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To cite this article: Chester Kalinda, Moses J. Chimbari, Mokgadi P. Malatji & Samson Mukaratirwa (2018) Influence of desiccation on the survival of *Bulinus globosus* under laboratory conditions, Journal of Freshwater Ecology, 33:1, 461-473, DOI: [10.1080/02705060.2018.1520157](https://doi.org/10.1080/02705060.2018.1520157)

To link to this article: <https://doi.org/10.1080/02705060.2018.1520157>



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Published online: 13 Nov 2018.



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Influence of desiccation on the survival of *Bulinus globosus* under laboratory conditions

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ABSTRACT

Environmental changes are generally known to influence the distribution and abundance of schistosome intermediate host snails (IHS). However, the influence of hydrologic changes per se on the length of survival of schistosome IHS is not fully understood. To explore how desiccation may influence the survival of *Bulinus globosus*, the main IHS of *Schistosoma haematobium* in southern Africa, we conducted a study under laboratory conditions where snails were subjected to periods of desiccation and their survival evaluated. Desiccation period from 28 to 49 days post-draining of water was associated with an increase in mortality of 33.2 and 42.4% in large (mean shell height 7.81 ± 0.44 mm) and small (mean shell height 5.94 ± 0.68 mm) *B. globosus* snails, respectively. Although the duration of desiccation had no effect on the depth of burrowing, large size snails burrowed deeper into the soil than small size snails. The LT₅₀ and LT₉₀ of snails designated as large (7.81 ± 0.44 mm) were 73.35 ± 10.32 and 110.61 ± 21.03 days, respectively. On the other hand, LT₅₀ and LT₉₀ for snails designated as small (5.94 ± 0.68 mm) were 59.64 ± 8.56 and 84.19 ± 12.09 days, respectively. The survival of *B. globosus* during desiccation depended on the size/age of the snail where large size snails aestivate and survive for a longer period by burrowing deeper into the soil. We therefore conclude that adult *B. globosus* may play a significant role in habitat recolonization after a period of drought which is a common phenomenon in schistosomiasis endemic areas when population crashes.

ARTICLE HISTORY



Received 15 June 2018
Accepted 30 August 2018

KEYWORDS

aestivation; *Bulinus globosus*; burrowing; desiccation endpoint; population recolonization; schistosomiasis; survival

Introduction

Schistosoma intermediate host snails (IHS) are vulnerable to climatic changes (Yang et al. 2007; Morley and Lewis 2013). Given their role in schistosomiasis transmission, it is important to evaluate their responses to predicted future changes in aquatic habitats due

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to climate change. Furthermore, increased anthropogenic activities may negatively affect aquatic and freshwater ecosystems (Lytle and Poff 2004; Tisseuil et al. 2012) resulting in altered functional diversity, integrity of the freshwater ecosystems (Konar et al. 2013) and abundance of freshwater organisms (Kingsford 2011; Lund et al. 2016). Increasing evidence also suggest that differences in the response of IHs to climate change may lead to changes in their interspecific and timing of interactions (Paull et al. 2012), distribution and abundance (Zhou et al. 2008; Stensgaard et al. 2013). Therefore, it is important to investigate the adaptation strategies of IHs to abiotic stresses such as water reduction and desiccation in order to predict their future potential responses to climate change.

Bulinus globosus (Gastropoda: Planorbidae) is the major IH snail of *Schistosoma haematobium* in southern Africa (Appleton and Madsen 2012). The snail is aquatic and breeds in fresh water habitats and can reproduce through selfing or outcrossing depending on the environmental conditions (Jarne et al. 1992). Hence, *Bulinus globosus* is considered to have a high biotic potential and can breed throughout the year in aquatic environments (O'keeffe 1985). Its rapid growth and re-population rate of habitats even after population crashes due to drought (Harrison and Shiff 1966; O'keeffe 1985; Marti 1986) makes it critical to gather information on the behavior of the specie during desiccation in search of strategies to enhance the effectiveness of vector-control in schistosomiasis control programs.

