A Call for Standardised Snail Ecological Studies to Support Schistosomiasis Risk Assessment and Snail Control Efforts

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Abstract

Freshwater snails act as intermediate hosts (IH) for schistosomiasis, a tropical disease affecting over 200 million people worldwide. Despite their medical importance, an extensive understanding of IH snail ecology remains absent. Especially data on the tolerance limits to different abiotic factors is fragmented and incomplete. Consequently, the construction of accurate species distribution models to identify snail habitats and guide targeted snail control efforts remains difficult. Here, we compiled a summary on the tolerance limits to abiotic factors of African IH snails of human schistosomiasis. A systematic search on Web of Science, Pubmed, and Embase identified 45 relevant studies. Synthesis of these studies indicates that research efforts differ greatly between IH snail species, life stages and abiotic factors. The importance of each abiotic factor in determining snail presence and abundance is discussed. Furthermore, attention was drawn to knowledge gaps and the lack of standardised experimental designs, which impedes comparisons between studies. This in turn prevents us from making firm conclusions and calls for best practices adopted by all malacologists. In doing so, IH snail ecological data could serve as a basis to assess schistosomiasis risk and guide snail control efforts in order to support schistosomiasis control.

Keywords

Abiotic factors, systematic review, tolerance limits, *Bulinus*, *Biomphalaria*, species distribution

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Introduction

Schistosomiasis is a parasitic disease caused by blood flukes of the genus *Schistosoma* (class: Trematoda), which depend on freshwater intermediate host (IH) snails for their transmission (Gryseels, 2012). The main causative agents of urinary and intestinal schistosomiasis in Africa are *Schistosoma haematobium* (Bilharz, 1852) and *Schistosoma mansoni* Sambon, 1907, respectively. Despite large control efforts made in the past decades, schistosomiasis remains one of the major global health concerns with over 220 million people infected, 93 % living in sub-Saharan Africa (WHO, 2015).

In Africa, human urinary and intestinal schistosomiasis are transmitted through IH snails of the genera *Bulinus* and *Biomphalaria*, respectively (Brown, 1994). These hermaphroditic snails have a high morphological plasticity and are typical r-species as they are characterised by a high reproduction potential which allows them to colonize new habitats quickly (Oyeyi & Ndifon, 1990; Dillon, 2000). Both genera are known to occupy various habitats including small pools, lakes, streams, dams and irrigation canals. Additionally, their wide tolerance ranges to ecological factors such as temperature, rainfall, and the chemical water composition result in a global distribution of both genera (Appleton, 1978; Brown, 1994). Despite these characteristics, the demographic aspects (e.g. population densities, size at reproduction) of IH snails are very sensitive to environmental fluctuations (Dillon, 2000). This causes IH snail distributions to be spatially clustered and largely determined by environmental characteristics (Dillon, 2000; Krauth et al., 2017), eventually leading to spatial heterogeneity in schistosomiasis transmission (Clennon et al., 2004; Assare et al., 2015).

Following the uncovering of the schistosome life cycle in 1913, IH snail control was used as the main tool to eliminate schistosomiasis (Shiff, 2017; Sokolow et al., 2018). Following the discovery of the anthelmintic drug praziquantel in 1970, the WHO shifted its focus from IH snail control to preventive chemotherapy, through mass drug administration (MDA) among school-aged children (WHO, 1985). However, this method alone proves to be insufficient as the prevalence of schistosomiasis remains high (WHO, 2015). Even though poverty convicts many people to risky water-related practices (King,

2010), limited knowledge, negative attitudes towards schistosomiasis prevention and treatment, and risky behaviour in high-risk zones remain key factors in facilitating disease transmission (Sacolo et al., 2018). Hence, increasingly more scientists argue for integrated control strategies where MDA is supplemented by “old fashioned” snail control, among other measures like sanitation, safe water supply, and health education (Hu et al., 2005; Grimes et al., 2014; King & Bertsch, 2015; Shiff, 2017; Lo et al., 2018; Sokolow et al., 2018; Ashepet et al., 2020). Schistosomes are capable of infecting multiple definitive hosts such as rodents (Catalano et al., 2020). Since these animals are not treated during MDA, they act as a reservoir for parasites. However, these parasites still require snails to complete their life cycle, turning snail control into an important part of schistosomiasis control strategies. Furthermore, snail habitat mapping can provide a good estimator of schistosomiasis transmission (Wood et al., 2019), which also illustrates the importance of snail control to reduce transmission risk. Integrated control strategies have demonstrated their effectiveness in Japan and the People’s Republic of China where they significantly reduced both human and snail infections, or even eradicated schistosomiasis completely (Tanaka & Tsuji, 1994; Qian et al., 2018). Hence, these strategies might be effective in Sub-Saharan Africa too.

An extensive understanding of IH snail ecology can help guide snail control efforts. Large-scale snail control using molluscicides is unachievable due to the high cost, difficulty to disperse, toxicity to non-target aquatic organisms and other ecologically adverse effects (Rollinson et al., 2013; King & Bertsch, 2015; Sokolow et al., 2018). Biological control efforts, too, are only feasible and ethically justified when applied on a small scale. However, the effective implementation of small-scale (targeted) control efforts is hampered by the fragmentation and incompleteness of ecological data on the IH snails (Adema et al., 2012; Monde et al., 2015; Shiff, 2017; Sokolow et al., 2018).

Due to the scarcity of information on the tolerance limits and life-history traits of IH snails, there is no clear overview of the effects of (a)biotic factors on the distribution or habitat preferences of these snails (Pedersen et al., 2014; Manyangadze et al., 2016; Shiff, 2017). Information on the tolerance

limits is especially relevant because the tolerable extremes often differ slightly among IH snail species, although the optimum conditions are mostly similar (Hubendick, 1958; Malek, 1958). Syntheses on the effects of ecological factors affecting African freshwater snails were made by Appleton (1978), Brown (1994), and Dillon (2000). Kalinda et al. (2017b) made an effort to synthesize existing information on the effect of temperature on the growth, fecundity and survival of IH snails transmitting human schistosomiasis, while Stensgaard et al. (2013) assessed the effect of climate change on the intestinal schistosomiasis and IH snail distribution in Africa. These reviews, however, do not consider the effects of biotic or abiotic factors (other than temperature) on the life-history traits and tolerance limits of IH snails. Incorporation of experimental data on the tolerance limits might result in more reliable predictions of future IH snails distributions, thereby improving schistosomiasis risk assessment in new areas (Monahan, 2009; Stensgaard et al., 2016).

This systematic review elaborates and draws upon the studies of Appleton (1978), Brown (1994), Dillon (2000) and Kalinda et al. (2017b), and aims to compile an exhaustive synthesis of the knowledge on the tolerance limits to abiotic factors of African schistosome IH snails of the genera *Bulinus* and *Biomphalaria*. Here, abiotic factors are defined as the non-living part of the ecosystem that shapes the environment, such as temperature, rainfall, stream velocity and the chemical water composition. The effect of each factor on life-history traits is reported. Knowledge gaps that impair the schistosomiasis risk assessment and the application of effective IH snail control actions are identified. Biotic factors, including population densities, competition and other ecological interactions, as well as tolerance to pollutants and physiological responses are outside the scope of this study and are therefore not discussed here.

Materials and methods

Search strategy

A systematic search of all peer reviewed articles published between 1864 and 2019 was conducted on 21/03/2019 via PubMed (Medline), Embase, Web of Science core collection, BIOSIS Citation Index,

Zoological Record, Current Contents Connect, SciELO Citation Index, Data Citation Index, Inspec, Derwent Innovations Index, KCI-Korean Journal Database and the Russian Science Citation Index. Relevant MeSH and Emtree terms were identified for PubMed (Medline) and Embase, respectively. MeSH terms included “*Biomphalaria*”, “*Bulinus*”, and expressions related to life-history traits and tolerance limits. These keywords were complemented with related searches in titles and abstracts to also include recent publications. The Boolean operators AND and OR were used to combine the search terms (full search string: Supplementary Material S1). The Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) guidelines were followed (Moher et al., 2009).

Eligibility criteria

The eligibility criteria were defined prior to the literature search. Only experimental, field studies or reviews published in peer reviewed journals were retained. Articles had to be published in English, French, Dutch, Afrikaans or Spanish in order to be considered for title and abstract screening. Studies had to report on the tolerance limits to abiotic factors of African schistosome IH snail species of the genera *Bulinus* and *Biomphalaria*. Studies mentioning merely the effects of pollution, heavy metals, molluscicides, vegetation, or biotic interactions (e.g. predation, competition, and parasitism) were excluded since they leaned more on biotic aspects rather than abiotic factors. All articles identified by Kalinda et al. (2017b), who reviewed the effect of temperature on the life-history traits of schistosome IH snails, were also assessed for eligibility in this systematic review. The main findings of each article are summarised in Supplementary Table 1.

Article selection process

References were extracted from the databases and imported into the reference manager EndNoteX9 (Clarivate analytics) for duplicate removal. The unduplicated references were uploaded to the web application Rayyan (Rayyan QCRI) for title and abstract screening (Ouzzani et al., 2016). The screening was carried out independently by two researchers (T.M. and C.H.). When eligibility was not clear, studies were retained for full text assessment to avoid elimination of valid papers.

Data collection

All eligible studies were collected in a spreadsheet which included information on authors, year and title of publication, species studied, snail origin, snail source (field or laboratory strains), environmental factors studied, life-history traits examined, the objectives of the study, and the relevant outcomes for this systematic review. The tolerance limits to each abiotic factor are reported in the results and discussion sections.

Results

A total number of 6271 papers were extracted from the 12 databases and another eight papers were identified through snowballing. After duplicate removal, 4210 papers were withheld of which 4055 were deemed unsuitable based on title and abstract. A total of 155 papers were retained for full text assessment of which 26 did not discuss life-history traits at all, 16 did not discuss life-history traits in relation to environmental factors, two did not report on the effect of environmental factors, 58 did not explicitly report on tolerance limits, three did not report on snails, and five were already included in the review by Kalinda et al. (2017b). Eventually, 45 studies were included in this review (Fig. 1). A graphical summary of the included studies is supplied (Fig. 2) while a summary table with the relevant findings for each study is compiled (Supplementary Table 1).

The abiotic factors examined are organized in the following categories: (1) climatic parameters, (2) physical properties of waterbodies, and (3) water composition. The results for each category are presented per abiotic factor, species, and life stage of the snails (eggs, juveniles and adults). An overview of the findings grouped per species is given in Supplementary Table 2 while an overview of the findings grouped per abiotic factor is given in Supplementary Table 3.

Climatic parameters

Temperature

The effect of temperature on the life-history traits of schistosome IH snails was recently reviewed by Kalinda et al. (2017b). Key findings on the tolerance limits of African species are summarised here and supplemented by more recent findings.

Egg mass production reduced above 27 °C and no eggs hatched above 35 °C for *Biomphalaria pfeifferi* (Krauss, 1848) (Sturrock, 1966; Appleton & Eriksson, 1984). Survival of this species was greatly reduced outside the temperature range of 14-31.5 °C (Sturrock, 1966; Appleton, 1977a; McCreesh & Booth, 2014a) and growth was severely stunted at 29°C (Appleton, 1977b). The number of eggs laid by *Bulinus nyassanus* (Smith, 1877) maintained at 22, 25, 28 or 31°C was not significantly different, although the net reproductive rate and growth were greatly reduced below 22 °C (Kubiriza et al., 2010). In a study by Kalinda et al. (2017a), the growth rate of *Bulinus globosus* (Morelet, 1866) was inhibited below 15.5 °C and reduced above 31 °C. *Bu. globosus* snails maintained at 22.5-23.5 °C had longer shell heights than those maintained at 14-16 °C and their intrinsic growth rate dropped when temperatures rose above 28.5 °C (Woolhouse & Chandiwana, 1990; O’Keeffe, 2006). When the same species was maintained at 15.5 and 36 °C, snails did not produce egg masses and survival was lowest (Kalinda et al., 2017a). *Bulinus abyssinicus* (Martens, 1866) had a maximum survival rate between 20 and 35 °C while this species did not survive at 40 °C (Dagal et al., 1985). *Bulinus africanus* (Krauss, 1848), *Bu. globosus* and *Bi. pfeifferi* did not survive longer than eight days at 8 °C while *Bulinus tropicus* (Krauss, 1848) survived 31 days at 4 °C (Joubert et al., 1984). Survival rates at 34 and 36 °C were higher for *Bu. globosus* than for *Bi. pfeifferi* and *Bu. africanus* (Joubert et al., 1985). Survival of *Biomphalaria alexandrina* (Ehrenberg, 1831) and *Bulinus truncatus* (Audouin, 1827) was reduced at temperatures above 33 °C and below 10 °C (El-Emam & Madsen, 1982; Pflüger et al., 1983).

190 Snails in temporary habitats are prone to desiccation during certain periods of the year. *Bu. truncatus*
191 can survive 7 months under desiccation conditions in the shade (Chu et al., 1967c) although Watson
192 (1958) reported that it tolerates desiccation periods of 9-10 months in Iraq. These results are
193 comparable to the 7 to 8 months survival time of *Bu. truncatus*, *Bu. globosus* and *Bulinus umbilicatus*
194 Mandahl-Barth, 1973 in desiccated habitats found by Diaw et al. (1988). Sturrock (1965) showed that
195 59% of *Bu. globosus* were still alive after 29 days of desiccation but that snail mortality increases
196 linearly with an increase in the length of the desiccation period. Cridland (1967), however, refines
197 these results somewhat as he found that small-sized *Bu. globosus* were almost all dead after seven
198 days of desiccation and only 4.5 % of large *Bu. globosus* were still alive after 30 days. The number of
199 surviving large snails increased to 14 % after 90 days when snails were buried in mud (Cridland, 1967).
200 Kalinda et al (2018b) also noted a marked difference between the survival times of large and small *Bu.*
201 *globosus* snails, with large snails surviving longer (50 % after 73 ± 10 days and 10 % after 111 ± 21 days)
202 than small snails (50 % after 60 ± 9 days and 10 % after 84 ± 12 days). However, this size-dependency
203 is challenged by a study of Chu et al. (1967a), where small *Bu. globosus* snails had longer survival times
204 than large ones outdoors. *Biomphalaria arabica* (Melvill & Ponsonby, 1896) and *Bu. truncatus* survive
205 desiccation periods of up to 50 and 60 days, respectively, in the lab, and 20 and 35 days, respectively,
206 outdoors (Ghandour, 1987). When kept on wet mud, snail survival times decreased to 16 and 20 days,
207 respectively, indoors and 10 and 12 days, respectively, outdoors. When snails were allowed to bury in
208 mud, survival times indoors increased to 90 days for *Bi. Arabica* and up to 120 days for *Bu. truncatus*,
209 but stayed constant outdoors (Ghandour, 1987).

