IMMUNOLOGY AND HOST-PARASITE INTERACTIONS - ORIGINAL PAPER

Patterns of *Sphaeridiotrema pseudoglobulus* infection in sympatric and allopatric hosts (*Bithynia tentaculata*) originating from widely separated sites across the USA

Gregory J. Sandland[1,2] · James P. Peirce[3,2]

Abstract

In circumstances where populations of invasive species occur across variable landscapes, interactions among invaders, their parasites, and the surrounding environment may establish local coevolutionary trajectories for the participants. This can generate variable infection patterns when parasites interact with sympatric versus allopatric hosts. Identifying the potential for such patterns within an invasive-species framework is important for better predicting local infection outcomes and their subsequent impacts on the surrounding native community. To begin addressing this question, we exposed an invasive snail (*Bithynia tentaculata*) from two widely separated sites across the USA (Wisconsin and Montana) to the digenean parasite, *Sphaeridiotrema pseudoglobulus*, collected from Wisconsin. Parasite exposures generated high infection prevalences in both sympatric and allopatric snails. Furthermore, host survival, host growth, the proportion of patent snails, and the timing of patency did not differ between sympatric and allopatric combinations. Moreover, passaging parasites through snails of different origins had no effect on transmission success to subsequent hosts in the life cycle. However, the number of parasites emerging from snails and the pattern of their release varied based on snail origin. These latter observations suggest the potential for local adaptation in this system, but subsequent research is required to further substantiate this as a key factor underlying infection patterns in the association between *S. pseudoglobulus* and *B. tentaculata*.

Keywords *Bithynia tentaculata* · Coevolution · Local adaptation · Species invasion · *Sphaeridiotrema pseudoglobulus*

Introduction

Species invasions are critical threats to the integrity and diversity of native communities worldwide (Simberloff et al. 2013; Macic et al. 2018; Blackburn et al. 2019). When evaluating species invasions across animal groups, mollusks, and more specifically gastropods, are some of the most common, widespread, and detrimental invaders (Alonso and Castro-Diez

2008; Strayer 2010; Horgan et al. 2014). A key concern regarding these invaders is that they can serve as hosts for a number of parasite taxa, including nematodes and digenean flatworms, that pose risks for native species (Kim et al. 2002; Karatayev et al. 2012; Teem et al. 2013). For instance, in the Southern United States, the invasive snail, *Melanoides tuberculatus*, harbors a trematode (*Centrocestus formosanus*) that infects the gills of numerous native fish species causing host morbidity and mortality (Mitchell et al. 2000; Mitchell et al. 2005; Fleming et al. 2011). This has generated concern for the native fish communities currently experiencing infections and those in other habitats at risk of invasion by the snail and its parasite (Mitchell et al. 2005).

Given that many invasive gastropods are widespread, they have the potential to interact with parasites across a range of environmental conditions, which, in turn could modulate coevolutionary trajectories and infection outcomes among different locations (Lively 1998). For snail-digenean interactions, the strong reciprocal selection between participants, migration rates of parasites relative to their hosts, and high

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✉ Gregory J. Sandland
  gsandland@uwlax.edu

1   Department of Biology, University of Wisconsin-La Crosse, 1725 State Street, La Crosse, WI 54601, USA

2   River Studies Center, University of Wisconsin-La Crosse, 1725 State Street, La Crosse, WI 54601, USA

3   Department of Mathematics, University of Wisconsin-La Crosse, La Crosse, WI 54601, USA

parasite virulence are expected to favor digeneans that are locally adapted to their gastropods (Lively 1999; Gandon and Michalakis 2002). Under this scenario, parasites are predicted to exhibit higher fitness (i.e., infection prevalence, and offspring production) when infecting local (sympatric) snails compared to those from other locations (allopatric hosts). Empirical tests of this theory have generated mixed results. For example, Lively (1989), Manning et al. (1995), and Ibikounlé et al. (2012) reported expected outcomes, with trematodes being better able to infect/exploit sympatric snail hosts compared to allopatric combinations, even at relatively small spatial scales. However, in a number of other cases, there has been either no consistent evidence for local adaptation (Coelho et al. 2009; Dar et al. 2013), or higher infection estimates in allopatric host-parasite combinations (Gasnier et al. 2000). From a species-invasion standpoint, understanding the coevolutionary dynamics of hosts and parasites from distinct geographic locations could provide important insights into the impacts that these interactions have on native communities and how uninfected invaders might respond to parasite exposures as they establish in new, uninfested areas (Adlard et al. 2015).

