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Seasonal distribution and cercarial shedding of *Bulinus* spp. snails: Implications for urogenital schistosomiasis control in the Simiyu Region, northwestern Tanzania

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ABSTRACT

Urogenital schistosomiasis is a neglected tropical disease of significant public health concern caused by the trematode species *Schistosoma haematobium*. Its transmission is localised and heterogeneous, with seasonal occurrences in Tanzania primarily facilitated by *Bulinus* spp. snails, which serve as intermediate hosts. To plan effective, data-driven control measures, it is crucial to understand the epidemiology of schistosomes in these snails. This study aimed to investigate the seasonal distribution, abundance, and *Schistosoma* spp. infections (assessed *via* cercarial emergence) in *Bulinus* spp. snails in two districts, Maswa and Meatu, in the Simiyu Region of Tanzania. Malacological surveys were conducted at 90 sites in total, comprising sites in 35 rivers, 32 ponds, and 23 branching streams. Each study site was sampled once during the rainy season and once during the dry season. Snails were collected using a standard scoop- and handpicking technique by two people for 15 min at each site. The collected snails were morphologically identified and subjected to a cercarial emergence experiment. Water physicochemical characteristics were recorded simultaneously with snail collection using a portable multiparameter water meter. The data were analysed using STATA v. 17. A total of 4997 *Bulinus* spp. snails were collected from 90 sites in the two districts. Of these, 91.4% (95% CI: 90.5–92.1%) were morphologically identified as *Bulinus nasutus* and 8.6% (95% CI: 7.8–9.4%) were identified as *Bulinus globosus*. *Bulinus* spp. snail abundance was almost evenly distributed across seasons, with 50.4% (95% CI: 48.9–51.7%) collected during the dry season and 49.6% (95% CI: 48.2–51.0%) collected during the rainy season. Water temperature and salinity were significantly negatively correlated with snail abundance (both $P < 0.001$). *Schistosoma* spp. cercarial emergence followed a seasonal pattern and was significantly higher during the rainy season ($P = 0.005$). Our findings underscore that *B. nasutus* was the most abundant freshwater snail distributed at nearly all the study sites during the rainy and dry seasons. Therefore, appropriate snail control strategies are recommended to complement ongoing schistosomiasis control strategies in the Simiyu Region.

1. Introduction

Schistosomiasis is a neglected tropical disease affecting approximately 260 million people worldwide (WHO, 2017). More than 90% of these cases occur in sub-Saharan Africa (Fuss et al., 2020; Zhang et al., 2022). Schistosomiasis is ranked the second most common parasitic disease after malaria in terms of public health impact (Gaye et al., 2021). The disease affects mainly poor and developing countries with low levels of sanitation and limited access to safe water (Jones et al., 2021). Tanzania is the second most affected country globally, with an estimated national prevalence of 52% (Fuss et al., 2020). More than two-thirds of the cases are urogenital schistosomiasis caused by *Schistosoma haematobium* (Mazigo et al., 2024). All age groups are affected in Tanzania, especially in the eastern and southeastern coastal regions, the

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northwestern hinterlands, and the islands of Zanzibar (Tumwebaze et al., 2019; Chibwana et al., 2020; Mushi et al., 2022).

Schistosoma haematobium has a complex life cycle that involves mammals as the definitive host and freshwater *Bulinus* spp. snails as the intermediate host (Mari et al., 2017; Liang et al., 2022). Adult worms reside in the vesical venous plexus and uterovaginal venous plexuses, where they produce eggs with terminal spines (Orish et al., 2022). Host's inflammatory response to the deposition of these eggs in vessels and organs leads to morbidity (Silvestri et al., 2022). Common symptoms start with haematuria which then leads to urological abnormalities like bladder calcification and deformities in the ureters and kidneys resulting in hydronephrosis. Chronic infection can also result in severe bladder morbidity, including cancer (Ng'weng'weta and Tarimo, 2017). Additional pathology observed in females referred to as female genital schistosomiasis, is also linked to HIV transmission (Orish et al., 2022; Zhang et al., 2022).

Bulinus spp. snails are key to *S. haematobium* transmission (Allan et al., 2020). The life-cycle of *Schistosoma haematobium* involves two hosts: humans and snails (Orish et al., 2022). Female worms residing in humans release eggs into waterbodies through urine. These eggs hatch into free-swimming miracidia, which infect snails. Inside the snails, the miracidia undergo asexual reproduction, producing cercariae. These cercariae seek out humans who come into contact with the water; upon skin penetration, they transform into schistosomula and continue the infection in the human host (Orish et al., 2022).

In northwestern Tanzania, S. *haematobium* transmission is seasonal (Webbe, 1962; Mazigo et al., 2024). Transmission also varies spatially on a micro-geographical scale directly related to snail abundance (Angelo et al., 2018); this results in variations in transmission across different locations and seasons (Starkloff et al., 2024). *Bulinus nasutus* is the primary snail species historically reported to be involved in the transmission of *S. haematobium* in northwestern Tanzania, including the Simiyu Region (Webbe, 1962; Lwambo, 1988). The other *Bulinus* spp. snails present in the region include *Bulinus globosus*, *Bulinus truncatus*, *Bulinus africanus*, and *Bulinus forskalii* (Angelo et al., 2023). These species can adapt to diverse geographical environments by colonising temporary waterbodies that form after the rainy season, leading to a swift increase in numbers (Angelo et al., 2014). The distribution and abundance of freshwater *Bulinus* spp. snails are influenced by water physicochemical (temperature, turbidity, salinity, conductivity, pH, and velocity) (Nwoko et al., 2022), environmental (food, competition, predators, and aquatic vegetation), and climatic (rainfall and temperature) factors (Manyangadze et al., 2021; Nwoko et al., 2023a).

This study investigates the seasonal distribution, abundance, and prevalence of *Schistosoma* spp. infection of *Bulinus* spp. snails in the Simiyu Region, northwestern Tanzania. The insights gained from this study are crucial to our understanding of snail adaptation to seasonal changes and the impact on *S. haematobium* transmission. This approach, which integrates snail epidemiology and ecological conditions, is vital for planning effective strategies to control and eliminate urogenital schistosomiasis in Tanzania and elsewhere.

2. Materials and methods

2.1. Study area

This study was conducted in the Maswa and Meatu districts in the Simiyu Region of northwestern Tanzania. Maswa and Meatu are among five districts in the region that are located between 3.1833° and 3.4979°S and between 33.7071° and 34.3310°E, respectively (Fig. 1).

