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Review Paper

The role of snail aestivation in transmission of schistosomiasis in changing climatic conditions

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Schistosomiasis vector snails are subjected to extreme seasonal changes, particularly in ephemeral rivers and lentic waterbodies. In the tropics, aestivation is one of the adaptive strategies for survival and is used by snails in times of extremely high temperatures and desiccation. Aestivation therefore plays an important role in maintaining the transmission of schistosomiasis. This review assesses the possible impacts of climate change on the temporal and spatial distribution of schistosomiasis-transmitting snails with special emphasis on aestivation, and discusses the effect of schistosome infection on aestivation ability. The impacts of parasite development on snails, as well as physiological changes, are discussed with reference to schistosomiasis transmission. This review shows that schistosome-infected snails have lower survival rates during aestivation, and that those that survive manage to get rid of the infection. In general, snail aestivation ability is poor and survival chances diminish with time. Longer dry periods result in fewer, as well as uninfected, snails. However, the ability of the surviving snails to repopulate the habitats is high.

Keywords: climate change, schistosomiasis transmission, vector ecology

Introduction

Schistosomiasis is caused by blood trematodes of the *Schistosoma* genus, which are internal parasites of vertebrates. The three main species infecting humans are *Schistosoma haematobium*, *S. japonicum* and *S. mansoni.* Two other species, more localised geographically, are *S. mekongi* and *S. intercalatum.* The life cycle involves two hosts. The primary host, where the flukes sexually reproduce, is the human host and asexual reproduction occurs in snail intermediate hosts.

Intermediate host snails play a central role in the transmission of schistosomiasis. Hence it is crucial that the ecology and the role of snails in transmitting schistosomiasis are seriously considered in designing control programmes. The currently recommended strategy for control of schistosomiasis is anchored on mass drug administration, using praziquantel as the drug of choice (WHO 2006; Utzinger et al. 2009). While this strategy significantly lowers the prevalence and intensity of the disease, and reduces the force of transmission through reduced contamination levels, it does not stop treated individuals from being reinfected (Chimbari 2012). It is therefore important to understand the ecology of the snail intermediate hosts.

For many decades in the past snail ecology was seriously studied (Appleton 1978; Brown 1994) and schistosomiasis control programmes were centred around snail control (Yuan et al. 2005), in combination in some instances with treatment and water and sanitation (Chandiwana and Taylor

1990; McCullough 1992; Souza 1995). Much success was registered through these strategies. These studies focused on defining snail distribution, abundance, infection status and interactions with humans and animals (Chandiwana and Taylor 1990; Makura and Kristensen 1991; McCullough 1992). Efforts were made to understand the schistosome/ snail interactions (Morand et al. 1996), survival strategies of snails (Storey and Storey 2012), biological control of the snails through various means including use of fish (Moyo 1995; Chimbari et al. 1996; Chimbari et al. 1997), competition with non-intermediate host snails (Ndlela et al. 2007), susceptibility to both synthetic and plant molluscicides (McCullough 1992; Chimbari and Shiff 2008), and susceptibility to other natural infections in the waterbodies (Chingwena et al. 2002). The advent of the safe single dose of praziquantel, now used for treating both *S. haematobium* and *S. mansoni*, and environmental concerns expressed against the use of synthetic molluscicides (McCullough 1992; Engels et al. 2002), shifted research attention away from snail studies. This shift downgraded the study of snails (malacology) to an academic discipline more appropriate for understanding biodiversity, rather than as a key component of understanding disease transmission.

Eradicating snail intermediate hosts would be ideal to curb reinfection. However, there is no doubt that indiscriminate killing of snails from a biodiversity point of view is unacceptable. Therefore, investing in molluscicides is not

encouraged, particularly given that alternative environmentally friendly, plant-based molluscicides have not been developed to a point where they could be used sustainably. However, it is important that the ecology of intermediate host snails is taken into account when designing schistosomiasis control programmes. In particular, control managers need to know when and where infected and non-infected snails are present in water. They need to understand how snail populations build up following periods of dry conditions along ephemeral rivers and lentic waterbodies, and how that influences schistosomiasis transmission locally.

