthica hosts. Although the results do not show clear evidence of the non–invasive nature of P. antipodarum, they may suggest an additional, indirect effect of this snail species on native malacofauna in new areas. Our results highlight the additional aspect of the influence of alien snail species on native malacofauna. Ecologists emphasize the direct changes caused by newcomers (Riley, Dybdahl & Hall Jr, 2008). In our opinion, especially in the case of research on freshwater snails, the aspect of their association with trematodes should be taken into account in analyses concerning the impact of alien species introduction.

**CONCLUSION**

The data represent a pilot study that precedes a wide–planned series of field and laboratory studies focused on the influence of alien molluscan species, namely P. antipodarum, on possible reduction of swimmer’s itch in European recreational water bodies. Our experimental work demonstrates that a high population density of P. antipodarum lowers the transmission of bird schistosomes miracidia to suitable snail hosts such as R. balthica. Further research will focus on the potential ability of P. antipodarum to limit native gastropod infections in natural conditions.

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ADDITIONAL INFORMATION AND DECLARATIONS

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Competing Interests
The authors declare there are no competing interests.

Author Contributions
• Anna Marszewska conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables.
• Anna Cichy analyzed the data.
• Jana Bulantova contributed reagents/materials/analysis tools.
• Petr Horak contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper.
• Elzbieta Zbikowska conceived and designed the experiments, analyzed the data, authored or reviewed drafts of the paper, approved the final draft.

Animal Ethics
The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):
The maintenance and care of experimental animals were carried out in accordance with the European Directive 2010/63/EU and Czech law (246/1992 and 359/2012) for biomedical research involving animals. Experiments have been performed under legal consent of the Expert Commission of the Section of Biology, Faculty of Science, Charles University in
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Data Availability
The following information was supplied regarding data availability:

The raw data are supplied in the Supplemental Files.

Supplemental Information
Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.5045#supplemental-information.

REFERENCES

Allan BF, Langerhans RB, Ryberg WA, Landesman WJ, Griffin NW, Katz RS, Oberle BJ, Schutzenhofer MR, Smyth KN, De St Maurice A, Clark L, Crooks KR, Hernandez DE, McLean RG, Ostfeld RS, Chase JM. 2009. Ecological correlates of risk and incidence of West Nile virus in the United States. Oecologia 158:699–708.

Alonso A. 2006. Rating the impact of environmental degradation on benthic macroinvertebrates at the head of the river Henares. Ecosistemas 15:1–5.

Amen RI, Meuleman EA. 1992. Isolation of mother and daughter sporocysts of Trichobilharzia ocellata from Lymnaea stagnalis. Parasitology Research 78:265–266 DOI 10.1007/BF00931739.

Angilletta Jr MJ. 2006. Estimating and comparing thermal performance curves. Journal of Thermal Biology 31:541–545 DOI 10.1016/j.jtherbio.2006.06.002.

Arle J, Wagner F. 2013. Effects of anthropogenic salinisation on the ecological status of macroinvertebrate assemblages in the Werra River (Thuringia, Germany). Hydrobiologia 701:129–148 DOI 10.1007/s10750-012-1265-z.

Begon M. 2008. Effects of host diversity on disease dynamics. In: Ostfeld RS, Keesing F, Eviner VT, eds. Infectious disease ecology: effects of ecosystems on disease and of disease on ecosystems. Princeton: Princeton University Press, 12–29.

Berg MS Van Den, Coops H, Noordhuis R, Van Schie J, Simon J. 1997. Macroinvertebrate communities in relation to submerged vegetation in two Chara-dominated lakes. Hydrobiologia 342:143–150 DOI 10.1023/A:1017094013491.

Blankespoor HD, Reimink RL. 1991. The control of swimmer’s itch in Michigan: past, present, future. Michigan Riparian 24:7–23.

Boycott AE. 1936. The habitats of fresh-water mollusca in Britain. Journal of Animal Ecology 5:116–186 DOI 10.2307/1096.

Brzeziński T, Kołodziejczyk A. 2001. Distribution of Potamopyrgus antipodarum (Gray, 1843) in waters of the Wigry National Park and the effect of selected habitat factors on its occurrence. Folia Malacologica 9:125–135 DOI 10.12657/fomal.009.015.