210 *Biomphalaria pfeifferi* survival was as low as 35 % after 28 days of desiccation when their habitat dried
211 up quickly (Badger & Oyerinde, 1996). Similar results were obtained by Cridland (1967), where 20 % of
212 large size *Bi. pfeifferi* snails survived after 30 days, and by Shiff (1960), where 38 % of *Bi. pfeifferi* snails
213 survived 21 days of desiccation. While the survival rate of *Bi. pfeifferi* was low when desiccated at an
214 ambient temperature of 15-21 °C (18 % after 48 days), it increased considerably at 21-27 °C (71 % after

215 57 days) (Shiff, 1960). *Biomphalaria angulosa* Mandahl-Barth, 1957 survived up to one month of severe
216 desiccation (Sturrock, 1965). *Bu. globosus* survival times increased when habitats dried up slowly (77
217 days) rather than quickly (42 days) (Hira, 1968). Annecke and Peacock (1951) observed *Bu. tropicus*
218 and *Bu. africanus* to survive as long as 18 months aestivating in grass roots while Van Aardt and Steytler
219 (2007) found *Bu. tropicus* to survive for five months in the shade but only 24 h in direct sunlight. This
220 species also showed increased survival rates at a higher relative humidity of 85-96 % (37-42 % still alive
221 after 60 days) in comparison to a lower relative humidity of 57 % (0 % still alive after 16 days) (Van
222 Aardt & Steytler, 2007).

223 *Physical properties*

224 flow velocity

225 Snails from the genera *Bulinus* and *Biomphalaria* generally withstand flow velocities up to 0.3 m/s
226 (Appleton, 1978; Utzinger et al., 1997b). Waterbodies with flow velocities between 0.03 and 0.11 m/s
227 seem to be avoided by *Bi. pfeifferi* (Utzinger et al., 1997b) while *Bulinus jousseaumei* (Dautzenberg,
228 1890) has been shown to withstand flow velocities as high as 0.86 m/s (Dussart, 1987).

229 Wave action and water depth

230 *Bulinus globosus* tolerates exposure to waves at least 10 cm high for prolonged periods of time
231 (Appleton, 1978). *Bi. pfeifferi* prefers shallow waters with a depth ranging between 2 and 7 cm in lentic
232 habitats (Utzinger et al., 1997b) although *Biomphalaria* snails have been observed at a depth of 15 m,
233 where they can still lay eggs (Gillet et al., 1960).

234 Light

235 Oviposition of *Bu. tropicus* was retarded by two weeks and fewer eggs were laid when snails were kept
236 under non-circadian light-dark regimes or in complete darkness, although these conditions did not
237 affect growth of juvenile snails (Chaudry & Morgan, 1986). Results published by El-Emam and Madsen
238 (1982) showed that both growth and egg laying rates were reduced for *Bu. truncatus* kept under
239 complete darkness for five weeks. These findings, however, were contradicted by the results of

Bayomy and Joosse (1987) and El-Emam and Mohammed (1979), who kept *Bu. truncatus* under different photoperiods for 17 weeks and found no difference in growth and egg laying capacity between them. Survival seems to be unaffected by the absence of light for this species (El-Emam & Mohamed, 1979; El-Emam & Madsen, 1982; Bayomy & Joosse, 1987). *Bi. alexandrina*, on the other hand, cannot tolerate maintenance under complete darkness (El-Emam & Madsen, 1982). However, in a study by Al-Hassan (2006a), no differences in metabolic rate, reproductive parameters or mortality rate could be observed between snails kept under total darkness and daylight conditions for five weeks.

Water composition

Calcium concentration and dissolved solids

According to Al-Sheikh and Dagal (2011), the maximum tolerated concentrations of dissolved solids and calcium carbonate for *Bulinus beccarii* (Paladilhe, 1872) are 1254 mg/l and 813 mg/l, respectively, and 455 mg/l and 603 mg/l, respectively, for *Bi. pfeifferi*. The lethal Ca^{2+} concentrations for adult and young *Bi. alexandrina* snails were determined at >3600 mg/l and >1440 mg/l, respectively (El-Hassan, 1974). Egg laying rates of *Bi. pfeifferi* were maximal at 10-36 mg/l Ca^{2+} but significantly dropped at Ca^{2+} concentrations above 80-100 mg/l (Harrison et al., 1966). A concentration of 2 mg/l Ca^{2+} and a calcium to magnesium ratio of 0.3 are close to the lower limits required for survival of *Bi. pfeifferi* (Nduku & Harrison, 1976). Lethal Ca^{2+} concentrations for *Bu. truncatus* snails were determined at >2880 mg/l and >1440 mg/l for adults and young snails, respectively (El-Hassan, 1974). According to Meier-Brook et al. (1987), egg laying rates of *Bu. truncatus* were reduced as Ca/Mg ratios dropped from 0.5/1 to 0.2/1 and halted at a ratio of 0.1/1. Reproduction ceased completely when snails were maintained for over half a year at ratios of <0.75/1 (Meier-Brook et al., 1987). Growth rate and net reproduction rate of *Bi. alexandrina* and *Bu. truncatus* snails increased with calcium concentrations of up to 10-20 mg/l and 5-10 mg/l, respectively (Madsen, 1987). For *Bu. tropicus* growth was partly inhibited at 80 mg/l Ca and completely inhibited at 320 mg/l (James et al., 2006). *Biomphalaria camerunensis* C.R. Boettger, 1941 grew best after four weeks in 40 and 80 mg/l Ca^{2+} but no significant growth effect of these

concentrations was apparent anymore after ten weeks. According to Madsen (1987), the hatching of eggs is not affected by the calcium concentration, although James et al. (2006) showed that the survival of hatched snails reduced slightly at a 0.00 mg/l Ca^{2+} treatment.

pH

Survival of *Bu. abyssinicus* is highest around pH 7.5, with a maximum range between pH 6-8 for both hatchability and survival (Harrison & Shiff, 1966; Dagal et al., 1985). *Bi. pfeifferi* has been shown to tolerate pH values between 5.3 and 9.0 (Klutse & Baleux, 1996) while *Bu. truncatus* tolerates pH values in the range of 4.5-10.0 (Deschiens, 1954).

Salinity

The maximum tolerated concentration of NaCl for the hatching of *Bu. abyssinicus* eggs was 2800 mg/l, eggs died at 3200 mg/l (Dagal et al., 1985). Eggs of *Bu. africanus* had a higher lethal concentration of 5250 mg/l while egg laying was recorded at concentrations of 4500 mg/l (Donnelly et al., 1983). Survival of hatchlings, however, started to decline at concentrations of 1000 mg/l and was lethal within six days at a concentration of 4500 mg/l (Donnelly et al., 1983). Salinity had no effect on juvenile or adult *Bu. abyssinicus* up to 5200 and 5600 mg/l, respectively, while adult snails had a maximum tolerable concentration of 7600 mg/l (Dagal et al., 1985). This concentration was much lower for *Bu. truncatus* at 2123 mg/l (Malek, 1958). Lethal concentrations were different among species, with *Bu. africanus* having the highest lethal concentration of 5250 mg/l (Donnelly et al., 1983) followed by *Bu. truncatus* with 3500 mg/l (Malek, 1958). Growth of *Bu. tropicus*, *Bu. truncatus* and *Bu. globosus* snails was unaffected in waters with salt concentrations up to 1460 mg/l (Watson, 1958; James et al., 2006) while survival of adult *Bu. africanus* was unaffected at salinities up to 3500 mg/l (Donnelly et al., 1983). When considering other salts, *Bu. truncatus* tolerates MgCl_2 up to a maximum of 510 mg/l and it is lethal at 2000 mg/l (Malek, 1958). Growth of *Bu. globosus* was inhibited at 760 mg/l according to James et al. (2006) while Deschiens (1954) reported 510 mg/l as the tolerance limit of *Bulinus* spp. to magnesium. Eggs of *Bi. pfeifferi* could not hatch at conductivities of 50 μS or below and hatching rates

dropped at conductivities of 750 μ S and higher while survival rates of adult *Bi. pfeifferi* snails were reduced at conductivities lower than 250 μ S and higher than 500 μ S (Jennings et al., 1973).

Observed trends and variability in research efforts

The outcomes of the included studies are summarised for each abiotic parameter in Supplementary Table 3. This table shows that little work has been carried out on the effect of temperature on the tolerance limits of IH snails. Data on both eggs and juveniles are absent for almost all species but *Bi. pfeifferi*. Adult upper tolerance limits vary from 27 to 36 °C depending on the species. Data on lower temperature tolerance limits is rare although it seems that lower tolerance limits of *Bu. truncatus* and *Bu. globosus* lie around 10 °C while *Bi. pfeifferi* tolerates temperatures of 14 °C . Thus, *Bulinus* spp. appear to withstand both cold and warm temperatures better than *Biomphalaria* spp. which is also reflected in the wider continental distribution of *Bulinus* spp. across Africa (Brown, 1994). However, it should be noted that the variation between *Bulinus* spp. is large.

Bulinus spp. prone to desiccation have longer survival times than *Biomphalaria* spp., although little data has been collected for the latter. Furthermore, large differences in survival times of juveniles and adults have been observed. These differences can be attributed to snail size, with medium sized snails having higher survival rates, and snail age, with young snails surviving longer than old snails. Finally, survival chances of individual snails heavily depend on the place of aestivation. Exposure to light and wet mud drastically lower survival rates while moist mud and especially the capacity to bury in mud offer the best survival chances.

There are limited differences in snail tolerances to stream velocities. Most species withstand stream velocities of about 0,3 m/s although some species such as *Bu. jousseaumei* tolerate stream velocities of up to 0,86 m/s. Consequently, stream velocities have a big impact on snail presence and abundance in streams and rivers. Water depth, on the contrary, seems less important since snails have been found at extreme water depths of up to 95 m (Wright et al., 1967), although they do prefer shallow waters. The snail's preference for shallow waters seems to be correlated with light availability, although light

in itself does not affect snails. This suggests light influences snail presence and abundance through indirect effects on food availability.

Snails tolerate calcium concentrations far above values frequently found in nature (Verlicchi & Grillini, 2020). However, calcium exerts an influence on life-history traits, such as egg-laying rates, at much lower concentrations. A minimum calcium concentration of about 5 mg/l is required for normal snail development. These findings seem to be similar for both *Biomphalaria* spp. and *Bulinus* spp. Most snail species have very wide tolerance ranges for chemicals. Therefore, chemicals will only affect IH snails in cases where concentrations are extremely low or high. Although eggs and juveniles are most sensitive to the chemical water composition, little data has been collected for these life stages. In addition, *Biomphalaria* spp. excel in their absence of data for all life stages (except for calcium). Besides the calcium concentration, the salt concentration is the chemical component that has been investigated the most, especially for *Bulinus* spp. This is also a factor that is expected to have a large influence on snail presence or absence, especially near estuaries prone to salt water intrusion.

Discussion

The aim of this study was to compile a comprehensive synthesis of the literature on the life-history traits and tolerance limits to abiotic factors of African schistosome IH snails. Based on the retrieved studies we constructed a state of knowledge, emphasised some limitations of this study, highlighted observations regarding the factors influencing snail distributions, and made recommendations to guide further research efforts.

Current state of knowledge

This review indicated that knowledge on the tolerance limits of IH snail species to abiotic factors is very fragmented (spanning several decades) and incomplete. Furthermore, research efforts differ greatly between species, snail life stages, geographical origins, abiotic factors studied, the type of study, etc. (Fig. 2). Most work has been conducted on adult snails of five species: *Bi. alexandrina*, *Bi. pfeifferi*, *Bu. globosus*, *Bu. tropicus* and *Bu. truncatus* with the majority of data available for *Bi. pfeifferi* and *Bu.*

truncatus (Fig. 2). This is not surprising given their role in schistosome parasite transmission in Africa (Brown, 1994). However, the lack of data on the egg and juvenile stages is striking because these stages are a vital element in the formation of sustainable populations and thus a key factor in determining snail distributions. Furthermore, the limited data on snail species other than *Bi. pfeifferi* and *Bu. truncatus* is an important issue. Schistosome parasites are known to be transmitted through a variety of intermediate snail hosts, each occupying slightly different niches (Brown, 1994; Hauffe et al., 2016). When an IH species disappears from a habitat, it might be replaced by another species which is also capable of transmitting the same schistosome parasite (Adekiya et al., 2020). Therefore, data on all IH species and life stages is vital to provide reliable estimates of schistosomiasis risk.

Climate exerts a major influence on geographical species distributions across many taxa (e.g. Damm et al., 2010; Dias et al., 2014; Van Bocxlaer et al., 2014). The tolerance of snails to different climatic parameters, however, is still understudied. Of the two major climatic parameters, temperature and rainfall, the latter has received the most attention under the form of desiccation resistance studies. Accurate data on tolerance limits to temperature remains scarce. The effect of temperature on fecundity, egg hatchability, and survival has recently been reviewed by Kalinda et al. (2017b). We refer to this study for a more in-depth discussion on the effect of temperature on these life-history traits. Furthermore, waterbody characteristics play a major role in determining distribution patterns on both a regional and continental scale (Aho, 1978; Dehling et al., 2010; Hauffe et al., 2016; Perez-Saez et al., 2016). As illustrated in Supplementary Table 3, accurate data on tolerances to these characteristics is limited. Although these data have the potential to guide targeted control efforts, they cannot be reliably used for this purpose yet. Finally, the role of water chemistry in determining snail distributions and abundances remains unclear. For *Biomphalaria* spp. most work has focused on the effect of calcium concentrations while for *Bulinus* spp. most work has been conducted on the effect of salinity.

Limitations of the current study

Here, we discuss five limitations of the current review that should be considered when interpreting the presented data. 1) The tolerance limits reported here cannot unambiguously be compared across studies, IH snail species or life stages due to the lack of standardisation. Different exposure periods to an abiotic factor across studies greatly influence survival rates of snails. 2) Many of the (mostly older) studies are constrained by flawed experimental designs such as small sample sizes (e.g. El-Emam & Mohamed, 1979; Bayomy & Joosse, 1987) or pseudo-replication (e.g. El-Emam & Madsen, 1982; Dagal et al., 1985). 3) Inbreeding of laboratory snail strains could affect the resilience to extremes when compared to their conspecifics that are freshly collected in the field. Results from laboratory strains might therefore not correspond to field observations. 4) The effect of snail origin on the obtained data has not been considered yet, although snail origin possibly affects the tolerance limits due to genetic differentiation and local adaptation (Kuo & Sanford, 2009; Eliason et al., 2011; Sanford & Kelly, 2011). Therefore, caution is advised when using the data presented in this review to guide snail control efforts as tolerance limits might differ between locations. A detailed overview of the different origins of the snails used in each study is provided in Supplementary Table 1. 5) Snail species used in lab experiments are rarely identified genetically. Species identification is generally based on morphological characteristics but this approach is not ideal given the high morphological plasticity of schistosome IH snail species (Brown, 1994), potentially leading to identification errors. The identification accuracy of the included studies could not be assessed as it would require obtaining the snails used in the experiment to conduct a molecular identification. For this reason it is unavoidable that data summarised here might originate from a different species than the one that is reported. Therefore, the results from studies lacking a genetic identification step should be interpreted with caution and ideally verified through new experiments. Considering the above limitations, this study should only act as a summary of what is currently known about the tolerance limits of African schistosome IH snails and as a tool to identify important knowledge gaps.