Despite considerable efforts to control schistosomiasis, changes in climate and land use practices have led to the creation of more suitable habitats for IHs with subsequent increase in disease transmission (Yang et al. 2007; Zhou et al. 2008; McCreesh et al. 2015; Stanton et al. 2017; Yigezu et al. 2018). In addition, experimental (Paull and Johnson 2011; Kalinda et al. 2017a), field studies (Marti 1986), and predictive models (Manyangadze et al. 2016b; Kalinda et al. 2018) concluded that a rise in temperature may lead to an increase in snail fecundity and hence abundance. This may in-turn increase the risks of transmission of schistosomiasis due to the abundance of IHs. Nevertheless, efforts are being advocated to significantly reduce morbidity due to schistosomiasis through mass drug administration programmes (MDA) (Fenwick et al. 2009; Wang et al. 2009).

In the climate change-schistosomiasis theory, much emphasis has been placed on the effect of temperature on IHs (Yang et al. 2007; Kalinda et al. 2017a, 2017b) and disease dynamics (Stensgaard et al. 2013; McCreesh et al. 2015; Ngarakana-Gwasira et al. 2016), however, studies on the effect of abiotic disturbances such as desiccation through long term and seasonal droughts are limited. Ephemeral rivers and seasonal water ponds which are the common habitat for IHs of *Schistosoma* parasites are subject to water level alterations and drying due to normal seasonal cycles, climatic and eco-hydrologic factors (Darby et al. 2008; Whitehead et al. 2009). Furthermore, hydro-ecological models have also predicted a potential increase in the frequency and intensity of droughts (Van Vliet and Zwolsman 2008). This may have long-term implications on the population structure and abundance of IHs of parasites of medical and veterinary importance (Woolhouse and Taylor 1990; Bavia et al. 1999).

In the context of predicted climate shifts, correctly identifying the mechanisms through which desiccation and resumption of favorable conditions may affect IHs will improve the accuracy of predicting the potential impact of climate change on schistosomiasis. Process-based experiments may be essential in providing significant cues on the potential impact of desiccation on freshwater snails. This will significantly contribute to critical knowledge needed for an integrated approach to eradicate schistosomiasis and other snail-borne diseases, especially in sub-Saharan Africa where snails are now found in habitats initially thought to be unfavorable (Stanton et al. 2017). In view of this, the

present study examined the survival of *Bulinus globosus* during substratum drying under laboratory simulated desiccation conditions.

Methods

Breeding of experimental animals

Bulinus globosus snails were collected from a habitat in *Ingwavuma* (latitude: -26.9965 , longitude: 32.27257) in *uMkhanyakude* district of KwaZulu-Natal province of South Africa (Manyangadze et al. 2016b; Kalinda et al. 2017a). Snails were allowed to breed to give F1 generation snails that were used in the study. To create two distinct age groups, the laying of egg masses was staggered by creating a three 3 weeks age difference. This allowed us to have two groups of snails with age difference of 3 weeks. Snails were allocated to experimental jars when the young snails were 4 weeks old (average shell height of 4.03 ± 0.56 mm) and the large snails were 7 weeks old (average shell height of 6.32 ± 0.71 mm). The F1 generation was maintained in 2 L cubical plastic aquaria (size: $18 \times 18 \times 10$) cm^3 which were filled with filtered pond water and maintained at room temperature (24.0 – 25.0 °C). The snails were fed ad libitum on blanched lettuce and Tetramin tropical fish food (Tetra®). The experimental room had a photoperiod of 12-hour light/12-hour dark.

