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Research Article

Risk of Human Exposure to the Intestinal Schistosome, *Schistosoma mansoni*, across Seasons along the Senegal River

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Abstract

Background: Schistosomiasis is an emerging disease associated with changes to the environment that have increased human contact rates with disease-causing parasites, flatworms that are released from freshwater snails. For example, schistosomiasis remains a major public health problem in Northern Senegal, where prevalence in schoolchildren often reaches 90%.

Aim: This study focuses on the impact of seasonality on the risk of human exposure (RHE) to *Schistosoma mansoni*, defined as the total number of cercariae (the free-living life stage that infects humans) shed from all *Biomphalaria pfeifferi* snails collected at a site using standardized methods. We focus on RHE because it is rarely quantified and a recent study demonstrated that snails stop shedding cercariae when snail densities increase and thus per capita snail resources become limited [2], suggesting that densities of snails might not be directly proportional to RHE to schistosomes.

Method: We sampled four water access points in three villages every other week during the early (Dry1) and later dry seasons (Dry2) and the rainy season, quantifying the abundance of infected and

non-infected snail intermediate hosts, cercariae released per infected snail, and water chemistry. We used simple and multiple linear regressions to assess how seasonality and environmental parameters affect non-infected and infected snail abundance and RHE.

Results: Although RHE was found across all seasons, the abundance of infected and non-infected snail intermediate hosts and cercariae, as well as prevalence (23.71%), were all highest in the rainy season. In the rainy season, RHE was positively associated with the density of snail hosts and their periphyton food resource.

Conclusion: Although previous studies have examined the influence of seasonality on snail densities, few studies have explored the effects of seasonality on cercarial densities, which is the primary source of infection to humans. Our study demonstrates that cercarial densities are greater in the rainy season than in the early or late dry seasons. Given that cercarial densities directly pose risk of infection to humans, unlike non-infected or infected snails, these findings should help to inform decision making and schistosomiasis control efforts in West Africa.

Keywords: Linear regression model; Risk of human exposure; Schistosomiasis; Seasonality

Background

Infectious diseases are emerging globally at an unprecedented rate [1], and hosts and parasites are heterogeneous entities that exist in dynamic environments [2]. Globally, over 230 million people are infected with schistosomiasis, an infectious disease that is caused by parasitic helminthes [3-5]. Schistosomiasis remains a significant health burden in many areas of the world and ranks among the most important water-based diseases of humans in developing countries [6].

Schistosoma mansoni, the trematode (flatworm) that causes intestinal schistosomiasis, has a complex life cycle. While a vast proportion of *S. mansoni* eggs fail to leave the definitive human host and evoke potentially life-threatening pathology [7], *S. mansoni* eggs must migrate from the mesenteric vessels, across the intestinal wall, and into the feces to exit the human body and progress to their successive snail host. The excreted eggs hatch in the water resulting in a free-swimming miracidium that penetrates the intermediate snail host [8,9]. The flatworm then reproduces asexually to release cercariae from the snail [10]. The cercariae swim through the water in the hopes of penetrating the skin of definitive human hosts [11]. The worm reproduces sexually in humans and releases eggs in feces. If these eggs enter freshwater containing intermediate hosts, the life cycle can restart.

The abundance of intermediate host snails of human schistosomes is often strongly driven by environmental factors [12] and seasonality [13,14]. For example, the transformation of ecosystems in and around the Senegal River has created favorable environmental conditions for snails [12] and schistosomiasis, as described in past studies [15]. Similarly, seasonality can influence the amount of rain and thus aquatic habitat for snails.

Although previous studies have examined the influence of seasonality on snail densities [9,10], few studies have explored the effects

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of seasonality on cercarial densities, which is the primary source of infection to humans. This is an important gap in the literature because it was recently shown that snails stop shedding cercariae when snail densities increase and thus per capita snail resources become limited [2]. This creates a potential scenario where densities of snails might not be directly proportional to densities of cercariae, a proxy of the risk of human exposure (RHE) to schistosomes.

The aim of this study was to investigate how seasonality affects RHE to *S. mansoni* (i.e., number of cercariae shed from snails collected at water access points using standardized methods) along the Senegal and Lampasar Rivers in St. Louis, Senegal. We sampled four water access points in three villages every other week from October 2019 to October 2020 ($n = 21$ visits per site), quantifying the abundance of infected and non-infected snail intermediate hosts, *Biomphalaria pfeifferi*, *S. mansoni* cercariae released per infected snail, and water chemistry. Thus, our sampling spanned the dry season that runs roughly from mid-October to mid-June, and the rainy season, which is approximately from late June to early October [16].