The effect of climatic factors and waterbody characteristics on snail distributions

The global and regional distributions of schistosome IH snails are shaped by an interplay between climatic factors and environmental characteristics. On a global scale, climate has been demonstrated to be one of the major factors affecting distribution patterns in freshwater species (Van Bocxlaer et al., 2008; Damm et al., 2010). This is also true for IH snails, which are strongly influenced by the interaction between temperature and rainfall (De Kock et al., 2004; De Kock & Wolmarans, 2005a). These two factors have been used successfully to model freshwater snail distribution on a regional or continental scale (Stensgaard et al., 2006, 2013; Pedersen et al., 2014; Manyangadze et al., 2016). These modelling studies showed that a rise in surface temperature due to climate change may increase snail fecundity, thereby increasing snail population sizes in temperate areas (Appleton & Eriksson, 1984; Marti, 1986; Brackenbury & Appleton, 1991; Kabatereine et al., 2004). However, in warmer areas higher temperatures might result in lower survival and growth rates of IH snails leading to a decrease in population sizes (Stensgaard et al., 2013; McCreesh & Booth, 2014b; Kalinda et al., 2017a). This is because organisms living near their upper thermal limits tend to have the least physiological reserve to cope with additional warming so that a few degrees change in ambient temperature may result in an order of magnitude difference in survival and fecundity (Dillon, 2000; Stillman, 2002; Denny et al., 2011; Sunday et al., 2014). Previous studies therefore concluded that climate change is more likely to shift, rather than expand geographic ranges of IH snails (Lafferty, 2009; Stensgaard et al., 2019). This will likely mean an expansion of snail distributions pole-ward, i.e. towards South-Africa and Europe, as monthly mean temperatures rise above 10 °C, and a decrease in snail prevalence in Central Africa as mean temperatures rise above 36 °C (De Leo et al., 2020). However, organisms also have the capacity to adapt to changing climates (Bradshaw & Holzapfel, 2001). Therefore it is vital to not only examine the tolerance limits of IH snails, but also their local adaptation capacity in order to understand the putative schistosomiasis transmission dynamics (Lafferty, 2009). Unfortunately, this information is currently lacking.

The effects of rainfall patterns on IH snail distributions depend on the types of waterbodies that are available and the aestivation capacity (i.e. desiccation resistance) of the IH snail species. In regions

with a lot of standing water, IH snail abundances might decline considerably during droughts while in regions with flowing water IH snail abundances might rise (Perez-Saez et al., 2016). This might also lead to different schistosomiasis transmission dynamics in relation to precipitation in different areas (Landesman et al., 2007; Perez-Saez et al., 2017). Many habitats harbouring IH snails in Africa are seasonal waterbodies where the diversity and abundance of snail species are constrained by desiccation periods (Hauffe et al., 2016). Snails prone to desiccation display a variety of adaptation strategies that increase their survival chances. Some *Bulinus* spp. like *Bu. truncatus* are capable of burying in the mud and survive extended periods of time in dried up habitats (Watson, 1958; Chu et al., 1967c). Furthermore, they quickly recolonize previously dried up habitats when water returns because of their high reproduction capacities (Oyeyi & Ndifon, 1990). Other species like *Bu. tropicus* and *Biomphalaria* spp. have little mud-burrowing capabilities and prevent water loss by aestivating amongst the vegetation to avoid exposure to direct sunlight. These species generally have shorter survival times than burying species (Watson, 1958; Chu et al., 1967b; Cridland, 1967; Appleton, 1978; Ghandour, 1987). This might also explain the preference of *Biomphalaria* spp. for permanent waterbodies (Chu et al., 1967b; Ndifon & Ukoli, 1989) while *Bulinus* spp. are more prevalent in seasonal waterbodies (Woolhouse & Taylor, 1990; Appleton & Madsen, 2012).

The survival rates of snails prone to desiccation depend on three main factors: (1) the length of the desiccation period and the size of the snails, (2) the conditions at the soil surface and (3) the speed of water level decrease. Firstly, during desiccation periods, snails cannot forage and depend entirely on their energy reserves. This results in large snails, which have built up more reserves, surviving longer than small snails (Cridland, 1967; Al-Hassan, 2006b; Kalinda et al., 2018b). This effect might be offset to some extent by snail age with young snails surviving longer than old snails (Chu et al., 1967a; Kalinda et al., 2018b). Additionally, survival chances of snails aestivating on the surface (e.g. *Biomphalaria* spp.) depend heavily on the size of their aperture. Survival chances of large snails are compromised by their large aperture size, causing them to lose water more easily (Chu et al., 1967b). Therefore, medium sized snails are best suited to withstand desiccation on the soil surface because of a more favourable

aperture size/weight ratio (Hira, 1968; Diaw et al., 1988). Secondly, humid soils offer better survival chances (Ohlweiler & Kawano, 2001; Kalinda et al., 2018a) although aerobic conditions remain a prerequisite (Chu et al., 1967a; Coles, 1969; Betterton, 1984; Ebele & Smith, 1990; Thomas & Daldorph, 1991). This explains why survival rates are lower in wet mud and places exposed to sunlight (Chu et al., 1967c; Hira, 1968; Van Aardt & Steytler, 2007) and why they increase when IH snails bury in moist mud (Chu et al., 1967a; Kalinda et al., 2018b). Finally, the speed at which water levels decrease is decisive for snail survival as it determines the time snails have to prepare for a desiccation period, i.e. to search for a suitable aestivation spot or to bury in the soil. The exact mechanism triggering snail aestivation remains unknown (Rubaba et al., 2016) but rapid drying of habitats is usually fatal (Watson, 1958) while snails are more tolerant to desiccation when their habitats dry up gradually (Hira, 1968; Ghandour, 1987; Badger & Oyerinde, 1996). These findings are important to consider when using desiccation as a means for IH snail control in manmade waterbodies. Drying out of snail habitats has to be fast and sustained for a prolonged period in order to be effective. Unfounded measures, however, might result in unwanted outcomes as some snail species can double their breeding intensity after a period of desiccation, thereby offsetting the mortality caused by the dry period (Chu et al., 1967c; Oyeyi & Ndifon, 1990).

Abiotic influences are rarely constant in time and space. Snails can actively move to microhabitats that are more suitable in otherwise unsuitable habitats (Harrison & Shiff, 1966; Lafferty, 2009; Chapperon & Seuront, 2011). Furthermore, the area and isolation of surface waters determines the distribution and species richness patterns of molluscs, mainly due to the effect of habitat availability and diversity (Aho, 1978; Dillon, 2000; Hauffe et al., 2016). Therefore, besides climate, also waterbody characteristics play an important role in determining regional snail distributions (Denny et al., 2011).

A distinction has to be made between lentic habitats, which are subjected to seasonal changes, and lotic habitats, in which a continuous water flow partially determines habitat suitability (Rollinson et al., 2002; De Kock et al., 2004; De Kock & Wolmarans, 2005b). Snails in both lentic and lotic habitats might

be subject to seasonal desiccation (see above) while snails in lotic environments risk being flushed away in periods of heavy rainfall (Dida et al., 2014; Perez-Saez et al., 2016). Furthermore, high flow velocities in lotic environments might limit food availability, thereby decreasing snail population sizes even more (Yigezu et al., 2018). Although the preferred flow velocity of each IH snail species is not clear (Dazo et al., 1966; Atia et al., 1984; Utzinger et al., 1997b), most snail species (both *Biomphalaria* spp. and *Bulinus* spp.) are flushed away when flow velocities exceed 0.3 m/s (Appleton, 1978; Utzinger et al., 1997b; Dida et al., 2014). It should be noted, however, that temporal (e.g. seasonal precipitation) and spatial variations (e.g. behind boulders) of flow velocities can create suitable microhabitats for snails to survive even when flow velocities exceed 0.3 m/s (Rollinson et al., 2002; Al-Sheikh & Dagal, 2011). Flow velocity is correlated with other factors such as river depth and width. Most studies indicate a negative correlation between river depth, river width and the abundance of snail species (Woolhouse & Chandiwana, 1989; Utzinger et al., 1997a; Ugbomoiko, 1998; Hussein et al., 2011; Tchakonté et al., 2014). This effect is most likely caused by higher flow velocities flushing away snails in wide and deep rivers. In the case of lentic habitats, water depth does not seem to play an important role since snails can survive up to 15 m below the surface and still lay eggs. Live *Bu. nyassanus* snails have been found at a depth of 95 m (Wright et al., 1967), although they do prefer shallow waters (Gillet et al., 1960; Utzinger et al., 1997a). The preference of both *Bulinus* and *Biomphalaria* spp. for shallow waters seems to be correlated with light availability (Dillon, 2000). Although light only plays a minor role in snail maintenance in the laboratory (Gaud, 1958; El-Emam & Mohamed, 1979; El-Emam & Madsen, 1982; Chaudry & Morgan, 1986; Bayomy & Joosse, 1987; Mostafa & Gad, 1997), it can have significant indirect effects in the field. In a study by Loreau and Baluku (1991), artificial shading of a natural breeding site eliminated a population of *Bi. pfeifferi* within six weeks. It took eight weeks to recolonize the site. The lengthy recolonization period suggests an indirect effect of light through its effect on food sources (Loreau & Baluku, 1991). The association between the abundance of *Bu. truncatus* and high algal densities, macrophytes and substrate parameters supports this conclusion (Malek, 1958; Baluku et al., 1989; Dillon, 2000; Chlyeh et al., 2006; Hussein et al., 2011).

Finally, shore characteristics of waterbodies influence snail presences. Steep shores are generally less favourable for IH snails than gentle slopes. However, in large waterbodies, waves exceeding 10 cm can significantly influence *Bulinus* spp. situated on gentle slopes (Appleton, 1978). *Bi. pfeifferi* is less resistant to wave height, which explains its preference for small pools and sheltered areas (Appleton, 1978). According to Utzinger et al. (1997a), substratum type is not important for snail habitat selection, although firm mud rich in decaying organic matter is generally associated with favourable snail habitats (Malek, 1958; Appleton, 1978; Agi, 1996; Genner & Michel, 2003). Sediment with small particle sizes is likely associated with a larger food availability and the soft sediment lifestyle of molluscs, resulting in higher snail abundances (Dillon, 2000; Genner & Michel, 2003).

Unclear role of water chemistry

The effect of the chemical water composition on snail distributions is not so evident. The chemical water composition of natural waters differs greatly among waterbodies and is largely controlled by regional geology. However, since IH snails are mostly generalist species, they do have very wide tolerance ranges for most of the chemicals present in water. This does not mean that snails are unaffected by chemicals even if concentrations fall within their tolerance limits (Teesdale, 1962; Schutte & Frank, 1964; Eleutheriadis & Lazaridou-Dimitriadou, 1995). Here, we attempt to point out how the chemical water composition might influence snail distributions and abundances based on the tolerance limits found in this review and on findings discussed in other studies.

Calcium is a key component in the development of freshwater snails as it is incorporated in their shells which should provide a strong and reliable shelter from outside influences (Dillon, 2000). Low calcium levels in the water result in fragile and flexible snail shells (Madsen, 1987) but high concentrations may also pose a problem by corroding the shells (Frank, 1963). Snail growth increases exponentially with the calcium concentration (Brodersen & Madsen, 2003) and freshwater snails therefore have higher abundances in habitats with higher calcium concentrations (Dillon, 2000; Abdel-Kader et al., 2005). However, calcium concentrations do not seem to play a major role in determining the distribution of

IH snails given that the high tolerance limits of most snails (Williams, 1970) are far beyond natural calcium values which rarely exceed 150 mg/l (Verlicchi & Grillini, 2020). Notwithstanding adult snails tolerate high calcium concentrations, egg laying rates, growth, and survival can be affected by calcium concentrations in normal ranges (Harrison et al., 1970; El-Hassan, 1974; Dillon, 2000; James et al., 2006; Al-Sheikh & Dagal, 2011). Data on the lower limits of calcium concentrations is less abundant, although a minimum concentration of 5 mg/l Ca^{2+} is needed for most IH snails. No obvious differences in tolerance limits have been observed between *Bulinus* spp. and *Biomphalaria* spp. which is not surprising given the importance of calcium for both genera. It should be noted that the ratio between calcium and other minerals such as magnesium or sodium seems to be more important than the concentration of calcium alone. Changes in these ratios have been shown to significantly influence egg laying rates (Harrison et al., 1966; Meier-Brook et al., 1987), possibly because these minerals compete for calcium uptake sites in the IH snails (Nduku & Harrison, 1976, 1980).

The pH tolerance limits of most IH snail species lie outside the 5.0-9.0 pH range frequently observed in natural waterbodies (Malek, 1958; Dagal et al., 1985; Ugbomoiko, 1998). Schistosome IH snails have been observed at pH values as low as 4.0 although it is theoretically impossible to deposit lime in the shell below pH 5.8 (Malek, 1958). This observation might be explained by large diurnal variations in pH levels of natural waterbodies (Boycott, 1936). Lime is deposited in the shell when pH values are within the tolerance limits of the species, and shells are eroded when pH values are below these limits. Therefore, caution must be taken when relating the distribution of schistosome IH snails to a particular pH range (Malek, 1958). Data on pH ranges of other species is lacking, although it should be noted that the correlation between calcium concentration, total hardness, pH, alkalinity and conductivity is very high in fresh waters (Dillon, 2000). Therefore, other variables such as tolerance to calcium concentrations can be used as a proxy for these other factors.

Most data on water chemistry is derived from field studies through correlative analysis but little experimental data exists. Field studies by Tchakonté et al. (2014) and El-Hassan (1974) showed that

the distribution of *Bi. pfeifferi* is affected by the water composition and that *Biomphalaria* habitats have higher values for various ions, dissolved solids, electric conductivity (EC) and pH than *Bulinus* habitats. In the study by El-Hassan (1974), habitats devoid of both *Bu. truncatus* and *Bi. alexandrina* showed one or more ions exceeding the tolerance limits of those species. However, the concentrations of chemicals in natural waters are mostly far below the lethal concentrations for IH snails. Nevertheless, chemical components falling within the tolerance range of IH snails can still impact their distribution indirectly. For example, high tolerance ranges for salinity might suggest that this factor does not determine snail distributions but this would neglect the increased sensitivity of eggs and juveniles in comparison to adults (Donnelly et al., 1983; Tolba & Awad, 1995; James et al., 2006). This might result in unsustainable populations even though the adult tolerance limits have not been exceeded (source-sink dynamics of metapopulations). Therefore, it is striking to see that so little work has been carried out on the effect of the chemical water composition on the egg and juvenile life stages of the IH snail. Furthermore, one should not forget that calcium, water hardness, alkalinity, pH and conductivity also influence aquatic organisms that serve as food or prey (Dillon, 2000). Consequently, the effects that these factors have on IH snail populations might be indirect, rather than reflecting the IH snail tolerance limits.