Much of the information on the ecology of snails is based on studies conducted during the 1950–1980 period. The limiting ecological parameters found in literature are based on these early studies and yet drastic ecological changes have occurred since then due to many factors including human population pressure (Vörösmarty et al. 2000), water development projects (Vörösmarty et al. 2000; Steinmann et al. 2006), land-use changes (Chaumba et al. 2003) and climate change/variability (McCarthy et al. 2001; Parry et al. 2007), to mention some. It is therefore imperative that more research be conducted on snail ecology to understand the current situation. For such research to be encouraged and promoted there is need for an audit of what has been done and what is known, and of what needs to be done to provide a knowledge base for young scientists. It is against this background that we conducted this review on aestivation, one of the key ecological phenomena of snails that have implications on schistosomiasis transmission. This review focuses on the freshwater planorbids, given their relative abundance and medical importance to human health.

Methods

This review is based on a systematic search in July 2014 for relevant literature on PubMed (http://www.ncbi.nlm.nih.gov/pubmed) electronic search engine, following the method used by Simoonga et al. (2009). This search considered studies in aestivation, schistosomiasis transmission, climate change and impact on parasitic diseases, following a combination of terms and Boolean operations: 'aestivation and schistosomiasis transmission', 'aestivation and climate change', 'schistosomiasis and climate change' (Table 1). The snowballing technique was used to obtain more literature based on the bibliography or reference list of previous reviews obtained using the search strategy described above. The articles that were not relevant to snail aestivation were left out.

Aestivation

Aestivation is defined as a survival strategy whereby organisms lower their metabolic activities to survive seasonally adverse conditions (hot and dry) with limited or no food (Guppy et al. 1994; Guppy 2004; Secor and Lignot 2010; Storey and Storey 2012). The word aestivation derives from the Latin for summer (*aestas*) or heat (*aestus*) (Storey and Storey 2012). While hibernation occurs in winter, aestivation occurs in dry summer months (Withers and Cooper 2010). Aestivation is achieved by metabolic depression or

Table 1: Articles of published literature related to aestivation retrieved from PubMed (http://www.ncbi.nlm.nih.gov/pubmed)

Search word combination	No. of articles retrieved	No. of articles considered
'Snail aestivation'	126	30
'Snail aestivation + schistosomiasis'	8	6
'Schistosomiasis + climate change'	41	14
'Snails + climate change'	77	15
'Aestivation + climate change'	2	0
'Snail aestivation + climate change'	1	0
'Schistosomiasis + aestivation + climate change'	0	0

hypometabolism. It is achieved by strong metabolic rate suppression, strategies to retain body water, conservation of energy and body fuel reserves, altered nitrogen metabolism, and mechanisms to preserve and stabilise organs, cells and macromolecules over many weeks or months of dormancy (Storey and Storey 2012). Table 2 shows some of the intermediate host snails for schistosomiasis and the respective schistosome species.

Effects of aestivation on parasite development

Brown (1980) noted that aestivation was central to the ecology of many African molluscs. At that time very little was known about the parasite–host interaction. Several studies have shown that infected snails are more likely to die during aestivation (Woolhouse and Taylor 1990; Badger and Oyerinde 1996; White et al. 2007). The studies showed that, following exposure to the miracidia of *S. mansoni*, *Biomphalaria pfeifferi* snails' survival chances decreased with time before being aestivated. That is, the longer the snails stayed with an infection before being put into aestivation mode, the lower their survival chances. It has also been demonstrated that there is a difference in mortality rate of cercariae from aestivated and non-aestivated *B. pfeifferi*, and that penetration, migration and maturation of cercariae into adult worms are not affected by the aestivation in *B. pfeifferi* snails (Badger and Oyerinde 2003). Barbosa (1956) demonstrated that when *Biomphalaria glabrata* infected with *S. mansoni* is in the phase of shedding cercariae, and is kept out of water in the laboratory over a two-week period, the surviving snails get rid of the infection. The same group (Barbosa and Barbosa 1958) also showed that primary sporocysts stopped their development at some point in their 90-day laboratory aestivating period to resume it as soon as the snails returned to the water. The secondary sporocysts were also able to enter into dormancy when the snails were kept out of water. Thus, the largest proportion of snails that survive desiccation is likely to be those without infection and this translates to a low transmission potential.