Experimental design

Snails were assigned to two groups; large size snails comprised of 7 weeks old F1 generation and small snails comprised of 4 weeks old young F1 generation. This was purposely designed to evaluate the influence of snail size/age on survival during desiccation. Four hundred and eighty snails split in two groups (experimental and control groups) were randomly allocated to 48 2-L cubical plastic aquaria, with each aquarium containing 10 snails. Two control groups with the same shell height range and age as the experimental groups were also included. Each aquarium was filled with a 5 cm layer of soil (to give sufficient depth for burrowing) collected from a natural breeding site of *B. globosus* (Manyangadze et al. 2016a; Kalinda et al. 2017a). Prior to its use, the soil was washed in hot boiling water to kill any organisms within it and a composite sample was profiled using the sedimentation method. Before snails were added to the experimental 2-L cubical plastic aquaria, each aquarium was filled with 400 mL of filtered pond water until the soil was saturated and the water level was 4 cm above the surface of the soil. After 48 hrs, *B. globosus* F1 generation snails from each group were randomly allocated to each

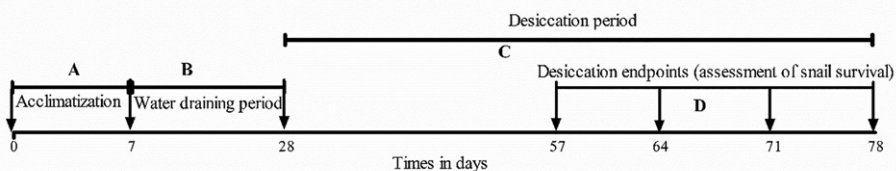


Figure 1. The timeline of experimental events; (A) acclimatization period, (B) water draining period to induce aestivation, (C) desiccation period to allow soil to dry and (D) desiccation endpoints at which snail survival was assessed in selected aquaria.

aquarium. The snails were acclimatized to the new environment for 7 days (Poznańska et al. 2015) before dewatering was initiated (Figure 1).

On day 8 after acclimatization, water was gradually drained from the aquaria of the experimental groups only. Three times a week (every after 2 days), 30 mL (cumulatively, 90 mL a week) of water was drained from each experimental aquarium using a graduated pipette (Koprivnikar et al. 2014; Poznańska et al. 2017). This process was done for a period of 3 weeks. In this period, 270 ml of water was drained from each aquarium. Feeding of snails in the experimental groups was stopped at day 21 from the beginning of the experiment while snails in the control group continued to be fed ad libitum. After water was drained in the experimental group, the soil was left to dry whereas water continued to be changed twice a week in the control group.

Measurement of water parameters, snail parameters and soil moisture

Water temperature, pH and conductivity in the experimental and control groups were monitored throughout the study period using the Hanna thermometer (Hanna Instruments HI 98129 PH/EC/TDS/°C Combo pocket instrument). The measurement of water quality parameters was stopped when the water dried off in the experimental group.

The study pre-determined the desiccation endpoints to be at day 57, 64, 71, and 78 (Betterson et al. 1988; Poznańska et al. 2015). At each desiccation endpoint (Figure 1), 12 aquaria were randomly selected to determine snail survival and revival. This included six aquaria from the experimental and six aquaria from the control groups. For the experimental aquaria, we carefully dug through the soil layers using a spatula in order to retrieve the snails buried in the soil without damaging their shells. The height of soil in each aquarium had been marked in order to distinctly determine the depth burrowing. Furthermore, the drying soil was carefully removed along its developing cracks to avoid damaging the shells of any snails. Since most snails would be attached to the soil at the time of digging, the undisturbed soils were collected, and the depth taken depending on the locations of the snails which were often visible. The depth at which each individual snail within the aquaria was found was measured and recorded. This was done at each desiccation endpoint (Figure 1) and the shell height of the snails was also measured.

We checked snail survival in the control experiments daily while in the experimental aquaria, this was done at each desiccation endpoint (Figure 1). To determine the status of snails dug at each desiccation endpoint (whether dead or alive), each snail was put in a small cup which had been filled with filtered pond water. The snails were then observed for three hours. Snails that opened their opercula with extension of their soft bodies were recorded as 'alive' and those that did not were recorded as 'dead'.