From the above it is obvious that water chemistry mediates IH snail abundances (Brown, 1994; Utzinger et al., 1997a; Hamed, 2010). However, the approach used in this review does not allow to analyse the effects of the different chemical components on snail abundances and these are therefore not extensively discussed here. Consequently, the results presented in this section cannot be used for schistosomiasis risk assessment nor to guide implementation of control measures without further research.

Knowledge gaps and future perspectives

Species distributions are mostly determined by extremes of environmental factors (e.g. highest or lowest temperature, longest dry period) rather than by averages or optima (Githeko et al., 2000;

Parmesan et al., 2000; Zimmermann et al., 2009; Smale & Wernberg, 2013). Therefore it is important to gather accurate data on the tolerance limits of IH snail species that could improve the accuracy of species distribution models (Kearney & Porter, 2009; Lafferty, 2009; Buckley et al., 2011; Huey et al., 2012; Sunday et al., 2014). Our review showed that knowledge on these limits is scarce and incomplete since most studies only report on optimal conditions and/or correlations between a factor and a trait. Additionally, much of the variance among IH snails is due to phenotypic plasticity but the genetic basis remains unknown (Dillon, 2000). Finally, the comparability of the studies reported here is limited by the lack of standardisation. Therefore, it remains difficult to suggest specific and effective snail control measures, as the current data is inadequate for this purpose.

Moreover, not only tolerance limits to abiotic factors should be considered when determining IH snail distributions. Biotic factors (such as competition, predation, vegetation coverage) play a major role in determining snail presences and abundances as well (Økland, 1983; Dillon, 2000; Ndione et al., 2018). This is exemplified by the study of Wood et al. (2019) who successfully used drone and satellite imagery to predict schistosomiasis transmission by assessing snail habitat suitability through vegetation mapping. Similarly, De Roeck et al. (2014) used environmental variables and high resolution satellite imagery to predict regional presences of freshwater snails that transmit liver flukes.

Assessing only the presence of IH snails in a given habitat does not provide a reliable estimate of schistosomiasis risk. The tolerance limits of schistosome parasites and infected snails differ from “healthy” snails (Badger & Oyerinde, 1996; Rubaba et al., 2016; Mulero et al., 2019) and schistosomiasis transmission mostly depends on snail abundance rather than merely snail presence (Rabone et al., 2019). Additionally, although the production of schistosome cercariae increases with temperature, schistosomiasis transmission will only increase if development rates and productivity of parasites can outpace increases in IH snail mortality rates (Poulin, 2006). Therefore it is important to also take into account the response of infected snails and their parasites to abiotic factors.

Most of the studies included in this review are carried out in a laboratory and only few field studies are reported. Both types of studies have their strengths and weaknesses, which should be considered

when interpreting the data. Laboratory studies are carried out in a controlled environment and mostly assess the effects of only a single or a few factors on the life-history or tolerance limits of IH snails (e.g. Nduku & Harrison, 1976; Brodersen & Madsen, 2003; Kalinda et al., 2018b). Interaction effects between various variables are not taken into account. Therefore, controlled lab experiments have limited predictive power when extrapolated to field conditions. Field studies on the other hand do include interaction effects but they are mostly restricted to correlative analysis between an abiotic factor and life-history traits, without defining clear limits (e.g. Genner & Michel, 2003; Abdel-Kader et al., 2005). Furthermore, life-history measurements in natural IH snail populations are not always consistent between different habitats (Dillon, 2000). Therefore, the recommended study type (field or laboratory) depends strongly on the aims of the study.

A broad range of issues must be addressed and knowledge gaps have to be filled before data on life-history and tolerance limits of African schistosome IH snails can be used reliably. Therefore, we suggest the following research priorities and best practises: (1) reliable species identification, (2) sound experimental designs with standard protocols including replication and sufficient sample sizes (with an absolute minimum of 20 individuals per condition and per replicate), randomisation, and standardised exposure times, (3) data collection for each snail species, life stage and (a)biotic factor with a focus on IH snail tolerance limits to temperature and desiccation, (4) assessment of the genetic basis of these traits through common garden or reciprocal transplant experiments, (5) further elucidation of the waterbody characteristics affecting IH snail distributions and abundances (e.g. water chemistry, shore characteristics, and the effects of shading), (6) assessment of the local adaptation capacity of IH snails by comparing life-history traits of snails from different origins , and (7) exploration of the capacity of biotic factors to predict IH snail distributions and abundances.

Conclusions

This review showed that our knowledge on the tolerance limits of schistosome IH snails to abiotic factors is far from complete. Few data has been collected on other snail species than *Bi. pfeifferi* and

Bu. truncatus. Furthermore, accurate information on the tolerance limits of eggs and juveniles remains scarce, despite their vital importance to form sustainable populations. Finally, IH snail distributions are mostly shaped by extremes of environmental conditions. Therefore it is striking that tolerance data is incomplete for all abiotic factors and that most work on temperature, one of the most important factors in shaping IH snail species' distributions, is focussed on optima rather than tolerance limits.

In addition to identifying knowledge gaps, we drew attention to the importance of sound and standardised experimental designs in IH snail ecological studies, including a reliable species identification step. Comparison of studies across different countries is virtually impossible because the local adaptation capacity of IH snails and the effects of snail origin on the tolerance limits have not been investigated yet. Finally, although biotic factors were not considered in this review, they cannot be neglected because of their large impact on local snail distributions and abundances. A better understanding of IH snail ecology, taking into account both the abiotic and biotic environment, might lead to more accurate models predicting schistosome IH snails distributions and putative schistosomiasis risk. Furthermore, novel integrated snail control measures might be designed which effectively limit schistosomiasis transmission. This way, research on IH snail ecology can become an important component in achieving schistosomiasis control and ultimately elimination of the disease.

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Declarations

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Conflict of Interest

The authors declare that they have no conflict of interest.

Availability of data and material

All data is available in the Supplementary Tables.

Code availability

NA.

Author contributions

All authors contributed to the study conception and design. The systematic search was designed and carried out by Tim Maes. Screening of the literature and data collection was carried out by Tim Maes and Cyril Hammoud. The first draft of the manuscript was written by Tim Maes and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Figure captions

Fig. 1 PRISMA diagram illustrating the selection process of the 45 studies included in the review.

Fig. 2 Graphical summary of the studies retained for this review. The sum of the numbers in the pie charts does not equal 45 (the total number of studies included in the review) in all the charts because some studies combined different categories; a) the country of snail origin, b) the snail species studied (blue = *Bulinus* spp.; green = *Biomphalaria* spp.), c) the abiotic factor studied (blue = climatic variable; green = water chemistry; yellow = waterbody characteristics), and d) the type of study.

Supplementary material S1: Full search string

S1.1 Search string PubMed (Medline)

("Biomphalaria"[Mesh] OR biomphalaria*[tiab] OR "Bulinus"[Mesh] OR bulinus[tiab]) AND ("Life Cycle Stages"[Mesh] OR "life history"[tiab] OR "Biological Variation, Individual"[Mesh] OR "Biological Variation, Population"[Mesh] OR "Life History Traits"[Mesh] OR Mortality[Mesh] OR "Body Size"[Mesh] OR "Adaptation, Physiological"[Mesh] OR "Body Constitution"[Mesh] OR "Growth and Development"[Mesh] OR Longevity[Mesh] OR "Stress, Physiological"[Mesh] OR Growth[tiab] OR survival[tiab] OR fecundity[tiab] OR hatch*[tiab] OR reproduc*[tiab] OR size[tiab] OR mortality[tiab])

S1.2 Search string Embase

('Bulinus'/exp OR bulinus:ti,ab,kw OR 'bulinud snail*':ti,ab,kw OR 'Biomphalaria'/de OR biomphalaria*:ti,ab,kw OR 'planorbis pfeifferi':ti,ab,kw OR 'Biomphalaria alexandrina'/exp OR 'Biomphalaria pfeifferi'/exp) AND ('life history trait'/exp OR 'life history':ti,ab,kw OR 'life history characteristic*'/exp OR 'population and population related phenomena'/exp OR 'growth, development and aging'/exp OR 'physical activity, capacity and performance'/exp OR 'adaptation'/exp OR Growth:ti,ab,kw OR survival:ti,ab,kw OR fecundity:ti,ab,kw OR hatch*:ti,ab,kw OR reproduc*:ti,ab,kw OR size:ti,ab,kw OR mortality:ti,ab,kw)

S1.3 Search string Web of Science (All databases)

(bulinus OR "bulinud snail*" OR "Planorbis pfeifferi" OR biomphalaria*) AND ("life history" OR Growth OR survival OR fecundity OR hatch* OR reproduc* OR size OR mortality)

Supplementary Table 1: Studies included in the qualitative synthesis (author and year) including the objective, snail species studied, country of snail origin, abiotic factor(s) studied, type of study (field study, laboratory study or review) and the main outcomes for each study.

Author and year	Objective	Snail species studied	Country of snail origin	Abiotic factor(s) studied	Type of study	Outcome
Abdel-Kader, 2005	To study the ecological factors that might affect the distribution of IH snails.	<i>Biomphalaria alexandrina</i> <i>Bulinus truncatus</i>	Egypt	Water chemistry	Field study	1. Calcium and potassium concentrations are higher in snail habitats. 2. Snails avoid habitats with low salt concentrations.
Al-Hassan, 2006a	To determine if the metabolic rate, reproductive parameters and survival of <i>Bi. alexandrina</i> are affected by total darkness conditions.	<i>Biomphalaria alexandrina</i>	Egypt	Light	Laboratory study	1. The metabolic rate is not affected by total darkness conditions over a period of 5 weeks. 2. Total darkness has no effect on reproductive parameters. 3. Mortality rate is not affected after 10 weeks.
Al-Sheikh and Dagal, 2011	To study the role of rainfall, ionic composition of water, water temperature, and pH on snail population densities and growth.	<i>Bulinus beccari</i> <i>Biomphalaria pfeifferi</i>	Egypt	Water chemistry Rainfall	Field study	1. <i>Bu. beccari</i> tolerates a maximum concentration of dissolved solids and calcium carbonate of 1254 and 813 mg/l respectively. 2. For <i>Bi. pfeifferi</i> these concentrations are 455 and 603 mg/l respectively. 3. Snail densities decrease when the intensity of rainfall increases in lotic water bodies
Appleton, 1977a	To assess the effects of constant above-optimal temperatures on the hatching, growth, survival, fecundity, and development of the ovotestis of <i>Bi. pfeifferi</i> .	<i>Biomphalaria pfeifferi</i>	South-Africa	Temperature	Laboratory study	1. Fecundity and survival are significantly reduced at 27 °C, hyperthermia occurs at 29 °C. 2. Growth is severely stunted at 29 °C.
Appleton, 1978	To collate and review the literature and indicate factors limiting IH snails distribution.	<i>Biomphalaria</i> spp. <i>Bulinus</i> spp.	Africa South-America	Water chemistry Salinity Turbidity Flow velocity Wave action Water depth Desiccation Light	Review	1. Low sodium/calcium ratios are unfavourable with only <i>Bi. pfeifferi</i> being found in ratios of 0.2. 2. Occurrence of species seems independent of the usual range of ionic composition of water bodies. 3. <i>Bulinus</i> and <i>Biomphalaria</i> spp. occur in waters with Ca ²⁺ conc. of 5-40 mg/l and HCO ₃ ⁻ conc. of 20 – 200 mg/l. 4. Population growth is related to rainfall and temperature. 5. Snails withstand stream velocities of approximately 0.3 m/s.

Author and year	Objective	Snail species studied	Country of snail origin	Abiotic factor(s) studied	Type of study	Outcome
						6. <i>Bu. globosus</i> withstands waves of at least 10 cm high. 7. Water pressure does not seem to play a role in usual snail habitats but snails are generally found in shallow water. 8. <i>Bulinus</i> and <i>Biomphalaria</i> spp. survives drying periods of 40 – 50 days. 9. <i>Bu. truncatus</i> survives 9 – 10 months out of the water in Iraq. 10. Survival after desiccation is highest in soils with low moisture content. 11. African snail species survive several generations in complete darkness. 12. Temperature and flow velocity are largely responsible for distribution patterns in Southern Africa. 13. Temperature is of greatest importance in lentic environments while flow velocity is the limiting factor in lotic environments.
Badger and Oyerinde, 1996	To assess the survival of laboratory bred infected and non-infected <i>Bi. pfeifferi</i> snails under desiccation conditions.	<i>Biomphalaria pfeifferi</i>	Unknown	Desiccation	Laboratory study	1. 35 % of <i>Bi. pfeifferi</i> survives 28 days of desiccation. 2. 0 % survives when infected with <i>Schistosoma</i> parasites.
Bayomy and Joosse, 1987	To study the effects of temperature and different photoperiods on body growth, fecundity, and survival of <i>Bu. truncatus</i> .	<i>Bulinus truncatus</i>	Unknown	Light	Laboratory study	1. Length of the photoperiod has no effect on mortality, growth or egg laying capacity.
Brodersen and Madsen, 2003	To assess the effect of different calcium concentrations on growth and crushing resistance of <i>Bi. sudanica</i> .	<i>Biomphalaria sudanica</i>	Ethiopia	Calcium concentration	Laboratory study	1. Growth increases linearly with the Ca concentration on a logarithmic scale. 2. Crushing resistance increases with increasing Ca concentration.
Chaudry and Morgan, 1986	To assess the effect of irregular photoperiods on various growth parameters and oviposition of <i>Bu. tropicus</i> .	<i>Bulinus tropicus</i>	Unknown	Light	Laboratory study	1. Growth of juvenile snails is unaffected by reversed circadian regimens. 2. Oviposition is considerably retarded by these reversed conditions.