Aestivation triggers

Most field-based studies have not pinpointed what triggers aestivation. However, it has been noted that several stresses, including conditions that restrict water and food availability, are the common trigger for aestivation and that these are usually accompanied by hot summer temperatures (Guppy 2004; Storey and Storey 2012). Betterton et

Table 2: Some snail species responsible for transmitting *Schistosomiasis* and their aestivation capabilities

Snail species	*Schistosomiasis* species	Aestivation ability and source
Biomphalaria glabrata	*S. mansoni*	Yes (Barbosa 1956)
Biomphalaria tenagophila	*S. mansoni*	Yes (Ohlweiler and Kawano 2001)
Biomphalaria pfeifferi	*S. mansoni*	Yes (Badger and Oyerinde 1996)
Bulinus truncatus	*S. haematobium*	Yes (Chu et al. 1967)
Bulinus globosus	*S. haematobium*	Yes (Betterton et al. 1988)
Bulinus senegalensis	*S. heamatobium*	Yes (Goll and Wilkins 1984)
Bulinus rohlfsi	*S. haematobium*	Yes (Betterton et al. 1988)
Bulinus forskalii	*S. haematobium, S. intercalatum, S. guineensis*	Yes (de Kock et al. 2002)
Bulinus africanus	*S. haematobium*	Yes (Heeg 1976)
Oncomelania hupensis	*S. japonicum*	Yes (Hong et al. 2002)
Neotricula aperta	*S. mekongi*	No (Attwood 1999)

al. (1988) point to some inconsistencies, and yet very little information relating to the stimulus for aestivation is given. This is probably because, in their study, *Bulinus rohlfsi* did not aestivate in the dry season, even although its habitat was drying due to evaporation, yet earlier it had been shown that snails aestivate before the pools dry up (Webbe 1962; Goll and Wilkins 1984). Water evaporation due to high air temperatures, and the resultant lower water temperatures signalling the end of the rainy season, have been correlated with a decline of *Bulinus senegalensis* populations (Vera et al. 1995), suggesting that a decrease in water temperature could be a stimulus for aestivation. Drying-off of a bloom of unicellular algae and environmental changes associated with this have also been cited as an aestivation trigger (Betterton et al. 1988). Aestivation triggers may be species-dependent. Cell signalling is crucial to achieving both a hypometabolic state and reorganising multiple metabolic pathways to optimise long-term viability during aestivation (Storey and Storey 2012). However, rapid river drying is not good for aestivation, as snails require gradually drying conditions to prepare themselves for aestivation (Barlow 1935). Barlow also noted that, if their habitat dried up suddenly, their survival chances were low, compared to under gradual drying. This may imply that the snails need time to prepare for aestivation or that they respond to certain stimuli associated with gradual drying. It is important to understand species-specific stimuli for aestivation mode triggers.

Physiological aspects of aestivation

Hypometabolism is controlled reversibly by controls that suppress cell functions (e.g. inhibiting activities of enzymes and functional proteins, and sequestering mRNA transcripts into stress granules) and changes in the amounts of selected proteins due to differential transcription, translation or degradation. This includes proteins that address aestivation-specific issues, for example, upregulation of urea cycle enzymes (Storey and Storey 2012). Protein synthesis is down-regulated in concert with metabolic depression (Guppy et al. 1994; Guppy and Withers 1999). An understanding of the aspects of cell biology that control metabolic depression therefore has widespread implications and applications, not only to the regulation of metabolically depressed organisms, but also in explaining the metabolic requirements of normal cells. But, to date, no molecular mechanism or process associated with the control

of metabolic depression has been comprehensively delineated, and the fundamental phenomenon of metabolic depression remains biochemically obscure (Guppy 2004). Barbosa and Barbosa (1958) observed that some snails survived until their weight was as low as 47–50% of their original weight, but that they usually died when their weight approached 60% of the original. Aestivation affects various metabolites. Polysaccharides, total lipids, lactic acid and volatile acids have been shown to be depleted in snails under aestivation as well as triglycerols (White et al. 2006) and phosphatidylcholine concentration significantly decreased during aestivation of the infected snails (White et al. 2007). Phosphatidylcholine has a structural role in cell membranes, so depletion of this lipid could indicate that the larval trematodes are somehow disrupting the cell membranes of snails. In general, physiological regulation of snail metabolism is vital for successful aestivation. It is important to have good understanding of this vital process.