Method

Study sites and seasonal displaying

To select sites for our study, we initially quantified the abundance of snail hosts and cercariae parasites in the water access points of several villages in the Delta of the Senegal River. We focused on four water access points after our initial survey because they had a considerable abundance of *B. pfeifferi* snails infected with *S. mansoni* and humans regularly entering the water access point. We sampled intermediate hosts every other week at these four water access points across three villages in Senegal, West Africa: Kaban (KA: 16° 3.338 N - 16°24.133 O) Minguegne (ME 1: 16°01.055' N - 16°21.397' O and ME2 :16°01.090' N - 16°21.369 O) and Ndiawdoune (NW: 16°4.075' N - 16°23.635' O). Kaban village is bordered by the Senegal River, Minguegne is bordered to the Ngalam outlet Senegal River in the “Trois marigots” zone and Ndiawdoune is bordered by the Lampasar River. Because the dry season spans roughly 9 months of the year in Senegal, we partitioned this season into early (Dry₁) and late dry seasons (Dry₂) corresponding to early in the season when temperatures were generally decreasing from late October to mid-January (29.4 C $\geq$ Dry₁ $\geq$ 15.6 C) and later in the season, from mid-January to late June, when temperatures were generally increasing (19.9 < T (Dry₂) $\leq$ 23.9).

Quantification of snail hosts

We used the snail sampling method described by Haggerty et al. [15]. Briefly, at each water access point, we conducted 10 1-m sweeps with a 2.5-mm mesh aquatic dipnet at random sampling points. To select random points, the access point was mapped ahead of time, partitioned into a grid, and sections of the grid were selected randomly. Any aquatic plants in the dipnet were placed into a wash pale with water, shaken vigorously to remove snails, and examined for any attached snails before weighing the vegetation mass using a spring scale. We recorded the number of *B. pfeifferi* snails captured per sweep (Figure 1). We defined the density of snails as the number of snail hosts captured per site and per visit.

All collected snails were brought to the laboratory to determine if they were infected by *S. mansoni*. In the laboratory, individuals were exposed to a lamp for one hour (1 h) to promote schistosome cercarial shedding. Once cercariae were shed, *S. mansoni*, the unique schistosome species infecting *B. pfeifferi* in Senegal, were identified by their

diagnostic forked tail and counted with the assistance of a dissecting microscope. Thus, RHE is defined as the total number of cercariae shed from all *B. pfeifferi* snails collected at a water access point using standardized methods during any snail collecting visit (Figure 1).



Figure 1: Risk of human exposure is defined as the total number of cercariae shed in collected snails at a water access point during any snail collecting visit and thus is the number of infected *Biomphalaria pfeifferi* (B.p.) x the mean number of *Schistosoma mansoni* (S.m.) cercariae shed per snail.

Environmental parameters predictors of hosts infection and RHE across seasonality

We recorded dissolved oxygen (DO), pH, water conductivity and water temperature using a YSI Professional Plus handheld multiparameter meter during each visit to each water access point. We also recorded periphyton and the phytoplankton fluorescence using an Aquapen AP 100-C handheld fluorometer. Periphyton was collected from a study site during snail sampling (see below) by wading into the water and cutting a stem of *Typha* spp. vegetation at the water surface and again at a depth of 10 cm below the water. The 10 cm section of *Typha* was taken to the lab and its surface scrubbed using a toothbrush. We then washed all algae off the *Typha* and brush using deionized water into a 50mL falcon tube and filled all samples to a standardized volume of 50 mL. Chlorophyll *a* was then quantified by shaking the Falcon tube vigorously to homogenize, transferring a subsample from the Falcon tube to a 1-mL cuvette, and recording Ft and Qy (which measure chlorophyll *a* and photosynthetic efficiency) values using the Aquapen. We recorded the surface area of *Typha* that was sampled and used it to standardize the periphyton fluorescence values based on sampling area. For the phytoplankton, we sampled open water at each site during each visit by transferring a 1-mL sample into a cuvette, and recording the Ft and Qy values using the Aquapen.