Carlsson R. 2000. The distribution of the gastropods Theodoxus fluviatilis (L.) and Potamopyrgus antipodarum (Gray) in lakes on the Åland Islands, southwestern Finland. Boreal Environment Research 5:187–195.
Chamot E, Toscani L, Rougemont A. 1998. Public health importance and risk factors for cercarial dermatitis associated with swimming in Lake Léman at Geneva, Switzerland. *Epidemiology and Infection* 120:305–314 DOI 10.1017/S0950268898008826.

Cianfanelli S, Lori E, Bodon M. 2007. Alien freshwater molluscs in Italy and their distribution. In: Gherardi F, ed. *Biological invaders in inland waters: profiles, distribution, and threats*. Dordrecht: Springer Press, 103–121.

Cichy A, Faltynkova A, Žbikowska E. 2011. Cearcariae (Trematoda, Digenea) in European freshwater snails a checklist of records from over one hundred years. *Folia Malacologica* 19:165–189 DOI 10.2478/v10125-011-0023-6.

Combes C, Moné H. 1987. Possible mechanisms of the decoy effect in *Schistosoma mansoni* transmission. *International Journal for Parasitology* 17:971–975.

Cort WW. 1936. Studies on schistosome dermatitis. IV. Further information on distribution in Canada and in the United States. *American Journal of Hygiene* 24:318–333 DOI 10.1093/oxfordjournals.aje.a118267.

Dorgelo J. 1987. Density fluctuations in populations 1982–1986 and biological observations of *Potamopyrgus jenkinsi* in two trophically differing lakes. *Aquatic Ecology* 21:95–110 DOI 10.1007/BF02255459.

Dubois JP. 2003. Effect of a sediment perturbation on the population of *Radix peregra ovata* in lake Annecy. In: *abstract book of 2nd workshop on bird schistosomes, Annecy*: 31.

Ebbs ET, Loker ES, Davis NE, Flores V, Veleizan A, Brant SV. 2016. Schistosomes with wings: how host phylogeny and ecology shape the global distribution of *Tribobilharzia querquedulae* (Schistosomatidae). *International Journal for Parasitology* 46:669–677 DOI 10.1016/j.ijpara.2016.04.009.

Eklu-Natey DT, Al-Khudri M, Gauthey D, Dubois JP, Wuest J, Vaucher C, Huggel H. 1985. Epidemiologie de la dermatite de baigneurs et morphologie de *Tribobilharzia cf. ocellate* dans le Lac Léman. *Revue Suisse De Zoologie* 92:939–953 DOI 10.5962/bhl.part.81924.

Extence CA. 1981. The effect of drought on benthic invertebrate communities in a lowland river. *Hydrobiologia* 83:217–224 DOI 10.1007/BF00008269.

Farahnak A, Essalat M. 2003. A study on cercarial dermatitis in Khuzestan province, south western Iran. *BMC Public Health* 3:35 DOI 10.1186/1471-2458-3-35.

Gaino E, Scoccia F, Lancioni T, Ludovisi A. 2008. The invader mudsnail *Potamopyrgus antipodarum* in the Tiber River basin (Central Italy). *Italian Journal of Zoology* 75:253–261 DOI 10.1080/11250000701885513.

Gérard C, Hervé M, Hechinger RF. 2017. Long-term population fluctuations of the exotic New Zealand mudsnail *Potamopyrgus antipodarum* and its introduced aporocotylid trematode in northwestern France. *Hydrobiologia* DOI 10.1007/s10750-017-3406-x.

Gérard C, Le Lannic J. 2003. Establishment of a new host-parasite association between the introduced invasive species *Potamopyrgus antipodarum* (Smith) (Gastropoda) and *Sanguinicola* sp. Plehn (Trematoda) in Europe. *Journal of Zoology* 261:213–216 DOI 10.1017/S0952836903004084.
Hall Jr RO, Tank JL, Dybdahl MF. 2003. Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. *Frontiers in Ecology and the Environment* 1:407–411 DOI 10.1890/1540-9295(2003)001[0407:ESDNAC]2.0.CO;2.

Hechinger RF. 2012. Faunal survey and identification key for the trematodes (Platyhelminthes: Digenea) infecting *Potamopyrgus antipodarum* (Gastropoda: Hydrobiidae) as first intermediate host. *Zootaxa* 3418:1–27.