Bithynia tentaculata is a dioecious aquatic snail that was first introduced into the Great Lakes from Europe in the late 1800s. Since that time, the snail has been reported from a number of additional waterbodies throughout North America including those in Quebec and Ontario, Canada (Gibson et al. 1972; Menard and Scott 1987; Lepitzki et al. 1994; Désy et al. 2000), lakes and rivers in the Eastern United States (Jokinen 1992; Harman 2000), lakes in Minnesota (Roy et al. 2016), the Mississippi River (Sauer et al. 2007; Weeks et al. 2017), and waterbodies in Montana, including Georgetown Lake (GTL) (Perez et al. 2016; DuBois 2017). At a number of these locations, the discovery of *B. tentaculata* has coincided with waterfowl mortality events attributed to trematode parasites that are transmitted through these snails. Three of these parasites, *Cyathocotyle bushiensis* (Khan, 1962), and two species of *Sphaeridiotrema* (*S. globulus* (Rudolphi, 1814) and *S. pseudoglobulus* (McLaughlin et al. 1993)), can utilize *B. tentaculata* as both first- and second-intermediate hosts (Gibson et al. 1972; Menard and Scott 1987; Lepitzki et al. 1994; Herrmann and Sorensen 2009; Sandland et al. 2013, 2014); *C. bushiensis* and *Sphaeridiotrema* spp. have been found in *B. tentaculata* populations from Montana and Wisconsin (Sauer et al. 2007; Sandland et al. 2013, 2014; Sandland pers. obs.).

Given the relatively wide distribution of *B. tentaculata* and its parasites across North America, and the potential for local adaptation in digenean-snail interactions, we undertook a study investigating infection patterns in hosts from two distant populations (WI and MT) exposed to *Sphaeridiotrema pseudoglobulus* acquired from WI. Results from this work may not only provide insights into the potential for local

adaptation in this system, but could also help to better predict the risk of naïve *B. tentaculata* becoming infected with *S. pseudoglobulus* in newly invaded habitats.

Materials and methods

Host material

In July 2017, adult *B. tentaculata* were haphazardly collected from Georgetown Lake (GTL), MT. (July 7) and Pool 8, WI. (July 13) which are separated by > 1700 km (Fig. 1). Georgetown Lake was created in 1885 in order to generate power for the surrounding communities. It now primarily serves as a recreational destination and as a source of water for local agriculture. The lake is a high-elevation site (approximately 1940 m above sea level) that covers 1140 ha; the average lake depth is 4.9 m (Georgetown Lake Montana 2019). Our sampling location at GTL (Comers Point; 46.1808° N, 113.3176° W) was comprised primarily of rocky substrates, including cobbles (64–256 mm) and boulders (> 256 mm). The second collection site was a rocky breakwater on the eastern side of Navigation Pool 8 of the Upper Mississippi River (43.6776° N, 91.2232° W) just north of the town of Stoddard, WI., which has served as one of our primary collection sites for the past 7 years. Pool 8 occurs between Lock and Dam 7 near Dresbach, MN, and Lock and Dam 8 at Genoa, WI. It spans a total of 37.7 km in length and encompasses approximately 8700 ha (Upper Mississippi River Restoration Program Long Term Resource Monitoring 2018; Carhart and De Jager 2019). The pool is approximately 190 m above sea level with an average depth < 2 m. The shoreline at our collection site was comprised of rocky substrates including riprap (150–250 mm) and boulders, which transitioned to sand approximately 2–3 m from shore.

For the GTL sample, all collected snails (> 400 individuals) were first added to 1-L plastic bags filled with lake water and then immediately placed on ice within a darkened cooler for transport back to UW-La Crosse (approximately 48 h later). Water temperature was monitored in each of the collection bags during the return trip to UW-La Crosse; temperatures remained between 2 and 3 C throughout that period. Once at the university, snails were placed into 250-mL plastic cups (with well-water) in groups of 10–12 individuals/cup. Snails were fed lettuce ad libitum and water was refreshed every 3 days; snails were maintained at room temperature (22–24 °C) on a natural light:dark cycle.

Adult bithyniids collected from Pool 8 (> 400 individuals) were immediately transported back to UW-La Crosse and placed in a darkened refrigerator (3–4 °C) for 24 h. This was done to approximate the conditions experienced by the GTL snails during transport from Montana to UW-La Crosse. After this period, snails were added to 250-mL cups in groups of

10–12 where they were maintained in the same manner as snails from MT.