Author and year	Objective	Snail species studied	Country of snail origin	Abiotic factor(s) studied	Type of study	Outcome
Chu et al., 1967a	To assess the survival rates of <i>Bu. truncatus</i> under desiccation conditions on wet mud.	<i>Bulinus truncatus</i>	Iran	Desiccation	Laboratory study	<ol style="list-style-type: none"> 1. Immature snails (4-8 mm) survive longer than mature ones (8-12 mm) under desiccation conditions. 2. <i>Bu. truncatus</i> survives for a maximum of 11 days in mud saturated with water. 3. The depth of burying is not correlated with survival rates. 4. The maximum survival time is 7 months in the shade.
Chu et al., 1967b	To assess the survival rates of IH snails under air-dried desiccation conditions.	<i>Bulinus truncatus</i> <i>Biomphalaria alexandrina</i>	Iran Egypt	Desiccation	Laboratory study	<ol style="list-style-type: none"> 1. <i>Bi. alexandrina</i> survives longer than <i>Bu. truncatus</i> under desiccation conditions 2. <i>Bu. truncatus</i> buries in mud, <i>Bi. alexandrina</i> has no capacity to do so.
Chu et al., 1967c	To assess the survival times and fecundity of <i>Bu. truncatus</i> under desiccation conditions on a mud substrate or no substrate at all.	<i>Bulinus truncatus</i>	Iran	Desiccation	Laboratory study	<ol style="list-style-type: none"> 1. Desiccated snails double their breeding intensity. 2. Survival times of snails kept in mud are higher than those of snails kept on no substrate.
Cridland, 1967	To assess the ability of IH snails to survive in the absence of water.	<i>Bulinus globosus</i> <i>Biomphalaria pfeifferi</i> <i>Bulinus africanus</i>	Zimbabwe	Desiccation	Laboratory study	<ol style="list-style-type: none"> 1. Small size <i>Bu. globosus</i> are all dead after 7 days of desiccation. 2. 4.5% of large <i>Bu. globosus</i> snails are still alive after 30 days. 3. 1 % of small <i>Bi. pfeifferi</i> survive after 21 days. 4. 20% of large <i>Bi. pfeifferi</i> survive after 30 days. 5. Medium sized <i>Bu. africanus</i> survive for 90 days on black sandy soil under rocks. 6. Large size <i>Bu. globosus</i> and <i>Bi. pfeifferi</i> show high survival rates at 30 and 60 days when buried. 7. 14% of buried large and 6% of small <i>Bu. globosus</i> are still alive after 90 days.
Dagal et al., 1985	To study the effects of salinity, water temperature and hydrogen ion concentration on egg hatching and the survival of juvenile and adult <i>Bu. abyssinicus</i> snails.	<i>Bulinus abyssinicus</i>	Somalia	Salinity Temperature pH	Laboratory study	<ol style="list-style-type: none"> 1. The optimum pH is 7.5 with a maximum range between pH 6 and 8 for survival and hatchability. 2. The maximum tolerated salt concentration for hatchability is 2800 mg/l. 3. The lethal salt concentration for eggs is 3200 mg/l. 4. Salinity has no effect on juveniles up to 5200 mg/l and 5600 mg/l for adults. 5. The maximum tolerable salt concentration is 7600 mg/l.

Author and year	Objective	Snail species studied	Country of snail origin	Abiotic factor(s) studied	Type of study	Outcome
Diaw et al., 1988	To study the effect of desiccation on the survival of <i>Bu. truncatus</i> , <i>Bu. globosus</i> and <i>Bu. umbilicatus</i> .	<i>Bulinus truncatus</i> <i>Bulinus globosus</i> <i>Bulinus umbilicatus</i>	Senegal	Desiccation	Laboratory study	1. <i>Bu. truncatus</i> , <i>Bu. globosus</i> and <i>Bu. umbilicatus</i> are capable of surviving 7 to 8 months of complete desiccation. 2. Snails of average size (6 to 8 mm) are best adapted to desiccation.
Donnelly et al., 1983	To study egg hatchability, fecundity, and survival of adult <i>Bu. africanus</i> in different salinities.	<i>Bulinus africanus</i>	South-Africa	Salinity	Laboratory study	1. Egg masses and hatchlings are more sensitive to salinity than adult snails. 2. Egg laying is recorded in salinities ≤ 4500 mg/l. 3. Hatching success reduces until a lethal concentration of 5250 mg/l for the eggs. 4. Survival of hatchlings starts to decline from 1000 mg/l. 5. Adult survival is unaffected in salinities <3500 mg/l. 6. At a salinity of 8700 mg/l, most adults die within 24h. 7. All snails are dead after 30 days in a salinity of 5250 mg/l. 8. Survival of snails infected with <i>Schistosoma</i> parasites is lower.
Dussart, 1987	To assess the detachment behaviour of several taxa of aquatic pulmonate molluscs in a tubed flowing water system.	<i>Bulinus jousseaumei</i>	Unknown	Flow velocity	Laboratory study	1. <i>Bu. jousseaumei</i> withstands stream velocities of 0.86 m/s.
El-Emam and Mohamed, 1979	To compare the influence of temperature, darkness and starvation on the growth and survival of <i>Bi. alexandrina</i> and <i>Bu. truncatus</i> .	<i>Biomphalaria alexandrina</i> <i>Bulinus truncatus</i>	Unknown	Light	Laboratory study	1. Complete darkness has no significant effect on the growth of <i>Bu. truncatus</i> . 2. Both control and exposed <i>Bi. alexandrina</i> were dead after 3 weeks.
El-Emam and Madsen, 1982	To assess the possibility of <i>Helisoma duryi</i> to act as a competitor and biological control agent for the control of <i>Bi. alexandrina</i> and <i>Bu. truncatus</i> .	<i>Biomphalaria alexandrina</i> <i>Bulinus truncatus</i>	Egypt	Light	Laboratory study	1. Growth and egg laying is reduced for <i>B. truncatus</i> kept under total darkness 2. <i>Bi. alexandrina</i> can't tolerate maintenance under total darkness.
El-Hassan, 1974	To elucidate the effect of the chemical water composition on	<i>Biomphalaria alexandrina</i>	Egypt	Water chemistry	Field study Laboratory study	1. <i>Bi. alexandrina</i> tolerates higher concentrations of various ions than <i>Bu. truncatus</i> . 2. Snails survive for 1 month in distilled water.

Author and year	Objective	Snail species studied	Country of snail origin	Abiotic factor(s) studied	Type of study	Outcome
	the distribution of <i>Bu. truncatus</i> and <i>Bi. alexandrina</i> .	<i>Bulinus truncatus</i>				<ol style="list-style-type: none"> Habitats devoid of both species show one or more ions at the minimum or maximum tolerable range. Habitat concentrations are mostly far below the lethal concentrations. Lethal Ca concentrations for adult <i>Bi. alexandrina</i> are determined at >3600 mg/l and at >1400 mg/l for young snails. Lethal Ca concentrations for adult <i>Bu. truncatus</i> are determined at > 2880 mg/l and at >1440 mg/l for young snails.
Gaud, 1958	To assess the ecology of <i>Bulinus</i> snails.	<i>Bulinus</i> spp.	Algeria	Light	Laboratory study	<ol style="list-style-type: none"> Light only plays a minor role in laboratory maintenance of snails.
Genner and Michel, 2003	To examine the habitat associations of gastropods in Lake Malawi.	<i>Bulinus nyassanus</i>	Malawi	Sediment size	Field study	<ol style="list-style-type: none"> Snails are more abundant in shallow waters with small sediment particle sizes, associated with greater food abundance and a soft sediment lifestyle.
Ghandour, 1987	To study the ability of IH snails of schistosomiasis in Saudi Arabia to survive desiccation under experimental conditions.	<i>Bulinus truncatus</i> <i>Biomphalaria Arabica</i>	Saudi-Arabia	Desiccation	Laboratory study	<ol style="list-style-type: none"> <i>Bi. arabica</i> and <i>Bu. truncatus</i> survive desiccation periods of up to 50 and 60 days, respectively, indoors and 20 and 35 days, respectively, outdoors. Survival declines on wet mud to 16 and 20 days, respectively, indoors and 10 and 12 days, respectively, outdoors. When buried, survival times are 90 days for <i>Bi. Arabica</i> and 120 days for <i>Bu. truncatus</i> indoors and 20 and 35 days, respectively, outdoors.
Harrison et al., 1966	To test the effects of a high magnesium to calcium ratio on the egg-laying rate of <i>Bi. pfeifferi</i> .	<i>Biomphalaria pfeifferi</i>	Zimbabwe	Calcium concentration	Laboratory study	<ol style="list-style-type: none"> Egg-laying rates are significantly lower in waters with high magnesium to calcium ratios. Egg-laying rates drop at 80 – 100 mg/l Ca²⁺.
Harrison and Shiff, 1966	To review some of the work carried out on the influence of temperature and water quality on <i>Bi. pfeifferi</i> and <i>Bu. globosus</i> .	<i>Bulinus globosus</i> <i>Biomphalaria pfeifferi</i>	South-Africa	Water chemistry	Review	<ol style="list-style-type: none"> Snails are absent from waters with a pH below 6 Snail incidence falls off in very soft waters of 2.4 mg/l Ca²⁺ and 22 mg/l CaCO₃.
Harrison et al., 1970	To determine if <i>Bi. pfeifferi</i> snails originating from different demes differ in their tolerance to HCO ₃ ⁻ and CaCO ₃ .	<i>Biomphalaria pfeifferi</i>	Zimbabwe	Calcium concentration	Laboratory study	<ol style="list-style-type: none"> <i>B. pfeifferi</i> is restricted to waters with calcium concentrations of more than 5 mg/l and bicarbonate concentrations of over 20 mg/l.

Author and year	Objective	Snail species studied	Country of snail origin	Abiotic factor(s) studied	Type of study	Outcome
						<ol style="list-style-type: none"> Population growth is maximal at Ca concentrations of 5 to 40 mg/l and bicarbonate concentrations of 20 to 200 mg/l. Optimum values are obtained for 12 mg/l Ca and 35 mg/l bicarbonate.
Hira, 1968	To elucidate the manner in which <i>Bu. globosus</i> overcomes the dry season and resumes the life cycle on the return of the rains.	<i>Bulinus globosus</i>	Nigeria	Desiccation	Field study Laboratory study	<ol style="list-style-type: none"> Medium sized snails are best suited to withstand desiccation due to aperture closing. After fast drying, none of the snails survives after 42 days of desiccation. After slow drying, none of the snails survives after 77 days of desiccation.
James et al., 2006	To establish dose-response relationships for major ions using growth and egg-laying bio-assays of bulinid snails.	<i>Bulinus tropicus</i> <i>Bulinus truncatus</i> <i>Bulinus globosus</i>	Unknown	Water chemistry	Laboratory study	<ol style="list-style-type: none"> Growth rate falls at NH₄Cl concentrations above 3 mM and is significantly inhibited at 4 mM. Concentrations above 6 mM are lethal after a week. Growth gradually declines at KCl concentrations above 3 mM until it is completely inhibited at 10 – 12 mM. Growth is inhibited at Ca concentrations of 80 mg/l and complete inhibition occurs at 320 mg/l. Growth is unaffected in waters with NaCl concentrations of up to 1460 mg/l. MgCl becomes inhibitory at concentrations of 760 mg/l Similar responses are observed for <i>Bu. truncatus</i> and <i>Bu. globosus</i>
Jennings et al., 1973	To assess the effects of the total dissolved salts concentration in water on the biology of <i>Bi. pfeifferi</i> .	<i>Biomphalaria pfeifferi</i>	South-Africa	Water chemistry	Laboratory study	<ol style="list-style-type: none"> No eggs hatch at conductivities of 50 μS. At conductivities of 750 and 1000 μS lower hatching percentages are recorded and very low survival rates occur after hatching At conductivities of 300 to 400 μS snails mature rapidly and survival rates are highest. At 100 and 250 μS snails move in search for more favourable environments. At 100, 250 and 500 μS, the survival rate is much lower and all snails die by the 13th week. Highest growth rates are obtained at 350 μS followed by 300, 500 and 400 μS.

Author and year	Objective	Snail species studied	Country of snail origin	Abiotic factor(s) studied	Type of study	Outcome
Kalinda et al., 2017a	To assess the effect of changing temperatures on the growth, fecundity and survival of schistosomiasis IH snails.	<i>Bulinus</i> spp. <i>Biomphalaria</i> spp.	Africa South-America	Temperature	Review	<ol style="list-style-type: none"> 1. <i>Bi. pfeifferi</i> egg mass production reduces above 27 °C. 2. <i>Bi. pfeifferi</i> survival is limited to the temperature range of 14 - 31.5 °C. 3. The growth and net reproductive rate of <i>Bu. nyssanus</i> are greatly reduced at 22 °C. 4. <i>Bu. globosus</i> growth rate is reduced at temperatures above 28.5 °C. 5. None of the snails survive longer than 8 days at 8°C. 6. No <i>Bu. abyssinicus</i> survive at temperatures of 40 °C. 7. Survival of <i>Bi. alexandrina</i> and <i>Bu. truncatus</i> is reduced at temperatures above 33 °C and below 10 °C.
Kalinda et al., 2017b	To assess the effect of temperature on the <i>Bu. globosus</i> - <i>Schistosoma haematobium</i> system.	<i>Bulinus globosus</i>	South-Africa	Temperature	Laboratory study	<ol style="list-style-type: none"> 1. Snails maintained at 15,5 and 36,0 °C do not produce egg masses. 2. Snail growth is inhibited at 15.5 °C and reduced at 31.0 °C.
Kalinda et al., 2018b	To examine the survival of <i>Bu. globosus</i> during substratum drying.	<i>Bulinus globosus</i>	South-Africa	Desiccation	Laboratory study	<ol style="list-style-type: none"> 1. Large snails burry deeper than small snails. 2. The length of the desiccation period and snail size has no effect on the depth of burying. 3. Snail mortality increases linearly with an increase in the length of the desiccation period. 4. Almost all snails die after 78 days of desiccation. 5. The lethal time (LT50) for large snails is 73.35 ± 10.32 days and 59.64 ± 8.56 days for small snails. 6. The LT90 values are 11.61 ± 21.03 and 84.19 ± 12.09 days respectively.
Klutse and Baleux, 1996	To assess the suitability of treated wastewater for <i>Bulinus</i> and <i>Biomphalaria</i> snails.	<i>Biomphalaria pfeifferi</i> <i>Bulinus truncatus</i>	Burkina Faso	Water chemistry	Laboratory study	<ol style="list-style-type: none"> 1. <i>Bi. pfeifferi</i> tolerates pH values between 5.3 and 9.0.
Loreau and Baluku, 1991	To carry out a first test of the effect of shade on the population density of <i>Bi. pfeifferi</i> .	<i>Biomphalaria pfeifferi</i>	DR Congo	Light	Field study	<ol style="list-style-type: none"> 1. Artificial shading of a breeding site eliminates a population of <i>Bi. pfeifferi</i> within 6 weeks. 2. The site is recolonized 8 weeks after removal of the shading.

Author and year	Objective	Snail species studied	Country of snail origin	Abiotic factor(s) studied	Type of study	Outcome
						3. The long duration of recolonization suggests that shade acts indirectly through its effects on food resources.
Madsen, 1987	To evaluate the potential of <i>Helisoma duryi</i> to establish populations in habitats in various schistosomiasis endemic areas.	<i>Biomphalaria alexandrina</i> <i>Biomphalaria camerunensis</i> <i>Bulinus truncatus</i>	Egypt DR Congo	Water chemistry	Laboratory study	<ol style="list-style-type: none"> Growth increases with calcium concentrations up to 0.25 – 0.50 mM for <i>Bi. alexandrina</i> and <i>Bu. truncatus</i>. Growth of <i>Bi. camerunensis</i> increases after 4 weeks in 1.00 and 2.00 mM calcium solutions. This growth is not apparent anymore after 10 weeks. The net reproductive rate increases with Ca concentrations up to 0.13 – 0.25 mM. Shells of snails reared at 0.00 and 0.0063 mM Ca²⁺ are very fragile and flexible. Hatching of eggs is not affected by the Ca concentration, except for <i>Bi. alexandrina</i> and <i>Bi. camerunensis</i>. Survival of hatched <i>Bi. alexandrina</i> and <i>Bi. camerunensis</i> snails is slightly reduced at 0.00 mM Ca²⁺.
Malek, 1958	To review factors conditioning the habitat of schistosomiasis IH snails.	<i>Bulinus truncatus</i> (<i>Bu. contortus</i>)	Unknown	Water chemistry desiccation	Review	<ol style="list-style-type: none"> Water with high silt concentrations can be harmful to snails. 1.5 % of <i>Bulinus</i> snails survive a drought period of 12 months on mud. Snails thrive better in the presence of animal and human excrement but do occur in unpolluted habitat as long as food is plentiful. <i>Bulinus</i> tolerates Mg concentrations of 510 mg/l. <i>Bu. truncatus</i> tolerates a pH range of 4.5 – 10.0.
Meier-Brook et al., 1987	To examine the variation of Ca/Mg ratios and their potential influence on the presence or absence of <i>Bu. truncatus</i> .	<i>Bulinus truncatus</i>	Tunesia Algeria	Water chemistry	Laboratory study	<ol style="list-style-type: none"> Egg-laying decreases with Ca/Mg ratios lower than 0.5/1 and got 0 at 0.1/1. Reproduction ceases when snails are maintained at ratios <0.75/1 for more than half a year. Egg-laying rates decrease significantly in Cl concentrations of 866 mg/l. <i>Bu. truncatus</i> are found in waters with a conductivity of 1220 – 2440 µmho and a total Cl concentration of 120 -602 mg/l.