Hertel J, Holweg A, Haberl B, Kalbe M, Haas W. 2006. Snail odour-clouds: spreading and contribution to the transmission success of *Trichobilharzia ocellata* (Trematoda: Digenea) miracidia. *Oecologia* 147:173–180 DOI 10.1007/s00442-005-0239-5.

Hinz W, Boeters HD, Guenther A. 1994. On the freshwater mollusc fauna in the Spanish Province of Cuenca. *Malakologische Abhandlungen* 17:65–81.

Hoeffler DF. 1974. Cercarial dermatitis. *Archives of Environmental Health* 29:225–229 DOI 10.1080/00039896.1974.10666573.

Horák P, Kolářová L. 2001. Bird schistosomes: do they die in mammalian skin? *Trends in Parasitology* 17:66–69 DOI 10.1016/S1471-4922(00)01770-0.

Horák P, Kolářová L, Dvořák J. 1998. *Trichobilharzia regenti* n. sp. (Schistosomatidae, Bilharziellinae) a new nasal schistosome from Europe. *Parasite* 5:349–357 DOI 10.1051/parasite/199805349.

Horák P, Mikeš L, Lichtenbergová L, Skála V, Soldánová M, Brant SV. 2015. Avian schistosomes and outbreaks of cercarial dermatitis. *Clinical Microbiology Reviews* 28:165–190 DOI 10.1128/CMR.00043-14.

Horák P, Mikeš L, Rudolfova J, Kolářová L. 2008. Penetration of *Trichobilharzia* cercariae into mammals: dangerous or negligible event? *Parasite* 15:299–303 DOI 10.1051/parasite/2008153299.

Hubendick B. 1950. The effectiveness of passive dispersal in *Hydrobia jenkinsi*. *Zoologiska Bidrag Från Uppsala* 28:93–504.

Hunter GW, Shillam DS, Trott OT, Howell EV. 1949. Schistosome dermatitis in Seattle, Washington. *Journal of Parasitology* 35:25–254 DOI 10.2307/3273299.

Huňová K, Kašný M, Hampl V, Leontovyc R, Kuběna A, Mikeš L, Horák P. 2012. *Radix* spp.: identification of trematode intermediate hosts in the Czech Republic. *Acta Parasitologica* 57:273–284 DOI 10.2478/s11686-012-0040-7.

Jarcho S, Van Burkalow A. 1952. A geographical study of swimmer’s itch in the United States and Canada. *Geographical Review* 42:212–226 DOI 10.2307/211386.

Johnson PTJ, Lund PJ, Hartson RB, Yoshino TP. 2009. Community diversity reduces *Schistosoma mansoni* transmission, host pathology and human infection risk. *Proceedings of the Royal Society B* 276:1657–1663 DOI 10.1098/rspb.2008.1718.

Johnson PTJ, Preston DL, Hoverman JT, Henderson JS, Paul SH, Richgels KLD, Redmond MD. 2012. Species diversity reduces parasite infection through crossgenerational effects on host abundance. *Ecology* 93:56–64.

Johnson PTJ, Thielges DW. 2010. Diversity, decoys and the dilution effect: how ecological communities affect disease risk. *Journal of Experimental Biology* 213:961–970 DOI 10.1242/jeb.037721.
Jouet D, Ferté H, Depaquit J, Rudolfová J, Latour P, Zanella D, Kaltenbach ML, Léger N. 2008. Trichobilharzia spp. in natural conditions in Annecy Lake, France. *Parasitology Research* **103**:51–58.

Kalinda C, Chimbari MJ, Mukaratirwa S. 2017. Effect of temperature on the *Bulinus globosus*—*Schistosoma haematobium* system. *Infectious Diseases of Poverty* **6**:57 DOI 10.1186/s40249-017-0260-z.

King CH, Bertsch D. 2015. Historical perspective: snail control to prevent schistosomiasis. *PLOS Neglected Tropical Diseases* **9**:e0003657 DOI 10.1371/journal.pntd.0003657.

King KC, Jokela J, Lively CM. 2011. Trematode parasites infect or die in snail hosts. *Biological Letters* **7**:265–268 DOI 10.1098/rsbl.2010.0857.