On 16 July 2017, snails from each location were transferred into new plastic cups where they laid eggs masses over the following 4 days. After that time, adults were removed from the cups and eggs were reared to hatching (15–23 days later). Removal of adult snails weeks prior to egg hatching prevented any cercarial transfer from infected parents to the offspring that were used in the experiment. Once hatching began in a cup, ground lettuce was added and water was refreshed every 3–4 days. When juvenile snails were 1–3 mm in size, they were transferred to smaller cups (100 mL) in groups of 20–30 individuals. Snails were again fed lettuce ad libitum and water was refreshed in these cups every 3–4 days. Juveniles were exposed to a natural light:dark photoperiod and maintained at room temperature (22–24 °C) during their rearing period. On 13 April 2018, cups containing juveniles from each location were transferred into an environmental chamber (Thermo Scientific) maintained at 22 °C on a 14-h-L:10-h-D photocycle. This was done to allow snails to acclimate to chamber conditions for approximately 3 weeks prior to the onset of the experiment. Total time between snail hatching and the start of the experiment was designed to minimize the influence of non-genetic factors (such as maternal effects) on infection outcomes in hosts collected from the two locations.

Parasite material

On 11 April 2018, we received two dead lesser scaup from 2 locations in Navigation Pool 7 of the UMR: a mature female from the shallows around Arrowhead Island (43.8989° N, 91.2858° W) and a mature male collected from the ABC Islands (43.8732° N, 91.3074° W). Birds were immediately placed in a refrigerator (3–4 °C) until necropsy on 13 April 2018. To acquire parasite eggs, the small intestine was first removed from the body of each bird and then opened longitudinally. Adult *S. pseudoglobulus* worms were removed and transferred into standard Petri plates with well water where they were teased apart to acquire eggs. Once eggs were removed from numerous worms, they were concentrated (by slowly swirling the water in each plate) and transferred to new Petri plates containing fresh well water. Parasite identification was determined using both adult worm and egg metrics (McLaughlin et al. 1993; McKindsey and McLaughlin 1994). Petri plates were then placed in a darkened drawer (at 22–24 °C) for 20 days after which they were removed and placed under incandescent light to induce miracidial hatching.

Exposures of first-intermediate hosts

On 03 May 2018, snails were placed individually into 3-mL plastic wells (Costar 24-well plates) with 2 mL of well-water and either sham-exposed (control) or exposed to 10 actively swimming miracidia (< 2 h old). The experiment included 90 bithyniids from GTL ($n = 31$ controls; $n = 59$ exposed) and 91 individuals from Pool 8 ($n = 33$ controls; $n = 58$ exposed). Attempts were made to size-match snails between locations (GTL and Pool 8) and treatments (sham-exposed controls and exposed). One hour after exposure, wells were checked to ensure that snails were out and active, and were not retracted