Determination of soil moisture was done using the gravimetric method (Reynolds 1970) at each desiccation endpoint. For the control aquaria, water was decanted from the aquaria and muddy soil was collected for determination of moisture content. For the soil from experimental aquaria, drying soil samples were also collected and three samples of 50 g of soil from each aquarium were oven dried at 105 °C in an incubator (EcoTherm Labotec) for 24 hours. After oven-drying, the soil was re-measured to obtain the soil water content. The experiment was run until day 79 when it was terminated. Although snails in the control aquaria were still alive, all the snails in experimental aquaria had died and hence it was not possible to make comparisons with survival of the control snails.

Data analysis

We summarized the water quality parameters as means and standard deviation. We also compared shell height of the snails among groups at each desiccation endpoint using a one-way analysis of variance (ANOVA) after carrying out parametric tests of normality and homogeneity of variance to satisfy ANOVA assumptions.

A generalized linear model with a Poisson link function was used to determine the influence of desiccation time on the number of snails that died after determining the number of snails that had resuscitated at each desiccation endpoint. The number of snails that died during the course of the experiment and those that were resuscitated was expressed as a proportion.

Probit regression model was also used to determine the lethal time (LT) of snail mortality of 50% (LT_{50}) and 90% (LT_{90}) for both large and small snails using the R package Mass (Ripley 2015). Data analysis was done using R 3.4.2 version (R Core Team. R: A language and environment for statistical computing, 2013).

Results

Water quality parameters

The soil that was used comprised 42% sand, 44% silt, and 14% clay. Water temperature (\pm SD) in the four treatments ranged from 23.02 ± 0.12 °C to 23.12 ± 0.03 °C while pH was generally neutral (7.58 ± 0.05 to 7.59 ± 0.01) in all experimental groups including the control. The mean total dissolved solids ranged from 604.7 ± 70.64 to 851.9 ± 20.81 604 in all experimental groups including the control.

Snail growth

Length of desiccation had no effect on the shell height of both control and experimental snails ($F_{3,32}=2.84$, $p=0.0536$). At desiccation endpoints day 57 and 78, the mean (\pm SD) shell height of small size control group was 6.50 ± 0.65 and 7.71 ± 0.72 mm, respectively. On the other hand, shell height of snails in the small size experimental group at desiccation endpoints day 57 and 78 was 5.27 ± 0.52 and 5.98 ± 0.56 mm, respectively (Figure 2A). Significant differences in the height of snails was observed at desiccation endpoints day 64 ($t=3.06$ $p=0.028$) and 78 ($t=2.72$, $p=0.042$). The interaction between

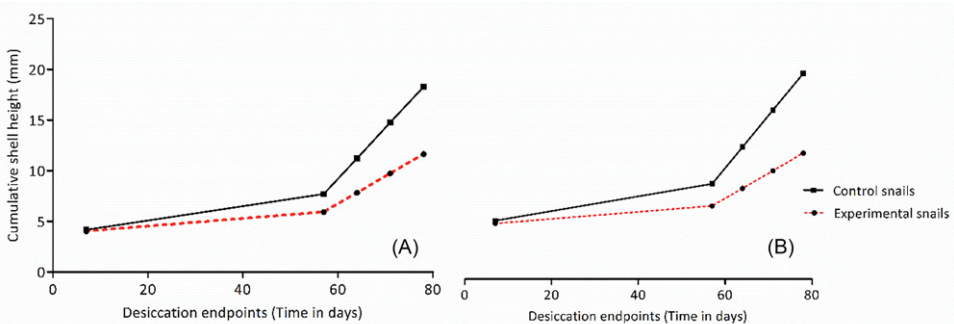


Figure 2. Cumulative shell height of *B. globosus* snails at different sampling points (desiccation end points). (A) = Shell height of experimental small snails and control at day 7 (initial measurements) and day 57, 64, 71, and 78 (Desiccation endpoints) of the experiment. (B) = Shell height of experimental large snails and control at day 7 (initial measurements) and day 57, 64, 71, and 78 (Desiccation endpoints) of the experiment.

initial size of the snail and desiccation time led to no significant difference in the growth of snails in the small size control and experimental groups ($F_{3,16}=0.48$, $p=0.699$).