Resuscitation

In general, aestivation appears to be a fairly 'light' dormancy involving no physiological changes that cannot be very rapidly reversed. Torrential summer rains have been cited as a stimulus for ending aestivation (Storey 2002). Studies of *Otala lactea* showed that arousal occurred within 10 minutes when aestivating snails were sprayed with water (Whitwam and Storey 1991). Uric acid is accumulated during aestivation of *Pomacea canaliculata* and may act as an antioxidant during the subsequent arousal to cope with harmful effects of reoxygenation (Giraud-Billoud et al. 2011). Very few studies have been carried out to understand the physiology of schistosomiasis-transmitting snails during aestivation. However, it has been established that the time taken to revive snails depends on species (Barlow 1935) and can range from two minutes to two hours. It has also been shown that there is differential mortality of different various size groups soon after the snails are revived (Betterton et al. 1988). Young snails tend to die off soon after revival, while old snails are more likely to die during aestivation (Hira 1968; Betterton et al. 1988).

Host–parasite interactions

Numerous studies have demonstrated the negative effects of larval trematodes on the fecundity, survival and growth

of the snail hosts. Immature *S. mansoni* larvae were shown to survive and develop within aestivating *Biomphalaria tenagophila* (Ohlweiler and Kawano 2001). However, the survival of the infected snails was lower than that of uninfected snails. Barbosa (1956) also demonstrated that *S. mansoni* can stop its development in *B. glabrata* when the snail aestivates in natural habitats that are subjected to annual drought. They confirmed the phenomenon, which had been observed under laboratory conditions (Barbosa and Barbosa 1958), in the field in aestivating snails found on the soil. The conditions created in the host tissues during the aestivation period make the trematode stop its development. The phenomenon is seasonal and is characterised by the temporary failure of growth and reproduction of the trematode during a change of the environment when the snail is subjected to adverse climatic factors. Gérard (2001) suggested that parasites had a regulatory impact on host populations based on a mathematical model which demonstrated an inverse relation between the frequency of the snails and the rate of parasitism.

Differential species aestivation abilities

Snails have different strategies for surviving long drought periods. Survival rates depend on many factors, including the species of the snail, whether habitats dry up gradually or rapidly, soil moisture and relative humidity (Appleton 1978; McCreesh and Booth 2013). Survival may be lower for snail populations with little history of previous desiccation (Appleton 1978; McCreesh and Booth 2013). Aestivation is more common in *Bulinus* species than in *Biomphalaria* species, and therefore plays a greater role in the transmission of *S. haematobium* than *S. mansoni* (Brown 1994; Appleton and Madsen 2012). *Biomphalaria glabrata* and *Biomphalaria straminea*, vectors for *S. mansoni*, were shown to survive by seeking protection under ground-level vegetation and not burrowing under the soil to avoid desiccation (Olivier 1956). The majority of the surviving snails were at the soil surface or in the top centimetre of the soil, possibly left stranded there when the water level fell and the pools dried up. However, Betterton et al. (1988) showed that *B. rohlfsi* and *Bulinus globosus* aestivated towards the bottom of their drying-out habitats. The authors noted that this behaviour is adaptively advantageous for temporary pool dwellers, since it prevents them from being revived too early after the first isolated rainfall of the season and enables them to emerge only when the pool is fairly full and well established. It has indeed been shown that different species have different tolerance to drought (Barlow 1933). The authors noted that, for *B. globosus*, survival rates during desiccation compared favourably with survival rates of free-living snails in the field. Differential species ability will no doubt influence schistosomiasis species distribution geographically if length of drought changes as some snail species will be pushed to extinction while others will thrive.