Fig. 1 *Bithynia tentaculata* collection locations in the USA (Map a). Snails were acquired from Georgetown Lake Montana (MT-Inset b) and Pool 8 of the Upper Mississippi River, Wisconsin (WI-Inset c) in 2017. Stars (★) identify the location within each state where snails were collected
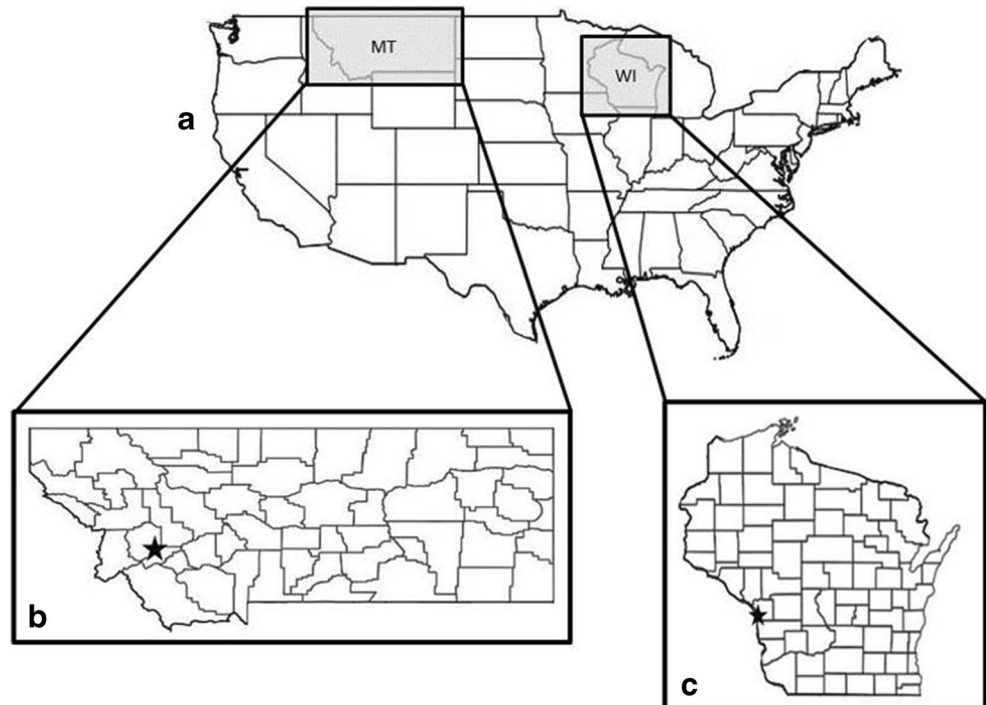
into their shells with the operculum closed. Control snails were treated in exactly the same manner but lacked parasite exposure. Snails were then placed back into the environmental chamber overnight. The following day, snails from each well were measured and transferred individually into 90-mL cups (Solo©) containing 70 mL of well water. Lettuce was added to each cup and snails were placed back into the chamber. Well water was replaced in each cup weekly, and snails were fed lettuce twice per week to maintain ad libitum conditions. Snails were measured weekly from the top of the spire to the bottom lip of the aperture using digital calipers. After each weekly measurement, > 50% of the snails were repositioned within the environmental chamber to reduce any potential influence of location on host and/or parasite responses. During the last 3 weeks of the experiment (weeks 8–10), snail wet-weights were determined in addition to lengths for all individuals. To acquire wet-weights, snails were patted dry using paper towel (to remove excess water) and then placed on to a standard balance.

At the start of week 5, snails were transferred from their cups to individual 17-mL plastic wells containing 12 mL of well water. This was done at 6:00 h when the lights came on in the chamber. After this, snails were assessed for cercarial shedding every 2 h until 20:00 h (lights off) using a dissecting microscope (× 10–20 magnification). Assessments continued weekly, until cercarial release was first observed. Once shedding had started, all snails were again isolated in 17-mL wells (Costar 6-well plates) with 12 mL of well water. Wells were checked hourly (from 6:00 to 22:00 h) for the presence of swimming cercariae indicating the infection had reached patency. If cercariae were observed in a well, that snail was identified as patent. These counts were used to generate prevalence values during weeks 9 and 10. At the end of week 10, all snails from control and exposed treatments were necropsied to determine snail sex and infection status. This endpoint was established to minimize the effects of cercarial re-infection on the life-history responses of shedding snails. Snail sex was determined based on the presence/absence of a penis (on top of the head).

During week 9, water samples (containing cercariae) were collected hourly from the wells of a subsample of infected, size-matched snails (2 females and 4 males/treatment) from 6:00 to 22:00 h. Each sample was added to a standard Petri plate, and then fixed with 70% EtOH. Wells (containing snails) were then refilled with fresh well-water and placed back into the environmental chamber. The following day, intact cercariae (plus cercariae tails) were counted in the Petri plate samples using a dissecting microscope at × 20–30 magnification. We repeated this procedure for the same subsample of infected snails during week 10.

Exposures of second-intermediate hosts

In order to more thoroughly assess parasite fitness based on snail origin, we gathered a second sample of cercariae from hosts during week 10 (1 day after the collection outlined above) and used them to assess transmission to naïve, second intermediate-host snails. For this experiment, parasites were collected from 5 size-matched infected snails from each of the two locations (Pool 8 or GTL). Cercariae were collected using the same procedure outlined above, but for this experiment, snails were shed for a single hour (16:00–17:00 h) to ensure larval viability. Once collected, cercariae were pooled based on snail origin. Twenty uninfected lab-reared bithyniids (originating from Pool 7 of the UMR) were size-matched and then individually exposed to 20 vigorously swimming cercariae shed from either GTL or Pool 8 hosts ($n = 10$ snails/treatment). One week later, these snails were necropsied and the numbers of encysted metacercariae were recorded.