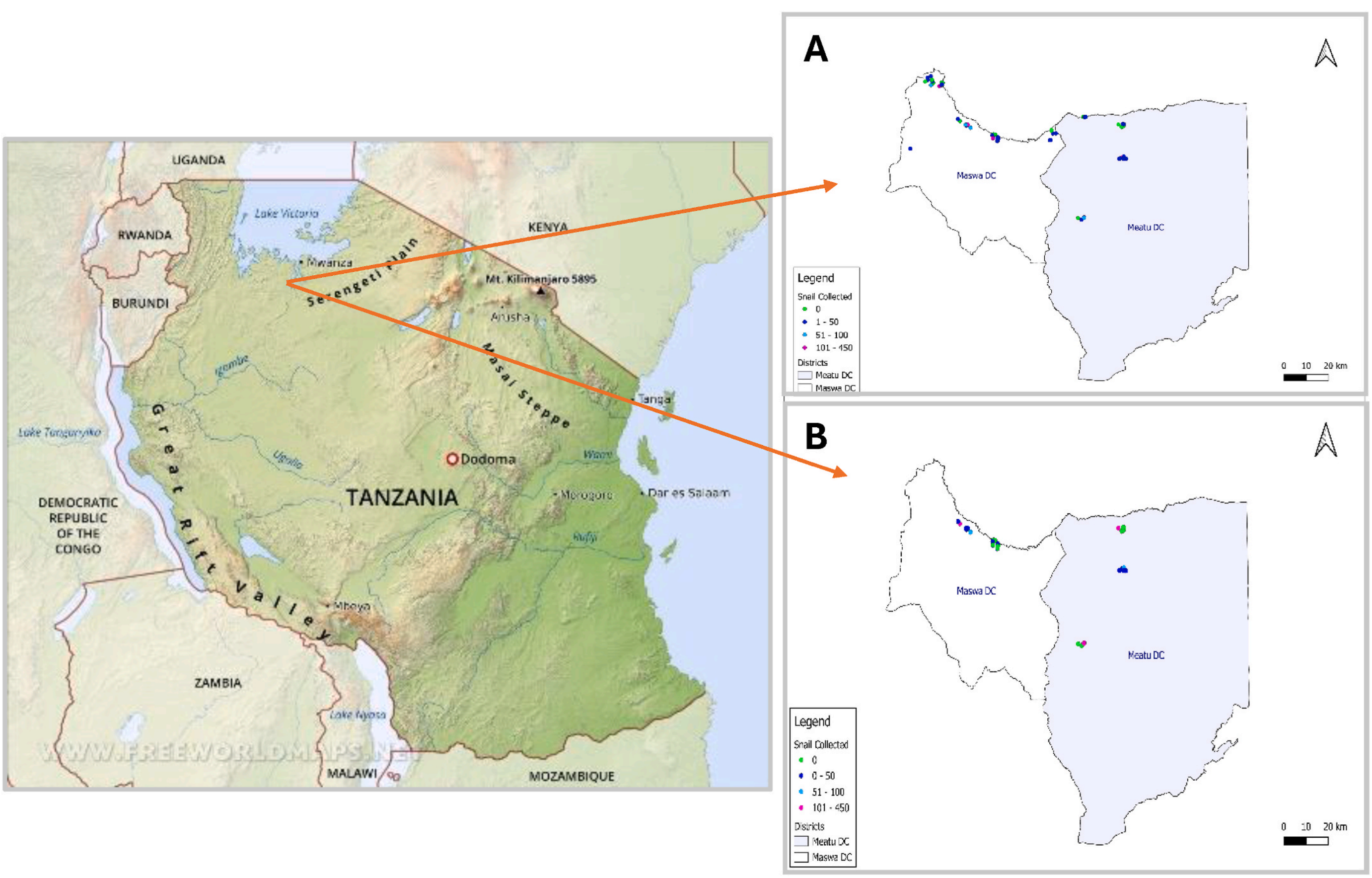

Fig. 1. Map of Tanzania showing the positions of the Maswa and Meatu districts. Location of the 90 snail survey sites during the rainy season (**A**) and the 56 snail survey sites during the dry season (**B**). (Tanzania map source: https://www.freeworldmaps.net/africa/tanzania/map.html).

According to administrative reports available for the districts, Maswa has 120 villages while Meatu has 109 villages. This tropical area has an annual rainfall ranging from 700 mm to 1000 mm (Justine et al., 2024). The average annual mean temperature ranges from 18.8 °C to 31.0 °C (Justine et al., 2024). The rainy season is from October to May and the dry season is from June to September. According to the 2022 census, the Simiyu Region had a total population of 2,140,497 people (NBS, 2022). The majority of the inhabitants of the two districts are involved in subsistence and livestock keeping and depend on water from rivers, streams, and temporary ponds for domestic activities, livestock maintenance, and irrigation for plant/food growth. The two districts are endemic for urogenital schistosomiasis in both adults and school-aged children (Mazigo et al., 2022a). Several seasonal waterbodies exist in these districts, with water levels reaching a peak in the rainy season followed by a water level decrease or complete drying out during the dry season. These factors account for the seasonal transmission of schistosomiasis in these areas and are attributed to the inhabitants' exposure to cercaria-infested waterbodies.

2.2. Study design and site selection

A longitudinal malacological survey was conducted within the two districts, Maswa and Meatu, in the Simiyu Region, Tanzania (Fig. 1). The study was conducted over two distinct periods: the rainy season (October-May) with sampling in December 2022, and the dry season (June-September) with sampling in June 2023. Out of 229 villages across the two districts, we randomly selected 11.

The selection of these villages was informed by precision mapping data from 2021, which indicated a schistosomiasis prevalence of 3.3–58.0% among schoolchildren in these districts (Mazigo et al., 2022b). In each village, we identified waterbodies frequently used for various human activities with the help of local leaders; these waterbodies, which were often used for different livelihood activities, were included as study sites. Our study involved 90 sites in total, consisting of sites in 35 rivers, 32 ponds, and 23 branching streams (Fig. 2).

2.3. Sampling of *Bulinus* spp. snails

At each sampling site, two people collected *Bulinus* spp. snails for 15 min. A wooden scoop with a 3-m handle and a 0.2 mm mesh net was used; snails were also handpicked from vegetation. The total number of snails collected at each site was counted and snails were placed in different collection pots/containers for each site along with a few wet roots/vegetation from each site. The containers were labelled with the site name, date, time, and number of *Bulinus* spp. snails before being stored in a cool box. Data collection forms were used to capture information on the waterbody name, type of water habitat, village name, site name, GPS coordinates, water physicochemical parameters, the number of snails collected, and human activities observed at each site.

2.4. Morphological identification of snails

Morphological identification of the *Bulinus* spp. snails followed the WHO keys for identification of East and Central African freshwater snails of medical and veterinary importance (Mandahl-Barth, 1962). Species within the genus *Bulinus* are characterized by their unique sinistral shell orientation (Mandahl-Barth, 1962). *Bulinus nasutus* was identified by having a fully grown shell consisting of 5–6 whorls, a broadly conical spire with a rather pointed apex; micro-sculptures often diffuse all over the shell, and the spire is rather low, approximately half as high as the aperture (Fig. 3). *Bulinus globosus* was identified by having a full-growth shell of 15–20 mm in height, consisting of 4–4.5 whorls, a short spire with a blunt apex and a distinct truncation of the columella (Fig. 3); micro-sculptures are restricted to the upper part of the shell or absent, spiral sculpture is more or less pronounced. Clean and fresh shells are usually glossy and light brown (Mandahl-Barth, 1962).