Kolářová L, Horák P, Skírnisson K. 2010. Methodical approaches in the identification of areas with a potential risk of infection by bird schistosomes causing cercarial dermatitis. *Journal of Helminthology* **84**:327–335 DOI 10.1017/S0022149X09990721.

Kolářová L, Skírnisson K, Horák P. 1999. Schistosome cercariae as the causative agent of swimmer’s itch in Iceland. *Journal of Helminthology* **73**:215–220 DOI 10.1017/S0022149X99000335.

Lagrue C, Poulin R. 2015. Local diversity reduces infection risk across multiple freshwater host-parasite associations. *Freshwater Biology* **60**:2445–2454 DOI 10.1111/fwb.12677.

Leedom WS, Short LB. 1981. *Cercaria pomaceae* sp. n., a dermatitis-producing schistosome cercaria from *Pomacea paludosa*, the Florida apple snail. *Journal of Parasitology* **67**:257–261 DOI 10.2307/3284521.

Lévesque B, Giovenazzo P, Guerrier P, Laverdiere D, Prud’Homme H. 2002. Investigation of an outbreak of cercarial dermatitis. *Epidemiology and Infection* **129**:379–386.

Lewin I, Smolinski A. 2006. Rare and vulnerable species in the mollusc communities in the mining subsidence reservoirs of an industrial area (The Katowicka Upland, Upper Silesia, Southern Poland). *Limnologica* **36**:181–191 DOI 10.1016/j.limno.2006.04.002.

Lichtenbergová L, Lassman H, Jones MK, Kolářová L, Horák P. 2011. *Trichobilharzia regenti*: host immune response in the pathogenesis of neuroinfection in mice. *Experimental Parasitology* **128**:328–335 DOI 10.1016/j.exppara.2011.04.006.

Lindblade KA. 1998. The epidemiology of cercarial dermatitis and its association with limnological characteristics of a northern Michigan Lake. *Journal of Parasitology* **84**:19–23 DOI 10.2307/3284521.

Loken BR, Spencer CR, Granath Jr WO. 1995. Prevalence and transmission of cercariae causing schistosome dermatitis in Flathead Lake, Montana. *Journal of Parasitology* **81**:646–649 DOI 10.2307/3283870.

Loker E, Hofkin B. 2015. Chapter 9: the challenge of parasite control. In: *Parasitology: a conceptual approach*. New York: Garland Science, 576p.

Macy RW. 1952. Studies on schistosome dermatitis in the Pacific Northwest. *Northwest Medicine* **51**:947–950.
Marszewska A, Cichy A, Heese T, Żbikowska E. 2016. The real threat of swimmers’ itch in anthropogenic recreational water body of the Polish Lowland. *Parasitology Research* **115**:3049–3056 DOI 10.1007/s00436-016-5060-z.

McCullough FS. 1992. The role of mollusciciding in schistosomiasis control. WHO/Schist/92.107.

Mehlhorn H. 2008. *Encyclopedia of parasitology*. Heidelberg: Springer.

Meuleman EA, Huyer AR, Mooij JH. 1984. Maintenance of the life cycle of *Trichobilharzia ocellata* via the duck *Anas platyrhynchos* and the pond snail *Lymnaea stagnalis*. *Netherlands Journal of Zoology* **34**:414–417.

Mitchell CE, Reich PB, Tilman D, Groth JV. 2003. Effects of elevated CO2, nitrogen deposition, and decreased species diversity on foliar fungal plant disease. *Global Change Biology* **9**:438–451 DOI 10.1046/j.1365-2486.2003.00602.x.

Moffitt CM, James CA. 2012. Response of New Zealand mudsnails *Potamopyrgus antipodarum* to freezing and near-freezing fluctuating water temperatures. *Freshwater Science* **31**:1035–1041 DOI 10.1899/11-160.1.

Moore JW, Herbst DB, Heady WN, Carlson SM. 2012. Stream community and ecosystem responses to the boom and bust of an invading snail. *Biological Invasions* **14**:2435–2446 DOI 10.1007/s10530-012-0240-y.

Morley NJ. 2008. The role of the invasive snail *Potamopyrgus antipodarum* in the transmission of trematode parasites in Europe and its implication for ecotoxicological studies. *Aquatic Sciences* **70**:107–114 DOI 10.1007/s00027-007-7052-7.