Data and statistical analyses

Because some of the snails died early on in the experiment (and early on in parasite development), we were unable to differentiate between exposed-uninfected snails and exposed-infected individuals. Furthermore, we were not confident sexing bithyniids at these early time points due to their small sizes. Therefore, our survival analysis (using binary logistic regression) was restricted to two levels of exposure status (exposed or control) and two levels of snail origin (GTL and Pool 8). Any snails dying before the end of the experiment were excluded from subsequent analyses. A total of 85 GTL snails ($n = 31$ controls; $n = 54$ infected) and 80 Pool 8 snails ($n = 29$ controls; $n = 51$ infected) survived until the end of the study.

At the start of the experiment (week 0), snail sizes were compared using 3-way ANOVA where snail origin (GTL or Pool 8), sex (male or female), and infection status (infected or control) were used as main effects in the model. Snail size was found to differ based on origin ($F_{1,157} = 6.361$, $P = 0.045$) with individuals from GTL being larger (6.18 ± 0.14 mm) than those from Pool 8 (5.76 ± 0.14 mm). To control for this, we subtracted snail sizes at week 0 from their final sizes at week 10 to get an estimate of growth during the study These estimates were then compared among treatments (after $\log_{10}$ transformation) using 3-way ANOVA; the main effects in the model were the same as those listed for the week 0 analysis.

Binary logistic regression was used to investigate differences in snail patency at weeks 9 and 10. Both snail origin and snail sex were used as predictor variables in these analyses. In order to compare the numbers of cercariae shed from a subsample of snails, we first standardized cercarial release based on snail weight. This allowed us to calculate estimates of cercariae release per centigram (wet-weight) of snail tissue.

These data were then used in a Repeated-Measures ANOVA, where time (weeks) and snail origin were incorporated as main effects into the model. To assess transmission success at subsequent stages in the life cycle, a t test was used to compare the number of *S. pseudoglobulus* metacercariae that successfully established in second-intermediate hosts after passage through *B. tentaculata* from GTL or Pool 8.

Results

Host life-history responses

Neither snail origin nor *S. pseudoglobulus* exposure served as good predictors of snail survival during the study (origin: Wald = 2.35, df = 1, $P = 0.125$; exposure status: Wald = 0.87, df = 1, $P = 0.351$). In fact, survival remained relatively high (> 87%) in snails across all of the experimental treatments.

Three-way ANOVA revealed significant effects of sex ($F_{1,157} = 5.21$; $P = 0.024$) and infection status ($F_{1,157} = 19.54$; $P < 0.001$) on snail growth during the 10-week study, with females growing more than males and infected snails growing more than control snails (Fig. 2). Neither snail origin nor any of the interaction terms were significant (all $P > 0.09$) at the end of the study.

Parasite life-history responses

Binary logistic regression revealed no effect of either snail origin or snail sex on the proportions of patent (shedding) snails during week 9 (all $P > 0.38$) and week 10 (all

$P > 0.62$); however, the proportions of shedding snails in each treatment increased over the 2-week period (Fig. 3). Necropsies of shedding and non-shedding snails at the end of the experiment revealed *S. pseudoglobulus* rediae in all exposed individuals from both sympatric and allopatric groups.

For weeks 9 and 10, the onset of cercarial shedding began after 15:00 h and ceased once the lights shut off in the environmental chamber (20:00 h) (Fig. 4a, b). The magnitude and shape of cercarial release were similar for snails during week 9 (Fig. 4a), but varied during week 10 (Fig. 4b). This led to a significant interaction between time and snail origin (repeated-measures ANOVA: $F_{1,10} = 5.93$; $P = 0.035$), where cercarial emergence from the sympatric host combination was greater than the allopatric combination at week 10 (Fig. 5).

Infections in second-intermediate hosts

There was no difference in the numbers of successfully encysted metacercariae ($t_{18} = 0.63$; $P = 0.54$) in naïve snails exposed to *S. pseudoglobulus* cercariae shed from either sympatric or allopatric hosts. On average, 77% (15.4 ± 0.50) of the cercariae from allopatric *B. tentaculata* and 80% (16.0 ± 0.82) of the larvae from sympatric snails successfully established as metacercariae in second-intermediate hosts.