Statistical analysis

We conducted our data analysis using R software version 4.0.5 (2021-03-31). To assess the significance of temperature on seasonality (**model 1**) and seasonality (Dry₁, Dry₂, and rainy) on RHE (**model 2**), we used two simple linear regression models. To elucidate how abiotic (pH, dissolved oxygen, water conductivity, water temperature, periphyton, phytoplankton) and biotic parameters (snail density, periphyton, phytoplankton, vegetation) affected the snail infection and RHE across seasons, we used three multiple linear regression models (**model 3: model 3a, model 3b and model 3c**), one for each of the three seasons Dry₁, Dry₂, and rainy. To each season we applied a model where the environmental parameters were predictors of RHE. To identify the best fit model, we included all variables as predictors and removed the single term with the highest non-significant *p*-value until the model contained only significant terms (S1 Table).

Results

Seasonal densities of *Biomphalaria pfeifferi*

Of the 895 *Biomphalaria pfeifferi* we collected in 840 sweeps across the four sites, 83 were collected in the Dry₁ season (9.27 %), 192 in the Dry₂ season (21.45 %), and 620 in the rainy (69.28 %) season (Table 1, Figure 2). All three seasons differed from one another in densities of snails ($P < 0.05$).

		Mean	Max
Seasons	Dry ₁ (N = 83)	3.46	18.00
	Dry ₂ (N = 192)	9.60	33.00
	Rainy (N = 620)	15.50	87.00
Total (N = 895)		10.65	87.00

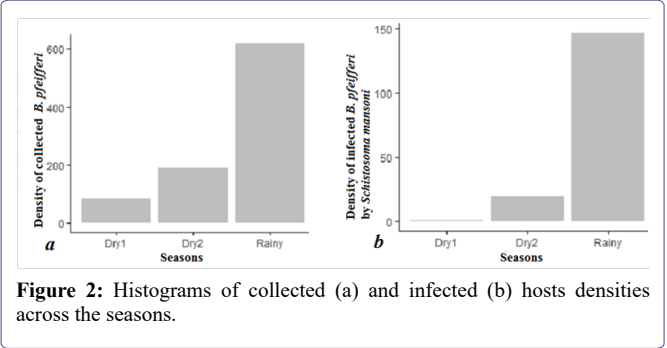
Table 1: Total mean and maximum of the total and seasonal densities of *Biomphalaria pfeifferi*.

Seasonality of infected *Biomphalaria pfeifferi*

Of the 895 *Biomphalaria pfeifferi* we collected, a total of 168 shed *S. mansoni* cercariae for an overall prevalence of 18.77%. Of the *S. mansoni*-infected snails, 147 were found in the rainy season (infection rate = 87.5%), 19 during Dry₂ (infection rate = 11.31 %) and only 2 individuals were found infected in the Dry₁ period (infection rate = 1.19 %) (Figure 2). Thus, prevalence in the rainy, Dry₂, and Dry₁ seasons was 23.71%, 9.90%, and 2.40%, respectively. There was no significant relationship between density of snail hosts and density of infected snails during the Dry₁ season (Figure 3), likely because of the extremely low prevalence during this season. In contrast, there was a significant relationship between total snail densities and infected snail densities in the Dry₂ and rainy seasons (Figure 3).

		Mean	Max
Seasons	Dry ₁ (N = 2)	0.08	1.00
	Dry ₂ (N = 19)	0.95	4.00
	Rainy (N = 147)	3.67	28.00
Total infected (N = 167)		1.99	28.00

Table 2: Total, mean and maximum of the total and seasonal infected individuals of *Biomphalaria pfeifferi*.



Environmental factors predicting the infection of snails per season

Associations between environmental parameters and the abundance of infected snails in the early dry season were not conducted because we caught too few infected snails (two) to justify these analyses. In Dry₂, the density of infected hosts was positively associated

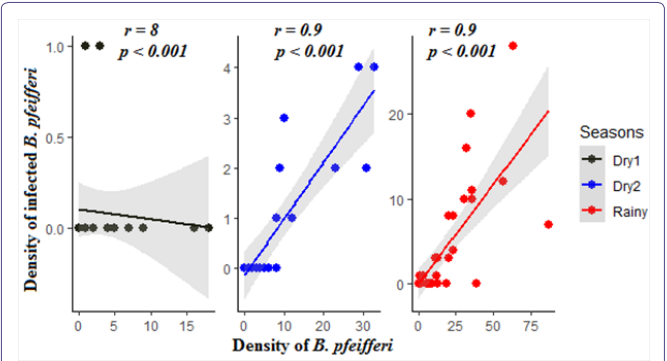


Figure 3: Linear relationship between density of hosts and infected hosts across seasonality.