Mouthon J, Dubois JP. 2001. Mollusc communities of the littoral zone of Annecy Lake (Savoie, France). *International Journal of Limnology* **37**:267–276 DOI 10.1051/limn/2001023.

Múrria C, Bonada N, Prat N. 2008. Effects of the invasive species *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca) on community structure in a small Mediterranean stream. *Fundamental and Applied Limnology* **171**:131–143 DOI 10.1127/1863-9135/2008/0171-0131.

Piechocki A, Wawrzyniak-Wydrowska B. 2016. *Guide to freshwater and marine mollusca of Poland*. Poznani: Bogucki Publishing House.

Pilz J, Eisels S, Disko R. 1995. Zerkariendermatitis (swimmer’s itch) Fallbericht einer Zerkariendermatitis durch Trichobilharzia (Digenea, Schistosomatidae). *Der Hautarzt* **46**:335–338 DOI 10.1007/s001050050262.

Pointier JP, David P, Jarne P. 2011. The biological control of the snail hosts of schistosomes: the role of competitor snails and biological invasions. In: Toledo R, Fried B, eds. *Biomphalaria snails and larval Trematodes*. New York: Springer Press, 215–238.

Ponder WF. 1988. *Potamopyrgus antipodarum*—a Molluscan colonizer of Europe and Australia. *The Journal of Molluscan Studies* **54**:271–285 DOI 10.1093/mollus/54.3.271.
Radea C, Louvrou I, Economou-Amilli A. 2008. First record of the New Zealand mud snail Potamopyrgus antipodarum J.E. Gray 1843 (Mollusca: Hydrobiidae) in Greece—notes on its population structure and the associated microalgae. *Aquatic Invasions* 3:341–344 DOI 10.3391/ai.2008.3.3.10.

Rempfer J, Livingstone DM, Blodau C, Forster R, Niederhauser P, Kipfer R. 2010. The effect of the exceptionally mild European winter of 2006–2007 on temperature and oxygen profiles in lakes in Switzerland: a foretaste of the future? *Limnology and Oceanography* 55:2170–2180 DOI 10.4319/lo.2010.55.5.2170.

Richards DC, Cazier LD, Lester GT. 2001. Spatial distribution of three snail species, including the invader Potamopyrgus antipodarum, in a freshwater spring. *Western North American Naturalist* 61:375–380 DOI 10.1080/1125000701885513.

Riley LA, Dybdahl MF, Hall Jr RO. 2008. Invasive species impact: asymmetric interactions between invasive and endemic freshwater snails. *Journal of the North American Benthological Society* 27:509–520 DOI 10.1899/07-119.1.

Sapp KK, Loker ES. 2000. Mechanisms underlying digenean-snail specificity: role of miracidial attachment and host plasma factors. *Journal of Parasitology* 86:1012–1019 DOI 10.1645/0022-3395(2000)086[1012:MUDSSR]2.0.CO;2.

Schniebs K, Gloer P, Vinarski MV, Hundsdorfer AK. 2011. Intraspecific morphological and genetic variability in Radix balthica (Linnaeus, 1758) (Gastropoda: Basommatophora: Lymnaeidae) with morphological comparison to other European Radix species. *Journal of Conchology* 40:657–678.

Simões M. 1988. Distribution in Portugal of Potamopyrgus jenkinsi (Prosobranchia Hydrobiidae). *Iberus* 8:243–244.

Skírnisson K, Kolárová L. 2005. Swimmer’s itch in Landmannalaugar, Iceland. *Laeknabladid* 91:729–736.

Smyth JD, Halton DW. 1983. *The physiology of Trematodes*. 2nd edition. Cambridge: Cambridge University Press.

Soldánová M, Selbach C, Kalbe M, Kostadinova A, Sures B. 2013. Swimmer’s itch: etiology, impact, and risk factors in Europe. *Trends in Parasitology* 29:65–74 DOI 10.1016/j.pt.2012.12.002.

Soldánová M, Selbach C, Sures B. 2016. The early worm catches the bird? Productivity and patterns of Trichobilharzia szidati cercarial emission from Lymnaea stagnalis. *PLOS ONE* 11:e0149678 DOI 10.1371/journal.pone.0149678.