2.5. Identification of *Schistosoma* spp. snail infections by cercarial emergence

Cercarial emergence detection assay was conducted on the day of snail collection. Snails from each collection container were transferred to a separate container and thoroughly washed. *Bulinus* spp. snails were then grouped into batches of 5–10 individuals and placed in 6-well plates or Petri dishes based on their sampling sites (Fig. 4B). Three-quarters of each well or Petri dish was filled with clean bottled water. The snails were then exposed to artificial light or indirect sunlight to stimulate cercarial emergence. Observations were made at intervals of 4–6 h under a dissecting microscope. If any cercariae were observed in a well or Petri dish, all snails in that well were thoroughly washed to prevent cercarial contamination. Each snail from that group was then individually placed in a separate well of a 6-well plate with clean bottled water to identify the individual snails shedding cercariae (Fig. 4D). *Schistosoma* spp. cercariae were identified and documented using the

Fig. 2. Photos of the sampling sites showing rivers (**A-C**), ponds (**D** and **E**), branching streams (**F** and **G**), and measurements of water physiochemical parameters (**H**).

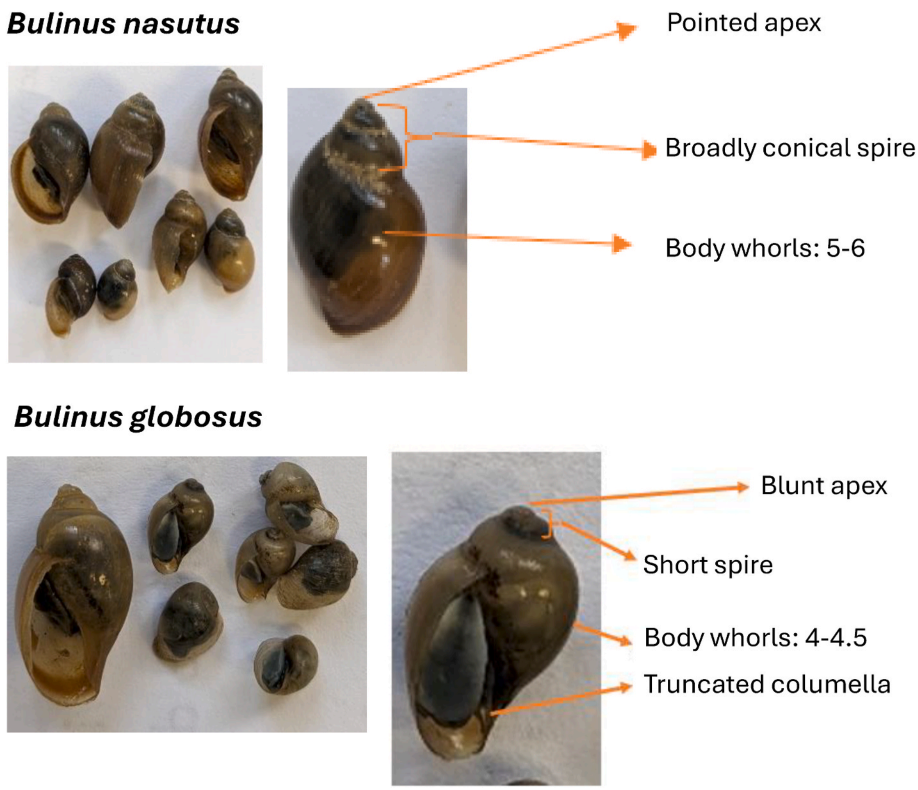

Fig. 3. Characteristic features enabling morphological identification of the two snail species (identification keys by Mandahl-Barth, 1962). *Bulinus nasutus* has a pointed apex and broadly conical spire whereas *Bulinus globosus* has a blunt apex, short spire and truncated columella.

Fig. 4. A Snail collection (scooping). **B** Setup for cercarial emergence assay. **C** Examination of cercariae under a dissecting microscope. **D** *Schistosoma* spp. cercariae.

keys by Frandsen and Christensen (2022). *Schistosoma* spp. cercariae are recognized by their unique characteristic of having tail furcae curved backwards when in resting position. Given that morphological identification keys cannot distinguish between the cercariae of human- or animal-infecting species of *Schistosoma*, they were all collectively classified as *Schistosoma* spp. cercariae.

2.6. Environmental and water physicochemical parameters

At each study site, water physicochemical parameters related to snail abundance and distribution were measured simultaneously with snail sampling. The parameters were measured using a portable multimeter device (PCE-PHD1; PCE Germany GmbH, Meschede, Germany). These parameters included temperature, pH, salinity (g/l), electrical conductivity (mS/cm), and dissolved oxygen (mg/l). Environmental and water habitat characteristics, including water habitat type, water level, substrate, vegetation, and presence of domestic and wild animals were also recorded. Human activities at the visited sites were recorded through direct observation (Nwoko et al., 2023b).

2.7. Data analysis

Data were entered into Microsoft Excel v.2019, and statistical analysis was performed using the software STATA v.17 (StataCorp.; College Station, TX, USA). Each snail collection site point (GPS code) was imported into Quantum GIS (QGIS) version 2.41.21 (Essen, Germany) for mapping of the schistosome infection sites. The number of each snail species collected from each site, season, and date of survey were statistically analysed. Prevalence of cercarial emergence was computed as the proportion of snails shedding cercariae. Snail distribution was analysed descriptively. A two-sample Mann-Whitney test (equivalent to Wilcoxon rank-sum test) was used to compare the abundance of snails collected with the binary grouping variables (district, season, snail species). A Kruskal-Wallis test was used to compare the abundance of snails across water habitats (river, pond, and branching stream). A multivariate analysis using generalized linear models (GLMs) with a Poisson distribution and log link function was performed to examine the influence of water physicochemical variables on the abundance of *Bulinus* spp. snails. As we did not find a significant difference in the abundance of snails between the dry and rainy seasons, we analysed the association between water physicochemical variables and snail abundance independently of the season. Due to collinearity, pH was excluded from the model. The best-fit was achieved with the variables water temperature, salinity, conductivity, and dissolved oxygen. A *P*-value < 0.05 was considered to indicate statistical significance.

3. Results

3.1. Distribution and abundance of Bulinus spp. during the rainy and dry seasons

A total of 4997 *Bulinus* spp. snails were collected during the dry and rainy seasons. Of these, 91.4% (4566/4997; 95% CI: 90.5–92.1%) were morphologically identified as *B. nasutus* and 8.6% (431/4997; 95% CI: 7.8–9.4%) were identified as *B. globosus.* Nearly half of all the snails (49.6%; 95% CI: 48.2–51.0%) were collected during the rainy season, while the other half (50.4%; 95% CI: 48.9–51.8%) were collected during the dry season (Mann-Whitney test, $Z = -0.602$, $P = 0.547$) (Table 1).

Table 1
Seasonal distribution of *Bulinus* spp. abundance in the two districts of the Simiyu Region, Tanzania.

Season	District	No. of sites	No. of snails collected		Total no. of snails
			B. nasutus	*B. globosus*	
Rainy	Maswa	60	1474	278	1752 (70.7%)
	Meatu	30	594	133	727 (29.3%)
	Total	90	2068 (83.4%)	411 (16.6%)	2479 (49.6%)
Dry	Maswa	31	1275	12	1287 (51.1%)
	Meatu	25	1223	8	1231 (48.9%)
	Total	56	2498 (99.2%)	20 (0.8%)	2518 (50.4%)
Total	Maswa		2749 (54.3%)	290 (67.3%)	3039 (60.8%)
	Meatu		1817 (39.8%)	141 (32.7%)	1958 (39.2%)

Among the 90 study sites, *Bulinus* spp. snails were collected from 79% (71/90) of the sites during the rainy season. Of the 2479 *Bulinus* spp. snails collected during the rainy season, 83.4% (2068/2479) were morphologically identified as *B. nasutus* and 16.6% (411/2479) were identified as *B. globosus* (Table 1). Among the 71 sites where *Bulinus* spp. were collected, *B. nasutus* was recorded at 63, while *B. globosus* was recorded at only 29 sites.