Author and year	Objective	Snail species studied	Country of snail origin	Abiotic factor(s) studied	Type of study	Outcome
Mostafa and Gad, 1997	To study the effect of UV-irradiation, gamma irradiation, and praziquantel on infected <i>Bi. alexandrina</i> snails.	<i>Biomphalaria alexandrina</i>	Egypt	Light	Laboratory study	1. UV irradiated snails show a mortality rate comparable to the control snails.
Nduku and Harrison, 1976	To assess the effects of a wide range of calcium ion concentrations in the absence of other cations on the biology of test snails. To assess the effects of differing ratios of calcium to magnesium, calcium to potassium and calcium to sodium ions on <i>Bi. pfeifferi</i> .	<i>Biomphalaria pfeifferi</i>	Zimbabwe	Water chemistry	Laboratory study	1. Survival, maturation and fecundity are low at bicarbonate concentrations under 10 mg/l or higher than 30 mg/l. 2. Survival is significantly lower at Ca concentrations below 1 mg/l. 3. Calcium sulphate buffering reduces survival rates, fecundity and net reproductive rate in comparison to calcium bicarbonate buffering. 4. At Ca/Mg ratios <1, fecundity and egg fertility drop. 5. At Ca/Na ratios <0.5 and Ca/Na ratios <0.25; fecundity fall off. 6. Hatching rates are lower in 0.5 mg/l Ca ²⁺ and >20 mg/l Ca ²⁺ . 7. A concentration of 2.0 mg/l Ca ²⁺ is near the lower limit for snail survival. 8. A Ca/Mg ratio of >0.3 is needed for survival.
Shiff, 1960	To study the capacity of IH snails to survive dry conditions.	<i>Biomphalaria pfeifferi</i> <i>Bulinus globosus</i>	Zimbabwe	Desiccation	Laboratory study	1. 38% of <i>Bi. pfeifferi</i> snails survive after 21 days of desiccation. 2. Only 18% of <i>Bi. pfeifferi</i> snails survive after 48 days of desiccation. 3. 71% of <i>Bi. pfeifferi</i> snails survive after 57 days when temperatures increased. 4. 87% of <i>Bi. pfeifferi</i> snails survive after 49 days under stable indoor conditions. 5. 59% of <i>Bu. globosus</i> are still alive after 29 days.
Sturrock, 1965	To study the biology and potential of <i>Bi. angulosa</i> as a host of <i>Schistosoma mansoni</i> .	<i>Biomphalaria angulosa</i>	Tanzania	Desiccation	Laboratory study	1. <i>Bi. angulosa</i> survives up to 1 month of desiccation.
Sturrock, 1966	To study the influence of temperature on the biology of <i>Bi. pfeifferi</i> .	<i>Biomphalaria pfeifferi</i>	Tanzania	Temperature	Laboratory study	1. No eggs hatch at 35°C. 2. Growth is fastest at 30 °C, although survival is lowest.
Ützinger et al., 1997b	To determine microhabitat availability for <i>Bi. pfeifferi</i> with	<i>Biomphalaria pfeifferi</i>	Tanzania	Flow velocity Water depth	Field study	1. Absence of <i>Bi. pfeifferi</i> is mainly associated with stream velocities exceeding 0.3 m/s.

Author and year	Objective	Snail species studied	Country of snail origin	Abiotic factor(s) studied	Type of study	Outcome
	respect to water depth, water velocity, and substratum type.			Substratum type		<ol style="list-style-type: none"> Stream velocities between 0.03 and 0.11 m/s are avoided. Snail size appears to be of no importance in spatial microhabitat selection. <i>Bi. pfeifferi</i> prefers depths between 2 and 7 cm. Substratum type is of no importance in habitat selection.
Van Aardt and Steytler, 2007	To determine the water permeability of the shell of <i>Bu. tropicus</i> . To determine survival rates under desiccation conditions with different relative humidity's.	<i>Bulinus tropicus</i>	South-Africa	Desiccation	Laboratory study	<ol style="list-style-type: none"> All snails are dead within 24 h when exposed to direct sunlight. Snails are still alive after 5 months without direct sunlight. After 60 days of desiccation, between 37 and 42% of snails are still alive at relative humidity's between 85 and 96 %. Snails kept at a relative humidity of 57 % are all dead after 16 days.
Watson, 1958	To give a comprehensive account of the current status of knowledge regarding the ecology and distribution of <i>Bu. truncatus</i> in the Middle East.	<i>Bulinus truncatus</i>	Middle-East	Desiccation Salinity Water chemistry	Review	<ol style="list-style-type: none"> Established and breeding colonies of <i>Bu. truncatus</i> are only found in more or less permanent collections of water and are unable to breed in temporary water bodies. <i>Bu. truncatus</i> prefers polluted waters and is therefore more abundant near human habitations. Less tolerant to heat than to cold. Daily mortality rate of 10% when temperature reaches 38 – 40°C. Slow drying up of habitats does not kill snails, fast drying is usually fatal. <i>Bu. truncatus</i> can survive in waters with a salinity of 1500 mg/l. <i>Bu. truncatus</i> is relatively tolerant to low oxygen tensions.

Supplementary Table 2: Findings structured per species (ranked alphabetically), life stage and abiotic factor studied (in the following order: temperature, desiccation, waterbody characteristics, water chemistry, and salinity). No data was available when an abiotic factor is not mentioned for a life stage.

Snail species	Life stage	Abiotic factor	Findings	Study
<i>Biomphalaria alexandrina</i> (Ehrenberg, 1831)	Eggs	/	/	/
	Juveniles	Water chemistry	1. The lethal Ca conc. for young <i>Bi. alexandrina</i> was determined at >1400 mg/l.	El-Hassan, 1974
			2. Survival of hatched <i>Bi. alexandrina</i> snails was slightly reduced at 0.00 mM Ca ²⁺ .	Madsen, 1987
	Adults	Temperature	1. Survival of <i>Bi. alexandrina</i> was reduced at temperatures above 33 °C and below 10 °C.	Kalinda et al., 2017a
		Desiccation	1. <i>Bi. alexandrina</i> survived longer than <i>Bu. truncatus</i> under desiccation conditions.	Chu et al., 1967b
			2. <i>Bi. alexandrina</i> had no mud burrowing capacities.	
		Light	1. The metabolic rate was not affected by total darkness conditions over a period of 5 weeks.	Al-Hassan, 2006a
			2. Total darkness had no effect on reproductive parameters.	
			3. Mortality rate was not affected after 10 weeks.	
			4. <i>Bi. alexandrina</i> could not tolerate maintenance under total darkness.	
		Water chemistry	5. UV irradiated snails showed a mortality rate comparable to control snails.	El-Emam and Madsen, 1982 Mostafa and Gad, 1997
			1. <i>Bi. alexandrina</i> tolerates higher concentrations of various ions than <i>Bu. truncatus</i> .	
			2. Snails can survive for 1 month in distilled water.	
			3. Habitats devoid of <i>Bi. alexandrina</i> showed one or more ions at the minimum or maximum tolerable range.	
			4. Habitat concentrations are mostly far below the lethal concentrations.	
			5. The lethal Ca concentration for adult <i>Bi. alexandrina</i> was determined at >3600 mg/l.	
			6. Growth increases with calcium concentrations up to 0.25 – 0.50 mM.	

Snail species	Life stage	Abiotic factor	Findings	Study
			7. The net reproductive rate increased with Ca concentrations up to 0.13 – 0.25 mM. 8. Shells of snails reared at 0.00 and 0.0063 mM Ca ²⁺ were very fragile and flexible.	Madsen, 1987
<i>Biomphalaria angulosa</i> Mandahl-Barth, 1957	Eggs	/	/	/
	Juveniles	/	/	/
	Adults	Desiccation	1. <i>Bi. angulosa</i> survives up to 1 month of desiccation.	Sturrock, 1965
<i>Biomphalaria Arabica</i> (Melvill & Ponsonby, 1896)	Eggs	/	/	/
	Juveniles	/	/	/
	Adults	Desiccation	1. <i>Bi. arabica</i> survives desiccation periods of up to 50 days indoors and 20 days outdoors. 2. Survival declines on wet mud to 16 days indoors and 10 days outdoors. 3. When buried, <i>Bi. arabica</i> survives for 90 days indoors and 20 days outdoors.	Ghandour, 1987
<i>Biomphalaria camerunensis</i> C.R. Boettger, 1941	Eggs	/	/	/
	Juveniles	Water chemistry	1. Survival of hatched <i>Bi. camerunensis</i> snails is slightly reduced at 0.00 mM Ca ²⁺ .	Madsen, 1987
	Adults	Water chemistry	1. Growth increased after 4 weeks in 1.00 and 2.00 mM calcium solutions. This growth was not apparent anymore after 10 weeks. 2. The net reproductive rate increases with Ca concentrations up to 0.13 – 0.25 mM. 3. Shells of snails reared at 0.00 and 0.0063 mM Ca ²⁺ are very fragile and flexible.	Madsen, 1987
<i>Biomphalaria pfeifferi</i> (Krauss, 1848)	Eggs	Temperature	1. No eggs hatched at 35°C.	Sturrock, 1966
		Water chemistry	1. No eggs hatched at conductivities of 50 µS.	Jennings et al., 1973
			2. At conductivities of 750 and 1000 µS lower hatching percentages were recorded and very low survival rates occurred after hatching. 3. Hatching rates were lower in 0.5 mg/l Ca ²⁺ and >20 mg/l Ca ²⁺ .	Nduku and Harrison, 1976

Snail species	Life stage	Abiotic factor	Findings	Study
	Juveniles	Temperature	1. Growth was fastest at 30 °C, although survival was lowest at this temperature.	Sturrock, 1966
	Adults	Temperature	1. Fecundity and survival were significantly reduced at 27 °C, hyperthermia occurred at 29 °C. 2. Growth was severely stunted at 29 °C. 3. Egg mass production reduced above 27 °C. 4. Survival is limited to the temperature range of 14 - 31.5 °C.	Appleton, 1977a Kalinda et al., 2017a
		Desiccation	1. 35 % of <i>Bi. pfeifferi</i> survived 28 days of desiccation. 2. 0 % survived when infected with Schistosoma parasites. 3. 1 % of small <i>Bi. pfeifferi</i> survived after 21 days. 4. 20% of large <i>Bi. pfeifferi</i> survived after 30 days. 5. Large size <i>Bi. pfeifferi</i> showed high survival rates at 30 and 60 days when buried. 6. 38% of <i>Bi. pfeifferi</i> snails survived after 21 days of desiccation. 7. Only 18% of <i>Bi. pfeifferi</i> snails survived after 48 days of desiccation. 8. 71% of <i>Bi. pfeifferi</i> snails survived after 57 days when temperatures increased. 9. 87% of <i>Bi. pfeifferi</i> snails survived after 49 days under stable indoor conditions.	Badger and Oyerinde, 1996 Cridland, 1967 Shiff, 1960
		Waterbody characteristics	1. Absence of <i>Bi. pfeifferi</i> is mainly associated with stream velocities exceeding 0.3 m/s. 2. Stream velocities between 0.03 and 0.11 m/s are avoided. 3. <i>Bi. pfeifferi</i> prefers water depths between 2 and 7 cm. 4. Substratum type is of no importance in habitat selection.	Ützinger et al., 1997b
		Light	1. Artificial shading of a breeding site eliminated a population of <i>Bi. pfeifferi</i> within 6 weeks. 2. The site was recolonized 8 weeks after removal of the shading.	Loreau and Baluku, 1991

Snail species	Life stage	Abiotic factor	Findings	Study
			3. The long duration of recolonization suggests that shade acts indirectly through its effects on food resources.	
		Water chemistry	1. <i>Bi. pfeifferi</i> tolerates a maximum concentration of dissolved solids and calcium carbonate of 455 and 603 mg/l respectively.	Al-Sheikh and Dagal, 2011
			2. Egg-laying rates significantly lowers in waters with high magnesium to calcium ratios.	Harrison et al., 1966
			3. Egg-laying rates drop at 80 – 100 mg/l Ca ²⁺ .	
			4. <i>B. pfeifferi</i> is restricted to waters with calcium concentrations of more than 5 mg/l and bicarbonate concentrations of over 20 mg/l.	Harrison et al., 1970
			5. Population growth is maximum at Ca concentrations of 5 to 40 mg/l and bicarbonate concentrations of 20 to 200 mg/l.	
			6. Optimum values were obtained for 12 mg/l Ca and 35 mg/l bicarbonate.	
			7. Snail incidence falls off in very soft waters of 2.4 mg/l Ca ²⁺ and 22 mg/l CaCO ₃ .	Harrison and Shiff, 1966
			8. Survival, maturation and fecundity are low at bicarbonate concentrations under 10 mg/l or higher than 30 mg/l.	Nduku and Harrison, 1976
			9. Survival was significantly lower at Ca concentrations below 1 mg/l.	
			10. Calcium sulphate buffering reduced survival rates, fecundity and net reproductive rate in comparison to calcium bicarbonate buffering.	
			11. At Ca/Mg ratios <1, fecundity and egg fertility dropped.	
			12. At Ca/Na ratios <0.5 and Ca/Na ratios<0.25; fecundity fell off.	
			13. A concentration of 2.0 mg/l Ca ²⁺ is near the lower limit for snail survival.	
			14. A Ca/Mg ratio of >0.3 is needed for survival.	
			15. Snails are absent from waters with a pH below 6.	