Implications of aestivation on schistosomiasis

The success of schistosomiasis control programmes depend to a great extent on an understanding of the

ecology of snails and subsequent schistosome transmission. It is essential to understand how aestivation affects the time necessary for the re-establishment of communities in a freshwater habitat after disturbance. Thus, a long-term study on the level of individual snails, populations of one species and complex snail communities is necessary to have a better understanding of the functioning of trematode–mollusc systems in the field. *Bulinus globosus* survival rates during desiccation were found to be similar to survival rates of free-living snails in the field (Woolhouse and Taylor 1990). Similarly Vera et al. (1995) found that another snail species, *B. senegalensis*, survived in two persistent and three ephemeral pools, including one that only had water for one month following an eleven-month dry period. This observed period of aestivation exceeded the six to seven months recorded in Gambia (Smithers 1956). This demonstrates the good adaptation of *B. senegalensis* to temporary waterbodies in Niger and confirms its classification as a good aestivator. This information is particularly important in cases where attempts to control snails in irrigated areas by the periodic draining of water courses. Periodic drainage of irrigation canals along with tailored engineering designs to increase water flow has been implemented to reduce snail densities (Thomson et al. 1996; Chimbari 2012). However, under drought conditions the survival rates of adult *B. globosus* are sufficiently high to call into question the effectiveness of drainage (to the extent that this simulates natural drought conditions) in controlling snail populations (Barlow 1933; Vera et al. 1995). Drainage may, however, interfere with snail breeding, and thus may be effective in reducing the density of snails with patent infections (owing both to reduced survival rates and loss of infection), and subsequently in temporarily reducing schistosomiasis transmission (Vera et al. 1995; Thomson et al. 1996; Chimbari 2012). Appleton (1978) noted that during the rainy season, the snail densities are low, with little or no breeding and that egg laying is increased just after aestivating snails are revived. Thus, treatment of ponds with molluscicide at the end of the rainy season and upon onset of rains, when the snails would be trying to repopulate, would be effective in controlling snails, thereby reducing transmission of schistosomiasis, as suggested by Senghor et al. (2015).

There are contradictory reports on the effect of infectivity on the survival of the snails. In a study involving 1 200 *B. glabrata* snails (Lancastre et al. 1989), there were no differences between snails infected for 3 days or 12 days before aestivation. However, when snails were either put on soil or buried in sealed or ventilated boxes, survival was better for the 'on soil' snails than for 'buried' snails. The surviving desiccated *B. glabrata* had a lower death rate and lesser cercarial production than infected snails kept in water. A statistically significant inferior production of male cercariae compared to female and to mixed cercariae was demonstrated. There were also no surviving snails in sealed boxes. Most importantly, it was demonstrated that a significantly large portion of snails die and do not make it through the dry period (Barbosa and Barbosa 1958). In short, aestivation ability is very poor.

Snail ecology and climate change

Climate change is now generally accepted as fact (Mas-Coma et al. 2008). It is conceivable then that, with climate change, the duration of dry/wet seasons has been changing over time and may become shorter or longer in the future. This may reduce or increase the chances of snail survival and breeding. An understanding of these dynamics is critical in formulating intervention control strategies. Climate variables are able to affect the prevalence, intensity and geographical distribution of helminths by directly influencing free-living larval stages, as well as indirectly influencing mainly the invertebrate, but also the vertebrate, hosts (Mas-Coma et al. 2008). Mature cercariae shed by post-aestivated *B. pfeifferi* and *B. glabrata* were shown to be as infective as those shed by non-aestivated snails (Eveland and Ritchie 1972; Badger and Oyerinde 2003). However, cercariae from post-aestivated *B. pfeifferi* became less motile more quickly during the first 12 hours after release. This was attributed to reduced energy reserves, which could have been due to the host itself having been starved and had its reserved energy depleted (Eveland and Ritchie 1972; Badger and Oyerinde 2003). It appears that snails occurring where there are longer drought periods have adapted to the drought conditions (Barlow 1933; Vera et al. 1995).