Of the 90 study sites, 34 were not surveyed during the dry season due to logistical challenges. Out of the 56 sites that were surveyed, 5 were dry. Therefore, complete data during the dry season were obtained from a total of 51 sites. A total of 2518 snails were collected during the dry season. Of these, 99.2% were morphologically identified as *B. nasutus* and 0.8% were identified as *B. globosus* (Table 1). *Bulinus nasutus* was collected at 65% (33/51) of the sites while *B. globosus* was collected at only 8% (4/51) of the sites.

Other freshwater snails, *Pila* spp., *Melanoides* spp., *Ceratopharus* spp., *Cleopatra* spp., *Biomphalaria* spp., *Bellamya* spp., and *Radix* spp., were also observed at the sites.

Among the 2479 snails collected during the rainy season, 70.7% (95% CI: 68.8–72.5%) were collected from Maswa, while only 29.3% (727/2479; 95% CI: 27.5–31.1%) were collected from Meatu; however, differences in snail abundance distribution were not significant (Mann-Whitney test, $Z = 0.271$, $P = 0.786$). Among the 2518 snails collected during the dry season, 51.1% (1287/2518) were collected from Maswa and 48.9% were collected from Meatu; there were no significant differences in snail abundance distribution (Mann-Whitney test, $Z = -0.220$, $P = 0.826$). Considering both seasons, 60.8% (3039/4997; 95% CI: 59.4–62.1%) *Bulinus* spp. snails were collected from Maswa and 39.2% (1958/4997; 95% CI: 37.8–40.6%) were collected from Meatu, with no significant differences in snail abundance distribution between districts (Mann-Whitney test, $Z = 0.171$, $P = 0.8639$) (Table 1).

3.2. Abundance and distribution of Bulinus spp. snails in various aquatic habitats

Sites in a total of 13 rivers, 26 ponds, and 21 branching streams were surveyed in Maswa District and sites in 22 rivers, 6 ponds, and 2 branching streams were surveyed in Meatu District. Snail populations varied across different habitats and seasons.

In Maswa District, ponds were the predominant habitat for *Bulinus* spp. in all seasons, accounting for 80.3% (1034/1287) and 55.0% of the total snail population during the dry and rainy season, respectively (Table 2). However, in Meatu District, a contrasting trend was observed, with rivers being the primary habitats for *Bulinus* spp. snails, harbouring 86.4% and 85.6% of the total snail population during the rainy and dry season, respectively (Table 2).

During the rainy season, the overall snail population was distributed as follows: 39% (967/2479) in ponds, 31.4% (778/2479) in rivers, and 29.6% (734/2479) in branching streams (Kruskal-Wallis test, $H = 1.541$, $df = 2$, $P = 0.463$). A somewhat different distribution pattern was observed during the dry season, with 43.1% (1086/2518) of snails found in rivers, 45.7% (1151/2518) in ponds, and a much lower proportion, 11.1% (281/2518) in branching streams; however, the differences in snail abundance distribution were not significant (Kruskal-Wallis test, $H = 0.640$, $df = 2$, $P = 0.7263$) (Table 2).

3.3. Environmental and human activities and water physicochemical parameters

The water habitats most frequently visited by humans were rivers (40.0%, 36/90), ponds (36.7%, 33/90), and branching streams (23.3%, 21/90). Nearly two-thirds (64%) of these habitats were temporary/seasonal. In these habitats, the common substrates observed were mud, rock sand, and gravel. During the dry season, the commonly observed vegetation included grasses, polygonum, sedges, and water lilies. In contrast, the rainy season was characterised by the presence of grass,

Table 2
Seasonal distribution of *Bulinus* spp. abundance in waterbodies by district.

District	Season	Waterbody type	No. of waterbodies	No. of snails examined		
				B. nasutus	*B. globosus*	Total
Maswa	Rainy	River	13	71	79	150 (8.6%)
		Pond	26	802	162	964 (55.0%)
		Branching stream	21	601	37	638 (36.4%)
	Dry	River	5	23	9	32 (2.5%)
		Pond	12	1034	0	1034 (80.3%)
		Branching stream	14	218	3	221 (17.2%)
Meatu	Rainy	River	22	528	100	628 (86.4%)
		Pond	6	3	0	3 (0.4%)
		Branching stream	2	63	33	96 (13.2%)
	Dry	River	18	1046	8	1054 (85.6%)
		Pond	5	117	0	117 (9.5%)
		Branching stream	2	60	0	60 (4.9%)

polygonum, sedges, and rushes. The domestic animals observed at the sites were mainly cows, goats, and sheep. During all the site visits, which were conducted in the daytime, no wild animals were observed at any of the sites. During the rainy season, the human activities observed in the branching streams and ponds included washing clothes, bathing/swimming, and washing bikes. Activities, including personal hygiene, water collection, fishing, animal grazing, and irrigation were observed mainly in the rivers during the dry season. The overall mean water temperature at all sites was nearly similar during the rainy and dry seasons respectively. However, water chemistry differed by season, with higher parameters recorded during the dry season compared to the rainy season (Table 3).

A multivariate analysis using generalized linear models with a Poisson distribution and log link function revealed that water temperature and salinity were significantly negatively associated with the abundance of *Bulinus* spp. snails (both *P*-values <0.001; Table 4).

Table 4
Associations between snail abundance and water physicochemical parameters during the rainy and dry seasons.

		Temperature	Conductivity	Salinity	DO
Snail abundance	r^2	−0.0048	0.0014	−0.0579	−0.0003
	P	< 0.001*	0.062	< 0.001*	0.513

*Statistically significant at $P < 0.05$.
Abbreviation: DO, dissolved oxygen.

3.4. Prevalence of *Schistosoma* spp. in *Bulinus* spp. as determined by cercarial emergence

Cercarial emergence of *Schistosoma* spp. was detected in *Bulinus* spp. collected at 26 out of 71 sites sampled in the rainy season (37%; 95% CI: 25.5–48.9%) and in 9 out of 35 sites sampled in the dry season (26%; 95% CI: 12.5–43.3%).

Schistosoma spp. cercarial emergence was detected in a total of 160 out of 4997 *Bulinus* spp. snails examined (3.2%; 95% CI: 2.7–3.7%). The overall prevalence of cercarial emergence in *Bulinus* spp. was significantly higher during the rainy season (3.9%; 95% CI: 3.2–4.8%) compared to the dry season (2.5%; 95% CI: 1.9–3.2%) ($\chi^2_{(1)} = 8.0084$, $P = 0.005$) (Table 5).