The shell height of snails in the large size control group at desiccation endpoints day 57 and 78 was 8.90 ± 0.41 and 10.3 ± 0.69 mm, respectively. The shell length of snails in the experimental group at desiccation endpoints day 57 and 78 was 7.8 ± 0.35 and 7.9 ± 0.44 mm, respectively (Figure 2B). The effect of the interaction between the initial size of the snail and desiccation time had no effect on the growth of snails in the large size control and experimental groups ($F_{3,16}=3.03$, $p=0.0653$). Nevertheless, significant differences in the shell height of snails was observed at desiccation endpoints day 64 ($t=3.05$, $p=0.0379$), 71 ($t=2.89$, $p=0.044$) and 78 ($t=3.40$, $p=0.0272$).

Snail size and depth of burrowing into the soil

We found a significant size effect on the depth of burrowing ($F_{1,16}=26.08$, $p=0.001$) such that large size snails burrowed deeper compared to small size snails (Figure 3). It was further observed that length of desiccation ($F_{3,16}=1.91$, $p=0.168$) and the interaction between snail size and length of desiccation ($F_{3,16}=1.01$, $p=0.417$) had no effect on depth of burrowing. On average, large size snails sampled on desiccation endpoints day 57 and 78 burrowed to the depth of 1.69 ± 0.27 and 2.09 ± 0.55 cm below the soil surface, respectively. On the other hand, small size snails sampled at desiccation endpoints day 57 and 78 burrowed to 0.84 ± 0.23 mm and 1.37 ± 0.33 cm below the soil surface.

There was a reduction in the amount of moisture content in the soil as the desiccation period increased (Figure 4A). The number of snails that were resuscitated decreased with an increase in desiccation period (Coeff: -0.0338 , $z=-2.71$, $p=0.007$; Figure 4B). Furthermore, snail mortality increased linearly with an increase in the length of desiccation (Coeff: 0.0314 , $z=3.52$, $p<0.001$; Figure 4C).

At day 57 and 78 of desiccation, the proportion of large experimental snails that had died was 0.341 (95% CI: 0.066–0.786) and 0.839 (95% CI: 0.399–1.219), respectively while 0.463 (95% CI: 0.183–1.066) and 0.918 (95% CI: 0.363–1.446) small experimental snails had died at day 57 and 78, respectively. On the other hand, 0.181 (95% CI 0.156–0.317) and 0.228 (95% CI: 0.193–0.722) control large size snails had died by 57 and 78, respectively. For small size control snails, 0.210 (95% CI: 0.112–0.604) and 0.268 (95% CI: 0.142–0.836) had died by day 57 and 78, respectively (Figure 4B, 4C).

Results show that large size snails were more resilient to desiccation than small size snails (Figure 5). The lethal time (LT) at which 50% (LT_{50}) of the experimental large size snails died was 73.35 ± 10.32 days while it was 59.64 ± 8.56 days for the small snails.

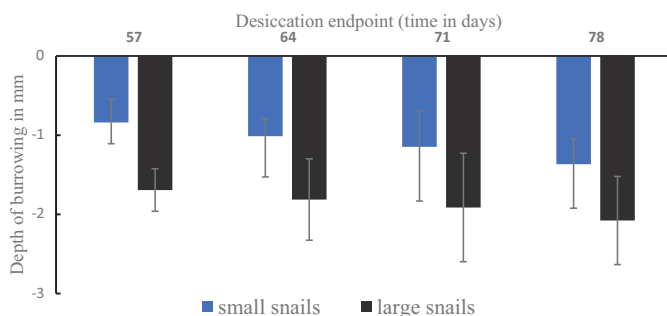


Figure 3. Depth of burrowing by large and small *B. globosus* snails at different desiccation periods.