Snail species	Life stage	Abiotic factor	Findings	Study
			16. <i>Bi. pfeifferi</i> tolerates pH values between 5.3 and 9.0.	Harrison and Shiff, 1966
			17. At conductivities of 300 to 400 μ S snails mature rapidly and survival rates are highest.	Klutse and Baleux, 1996
			18. At 100 and 250 μ S snails moved in search for more favourable environments. At 100, 250 and 500 μ S, the survival rate was much lower and all snails died by the 13th week.	Jennings et al., 1973
			19. Highest growth rates are obtained at 350 μ S followed by 300,500 and 400 μ S.	
<i>Biomphalaria sudanica</i> (Martens, 1870)	Eggs	/	/	/
	Juveniles	/	/	/
	Adults	Water chemistry	1. Growth increases linearly with the Ca concentration on a logarithmic scale. 2. Crushing resistance increased with increasing Ca concentration.	Brodersen and Madsen, 2003
<i>Bulinus abyssinicus</i> (Martens, 1866)	Eggs	Water chemistry	1. The optimum pH for hatchability ranges between pH 6 en 8.	Dagal et al., 1985
		Salinity	1. The maximum tolerated salt concentration for hatchability is 2800 mg/l. 2. The lethal salt concentration for eggs is 3200 mg/l.	Dagal et al., 1985
	Juveniles	Salinity	1. Salinity has no effect on juveniles up to 5200 mg/l.	Dagal et al., 1985
	Adults	Temperature	1. No <i>Bu. abyssinicus</i> survive at temperatures of 40 °C.	Kalinda et al., 2017a
		Water chemistry	1. The optimum pH for survival ranges between pH 6 and 8.	Dagal et al., 1985
		Salinity	1. Salinity has no effect on adults up to 5600 mg/l. 2. The maximum tolerable salt concentration is 7600 mg/l.	Dagal et al., 1985
	Eggs	Salinity	1. Egg masses are more sensitive to salinity than adult snails. 2. Hatching success reduces until a lethal concentration of 5250 mg/l for the eggs.	Donnelly et al., 1983
<i>Bulinus africanus</i> (Krauss, 1848)	Juveniles	Salinity	1. Hatchlings are more sensitive to salinity than adult snails.	Donnelly et al., 1983

Snail species	Life stage	Abiotic factor	Findings	Study
	Adults	Desiccation	2. Survival of hatchlings starts to decline from 1000 mg/l. 1. Medium sized <i>Bu. africanus</i> survive for 90 days on black sandy soil under rocks.	Cridland, 1967
		Salinity	1. Egg laying is recorded in salinities ≤ 4500 mg/l. 2. Adult survival is unaffected in salinities <3500 mg/l. 3. At a salinity of 8700 mg/l, most adults die within 24h. 4. No snails survive after 30 days in a salinity of 5250 mg/l. 5. Survival of snails infected with <i>Schistosoma</i> parasites is lower.	Donnelly et al., 1983
<i>Bulinus beccari</i> (Paladilhe, 1872)	Eggs	/	/	/
	Juveniles	/	/	/
	Adults	Water chemistry	1. <i>Bu. beccari</i> tolerates a maximum concentration of dissolved solids and calcium carbonate of 1254 and 813 mg/l respectively.	Al-Sheikh and Dagal, 2011
<i>Bulinus globosus</i> (Morelet, 1866)	Eggs	/	/	/
	Juveniles	Desiccation	1. Small size <i>Bu globosus</i> are all dead after 7 days.	Cridland, 1967
	Adults	Temperature	1. Growth rate is reduced at temperatures above 28.5 °C.	Kalinda et al., 2017a
			2. No snails survive longer than 8 days at 8°C.	Kalinda et al., 2017b
			3. Snails maintained at 15,5 and 36,0 °C do not produce egg masses.	
			4. Snail growth is inhibited at 15.5 °C and reduced at 31.0 °C.	
		Desiccation	1. 4.5 % of large snails are still alive after 30 days.	Cridland, 1967
			2. Large size <i>Bu. globosus</i> show high survival rates at 30 and 60 days when buried.	Diaw et al., 1988
			3. 14% of buried large and 6% of small <i>Bu globosus</i> can survive for 90 days.	
			4. <i>Bu. globosus</i> is capable of surviving 7 to 8 months of complete desiccation.	
			5. Snails of average size (6 to 8 mm) are best adapted to desiccation.	Hira, 1968
			6. Medium sized snails are best suited to withstand desiccation due to aperture closing.	

Snail species	Life stage	Abiotic factor	Findings	Study
			7. After fast drying, no snails survive after 42 days of desiccation.	Kalinda et al., 2018b
			8. After slow drying, no snails survive after 77 days of desiccation.	
			9. Large snails burry deeper than small snails.	
			10. The length of the desiccation period and snail size have no effect on the depth of burying.	
			11. Snail mortality increases linearly with an increase in the length of the desiccation period.	
			12. Almost all snails die after 78 days of desiccation.	Shiff, 1960
			13. The lethal time (LT50) for large snails is 73.35 ± 10.32 days and 59.64 ± 8.56 days for small snails.	
			14. The LT90 values are 11.61 ± 21.03 and 84.19 ± 12.09 days respectively.	
			15. 59% of <i>Bu. globosus</i> survive after 29 days.	
		Waterbody characteristics	1. Adults can withstand waves of at least 10 cm high.	Appleton, 1978
		Water chemistry	1. Snails are absent from waters with a pH below 6. 2. Snail incidence falls off in very soft waters of 2.4 mg/l Ca^{2+} and 22 mg/l CaCO_3 .	Harrison and Schiff, 1966
<i>Bulinus jousseaumei</i> (Dautzenberg, 1890)	Eggs	/	/	/
	Juveniles	/	/	/
	Adults	Waterbody characteristics	1. <i>Bu. jousseaumei</i> can withstand stream velocities of 0.86 m/s.	Dussart, 1987
<i>Bulinus nyssanus</i> (Smith, 1877)	Eggs	/	/	/
	Juveniles	/	/	/
	Adults	Temperature	1. The growth and net reproductive rate of <i>Bu. nyssanus</i> are greatly reduced at 22 °C.	Kalinda et al., 2017a
		Waterbody characteristics	1. Snails are more abundant in shallow waters with small sediment particle sizes, associated with greater food abundance and a soft sediment lifestyle.	Genner and Michel, 2003
	Eggs	/	/	/

Snail species	Life stage	Abiotic factor	Findings	Study
<i>Bulinus tropicus</i> (Krauss, 1848)	Juveniles	Light	1. Growth of juvenile snails is unaffected by reversed circadian regimens	Chaudry and Morgan, 1986
	Adults	Desiccation	1. All snails are dead within 24 h when exposed to direct sunlight. 2. Snails survive 5 months without direct sunlight. 3. After 60 days of desiccation, between 37 and 42% of snails are still alive at relative humidity's between 85 and 96 %. 4. Snails kept at a relative humidity of 57 % were all dead after 16 days.	Van Aardt and Steytler, 2007
		Light	1. Oviposition is considerably retarded by reversed circadian regimens.	Chaudry and Morgan, 1986
		Water chemistry	1. Growth rates fall at NH ₄ Cl concentrations above 3 mM and are significantly inhibited at 4 mM. Concentrations above 6 mM are lethal after a week. 2. Growth gradually declines at KCl concentrations above 3 mM until it is completely inhibited at 10 – 12 mM. 3. Growth is inhibited at Ca concentrations of 80 mg/l and complete inhibition occurs at 320 mg/l. 4. Growth is unaffected in waters with NaCl concentrations of up to 1460 mg/l. 5. MgCl becomes inhibitory at concentrations of 760 mg/l.	James et al., 2006
	<i>Bulinus truncatus</i> (Audouin, 1827)	Eggs	Water chemistry	1. Hatching success of eggs is not affected by Ca concentration.
	Juveniles	Desiccation	1. Immature snails (4-8 mm) survive longer than mature ones (8-12 mm) under desiccation conditions.	Chu et al., 1967a
		Water chemistry	1. The lethal Ca concentration for young <i>Bu. truncatus</i> is determined at >1440 mg/l.	El-Hassan, 1974
	Adults	Temperature	1. Survival of <i>Bu. truncatus</i> is reduced at temperatures above 33 °C and below 10 °C. 2. <i>Bu. truncatus</i> is less tolerant to heat than to cold. 3. Daily mortality rate of 10% when the temperature reaches 38 – 40°C.	Kalinda et al., 2017a Watson, 1958

Snail species	Life stage	Abiotic factor	Findings	Study
		Desiccation	<ol style="list-style-type: none"> 1. Adult snails survive 9-10 months out of the water in Iraq. 2. <i>Bu. truncatus</i> survives for a maximum of 11 days in mud saturated with water. 3. The depth of burying was not correlated with survival rates. 4. The maximum survival time observed was 7 months in the shade. 5. Desiccated snails double their breeding intensity. 6. Survival times of snails kept in mud were higher than those of snails kept on no substrate. 7. <i>Bu. truncatus</i> is capable of surviving 7 to 8 months of complete desiccation. 8. Snails of average size (6 to 8 mm) are best adapted to desiccation. 9. <i>Bu. truncatus</i> survives desiccation periods of up to 60 days indoors and 35 days outdoors. 10. Survival rates decline on wet mud to 20 days indoors and 12 days outdoors. 11. When buried, snails survive for 120 days indoors and 35 days outdoors. 12. 1.5 % of <i>Bulinus</i> snails survive a drought period of 12 months on mud. 13. Established and breeding colonies of <i>Bu. truncatus</i> are only found in more or less permanent collections of water and are unable to breed in temporary water bodies. 14. Slow drying up of habitats does not kill snails, fast drying is usually fatal. 	<p>Appleton, 1978</p> <p>Chu et al., 1967a</p> <p>Chu et al., 1967c</p> <p>Diaw et al., 1988</p> <p>Ghandour, 1987</p> <p>Malek, 1958</p> <p>Watson, 1958</p>
		Light	<ol style="list-style-type: none"> 1. The length of the photoperiod has no effect on mortality, growth or egg laying capacity. 2. Complete darkness has no significant effect on the growth of <i>Bu. truncatus</i>. 	<p>Bayomy and Joosse, 1987</p> <p>El-Emam and Mohamed, 1979</p>

Snail species	Life stage	Abiotic factor	Findings	Study
			3. Growth and egg laying were reduced for <i>B. truncatus</i> kept under total darkness.	El-Emam and Madsen, 1982
		Water chemistry	1. The lethal Ca concentration for adult <i>Bu. truncatus</i> is determined at > 2880 mg/l.	El-Hassan, 1974
			2. Growth increases with calcium concentrations up to 0.25 – 0.50 mM.	Madsen, 1987
			3. The net reproductive rate increases with Ca concentrations up to 0.13 – 0.25 mM.	
			4. Shells of snails reared at 0.00 and 0.0063 mM Ca ²⁺ are very fragile and flexible.	
			5. Water with high silt concentrations can be harmful to snails.	Malek, 1958
			6. Snails thrive better in the presence of animal and human excrement but do occur in unpolluted habitat as long as food is plentiful.	
			7. <i>Bu. truncatus</i> tolerates a pH range of 4.5 – 10.0.	
			8. <i>Bu. truncatus</i> can tolerate Mg concentrations of 510 mg/l.	
			9. Egg-laying rates decrease with Ca/Mg ratios lower than 0.5/1 and get 0 at 0.1/1.	Meier-Brook et al., 1987
			10. Reproduction ceases when snails are maintained at Ca/Mg ratios <0.75/1 for more than half a year.	
			11. Egg-laying rates decrease significantly in Cl concentrations of 866 mg/l.	
			12. <i>Bu. truncatus</i> are found in waters with a conductivity of 1220 – 2440 µmho and a total Cl concentration of 120 - 602 mg/l.	
			13. <i>Bu. truncatus</i> prefers polluted waters and is therefore more abundant near human habitations.	Watson, 1958
			14. <i>Bu. truncatus</i> can survive in waters with a salinity of 1500 mg/l.	
			15. <i>Bu. truncatus</i> is relatively tolerant to low oxygen tensions.	

Snail species	Life stage	Abiotic factor	Findings	Study
<i>Bulinus</i>	Eggs	/	/	/
<i>umbilicatus</i>	Juveniles	/	/	/
Mandahl-Barth, 1973	Adults	Desiccation	<ol style="list-style-type: none"> 1. <i>Bu. umbilicatus</i> is capable of surviving 7 to 8 months of complete desiccation. 2. Snails of average size (6 to 8 mm) are best adapted to desiccation. 	Diaw et al., 1988

Supplementary Table 3: Findings structured per abiotic parameter, species and life stage. References for the respective findings can be found in Supplementary Table 1.

Snail species	Eggs	Juveniles	Adults
Temperature			
<i>Biomphalaria alexandrina</i> (Ehrenberg, 1831)	/	/	1. Survival of <i>Bi. alexandrina</i> was reduced at temperatures above 33 °C and below 10 °C.
<i>Biomphalaria pfeifferi</i> (Krauss, 1848)	1. No eggs hatched at 35°C.	1. Growth was fastest at 30 °C, although survival was lowest at this temperature.	1. Fecundity and survival were significantly reduced at 27 °C, hyperthermia occurred at 29 °C. 2. Growth was severely stunted at 29 °C. 3. Egg mass production reduced above 27 °C. 4. Survival is limited to the temperature range of 14 - 31.5 °C.
<i>Bulinus abyssinicus</i> (Martens, 1866)	/	/	1. No <i>Bu. abyssinicus</i> survive at temperatures of 40 °C.
<i>Bulinus globosus</i> (Morelet, 1866)	/	/	1. Growth rate is reduced at temperatures above 28.5 °C. 2. No snails survive longer than 8 days at 8°C. 3. Snails maintained at 15,5 and 36,0 °C do not produce egg masses. 4. Snail growth is inhibited at 15.5 °C and reduced at 31.0 °C.
<i>Bulinus nyassanus</i> (Smith, 1877)	/	/	1. The growth and net reproductive rate of <i>Bu. nyassanus</i> are greatly reduced at 22 °C.
<i>Bulinus truncatus</i> (Audouin, 1827)	/	/	1. Survival of <i>Bu. truncatus</i> is reduced at temperatures above 33 °C and below 10 °C. 2. <i>Bu. truncatus</i> is less tolerant to heat than to cold. 3. Daily mortality rate of 10% when the temperature reaches 38 – 40°C.

Snail species	Eggs	Juveniles	Adults
Desiccation			
<i>Biomphalaria alexandrina</i> (Ehrenberg, 1831)	/	/	<ol style="list-style-type: none"> 1. <i>Bi. alexandrina</i> survived longer than <i>Bu. truncatus</i> under desiccation conditions. 2. <i>Bi. alexandrina</i> had no mud burrowing capacities.
<i>Biomphalaria angulosa</i> Mandahl-Barth, 1957	/	/	<ol style="list-style-type: none"> 1. <i>Bi. angulosa</i> survives up to 1 month of desiccation.
<i>Biomphalaria Arabica</i> (Melvill & Ponsonby, 1896)	/	/	<ol style="list-style-type: none"> 1. <i>Bi. arabica</i> survives desiccation periods of up to 50 days indoors and 20 days outdoors. 2. Survival declines on wet mud to 16 days indoors and 10 days outdoors. 3. When buried, <i>Bi. arabica</i> survives for 90 days indoors and 20 days outdoors.
<i>Biomphalaria pfeifferi</i> (Krauss, 1848)	/	/	<ol style="list-style-type: none"> 1. 35 % of <i>Bi. pfeifferi</i> survived 28 days of desiccation. 2. 0 % survived when infected with <i>Schistosoma</i> parasites. 3. 1 % of small <i>Bi. pfeifferi</i> survived after 21 days. 4. 20% of large <i>Bi. pfeifferi</i> survived after 30 days. 5. Large size <i>Bi. pfeifferi</i> showed high survival rates at 30 and 60 days when buried. 6. 38% of <i>Bi. pfeifferi</i> snails survived after 21 days of desiccation. 7. Only 18% of <i>Bi. pfeifferi</i> snails survived after 48 days of desiccation. 8. 71% of <i>Bi. pfeifferi</i> snails survived after 57 days when temperatures increased.