The overall prevalence of *Schistosoma* spp. cercarial emergence in *Bulinus* spp. was significantly higher in Meatu District (4.1%; 81/1958) than in Maswa District (2.6%; 79/3039) ($\chi^2_{(1)} = 8.79$, $P = 0.003$); this relation was similar for both seasons but only significant for the rainy season (rainy: 5.9 *vs* 3.1%; $\chi^2_{(1)} = 7.431$, $P = 0.006$; dry: 3.1 *vs* 1.9%; $\chi^2_{(1)} = 3.378$, $P = 0.066$) (Table 5).

The overall prevalence of *Schistosoma* spp. cercarial emergence in *B. nasutus* was somewhat greater but not significantly different from that in *B. globosus* (3.3 *vs* 1.9%; $\chi^2_{(1)} = 2.756$, $P = 0.097$). During the rainy season, the prevalence of *Schistosoma* spp. in *B. nasutus* was significantly greater than in *B. globosus* (4.4 *vs* 1.5%; $\chi^2_{(1)} = 7.885$, $P = 0.005$)

Table 5
Seasonal distribution of *Schistosoma* spp. prevalence as determined by cercarial emergence assay.

Season	District	*B. nasutus*		*B. globosus*		Overall	
		n/N	P (%)	*n/N*	P (%)	*n/N*	P (95% CI) (%)
Rainy	Maswa	51/1474	3.4	3/278	1.1	54/1752	3.1 (2.3–4.0)
	Meatu	40/594	6.7	3/133	2.3	43/727	5.9 (4.3–7.8)
	Total	91/2068	4.4	6/411	1.5	97/2479	3.9 (3.2–4.8)
Dry	Maswa	23/1275	1.8	2/12	16.7[a]	25/1287	1.9 (1.3–2.9)
	Meatu	38/1223	3.1	0/8	0	38/1231	3.1 (2.2–4.2)
	Total	61/2498	2.4	2/20	10.0[a]	63/2518	2.5 (1.9–3.2)

Abbreviations: *n*, number of snails shedding *Schistosoma* spp. cercariae; *N*, number of snails examined; P (%), Prevalence of *Schistosoma* spp. cercarial emergence in percent; CI, confidence interval.
[a] Sample size too small to allow a meaningful prevalence estimate.

Table 3
Physicochemical parameter values (median ± interquartile range) of waterbodies studied during the rainy and dry seasons.

Season	Waterbody type	T (° C)	pH	Salinity (g/l)	Conductivity (mS/cm)	DO (mg/l)
Rainy	Branching stream	25.00 ± 10.90	7.80 ± 1.30	0.02 ± 0.04	0.36 ± 1.09	20.40 ± 51.30
	Pond	27.40 ± 12.30	8.10 ± 2.95	0.01 ± 0.06	0.29 ± 1.02	10.90 ± 30.40
	River	25.40 ± 11.90	8.14 ± 1.36	0.03 ± 0.11	0.59 ± 2.08	7.70 ± 39.46
	Total	26.20 ± 13.10	7.98 ± 2.95	0.02 ± 0.12	0.38 ± 2.13	10.25 ± 55.76
Dry	Branching stream	25.75 ± 6.30	10.86 ± 0.80	0.05 ± 0.06	0.78 ± 1.29	13.75 ± 15.30
	Pond	26.75 ± 10.70	10.63 ± 0.83	0.02 ± 0.03	0.33 ± 0.63	15.65 ± 25.50
	River	26.40 ± 10.50	10.50 ± 1.54	0.06 ± 1.77	1.06 ± 3.33	16.40 ± 33.80
	Total	26.50 ± 11.80	10.60 ± 1.54	0.04 ± 1.78	0.79 ± 3.85	15.70 ± 39.20

Abbreviations: T, temperature; DO, dissolved oxygen.

(Table 5). No valid comparison could be made for the dry season due to the very small sample sizes for *B. globosus*.

4. Discussion

Understanding *S. haematobium* transmission dynamics is a prerequisite for effective and data-driven control strategies. This study provides insights into the seasonal distribution, abundance, and distribution of *Schistosoma*-infected *Bulinus* spp. snails, which are involved in the transmission of urogenital schistosomiasis, across the rainy and dry seasons in northwestern Tanzania. The study found a high number of *Bulinus* spp. snails in both the rainy and dry seasons, with *B. nasutus* being more prevalent and widely distributed than *B. globosus*. Among the physicochemical variables examined, snail abundance was significantly negatively associated with salinity and water temperature. Additionally, *Bulinus* spp. snails were observed to shed more *Schistosoma* spp. cercariae during the rainy season.

We collected around five thousand *Bulinus* spp. snails in both seasons, indicating a high presence. However, we did not find a significant difference in snail abundance between the dry and rainy seasons. This contrasts with other studies, such as the mapping surveys in six districts of northwestern Tanzania, which reported slightly more snails during the rainy season (Angelo et al., 2023; Starkloff et al., 2024). The difference in findings could be due to monthly samplings throughout the year from 467 sites in the mapping surveys, while our study involved a single sampling during each of the rainy and dry seasons from 90 sites. The dominance of *Bulinus* spp. snails in rainy and dry seasons highlight the potential for urogenital schistosomiasis transmission. This is particularly concerning in the study areas if behavioural risks such as open urination, swimming, and use of open water sources for livelihood activities persist.

In this study, *B. nasutus* was more prevalent and widespread than *B. globosus* in both seasons, corroborating findings from extensive surveys in Mwanza, Tanzania (Angelo et al., 2014). This pattern could be attributed to a variety of ecological and environmental factors. For example, the rainy season might offer an ideal environment for food availability and reproduction, contributing to the overall snail prevalence (Starkloff et al., 2024). Conversely, during the dry season, snails survive through a dormancy phase known as aestivation (Hang et al., 2022). A study conducted in Maun, Botswana, emphasised that *B. nasutus* can endure harsh climatic conditions, including droughts and floods (Chimbari et al., 2020). Furthermore, *B. nasutus* have been noted to use drainage pathways for dispersal and breeding (Chimbari et al., 2020). This resilience could account for the extensive distribution and overall prevalence of this snail species.

The only significant associations between snail abundance and physicochemical variables were water temperature and salinity. Water temperature was significantly negatively associated with snail abundance, suggesting snails are less tolerant to heat. Evidence shows that a monthly average temperature of 18–32 °C is optimal for *Bulinus* spp. fecundity and metabolism (Abdel-Malek, 1958; Wepnje et al., 2023). However, higher temperatures (> 31.5 °C) act negatively on *Bulinus* spp. snails, especially in small waterbodies such as ponds and streams, due to the reduction of dissolved oxygen levels and water volume, leading to a reduced snail population (Abdoulaye Ndione et al., 2020). Other studies have also reported a negative association between snail abundance and temperature in similar situations (Olkeba et al., 2020; Manyangadze et al., 2021; Ismail et al., 2022).

Higher salinity poses a significant threat to *Bulinus* spp. snails primarily due to osmotic stress (Donnelly et al., 1983). As salt concentrations increase in their environment, snails begin to lose water through osmosis, resulting in dehydration that can severely impact their overall health and survival. Additionally, elevated salinity can disrupt their physiological processes, such as reproduction and growth, further reducing their abundance in saline environments. To our knowledge, no significant relationship between salinity and *Bulinus* spp. abundance was observed in two studies (Nwoko et al., 2023b; Wepnje et al., 2023).