with the density of hosts and dissolved oxygen, and negatively associated with water temperature (Table 3). In the rainy season, the density of infected snails was positively associated with the density of snails and periphyton abundance, and negatively associated with pH, water temperature, and the density of *Bulinus* snails that are likely competitors with *B. pfeifferi* (Table 4).

Season	Predictors	Estimate	Std. Error	t value	Pr(> t)
Dry2	(Intercept)	-5.39417	2.28482	-2.361	0.030 **
	Density of hosts	0.08755	0.01776	4.930	< 0.001***
	Dissolved oxygen	0.75913	0.32777	2.316	0.030*
Rainy	(Intercept)	61.564843	21.117682	2.915	0.006 **
	Density of hosts	0.216169	0.029935	7.221	< 0.001***
	pH	-3.869580	1.464975	-2.641	0.010*
	Water Temperature	-1.138422	0.401187	-2.838	0.007 **
	Periphyton	0.006423	0.001412	4.548	< 0.001***
	<i>Bulinus spp</i>	-0.027456	0.009795	-2.803	0.008**

Table 3: Abiotic and biotic factors associated with the abundance of infected snails in the later dry season (Dry₂) and the rainy season. Analyses were not conducted in the early dry season because we caught too few infected snails (two) to justify analyses.

From the 167 infected *B. pfeifferi*, a total of 10,644 *S. mansoni* cercariae were shed. Sixteen cercariae were produced in Dry₁ (rate of parasite density = 0.15 %), 1,751 in Dry₂ (rate of parasite density = 16.45%) and 8,877 (rate of parasite density = 83.4 %) in the rainy season.

		Mean	Max
Seasons	Dry ₁ (N = 16)	0.66	10
	Dry ₂ (N = 1751)	87.55	449
	Rainy (N = 8877)	221.93	2370
Total infected (N = 10644)		126.71	2370

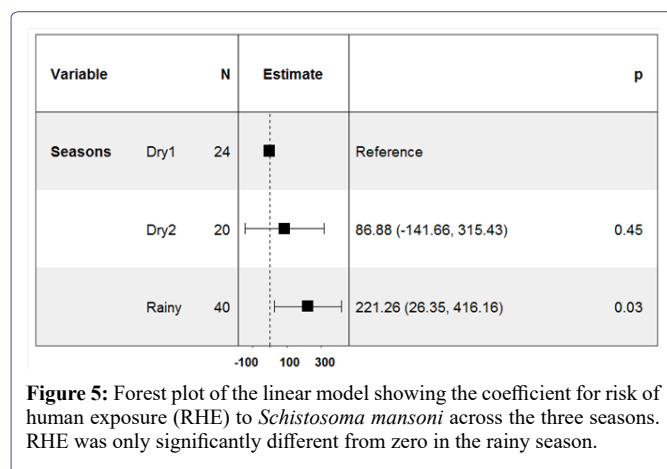
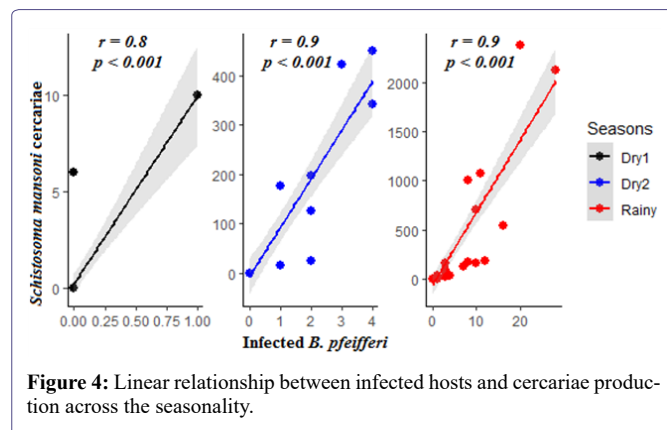
Table 4: Total, mean, and maximum of seasonal cercariae shed.

