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PRIMARY RESEARCH PAPER

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 are 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.

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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 colonise 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). After 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 provides 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 synthesise 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 that 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 organised 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

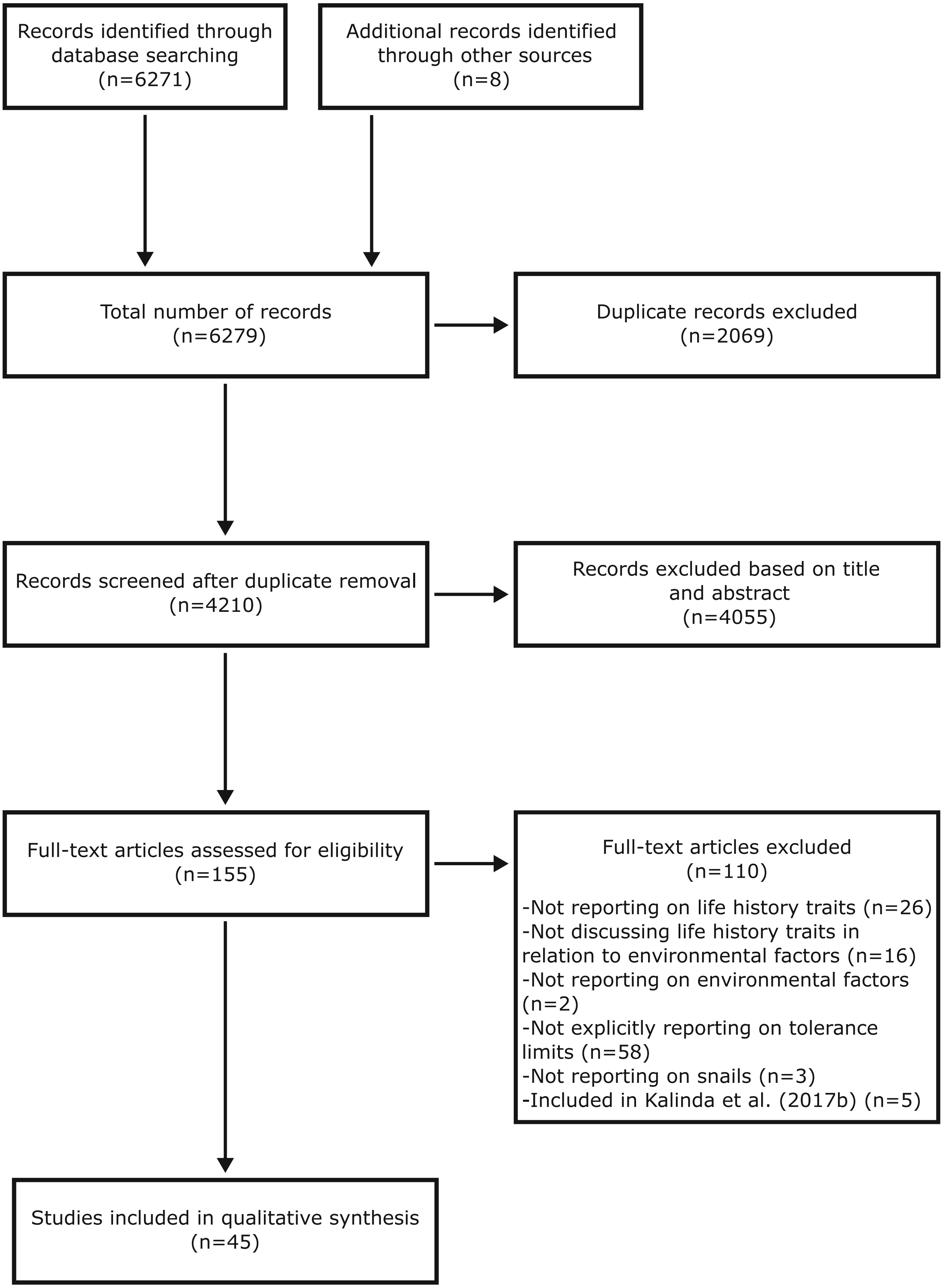
The effect of temperature on the life-history traits of schistosome IH snails was recently reviewed by Kalinda et al. (2017b). Key findings on the tolerance limits of African species are summarised here and supplemented by more recent findings.