Discussion

Bithynia tentaculata has emerged as an important, invasive species in North American waterbodies due to its potential

Fig. 2 Mean growth (mm) of male and female snails from Pool 8, WI, and Georgetown Lake (GTL), MT that were either sham-exposed (control) to or exposed-infected by *Sphaeridiotrema pseudoglobulus* acquired from the Upper Mississippi River, WI
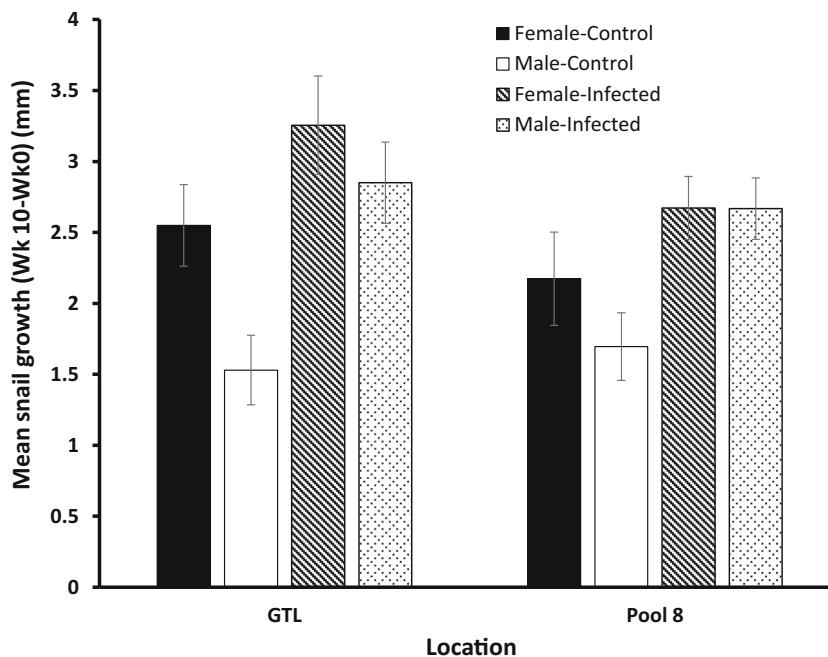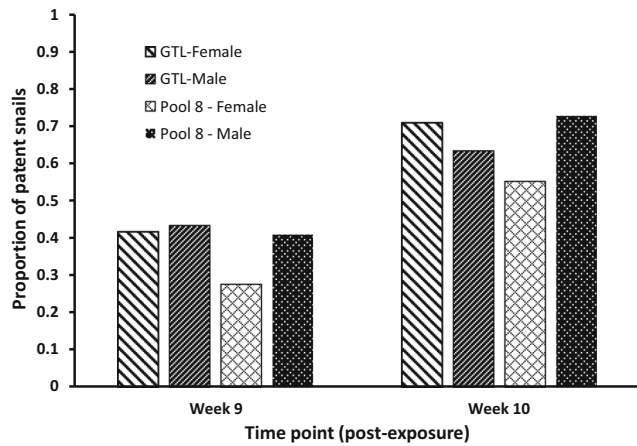
Fig. 3 Proportion of male and female snails from Pool 8,WI, and Georgetown Lake (GTL), MT shedding *Sphaeridiotrema pseudoglobulus* cercariae during weeks 9 and 10 of the experiment

to directly impact native species (Harman 2000) and its capacity to facilitate outbreaks of wildlife disease by transmitting digenean parasites to migrating waterfowl (Gibson et al. 1972; Hoeve and Scott 1988; Herrmann and Sorensen 2011). Although *B. tentaculata* invasion is widespread across areas of North America, little information exists regarding
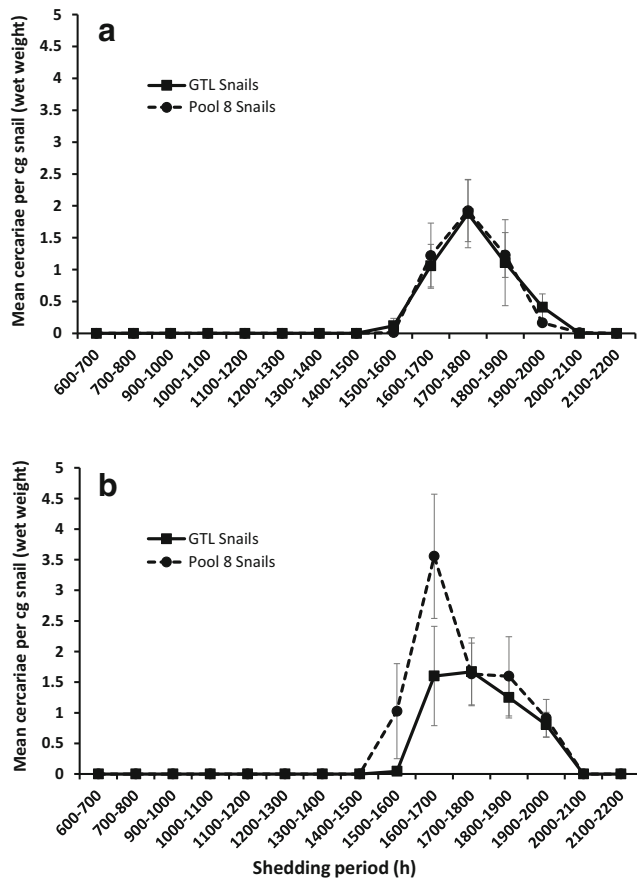