There was a strong and significant relationship between density of infected snails and the RHE in all seasons (Figure 4).

Even if the density of infected snail hosts was significantly associated to the RHE in all seasons, RHE was only significantly different from zero in the rainy season ($P = 0.03$) (Figure 5).

Environmental factors predicting the RHE per season

In Dry₁, RHE was associated positively with water temperature, and negatively with the density of *Bulinus* spp. snails and water



conductivity (Table 5). In Dry₁, RHE was associated positively with the density of *Bulinus* spp. snails (Table 5). In the rainy season, RHE was associated positively with the density of *B. pfeifferi* and periphyton, and negatively with the abundance of *Bulinus* spp. snails (Table 5).

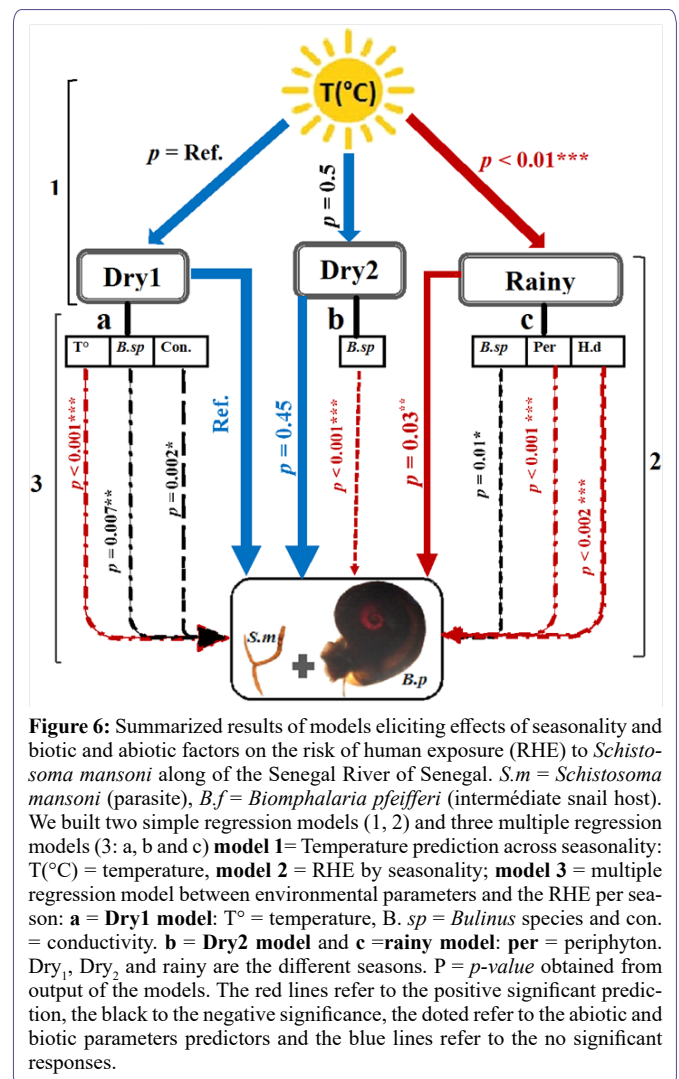
		Predictors	Estimate	Std. Error	t value	Pr(> t)
Seasons	Dry ₁	(Intercept)	-3.38719	2.10890	-1.606	0.123917
		Water Temperature	0.57016	0.13976	4.080	< 0.001***
		Bulinussp	-0.03956	0.01306	-3.028	0.007 **
		Water Conductivity	-0.05316	0.01478	-3.597	0.002**
	Dry ₂	(Intercept)	-46.989	32.705	-1.437	0.168
		Bulinusspp	2.097	0.387	5.419	< 0.001***
	Rainy	(Intercept)	-167.0064	94.2808	-1.771	0.08.
		Density of hosts	12.3690	3.7162	3.328	0.002 **
		Bulinussp	-3.1513	1.1795	-2.672	0.01 *
		Periphyton	0.7327	0.1641	4.465	< 0.001***

Table 5: Multiple regression model results predicting RHE across seasons.