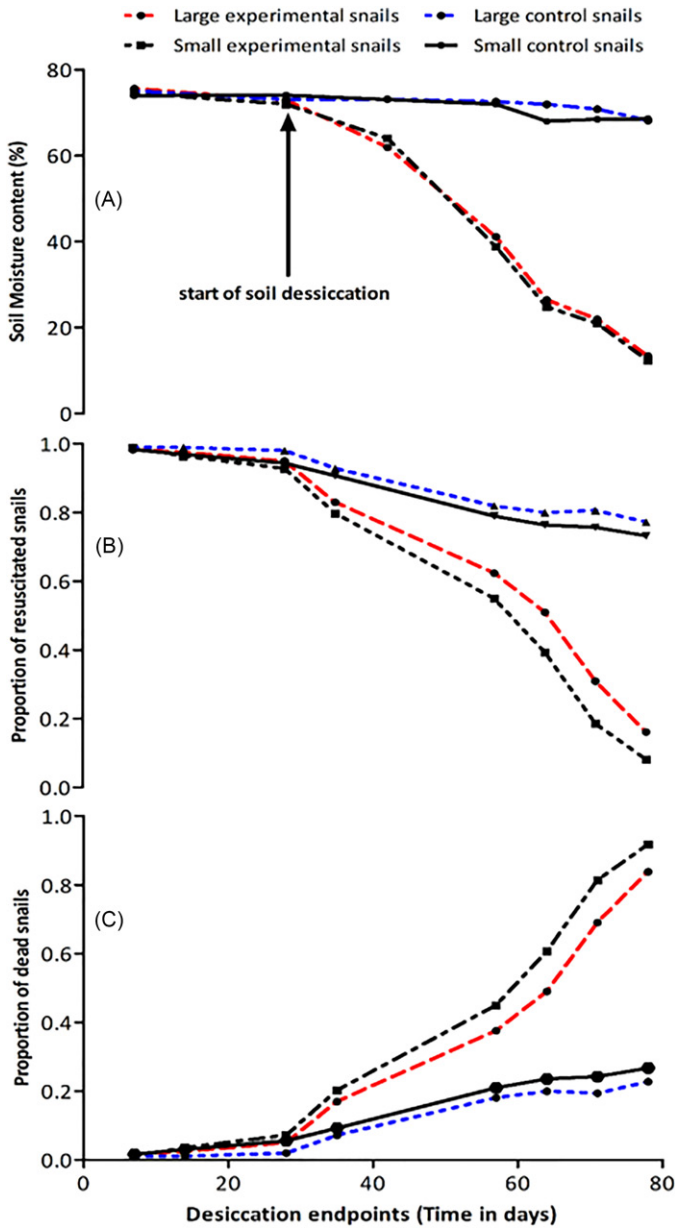


Figure 4. Soil moisture content measured at different time points (A) proportion of *B. globosus* snails that resuscitated at different desiccation time points (B) proportion of snails that died at different desiccation time points (C).

Furthermore, LT_{90} for large size snails was 110.61 ± 21.03 days while it was 84.19 ± 12.09 days for the small size snails.

Discussion

This study was designed to mimic conditions to which snails are exposed to in their natural habitats. It was observed that *B. globosus* was tolerant to drying conditions and

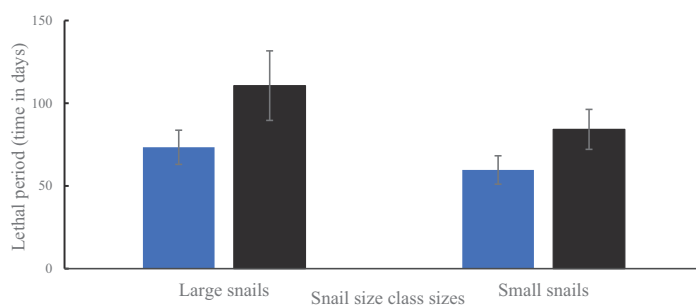


Figure 5. Lethal time (LT): 50% (LT₅₀, Blue) and 90% (LT₉₀, Black) for mortality of large and small *B. globosus* snails.