Snail species	Eggs	Juveniles	Adults
			9. 87% of <i>Bi. pfeifferi</i> snails survived after 49 days under stable indoor conditions.
<i>Bulinus africanus</i> (Krauss, 1848)	/	/	1. Medium sized <i>Bu. africanus</i> survive for 90 days on black sandy soil under rocks.
<i>Bulinus globosus</i> (Morelet, 1866)	/	1. Small size <i>Bu globosus</i> are all dead after 7 days.	1. 4.5 % of large snails are still alive after 30 days. 2. Large size <i>Bu. globosus</i> show high survival rates at 30 and 60 days when buried. 3. 14% of buried large and 6% of small <i>Bu globosus</i> can survive for 90 days. 4. <i>Bu. globosus</i> is capable of surviving 7 to 8 months of complete desiccation. 5. Snails of average size (6 to 8 mm) are best adapted to desiccation. 6. Medium sized snails are best suited to withstand desiccation due to aperture closing. 7. After fast drying, no snails survive after 42 days of desiccation. 8. After slow drying, no snails survive after 77 days of desiccation. 9. Large snails burry deeper than small snails. 10. The length of the desiccation period and snail size have no effect on the depth of burying. 11. Snail mortality increases linearly with an increase in the length of the desiccation period. 12. Almost all snails die after 78 days of desiccation. 13. The lethal time (LT50) for large snails is 73.35 ± 10.32 days and 59.64 ± 8.56 days for small snails.

Snail species	Eggs	Juveniles	Adults
			<p>14. The LT90 values are 11.61 ± 21.03 and 84.19 ± 12.09 days respectively.</p> <p>15. 59% of <i>Bu. globosus</i> survive after 29 days</p>
<i>Bulinus tropicus</i> (Krauss, 1848)	/	/	<p>1. All snails are dead within 24 h when exposed to direct sunlight.</p> <p>2. Snails survive 5 months without direct sunlight.</p> <p>3. After 60 days of desiccation, between 37 and 42% of snails are still alive at relative humidity's between 85 and 96 %.</p> <p>4. Snails kept at a relative humidity of 57 % were all dead after 16 days.</p>
<i>Bulinus truncatus</i> (Audouin, 1827)	/	<p>1. Immature snails (4-8 mm) survive longer than mature ones (8-12 mm) under desiccation conditions.</p>	<p>1. Adult snails survive 9-10 months out of the water in Iraq.</p> <p>2. <i>Bu. truncatus</i> survives for a maximum of 11 days in mud saturated with water.</p> <p>3. The depth of burying was not correlated with survival rates.</p> <p>4. The maximum survival time observed was 7 months in the shade.</p> <p>5. Desiccated snails double their breeding intensity.</p> <p>6. Survival times of snails kept in mud were higher than those of snails kept on no substrate.</p> <p>7. <i>Bu. truncatus</i> is capable of surviving 7 to 8 months of complete desiccation.</p> <p>8. Snails of average size (6 to 8 mm) are best adapted to desiccation.</p> <p>9. <i>Bu. truncatus</i> survives desiccation periods of up to 60 days indoors and 35 days outdoors.</p> <p>10. Survival rates decline on wet mud to 20 days indoors and 12 days outdoors.</p>

Snail species	Eggs	Juveniles	Adults
			<ol style="list-style-type: none"> When buried, snails survive for 120 days indoors and 35 days outdoors. 1.5 % of <i>Bulinus</i> snails survive a drought period of 12 months on mud. Established and breeding colonies of <i>Bu. truncatus</i> are only found in more or less permanent collections of water and are unable to breed in temporary water bodies. Slow drying up of habitats does not kill snails, fast drying is usually fatal.
<i>Bulinus umbilicatus</i> Mandahl-Barth, 1973	/	/	<ol style="list-style-type: none"> <i>Bu. umbilicatus</i> is capable of surviving 7 to 8 months of complete desiccation. Snails of average size (6 to 8 mm) are best adapted to desiccation.
Waterbody characteristics			
<i>Biomphalaria pfeifferi</i> (Krauss, 1848)	/	/	<ol style="list-style-type: none"> Absence of <i>Bi. pfeifferi</i> is mainly associated with stream velocities exceeding 0.3 m/s. Stream velocities between 0.03 and 0.11 m/s are avoided. <i>Bi. pfeifferi</i> prefers water depths between 2 and 7 cm. Substratum type is of no importance in habitat selection. Artificial shading of a breeding site eliminated a population of <i>Bi. pfeifferi</i> within 6 weeks. The site was recolonized 8 weeks after removal of the shading. The long duration of recolonization suggests that shade acts indirectly through its effects on food resources.

Snail species	Eggs	Juveniles	Adults
<i>Bulinus globosus</i> (Morelet, 1866)	/	/	1. Adults can withstand waves of at least 10 cm high.
<i>Bulinus jousseaumei</i> (Dautzenberg, 1890)	/	/	1. <i>Bu. jousseaumei</i> can withstand stream velocities of 0.86 m/s.
<i>Bulinus nyassanus</i> (Smith, 1877)	/	/	1. Snails are more abundant in shallow waters with small sediment particle sizes, associated with greater food abundance and a soft sediment lifestyle.
<i>Bulinus tropicus</i> (Krauss, 1848)	/	1. Growth of juvenile snails is unaffected by reversed circadian regimens	/
Water chemistry			
<i>Biomphalaria alexandrina</i> (Ehrenberg, 1831)	/	<ol style="list-style-type: none"> 1. The lethal Ca conc. for young <i>Bi. alexandrina</i> was determined at >1400 mg/l. 2. Survival of hatched <i>Bi. alexandrina</i> snails was slightly reduced at 0.00 mM Ca²⁺. 	<ol style="list-style-type: none"> 1. <i>Bi. alexandrina</i> tolerates higher concentrations of various ions than <i>Bu. truncatus</i>. 2. Snails can survive for 1 month in distilled water. 3. Habitats devoid of <i>Bi. alexandrina</i> showed one or more ions at the minimum or maximum tolerable range. 4. Habitat concentrations are mostly far below the lethal concentrations. 5. The lethal Ca concentration for adult <i>Bi. alexandrina</i> was determined at >3600 mg/l. 6. Growth increases with calcium concentrations up to 0.25 – 0.50 mM. 7. The net reproductive rate increased with Ca concentrations up to 0.13 – 0.25 mM. 8. Shells of snails reared at 0.00 and 0.0063 mM Ca²⁺ were very fragile and flexible.

Snail species	Eggs	Juveniles	Adults
<i>Biomphalaria camerunensis</i> C.R. Boettger, 1941	/	1. Survival of hatched <i>Bi. camerunensis</i> snails is slightly reduced at 0.00 mM Ca ²⁺ .	<ol style="list-style-type: none"> 1. Growth increased after 4 weeks in 1.00 and 2.00 mM calcium solutions. This growth was not apparent anymore after 10 weeks. 2. The net reproductive rate increases with Ca concentrations up to 0.13 – 0.25 mM. 3. Shells of snails reared at 0.00 and 0.0063 mM Ca²⁺ are very fragile and flexible.
<i>Biomphalaria pfeifferi</i> (Krauss, 1848)	<ol style="list-style-type: none"> 1. No eggs hatched at / conductivities of 50 µS. 2. At conductivities of 750 and 1000 µS lower hatching percentages were recorded and very low survival rates occurred after hatching. 3. Hatching rates were lower in 0.5 mg/l Ca²⁺ and >20 mg/l Ca²⁺. 		<ol style="list-style-type: none"> 1. <i>Bi. pfeifferi</i> tolerates a maximum concentration of dissolved solids and calcium carbonate of 455 and 603 mg/l respectively. 2. Egg-laying rates are significantly lower in waters with high magnesium to calcium ratios. 3. Egg-laying rates drop at 80 – 100 mg/l Ca²⁺. 4. <i>B. pfeifferi</i> is restricted to waters with calcium concentrations of more than 5 mg/l and bicarbonate concentrations of over 20 mg/l. 5. Population growth is maximum at Ca concentrations of 5 to 40 mg/l and bicarbonate concentrations of 20 to 200 mg/l. 6. Optimum values were obtained for 12 mg/l Ca and 35 mg/l bicarbonate. 7. Snail incidence falls off in very soft waters of 2.4 mg/l Ca²⁺ and 22 mg/l CaCO₃. 8. Survival, maturation and fecundity are low at bicarbonate concentrations under 10 mg/l or higher than 30 mg/l. 9. Survival was significantly lower at Ca concentrations below 1 mg/l. 10. Calcium sulphate buffering reduced survival rates, fecundity and net reproductive rate in

Snail species	Eggs	Juveniles	Adults
			<p>comparison to calcium bicarbonate buffering.</p> <p>11. At Ca/Mg ratios <1, fecundity and egg fertility dropped.</p> <p>12. At Ca/Na ratios <0.5 and Ca/Na ratios <0.25; fecundity fell off.</p> <p>13. A concentration of 2.0 mg/l Ca²⁺ is near the lower limit for snail survival.</p> <p>14. A Ca/Mg ratio of >0.3 is needed for survival.</p> <p>15. Snails are absent from waters with a pH below 6.</p> <p>16. <i>Bi. pfeifferi</i> tolerates pH values between 5.3 and 9.0.</p> <p>17. At conductivities of 300 to 400 µS snails mature rapidly and survival rates are highest.</p> <p>18. At 100 and 250 µS snails moved in search for more favourable environments. At 100, 250 and 500 µS, the survival rate was much lower and all snails died by the 13th week.</p> <p>19. Highest growth rates are obtained at 350 µS followed by 300, 500 and 400 µS.</p>
<i>Biomphalaria sudanica</i> (Martens, 1870)	/	/	<p>1. Growth increases linearly with the Ca concentration on a logarithmic scale.</p> <p>2. Crushing resistance increased with increasing Ca concentration.</p>
<i>Bulinus abyssinicus</i> (Martens, 1866)	<p>1. The optimum pH for hatchability ranges between pH 6 and 8.</p> <p>2. The maximum tolerated salt concentration for hatchability is 2800 mg/l.</p> <p>3. The lethal salt concentration for eggs is 3200 mg/l.</p>	<p>1. Salinity has no effect on juveniles up to 5200 mg/l.</p>	<p>1. The optimum pH for survival ranges between pH 6 and 8.</p> <p>2. Salinity has no effect on adults up to 5600 mg/l.</p> <p>3. The maximum tolerable salt concentration is 7600 mg/l.</p>

Snail species	Eggs	Juveniles	Adults
<i>Bulinus africanus</i> (Krauss, 1848)	<ol style="list-style-type: none"> 1. Egg masses are more sensitive to salinity than adult snails. 2. Hatching success reduces until a lethal salt concentration of 5250 mg/l for the eggs. 	<ol style="list-style-type: none"> 1. Hatchlings are more sensitive to salinity than adult snails. 2. Survival of hatchlings starts to decline from 1000 mg/l. 	<ol style="list-style-type: none"> 1. Egg laying is recorded in salinities $\leq$ 4500 mg/l. 2. Adult survival is unaffected in salinities < 3500 mg/l. 3. At a salinity of 8700 mg/l, most adults die within 24h. 4. No snails survive after 30 days in a salinity of 5250 mg/l. 5. Survival of snails infected with <i>Schistosoma</i> parasites is lower.
<i>Bulinus beccari</i> (Paladilhe, 1872)	/	/	<ol style="list-style-type: none"> 1. <i>Bu. beccari</i> tolerates a maximum concentration of dissolved solids and calcium carbonate of 1254 and 813 mg/l respectively.
<i>Bulinus globosus</i> (Morelet, 1866)	/	/	<ol style="list-style-type: none"> 1. Snails are absent from waters with a pH below 6. 2. Snail incidence falls off in very soft waters of 2.4 mg/l Ca^{2+} and 22 mg/l CaCO_3.
<i>Bulinus tropicus</i> (Krauss, 1848)	/	/	<ol style="list-style-type: none"> 1. Growth rates fall at NH_4Cl concentrations above 3 mM and are significantly inhibited at 4 mM. Concentrations above 6 mM are lethal after a week. 2. Growth gradually declines at KCl concentrations above 3 mM until it is completely inhibited at 10 – 12 mM. 3. Growth is inhibited at Ca concentrations of 80 mg/l and complete inhibition occurs at 320 mg/l. 4. Growth is unaffected in waters with NaCl concentrations of up to 1460 mg/l. 5. MgCl becomes inhibitory at concentrations of 760 mg/l.

Snail species	Eggs	Juveniles	Adults
<i>Bulinus truncatus</i> (Audouin, 1827)	1. Hatching success of eggs is not affected by Ca concentration.	1. The lethal Ca concentration for young <i>Bu. truncatus</i> is determined at >1440 mg/l.	1. The lethal Ca concentration for adult <i>Bu. truncatus</i> is determined at > 2880 mg/l. 2. Growth increases with calcium concentrations up to 0.25 – 0.50 mM. 3. The net reproductive rate increases with Ca concentrations up to 0.13 – 0.25 mM. 4. Shells of snails reared at 0.00 and 0.0063 mM Ca ²⁺ are very fragile and flexible. 5. Water with high silt concentrations can be harmful to snails. 6. Snails thrive better in the presence of animal and human excrement but do occur in unpolluted habitat as long as food is plentiful. 7. <i>Bu. truncatus</i> tolerates a pH range of 4.5 – 10.0. 8. <i>Bu. truncatus</i> can tolerate Mg concentrations of 510 mg/l. 9. Egg-laying rates decrease with Ca/Mg ratios lower than 0.5/1 and get 0 at 0.1/1. 10. Reproduction ceases when snails are maintained at Ca/Mg ratios <0.75/1 for more than half a year. 11. Egg-laying rates decrease significantly in Cl concentrations of 866 mg/l. 12. <i>Bu. truncatus</i> are found in waters with a conductivity of 1220 – 2440 µmho and a total Cl concentration of 120 -602 mg/l. 13. <i>Bu. truncatus</i> prefers polluted waters and is therefore more abundant near human habitations. 14. <i>Bu. truncatus</i> can survive in waters with a salinity of 1500 mg/l.

Snail species	Eggs	Juveniles	Adults
			15. <i>Bu. truncatus</i> is relatively tolerant to low oxygen tensions.