Discussion

Seasonal densities of *Biomphalaria pfeifferi*

Snail density contributes directly to the force of human infection [17,18], as schistosomiasis transmission is dependent on the presence of compatible snail intermediate hosts at water-contact sites [14]. The transformation of ecosystems in the Senegal River has created favorable biotopes to the development of intermediate host snails of human



schistosomes [12]. The presence of the intermediate host *B. pfeifferi* in our study region was previously described by several other authors [12,13,15,19,20], and is only second to *Bulinus truncatus* in abundance in this part of Senegal. We found the greatest density of the snail hosts during the rainy season. This finding is likely because of the dependence of *B. pfeifferi* on freshwater environments and resource availability in these environments. This hypothesis is consistent with the documentation that seasonal variation in temperature, rainfall and resource availability ubiquitously exert strong pressures on host-parasite systems [21]. The lowest densities of snails were found during the Dry₁ season, corresponding to decreasing temperatures. Given the role of temperature on natural process, declining temperature might slow down host development and limit food resources.

Seasonality dynamic and environmental factors predicting snail hosts infection and the RHE

Environmental conditions experienced by hosts are known to affect parasite transmission [22] and may mediate the outcome of infection [23]. These environmental factors, coupled with human behavior, likely act together to facilitate the acquisition and accumulation of schistosome infections across space and time [24]. Both snail infection and RHE were significantly associated with several biotic and abiotic factors and seasonality. We found that there was a significant

seasonal signature on the density of infected hosts and RHE, consistent with the findings of Gurarie et al. [17]. In general, across both the Dry2 and rainy season RHE was positively associated with the density of snails and periphyton. The density of hosts and dissolved oxygen (with their greatest measures) were associated with the number of infected hosts but not with the RHE during Dry2. The RHE was only predicted by the density of *Bulinus* species that we collected simultaneously with *B. pfeifferi* during this period. In contrast to *B. pfeifferi*, the density of *Bulinus* species was negatively associated with RHE in the rainy season. Interestingly, *Bulinus* species are competitors with *B. pfeifferi* and had a negative relationship with *B. pfeifferi* in the Dry2 season when resources are scarcer than in the rainy season, but a positive relationship with *B. pfeifferi* in the rainy season when food resources are more abundant. This finding is consistent with Civitello et al. [2] who showed in outside mesocosms that snails stop shedding cercariae when snail densities, and thus per capita snail resources, become limited.

The rainy season harbored over 87% of infected hosts. We did not quantify inputs of chemical fertilizers but, during the rainy season, water bodies regularly receive runoff from crop fields. This process can increase the growth of aquatic vegetation and periphytic algae that constitute the habitat and food resource, respectively, for snail hosts [26-28]. In past studies, authors found that agrochemicals might affect the transmission of schistosomes and other trematodes, as well as snail intermediate hosts, snail predators, and snail algal resources [6,26-38]. Periphyton was most abundant in the rainy season and the schistosome parasites rely on host feeding for their own growth, survival, and reproduction [39,40]. The fact that the abundance of infected hosts was associated negatively with temperature during the rainy season may be explained by maximal temperatures during this season (32.5 °C) being detrimental to snails or to free-living larval stages of the parasite [41]. Importantly, parasitism, including schistosomiasis, is expected to change in a warmer world [42-47]. For example, several authors predict that *S. mansoni* infection risk may increase across much of eastern Africa as temperatures increase over the next few decades [48,49].

Conclusion

Few studies have explored the effects of seasonality on cercarial densities, which is the primary source of infection to humans. This is an important gap in the literature because snails stop shedding cercariae when snail densities increase and thus per capita snail resources become limited [2]. This creates a potential scenario where densities of snails might not be directly proportional to densities of cercariae, a proxy of the RHE to schistosomes [50]. Although snails shed less when snail densities peak, we did find a strong seasonal signature to RHE. RHE was unequivocally the highest in the rainy season relative to the early and late dry seasons. Additionally, densities of both noninfected and infected snails were also highest in the rainy season. Thus, despite resource competition and limitations affecting RHE, risk of schistosomiasis along the Senegal River is highest in the productive rainy season.