In this study, no significant differences were observed in the overall *Bulinus* spp. abundance between Maswa and Meatu across both seasons. This finding contrasts with findings from Cameroon, where significant seasonal variations in abundance were recorded for *Bulinus* spp. and other genera, with higher numbers during the dry season (Wepnje et al., 2023).

Although ponds appeared to be the primary habitat for *Bulinus* spp. snails during the rainy season, representing 39% of the total population, rivers emerged as the predominant habitat in the dry season, accounting for 43.1% of the total snail population. However, no significant differences in snail abundance distribution were detected across the three habitat types. This finding is consistent with the relationship observed between *Bulinus* snails and water habitats in KwaZulu-Natal province, South Africa (Nwoko et al., 2023a). This underscores the observation that many ponds in these districts are seasonal, filling with water only during the rainy season and drying up during the dry season, while rivers prevail and harbor a significant number of snails. These data therefore indicate a homogeneous abundance distribution of *Bulinus* spp. concerning geography, season, and habitat.

Cercarial emergence from *Bulinus* spp. snails was observed during both the rainy and dry seasons, with a significantly higher rate of 3.9% during the rainy season compared to 2.5% in the dry season. This pattern contrasts with previous surveys in Iringa, Tanzania, where *Schistosoma* spp. cercarial emergence was observed in 8 out of 148 *Bulinus* spp. snails (5.4%) during the dry season and no cercarial emergence was detected during the rainy season (Nzalawahe et al., 2015). However, our findings corroborate the pattern observed in Shinyanga, Tanzania (Angelo et al., 2018) and in KwaZulu-Natal in South Africa, where the prevalence of *Schistosoma* spp. in *B. globosus* snails was higher (5.19%) during the rainy season compared with post-rainfall season (3.30%) (Nwoko et al., 2023a). In the latter study, infections with *Schistosoma* spp. were detected by cercarial emergence assay followed by snail dissection. It is worth noting that the actual levels of infection with *Schistosoma* spp. in the present study may be higher because prepatent infections are missed in cercarial emergence assays.

We observed a significantly higher overall prevalence of *Schistosoma* spp. cercarial emergence in *Bulinus* spp. in Meatu district for both seasons. This observation indicates higher transmission rates of *S. haematobium* in Meatu than in Maswa similar to the prevalence survey conducted among schoolchildren in these districts (Justine et al., 2024). A significantly higher prevalence of *Schistosoma* spp. in *B. nasutus* was also observed during the rainy season compared with *B. globosus*, this may be attributed to the higher abundance of *B. nasutus* in both dry and rainy seasons and across the two districts. Therefore, although the abundance distribution of *Bulinus* spp. in the two districts and during both seasons was homogeneous, *Schistosoma* spp. infection rates revealed regional differences and that *B. nasutus* serves as the main host for *Schistosoma* spp. in the region.

The variations in the prevalence of cercarial shedding can have a significant impact on the transmission and control of urogenital schistosomiasis in both seasons (Ismail et al., 2021; Kagabo et al., 2023). During the rainy season, numerous habitats are created for snail reproduction, which increases opportunities for human contact with cercaria-infested water and, consequently, transmission. Conversely, during the dry season, the scarcity of water sources can lead to a concentration of *Bulinus* spp. snails in the limited waterbodies, making *Bulinus* spp. snails more likely to become infected. This, coupled with frequent contact due to the heightened need for water, could result in higher exposure of the snails to miracidia and consequently, increased snail infections, thereby elevating the risk of infection in humans (Starkloff et al., 2024).

The WHO recommends that mass drug administration (MDA) should be conducted when the risk of reinfection is low (WHO, 2017). This is because higher reinfection rates cause the prevalence of infection to return to pre-treatment levels. To complement this, it is advised to reduce snail populations by applying molluscicides at least 5–7 weeks before MDA. This strategy ensures a reduced snail population and subsequently, a lower risk of reinfection (WHO, 2017). Our findings indicate higher overall cercarial emergence rates in December (rainy season) and lower rates at the beginning of the dry season in June. Based on this, we propose that application of molluscicides in June followed by MDA in September could be the most effective approach. However, it is important to note that data from just one month may not accurately reflect the transmission dynamics for the entire season. Furthermore, standard cercarial emergence methods might underestimate snail prepatent infections when compared to molecular techniques. Therefore, to validate this hypothesis, a well-designed study employing molecular xenomonitoring tools is necessary. It is also worth noting that *Schistosoma* spp. cercariae cannot be identified to the species level based on morphological features alone (Starkloff et al., 2024). The observed active transmission of *Schistosoma* spp. cercariae suggests human and/or bovine schistosomiasis agents. Future studies should use molecular methods for precise species identification and to confirm the contribution of the detected snails to the endemicity of urogenital schistosomiasis in the study areas. Despite these limitations, our findings offer valuable insights into the distribution and abundance of *Bulinus* spp. snails and the risk that they pose for urogenital schistosomiasis transmission. Such information can be instrumental in managing and developing effective snail control programmes to complement other initiatives for disease control, such as MDA, water, sanitation, hygiene, and health education.

5. Conclusions

This study revealed a high abundance of *Bulinus* spp. snails in both the rainy and dry seasons. *Bulinus nasutus* was widely distributed across both seasons, while *B. globosus* showed a limited distribution within the study sites. Notably, snail abundance was significantly negatively associated with water temperature and salinity. The detection of *Schistosoma* spp. cercariae emerging from *Bulinus* spp. snails in both the rainy and dry seasons, with a higher prevalence during the rainy season, suggests a consistent risk of transmission and potential water contamination from human excreta. To mitigate these risks, frequently contacted waterbodies, such as domestic ponds, should be screened or fenced to reduce contamination. The findings underscore the value of malacological surveys as complementary tools to disease prevalence surveys, aiding in the planning and management of schistosomiasis control in endemic areas. These insights can inform specific, data-driven strategies to control schistosomiasis, particularly in regions with seasonal transmission dynamics. Further research is warranted to investigate the year-round occurrence and diversity of potential snail hosts for *Schistosoma* spp. across a broad geographical region. Enhancing these surveys with molecular methods based on cercarial emergence will provide a more comprehensive understanding of the transmission dynamics.

CRediT authorship contribution statement

Nyanda C. Justine: Conceptualization, Methodology, Data curation, Formal analysis, Project administration, Writing – original draft, Writing – review & editing. **Humphrey D. Mazigo:** Supervision, Conceptualization, Funding acquisition, Methodology, Project administration, Writing – review & editing. **Antje Fuss:** Supervision, Writing – review & editing. **Bonnie L. Webster:** Supervision, Writing – review & editing. **Eveline T. Konje:** Supervision, Writing – review & editing. **Klaus Brehm:** Supervision, Writing – review & editing. **Andreas Mueller:** Supervision, Funding acquisition, Methodology, Writing – review & editing. All authors read and approved the final manuscript.

Ethical approval

This study, which was part of an epidemiological study of urogenital schistosomiasis in northwestern Tanzania, was reviewed, and ethical approval was obtained from the National Institute for Medical Research of Tanzania (Approval No: MR/53/100/718) and the Institutional Review Board of the Bugando Medical Centre/Catholic University of Health and Allied Sciences (Approval No: CREC/667/2023). The necessary permissions to carry out the study were granted by the administrative authorities of the Simiyu Region and the relevant districts.