capable of surviving and resuscitation after being exposed to desiccating conditions for 50 days. The observed resilience of these snails to drying and their eventual resuscitation at the resumption of favorable conditions may potentially lead to repopulating habitats. These findings are in consonant with the conclusions made by Harrison and Shiff (1966) who suggested that *B. globosus* can rapidly colonize habitats and re-build its population density following resumption of favorable conditions. The study further showed that soil moisture is an important determinant of snail survival during desiccations. According to Stubbington and Detry (2013), IHs can remain alive in the soil as long as it remains moist. The results from the current study, in a broader sense, agree with earlier studies done by Shiff (1960) and Woolhouse and Taylor (1990). Snail size was associated with high tolerance to desiccation and reduced mortality. Although earlier studies had exposed snails to damp mud/soil (Shiff 1960; Chu et al. 1967; Woolhouse and Taylor 1990) to evaluate their resistance to desiccation, the inclusion of water and its gradual reduction in this study allowed us to explicitly observe the response of *B. globosus* snails to progressive desiccation.

Both large and small size snails burrowed into the soil, nevertheless, large size *B. globosus* snails burrowed deeper in search of moisture and this increased its survival. According to Poznańska et al. (2015), IHs burrow into the soil as they follow the decreasing water levels and this increases chances of survival. Furthermore, the current study indicates that soil moisture content is a vital factor determining the length of snail survival and the number of snails that resuscitate. Our findings are corroborated by Barlow (1935) and Betterton et al. (1988) who suggested that desiccation rate affects both the survival and resuscitation of snails negatively. In the current study, the differences in the number of snails that resuscitated between the two groups may be particularly important in the repopulation of snail habitats. Large size snails with the shell height of 8 mm burrowed deeper into the soil. This collaborates with the finding of Betterton et al. (1988) who found that *B. globosus* with the shell height of about 9 mm burrowed deeper into the soils. Furthermore, Hira (1968) also observed that the survival of *B. globosus* was higher for snails with the shell height of 8.1–12.9 mm. On the other hand, Chu et al. (1967) indicated that *Bulinus truncatus* snails with the shell height of 4–8 mm survived far longer than those with the shell height of 8–12 mm. Collectively, our results suggest that tolerance to desiccation may be strongly associated with the size or age of the snail at the time of desiccation. Furthermore, our results suggest that adult *B. globosus* may play a significant role in habitat recolonization after a period of drought which is a common phenomenon in schistosomiasis endemic areas when population crashes.

Although studies focusing on the desiccation capacity and burrowing of IHs have largely been neglected, their importance may increase as the need to incorporate the

ecology of snails in schistosomiasis control programs rise. Our study found that the survival of snails reduced linearly with an increase in desiccation time. The proportion of snails that may resuscitate at the end of the desiccation period may directly be influenced by the duration of the desiccation period. According to Paraense (1975), desiccation period longer than five months led to a complete eradication of *Biomphalaria glabrata*. On the other hand, Woolhouse and Taylor (1990) observed that *B. globosus* was resilient to desiccation. This may have been enhanced by its ability burrow into the soil (Rubaba et al. 2016). A study by Sturrock (1970) further suggested that desiccation can reduce the population density of IHs and alter the age structure of resuscitating snails. Furthermore, Whitehead et al. (2009) suggested that desiccation at schistosomiasis transmission sites disrupts the population build-up of snails and increase snail mortality thus reduce the risks of schistosomiasis transmission. This process had earlier been used in Zimbabwe by Chandiwana et al. (1988) who demonstrated that effective management of water in irrigation schemes could reduce snail population. Results from the current study and studies done by others demonstrate the importance of manipulating snail habitats in combination with MDA for increased success of reducing the prevalence of schistosomiasis.