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Supporting information

Predictors	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-2.0429524	6.4340374	-0.318	0.751754
Density of hosts	0.2110943	0.0290041	7.278	3.17e-10 ***
pH	-0.1421507	0.4206818	-0.338	0.736404
Temperature	0.1233653	0.1213435	1.017	0.312672
<i>Bulinus spp</i>	-0.0174996	0.0079046	-2.214	0.029964 *
Periphyton	0.0034901	0.0009815	3.556	0.000665 ***
Vegetation mass	-0.0001518	0.0002398	-0.633	0.528690
Dissolved oxygen	0.0277973	0.2769924	0.100	0.920338
Conductivity	-0.0010181	0.0203757	-0.050	0.960284
Phytoplankton	-0.0098581	0.0056870	-1.733	0.087240
Salinity	24.2520062	34.2393410	0.708	0.481010

S1 Table: List of all used predictors in the starting full model: host density (*Biomphalaria pfeifferi* individuals), temperature, conductivity, pH, salinity, dissolved oxygen, vegetation mass, periphyton, competitors (*Bulinus* sp) and phytoplankton. If t-statistics < 0.05, associated predictor was retained in a model, while t-statistics > 0.05, the associated predictor was dropped. To fit the best model, we included all variables (abiotic and biotic) as predictors in the model and we removed the single term with the highest non-significant p-value until the model contains only significant terms. **Example:** full starting model on an overall prediction of snail's infection by factors.

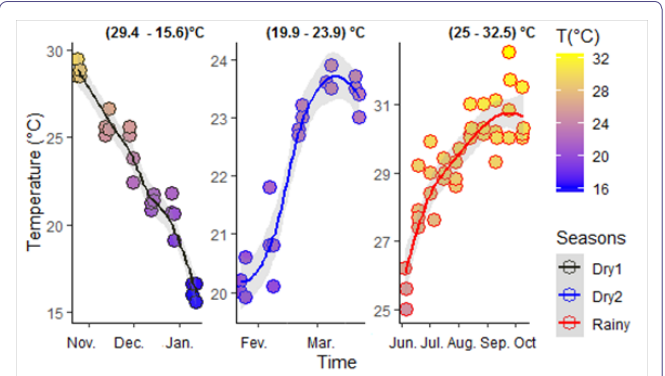
Social Human Activities	Seasons		
	Dry1	Dry2	Rainy
Swimming	+	+++	+++
Irrigation	+++	+++	---
Dishes wash	+++	+++	+++
Landry wash	+++	+++	+++
Fishing	+++	+++	+++

S2 Table: Social human activities linked to human risk exposure.

(+) = presence of activity and (-) = absence of activity. Human was frequented freshwater (Table 1). Most of the time they were making their domestically activities: washing-up, swimming, fishing or drawing water for crops irrigation. During all our monitoring in all seasons we had found at each site to each sample visit, humans making their activities into the water and they were directly exposed to infection (if cercariae are produced by snail), indirectly exposed (if snails were infected), or not exposed to the aquatic free-life stage (cercariae) of *Schistosoma mansoni* (when there was any snail host infected).

Predictors	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	0.6667	77.4424	0.009	0.9932
Dry2	86.8833	114.8656	0.756	0.4516
Rainy	221.2583	97.9577	2.259	0.0266 *

S3 Table: Significant response from a simple linear regression model of the RHE prediction by seasonality factor, p-value = 0.03.



S1 Figure: Seasonal dynamic of water temperature recording.

There was a linear dynamic of temperature that was highly in variation per season (e.g.: 25°- 32.5° during Rainy) and from a season to another: e.g.: (29.4°-15.6° in Dry1 and 19.9°-23.9° in Dry2). The measures decrease and fall to 15.6° C (minimum) in Dry1 season. When it was in increasing in Dry2 and Rainy seasons, it reached a peak (maximum) of 32.5° C. This greatest water temperature (32.5° C) was found in Rainy period and the weakest (15.6° C) during the Dry1 season. However, temperature declined earlier in October. The Rainy season was significantly associated to the temperature (p-value = 0.001).

S1 Table: List of all used predictors in the starting full model: host density (*Biomphalaria pfeifferi* individuals), temperature, conductivity, pH, salinity, dissolved oxygen, vegetation mass, periphyton, competitors (*Bulinus sp*) and phytoplankton. If t-statistics < 0.05, associated predictor was retained in a model, while t-statistics > 0.05, the associated predictor was dropped. To fit the best model, we included all variables (abiotic and biotic) as predictors in the model and we removed the single term with the highest non-significant *p-value* until the model contains only significant terms. **Example:** full starting model on an overall prediction of snail's infection by factors.

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S3 Table: Significant response from a simple linear regression model of the RHE prediction by seasonality factor, *p-value* = 0.03.



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