Fig. 4 Patterns of *S. pseudoglobulus* cercarial emergence (per cg wet-weight of host) from Pool 8 (sympatric) and Georgetown Lake (GTL) (allopatric) snails during **a** week 9 and **b** week 10 post-exposure

coevolutionary dynamics within this system and what these patterns might mean for native communities in different locations.

Infection prevalence is often compared between sympatric and allopatric host-parasite combinations in order to elucidate the strength of local adaptation in digenean-snail interactions (Lively 1989; Manning et al. 1995; Morand et al. 1996; Tchuem Tchuente et al. 1999; Krist et al. 2000; Southgate et al. 2000; Osnas and Lively 2004). In our study, prevalence of *S. pseudoglobulus* infection did not differ between sympatric and allopatric snail combinations, which was somewhat surprising given the distance (> 1700 km) between collection locations, the altitudinal difference between sites, and reports of local adaptation from previous studies (Lively 1989; Manning et al. 1995; Morand et al. 1996). One explanation for the pattern observed in our study is that the snails found in the UMR and GTL have similar genetic backgrounds, particularly at loci mediating *S. pseudoglobulus* infection. Recent work using microsatellites has shown that *B. tentaculata* from the UMR share a number of alleles with snails from GTL (Perez et al. 2016), likely indicating that these two populations originated from the same initial invasion location. If snails from the two populations also share alleles under selection (such as those involved in initial parasite recognition and encapsulation), infection differences would be less-pronounced or non-existent between the sympatric and allopatric parasite-host combinations (Kaltz and Shykoff 1998). Alternatively, parasite factors such as the diversity of genotypes represented in our exposures (Theron et al. 2014; Galinier et al. 2017) and/or the capacity of individual *S. pseudoglobulus* miracidia to infect an array of host genotypes could also have led to the prevalence patterns seen here, even if differences exist in the genetic backgrounds of *B. tentaculata* from the two populations. Procedurally, the miracidial dose used in our study may also have contributed to the prevalence pattern as it was higher (n = 10 larvae/snail) than those used in some of the previous
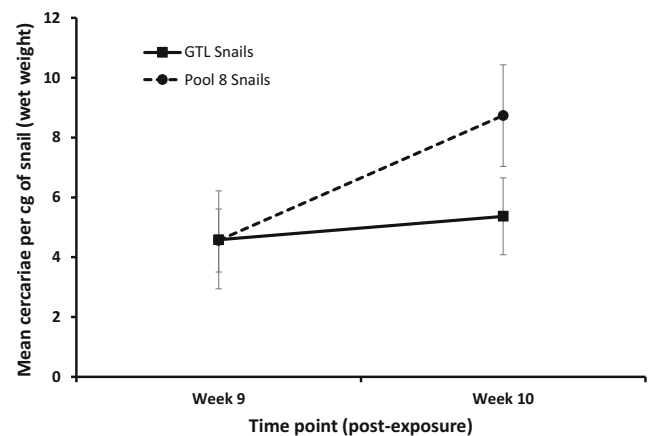

Fig. 5 Mean number of *S. pseudoglobulus* cercariae emerging (per cg wet-weight of host) from Pool 8 (sympatric) and Georgetown Lake (GTL) (allopatric) snails during weeks 9 and 10 post-exposure

investigations reporting parasite local adaptation (i.e., Manning et al. 1995). Given that higher miracidial doses can result in higher parasite prevalences (Theron et al. 2014), even in allopatric snails (Lima et al. 2019), it is possible that our larval numbers overwhelmed defense mechanisms (such as hemocytes and/or lectins) that would have otherwise been successful if GTL *B. tentaculata* had been exposed to fewer parasites.