Soler J. 2006. Diversity and distribution of freshwater molluscs in the Community of Madrid (Spain). *Graellsia* 62:201–252 DOI 10.3989/graeellsia.2006.v62.iExtra.119.

Son MO, Nabozhenko MV, Shokhin IV. 2008. The Don River basin is a new stage of expansion of Potamopyrgus jenkinsi (Smith, 1889) (Gastropoda, Hydrobioidae) in Europe. *Doklady Biological Sciences* 419:129–130 DOI 10.1134/S0012496608020178.

Sousa R, Guilhermino L, Antunes C. 2005. Molluscan fauna in the freshwater tidal area of the River Minho estuary, NW of Iberian Peninsula. *Annales de Limnologie-International Journal of Limnology* 41:141–147 DOI 10.1051/limn/2005009.
Städler T, Frye M, Neiman M, Lively CM. 2005. Mitochondrial haplotypes and the New Zealand origin of clonal European Potamopyrgus, an invasive aquatic snail. *Molecular Ecology* **14**:2465–2473 DOI 10.1111/j.1365-294X.2005.02603.x.

Strzelec M, Krodkiewska M, Królczyk A. 2014. The impact of environmental factors on the diversity of gastropod communities in sinkhole ponds in a coal mining region (Silesian Upland, Southern Poland). *Biologia* **69**:780–789 DOI 10.2478/s11756-014-0369-5.

Strzelec M, Spyra A, Krodkiewska M. 2006. Freshwater snails of the sand-pits in Upper-silesia Industrial Area (Poland). *Teka Komisji Ochrony i Kształtowania Środowiska Przyrodniczego* **3**:187–194.

Sullivan JT, Yeung JT. 2011. Incompatibility between miracidia of *Schistosoma mansoni* and *Helisoma duryi* occurs at two stages: penetration and intramolluscan establishment. *Journal of Parasitology* **97**:743–745 DOI 10.1645/GE-2758.1.

Thomsen MS, Wernberg T, Silliman BR, Josefson AB. 2009. Broad-scale patterns of abundance of non-indigenous soft-bottom invertebrates in Denmark. *Helgoland Marine Research* **63**:159–167 DOI 10.1007/s10152-008-0142-7.

Urbański J. 1938. Beiträge zur Kenntnis der Molluskenfauna der Wojewodschaft Poznań. II. *Fragmenta Faunistica Musei Zoologici Polonici* **3**:439–467.

Wagner S. 2000. Mollusk population in the Main River near Muehlheim/Dietesheim, Germany. *Mitteilungen Der Deutschen Malakozoologischen Gesellschaft* **65**:23–33.

Walter JE. 1980. A new snail in the Lake of Zurich Switzerland *Potamopyrgus jenkinsi* New Record Gastropoda Prosobranchia. *Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich* **125**:197–200.

Żbikowska E. 2003. Is there a potential danger of “swimmer’s itch” in Poland. *Parasitology Research* **89**:59–62 DOI 10.1007/s00436-002-0684-6.

Żbikowska E, Nowak A. 2009. One hundred years of research on the natural infection of freshwater snails by trematode larvae in Europe. *Parasitology Research* **105**:301–311 DOI 10.1007/s00436-009-1462-5.

Żbikowska E, Wójcik AR, Grygon-Franckiewicz B. 2002. “Wysypka pływaków” (swimmer’s itch) - dermatota o objawach chorobowych podobnych do zmian wywołanych przez pasożytnicze, alergogenne i jadowite stawonogi. In: Buczek A, Błaszak C, eds. *Stawonogi w Medycynie*. Lublin: Liber, 229–237.

Żbikowski J, Żbikowska E. 2009. Invaders of an invader—trematodes in *Potamopyrgus antipodarum* in Poland. *Journal of Invertebrate Pathology* **101**:67–70 DOI 10.1016/j.jip.2009.02.005.

Zettler ML, Richard D. 2004. Freshwater molluscs from Corsica. Notated collections from summer 2003 with emphasis on *Theodoxus fluviatilis*. *Malakologische Abhandlungen* **22**:3–16.

Zieritz A, Waringer J. 2008. Distribution patterns and habitat characterization of aquatic Mollusca in the Weidlingbach near Vienna, Austria. *Archiv für Hydrobiologie* **166**:271–292 DOI 10.1127/18/2008/271.