Consent for publication

Permission to publish this study was granted by the National Institute for Medical Research in Tanzania with reference number BD.242/437/01B/28.

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Declaration of competing interests

The authors declare that there are no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.crpvbd.2025.100248.

Data availability

The data supporting the conclusions of this article are included within the article and its supplementary file.

References

Abdel-Malek, E., 1958. Factors conditioning the habitat of bilharziasis intermediate hosts of the family Planorbidae. Bull. World Health Organ. 18, 785–818.

Abdoulaye Ndione, R., Bakhoum, S., Haggerty, C., Jouanard, N., Senghor, S., Demba Ndao, P., et al., 2020. Intermediate host snails of human schistosomes in the Senegal River Delta: Spatial distribution according to physicochemical parameters. In: Ray, S., Diarte-Plata, G., Escamilla-Montes, R. (Eds.), Invertebrates - Ecophysiology and Management. IntechOpen. https://doi.org/10.5772/intechopen.85842.

Allan, F., Ame, S.M., Tian-Bi, Y.-N.T., Hofkin, B.V., Webster, B.L., Diakité, N.R., et al., 2020. Snail-related contributions from the Schistosomiasis Consortium for Operational Research and Evaluation Program including xenomonitoring, focal molluscicciding, biological control, and modeling. Am. J. Trop. Med. Hyg. 103, 66–79. https://doi.org/10.4269/ajtmh.19-0831.

Angelo, T., Buza, J., Kinung'hi, S.M., Kariuki, H.C., Mwanga, J.R., Munisi, D.Z., Wilson, S., 2018. Geographical behavioural risks associated with *Schistosoma haematobium* infection in an area of complex transmission. Parasites Vectors 11, 481. https://doi.org/10.1186/s13071-018-3064-5.

Angelo, T., Shahada, F., Kassuku, A.A., Mazigo, H., Kariuki, C., Gouvras, A., et al., 2014. Population abundance and disease transmission potential of snail intermediate hosts of human schistosomiasis in fishing communities of Mwanza Region, north-western, Tanzania. Indian J. Sci. Res. 3 https://doi.org/02015510.

Angelo, T., Starkloff, N.C., Mahalila, M.P., Charles, J., Civitello, D.J., Kinung'hi, S., 2023. Mapping of snail intermediate host habitat reveals variability in schistosome and non-schistosome trematode transmission in endemic settings. bioRxiv. https://doi.org/10.1101/2023.06.04.543635.

Chibwana, F.D., Tumwebaze, I., Mahulu, A., Sands, A.F., Albrecht, C., 2020. Assessing the diversity and distribution of potential intermediate hosts snails for urogenital schistosomiasis: *Bulinus* spp. (Gastropoda: Planorbidae) of Lake Victoria. Parasites Vectors 13, 418. https://doi.org/10.1186/s13071-020-04281-1.

Chimbari, M.J., Kalinda, C., Siziba, N., 2020. Changing patterns of *Schistosoma* host snail population densities in Maun, Botswana. Afr. J. Aquat. Sci. 45, 493–499. https://doi.org/10.2989/16085914.2020.1753009.

Donnelly, F.A., Appleton, C.C., Schutte, C.H.J., 1983. The influence of salinity on certain aspects of the biology of *Bulinus* (*Physopsis*) *africanus*. Int. J. Parasitol. 13, 539–545.

Frandsen, F., Christensen, N.Ø., 2022. An introductory guide to the identification of cercariae from African freshwater snails with special reference to cercariae of trematode species of medical and veterinary importance. Acta Trop. 41, 181–202. https://doi.org/10.5169/seals-313293.

Fuss, A., Mazigo, H.D., Müller, A., Mueller, A., Mueller, A., 2020. Malacological survey to identify transmission sites for intestinal schistosomiasis on Ijinga Island, Mwanza, north-western Tanzania. Acta Trop. 203, 105289. https://doi.org/10.1016/j.actatropica.2019.105289.

Gaye, P.M., Doucoure, S., Senghor, B., Faye, B., Goumballa, N., Sembène, M., et al., 2021. *Bulinus senegalensis* and *Bulinus umbilicatus* snail infestations by the *Schistosoma haematobium* group in Niakhar, Senegal. Pathogenetics 10, 860. https://doi.org/10.3390/pathogens10070860.

Hang, De-R., Feng, Y., Zhang, J.-F., Wang, Y.-H., Zhang, B., Juma, S., et al., 2022. Studies on the ecology of *Bulinus globosus* snails: Evidence against burrowing into the soil during the dry season. Front. Environ. Sci. 10. https://doi.org/10.3389/fenvs.2022.925065.

Ismail, H., Ahmed, A., Lee, Y.-H., Elhag, M.S., Kim, Y., Cha, S., Jin, Y., 2021. Population dynamics of intermediate-host snails in the White Nile River, Sudan: A year-round observational descriptive study. Korean J. Parasitol. 59, 121–129. https://doi.org/10.3347/kjp.2021.59.2.121.

Ismail, H.A., Ahmed, A.E., Cha, S., Jin, Y., 2022. The life histories of intermediate hosts and parasites of *Schistosoma haematobium* and *Schistosoma mansoni* in the White Nile River, Sudan. Int. J. Environ. Res. Public. Health 19, 1508. https://doi.org/10.3390/ijerph19031508.

Jones, I.J., Sokolow, S.H., Chamberlin, A.J., Lund, A.J., Jouanard, N., Bandagny, L., et al., 2021. Schistosome infection in Senegal is associated with different spatial extents of risk and ecological drivers for *Schistosoma haematobium* and *S. mansoni*. PLoS Negl. Trop. Dis. 15, e0009712. https://doi.org/10.1371/journal.pntd.0009712.

Justine, N.C., Leeyio, T.R., Fuss, A., Brehm, K., Mazigo, H.D., Mueller, A., 2024. Urogenital schistosomiasis among school children in northwestern Tanzania: Prevalence, intensity of infection, associated factors, and pattern of urinary tract morbidities. Parasite Epidemiol. Control. 27, e00380. https://doi.org/10.1016/j.parepi.2024.e00380.

Kagabo, J., Kalinda, C., Nshimiyimana, P., Mbonigaba, J.B., Ruberanziza, E., Nyandwi, E., Rujeni, N., 2023. Malacological survey and spatial distribution of intermediate host snails in schistosomiasis endemic districts of Rwanda. Trop. Med. Infect. Dis. 8, 295. https://doi.org/10.3390/tropicalmed8060295.

Liang, S., Ponpetch, K., Zhou, Y.-B., Guo, J., Erko, B., Stothard, J.R., et al., 2022. Diagnosis of *Schistosoma* infection in non-human animal hosts: A systematic review and meta-analysis. PLoS Negl. Trop. Dis. 16, e0010389. https://doi.org/10.1371/journal.pntd.0010389.

Lwambo, N.J.S., 1988. Transmission of urinary schistosomiasis in Sukumaland, Tanzania. 1. Snail infection rates and incidence of infection in school children. J. Helminthol. 62, 213–217. https://doi.org/10.1017/S0022149X00011536.

Mandahl-Barth, G., 1962. Key to the identification of East and Central African freshwater snails of medical and veterinary importance. Bull. World Health Organ. 27, 135–150.