Our study provides insights into the relationship between snail survival, population extinctions, and recolonization of habitats. Field and experimental work has shown that the availability and persistence of water at transmission sites may increase snail population and potentially increase transmission of schistosomiasis. For example, water projects such as irrigation schemes were observed to enhance the creation of suitable site for IHs (Yang et al. 2005, Steinmann et al. 2006), increasing the potential risk of transmission of schistosomiasis. Our data showed that a reduction in soil moisture led to an increase in snail mortality. Predictive models have continued to project altered rainfall and water availability in certain parts of sub-Saharan Africa where *B. globosus* is the main IHs of *S. haematobium*. Results from our study indicate that such changes will be vital in the recolonization of snail breeding sites. Recolonization of habitats by IHs after resumption of favorable conditions such as water availability is consistent with results from other field experiments (Betterson et al. 1988; Manyangadze et al. 2016b). *Bulinus globosus* is a highly fecund snail (Marti 1986; Kalinda et al. 2017a) and rapidly recovers to populate habitats quickly (Harrison and Shiff 1966).

The current study focused on the potential influence of habitat change through water reduction on *B. globosus* population dynamics in terms of mortality and recovery. Burrowing and snail size played an important role in the survival of *B. globosus* snails. Increased snail survival especially at transmission sites increases the probability of recolonization and the risks of schistosomiasis transmission. Taking *B. globosus* as a model snail in the fight against schistosomiasis, increased duration of desiccation and potentially application of molluscicides at the inception of rains may further reduce snail population size and habitat recolonization.

Ethics approval

All experimental protocols and procedures of this study were reviewed and approved by the Animals Ethics Committee of the University of KwaZulu-Natal (UKZN) (Ref: REC/052/017PD) in accordance with the South African national guidelines on animal care, handling and use for biomedical research.

Availability of data and material

The data supporting the writing of this manuscript can be accessed from the project Centre of the Tackling Infection to Benefit Africa (TIBA), University of KwaZulu-Natal. Data can be requested by following the guidelines laid out in the Data Access Policy of the University of KwaZulu-Natal.

Acknowledgments

This research was commissioned by the National Institute of Health Research using Official Development Assistance (ODA) funding. The views expressed in this publication are those of the author(s) and not necessarily those of the NHS, the National Institute of Health Research, or the Department of Health. The College of Health Sciences, University of KwaZulu-Natal co-funded the study through the postdoctoral fellowship that was awarded to Chester Kalinda. The authors also acknowledge the precious inputs from the editors and anonymous reviewers who helped improve the content and quality of the paper.

Disclosure Statement

The authors declare that they have no competing interests

Funding

The writing of this manuscript was supported by University of KwaZulu-Natal, College of Health Sciences through the Post-doctoral fellowship awarded to the KC.

Authors' contributions

KC, SM, and MJC conceptualized the study. KC and PM performed the experiments and collected the data. KC analyzed the data and wrote the manuscript. MJC and SM read and edited the manuscript. All the authors approved the final version and agree to be accountable for any aspects of the work.

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Chester Kalinda has a PhD degree Public Health from the University of KwaZulu-Natal in Durban, South Africa. He is broadly interested in studying how cross-ecosystem interactions may influence infectious disease risk. Much of his research focuses on how climate change may affect intermediate hosts and vectors and transmission of parasites especially those of neglected tropical diseases.

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Mokgadi P. Malatji is a PhD student at the University of KwaZulu-Natal. Her research focuses on host-parasite interactions and how these interactions influence infectious disease risks. Her research interests also include molecular biology; medical and veterinary parasitology and tropical diseases. Currently, she is studying the taxonomy of *Lymnaeidae* species and *Fasciola* species.

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