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).

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

Desiccation

Snails in temporary habitats are prone to desiccation during certain periods of the year. *Bu. truncatus* can survive 7 months under desiccation conditions in the shade (Chu et al., 1967c) although Watson (1958) reported that it tolerates desiccation periods of 9–10 months in Iraq. These results are comparable to the 7 to 8 months survival time of *Bu. truncatus, Bu. globosus*, and *Bulinus umbillicatus* Mandahl-Barth, 1973, in desiccated habitats found by Diaw et al. (1988). Sturrock (1965) showed that 59% of *Bu. globosus* were still alive after 29 days of desiccation


Records identified through database searching (n=6271)
Additional records identified through other sources (n=8)
Total number of records (n=6279)
Duplicate records excluded (n=2069)
Records screened after duplicate removal (n=4210)
Records excluded based on title and abstract (n=4055)
Full-text articles assessed for eligibility (n=155)
Full-text articles excluded (n=110)
-Not reporting on life history traits (n=26)
-Not discussing life history traits in relation to environmental factors (n=16)
-Not reporting on environmental factors (n=2)
-Not explicitly reporting on tolerance limits (n=58)
-Not reporting on snails (n=3)
-Included in Kalinda et al. (2017b) (n=5)
Studies included in qualitative synthesis (n=45)