Although *S. pseudoglobulus* prevalence did not differ between sympatric and allopatric snails, significantly more cercariae emerged from sympatric hosts at certain points during patency. Furthermore, the shape of cercarial release differed between sympatric and allopatric combinations. These results suggest that the degree of "compatibility" between parasites and their hosts may emerge at later points in the infection process (i.e., after successful parasite establishment) (Hall and Ebert 2012). Support for this idea comes from other digenean-snail systems as well. For instance, Munoz-Antoli et al. (2010) found no difference in infection prevalence between sympatric and allopatric snails exposed to *Euparyphium chinensis*; however, host life-span, patency period, and overall cercarial production were greater in sympatric host-parasite combinations. Although our observations are suggestive of parasite local adaptation, further support requires fully balancing host exposures (Kawecki and Ebert 2004) by including parasites from additional populations, such as GTL. Expanding future experiments to include both hosts and parasites from a number of different locations across North America will help to better resolve whether the cercarial emergence patterns observed in this study are the result of local adaptation or are simply due to inherent characteristics of snail hosts from particular locations.

Even though the numbers of *S. pseudoglobulus* cercariae shed from sympatric and allopatric snails differed, the timing of cercarial emergence was relatively consistent across host-parasite combinations, occurring between 15:00 and 20:00 h in weeks 9 and 10. Previous preliminary experiments have shown similar shedding patterns for this parasite-host interaction as well (Sandland, pers. obs.). Distinct temporal cycles of cercarial emergence are often presumed to be adaptive, favoring transmission of these relatively short-lived larvae to subsequent hosts in the life cycle (Theron 2015; Hannon et al. 2018). For *S. pseudoglobulus*, the relatively narrow window of cercarial emergence may correspond with a number of biotic and/or abiotic factors that enhance transmission. For example, the timing of larval release may correspond to daily periods when second-intermediate hosts are in close proximity (Bell et al. 1999; Theron 2015), perhaps due to temporal patterns in behaviors such as feeding, reproduction, and/or predator-avoidance. Another possibility is that larval emergence occurs during periods when cercarial predators (such as fish, or aquatic invertebrates) are less active or are at relatively low numbers (Shostak and Esch 1990). Finally, diurnal cycles in

abiotic variables (such as UV intensity and water velocity) may also select for particular cercarial emergence patterns if these factors substantially contribute to parasite mortality (Hannon et al. 2018). Testing these hypotheses would be relatively straight-forward in this system and could provide a better understanding of *S. pseudoglobulus* infection patterns, particularly in hosts from the Upper Mississippi River.

To better predict infection dynamics at local scales, it is important to understand the potential for subsequent parasite transmission after passage through sympatric and allopatric host combinations (Gasnier et al. 2000). Our work shows that passaging *S. pseudoglobulus* through sympatric and allopatric snail combinations has no influence on metacercarial establishment in second-intermediate hosts. The fact that *S. pseudoglobulus* miracidia can efficiently infect allopatric *B. tentaculata*, can lead to gigantism in these snails, and then can successfully transmit from these hosts as cercariae, suggests that the parasite has the potential to establish and spread within naïve populations of *B. tentaculata*, even if it arrives from distant locations (i.e., via migrating waterfowl). Parasite transmission throughout local habitats could be exacerbated by the fact that *S. pseudoglobulus* cercariae can also infect a number of native snail species as second-intermediate hosts (Sandland et al. 2014). These infection patterns in first- and second-intermediate hosts may help to explain why *Sphaeridiotrema* spp. has been associated with both *B. tentaculata* populations and outbreaks of waterfowl disease at different sites across North America (Hoeve and Scott 1988; Lepitzki et al. 1994; Sauer et al. 2007; Herrmann and Sorensen 2009, 2011; Roy and St-Louis 2017).

Patterns of parasite emergence in this study suggest the potential for local adaptation in the *S. pseudoglobulus-B. tentaculata* system. However, our work also revealed no differences in other infection metrics, such as infection prevalence and time-to-patency, based on snail origin. These latter results are particularly concerning when considering *B. tentaculata*'s potential to spread, as newly established populations may be at high risk of parasite establishment leading to subsequent outbreaks of waterfowl disease. A broader assessment of how local coevolutionary dynamics influence infection outcomes between digeneans and their invasive mollusks should provide a more comprehensive understanding of the consequences associated with species invasions in local communities.

Authors' contributions GS and JP conceptualized the study, performed the collections, and wrote the manuscript. GS conducted the experiments and analyses.

Compliance with ethical standards

Conflicts of interest/competing interests The authors declare that they have no conflict of interest.

Ethics approval Because our study focused on invertebrate animals, IACUC protocols were not required.

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