Manyangadze, T., Chimbari, M.J., Rubaba, O., Soko, W., Mukaratirwa, S., 2021. Spatial and seasonal distribution of *Bulinus globosus* and *Biomphalaria pfeifferi* in Ingwavuma, uMkhanyakude district, KwaZulu-Natal, South Africa: Implications for schistosomiasis transmission at micro-geographical scale. Parasites Vectors 14, 222. https://doi.org/10.1186/s13071-021-04720-7.

Mari, L., Ciddio, M., Casagrandi, R., Perez-Saez, J., Bertuzzo, E., Rinaldo, A., et al., 2017. Heterogeneity in schistosomiasis transmission dynamics. J. Theor. Biol. 432, 87–99. https://doi.org/10.1016/j.jtbi.2017.08.015.

Mazigo, H.D., Kayange, N., Ambrose, E.E., Zinga, M.M., Mugassa, S., Ruganuza, D., et al., 2024. Efficacy of praziquantel drug against *Schistosoma haematobium* and performance of urine reagent strips among pre-and-school aged children during the high transmission season in North-Western Tanzania. Acta Trop. 256, 107232. https://doi.org/10.1016/j.actatropica.2024.107232.

Mazigo, H.D., Mwingira, U.J., Zinga, M.M., Uisso, C., Kazyoba, P.E., Kinung'hi, S.M., Mutapi, F., 2022a. Urogenital schistosomiasis among pre-school and school-aged children in four districts of north-western Tanzania after 15 years of mass drug administration: geographical prevalence, risk factors and performance of haematuria reagent strips. PLoS Negl. Trop. Dis. 16, e0010834. https://doi.org/10.1371/journal.pntd.0010834.

Mazigo, H.D., Zinga, M.M., Kepha, S., Yard, E., McRee-Mckee, K., Kabona, G., et al., 2022b. Precision and geographical prevalence mapping of schistosomiasis and soil-transmitted helminthiasis among school-aged children in selected districts of north-western Tanzania. Parasites Vectors 15, 492. https://doi.org/10.1186/s13071-022-05547-6.

Mushi, V., Zacharia, A., Shao, M., Mubi, M., Tarimo, D., 2022. Persistence of *Schistosoma haematobium* transmission among school children and its implication for the control of urogenital schistosomiasis in Lindi, Tanzania. PLoS One 17, e0263929. https://doi.org/10.1371/journal.pone.0263929.

NBS, 2022. Population and Housing Census. National Bureau of Statistics, Ministry of Finance, The United Republic of Tanzania.

Ng'weng'weta, S.B., Tarimo, D.S., 2017. Urinary schistosomiasis among preschool-age children in an endemic area of Kinondoni municipality, Dar es Salaam, Tanzania 2016. Asian Pac. J. Trop. Dis. 7, 162–168. https://doi.org/10.12980/apjtd.7.2017D6-359.

Nwoko, O.E., Kalinda, C., Manyangadze, T., Chimbari, M.J., 2022. Species diversity, distribution, and abundance of freshwater snails in KwaZulu-Natal, South Africa. Water 14, 2267. https://doi.org/10.3390/w14142267.

Nwoko, O.E., Manyangadze, T., Chimbari, M.J., 2023a. Spatial and seasonal distribution of human schistosomiasis intermediate host snails and their interactions with other freshwater snails in 7 districts of KwaZulu-Natal province, South Africa. Sci. Rep. 13, 7845. https://doi.org/10.1038/s41598-023-34122-x.

Nwoko, O.E., Manyangadze, T., Chimbari, M.J., 2023b. Spatial distribution, abundance, and infection rates of human schistosome-transmitting snails and related physicochemical parameters in KwaZulu-Natal (KZN) province, South Africa. Heliyon 9, e12463. https://doi.org/10.1016/j.heliyon.2022.e12463.

Nzalawahe, J., Kassuku, A.A., Stothard, J.R., Coles, G.C., Eisler, M.C., 2015. Associations between trematode infections in cattle and freshwater snails in highland and lowland areas of Iringa Rural District, Tanzania. Parasitology 142, 1430–1439. https://doi.org/10.1017/S0031182015000827.

Olkeba, B.K., Boets, P., Mereta, S.T., Yeshigeta, M., Akessa, G.M., Ambelu, A., Goethals, P.L.M., 2020. Environmental and biotic factors affecting freshwater snail intermediate hosts in the Ethiopian Rift Valley region. Parasites Vectors 13, 292. https://doi.org/10.1186/s13071-020-04163-6.

Orish, V.N., Morhe, E.K.S., Azanu, W., Alhassan, R.K., Gyapong, M., 2022. The parasitology of female genital schistosomiasis. Curr. Res. Parasitol. Vector Borne Dis. 2, 100093. https://doi.org/10.1016/j.crpvbd.2022.100093.

Silvestri, V., Mushi, V., Mshana, M.I., Bonaventura, W.M., Justine, N.C., Sabas, D., Ngasala, B., 2022. Blood flukes and arterial damage: A review of aneurysm cases in patients with schistosomiasis. Can. J. Infect Dis. Med. Microbiol. 2022, 6483819. https://doi.org/10.1155/2022/6483819.

Starkloff, N.C., Angelo, T., Mahalila, M.P., Charles, J., Kinung'hi, S., Civitello, D.J., 2024. Spatio-temporal variability in transmission risk of human schistosomes and animal trematodes in a seasonally desiccating East African landscape. Proc. R. Soc. B Biol. Sci. 291, 20231766. https://doi.org/10.1098/rspb.2023.1766.

Tumwebaze, I., Clewing, C., Dusabe, M.C., Tumusiime, J., Kagoro-Rugunda, G., Hammoud, C., Albrecht, C., 2019. Molecular identification of *Bulinus* spp. intermediate host snails of *Schistosoma* spp. in crater lakes of western Uganda with implications for the transmission of the *Schistosoma haematobium* group parasites. Parasites Vectors 12, 565. https://doi.org/10.1186/s13071-019-3811-2.

Webbe, G., 1962. The transmission of *Schistosoma haematobium* in an area of Lake Province, Tanganyika. Bull. World Health Organ. 27, 59–85.

Wepnje, G.B., Peters, M.K., Green, A.E., Nkuizin, T.E., Kenko, D.B.N., Dzekashu, F.F., et al., 2023. Seasonal and environmental dynamics of intra-urban freshwater habitats and their influence on the abundance of *Bulinus* snail host of *Schistosoma haematobium* in the Tiko endemic focus, Mount Cameroon region. PLoS One 18, e0292943. https://doi.org/10.1371/journal.pone.0292943.

WHO, 2017. Field use of molluscicides in schistosomiasis control programs: An operational manual for program managers. World Health Organization, Geneva, Switzerland. https://iris.who.int/handle/10665/254641.

Zhang, S.-M., Bu, L., Lu, L., Babbitt, C., Adema, C.M., Loker, E.S., 2022. Comparative mitogenomics of freshwater snails of the genus *Bulinus*, obligatory vectors of *Schistosoma haematobium*, causative agent of human urogenital schistosomiasis. Sci. Rep. 12, 5357. https://doi.org/10.1038/s41598-022-09305-7.