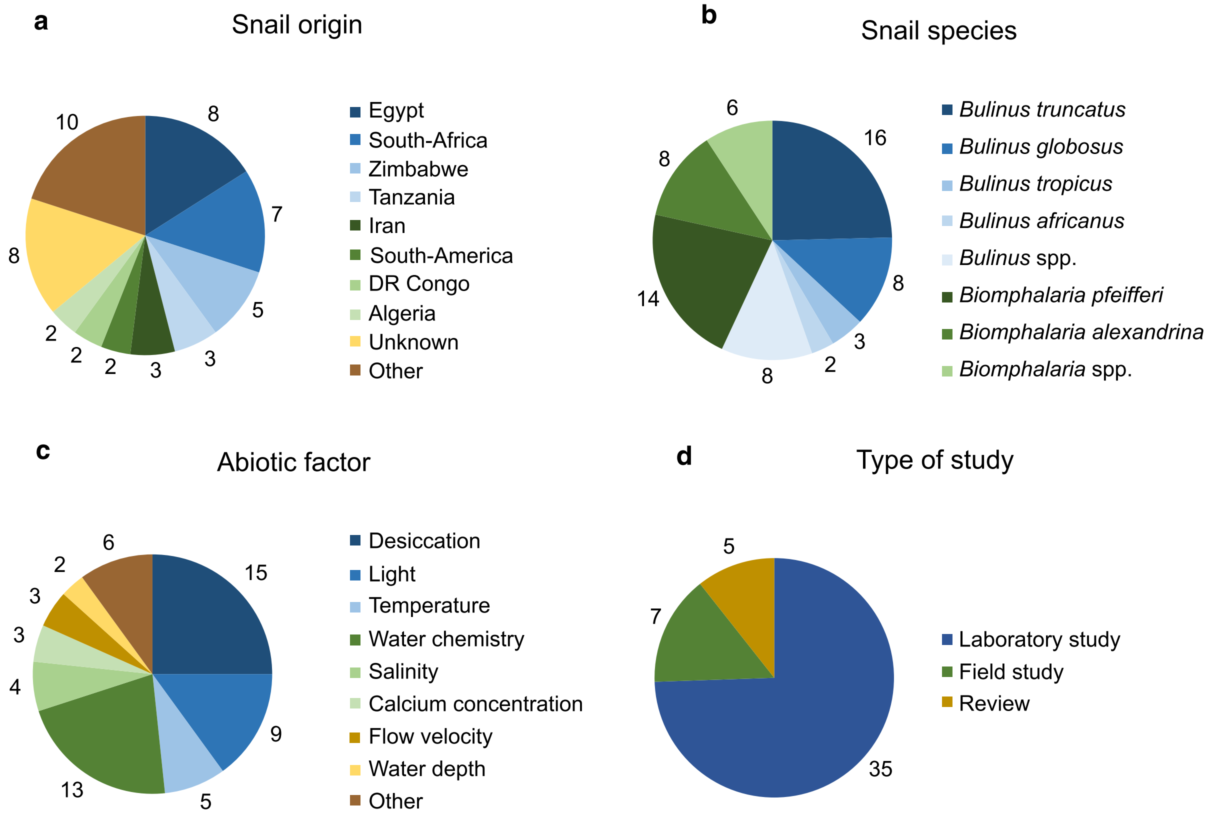


Fig. 2 Graphical summary of the studies retained for this review. The sum of the numbers in the pie charts does not equal 45 (the total number of studies included in the review) in all the charts because some studies combined different categories; **a** the country of snail origin, **b** the snail species 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

but that snail mortality increases linearly with an increase in the length of the desiccation period. Cridland (1967), however, refines these results somewhat as he found that small-sized *Bu. globosus* were almost all dead after seven days of desiccation and only 4.5% of large *Bu. globosus* were still alive after 30 days. The number of surviving large snails increased to 14% after 90 days when snails were buried in mud (Cridland, 1967). Kalinda et al. (2018b) also noted a marked difference between the survival times of large and small *Bu. globosus* snails, with large snails surviving longer (50% after 73 ± 10 days and 10% after 111 ± 21 days) than small snails (50% after 60 ± 9 days and 10% after 84 ± 12 days). However, this size dependency is challenged by a study of Chu et al. (1967a), where small *Bu. globosus* snails had longer survival times than large ones outdoors. *Biomphalaria arabica* (Melvill & Ponsonby, 1896) and *Bu. truncatus* survive desiccation periods of up to 50 and 60 days, respectively, in the lab, and 20 and 35 days, respectively, outdoors (Ghandour, 1987). When kept on wet mud, snail survival times decreased to 16 and 20 days, respectively, indoors and 10 and 12 days, respectively, outdoors. When snails were allowed to bury in mud, survival times indoors increased to 90 days for *Bi. Arabica* and up to 120 days for *Bu. truncatus*, but stayed constant outdoors (Ghandour, 1987).

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

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

Physical properties

Flow velocity

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

Wave action and water depth

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

Light

Oviposition of *Bu. tropicus* was retarded by 2 weeks and fewer eggs were laid when snails were kept under non-circadian light–dark regimes or in complete darkness, although these conditions did not affect growth of juvenile snails (Chaudry & Morgan, 1986). Results published by El-Emam and Madsen (1982) showed that both growth and egg-laying rates were reduced for *Bu. truncatus* kept under complete darkness for 5 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 5 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 beccari* (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 4 weeks in 40 and 80 mg/l Ca^{2+} but no significant growth effect of these concentrations was apparent anymore after 10 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 6 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 µS and higher while survival rates of adult *Bi. pfeifferi* snails were reduced at conductivities lower than 250 µS and higher than 500 µS (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 are rare, although it seems that the 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 have 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 have 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. (Figure 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* are 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 are 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 remain 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 are 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 poleward, 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 recolonise 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 among 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 determine 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 6 weeks. It took 8 weeks to recolonise the site. The lengthy recolonisation 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 are 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 are lacking, although 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 exist. 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 are 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 have 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 are 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 that 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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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

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