The abilities of snail species to survive different lengths and severities of desiccation in natural conditions are not well understood (McCreesh and Booth 2013). Droughts can lengthen the time that temporary waterbodies are without water and may result in permanent drying of some waterbodies. Climatic factors affect several ecological processes at different levels – from the performance of individual organisms, to the dynamics of populations and community interactions, up to the distribution of species (Mas-Coma et al. 2009a). The development and transmission rates of parasitic organisms are particularly sensitive to weather conditions. Climate change (global warming) is likely to affect the distribution and survival rate of parasite vectors and intermediate hosts and also directly influence the reproduction and maturation rate of parasites carried by them (McCarthy et al. 2001). The expansion of suitable habitats for invertebrate hosts of waterborne parasites could result in risk of waterborne infections in humans and animals and increased distribution of the disease. There are different environmental factors that impact on the distribution of schistosomiasis. Temperature, waterbody type, rainfall, water velocity and altitude can all have a significant effect on the schistosome life cycle and survival of the intermediate snail host (Fenwick et al. 2006). Climatic changes are likely to affect the known geographical distribution of freshwater snails such as *Biomphalaria* spp., the invertebrate hosts of *Schistosoma* spp. transmissible to humans, livestock and other animals (Morgan et al. 2001). For example, high temperatures may explain the absence of *Biomphalaria* spp. from coastal East Africa and the consequent absence of *S. mansoni* transmission (Sturrock 1966). Similarly, high mortality of *B. pfeifferi* in South Africa is associated with periods of continuous high temperatures (Appleton 1977). However, cercarial production may

increase at higher temperatures and the snail physiological processes also increase markedly at high temperatures (Mas Coma et al. 2009b). Thus, schistosomiasis is among the diseases which may change both its local infection and geographic expansion due to global warming. Populations of freshwater snails are subjected to severe ecological constraints imposed by large temporal fluctuations in their environment. Their success depends on their physiological capacity to tolerate these fluctuations (Hunter 1961). Temperature can also act as a stressor on hosts and may lead to an increase in parasite-induced mortality (Esch et al. 1975; Studer et al. 2010). The impact on individual hosts may then also translate into effects at the population level which, in turn, may negatively affect the parasite's success at completing its life cycle. Esch et al. (1975) noted that the varied response to the stressor input at the individual or population levels is dictated by the capacity for adaptability present at each level, and also that response may be modified, by the unique combination of environmental characteristics at the time of stressor input. Field observations have suggested that there is interspecific competition among snails in the waterbodies (Vera et al. 1995) when a temporary pool colonised by both *B. senegalensis* and *Bulinus truncatus* was studied. It was also shown that *B. senegalensis* was present in the temporary pools whatever their duration, whereas *B. truncatus* was only found in the more persistent pools. *Bulinus senegalensis* populations developed mostly during the rainy season when the water temperature was warm while *B. truncatus* was more abundant after the rainy season when the water temperature was cooler, but occasionally increased when the water temperature was warmer during unusual rainy seasons with low and intermittent rainfall. This has greater implications for intermediate host snails. The ability to aestivate and wait for the next season or to be modulated by water temperature can result in different temporal and spatial distribution and abundance. In unfavourable climatic conditions there is a possibility that the interspecies competition may be tilted in the favour of one species at the expense of the other. This would result in an increased presence of the other. If the favoured species is a parasite vector, this would lead to increased transmission. Thus climate change will have important implications on snail ecology and schistosomiasis transmission.

Climate change scenario

The Intergovernmental Panel on Climate Change (IPCC 2007) predicts an overall increase in the amount of rainfall at high altitudes and an overall decrease in most subtropical regions. The annual mean rainfall increase in tropical and East Africa, winter decrease for southern Africa, likely annual mean decrease in North Africa, northern Sahara, and likely summer mean increase in southern South-East Asia and south-eastern South America have been predicted (IPCC 2007). If these predictions become a reality, that will inevitably influence both the distribution and incidences of schistosomiasis (McCreesh and Booth 2013). Several models have indicated the importance of the length of the rainy season in determining the survival and breeding of snails (Martens et al. 1997; Douglas et al. 2008; Zhou et al.

2008; Stensgaard et al. 2013). Fecundity and survival are influenced by drastic alterations of the habitat (Appleton 1978). Increased surface water may result in an increase in schistosomiasis transmission. However, flash floods are likely to wash away the snails or dislodge them from their preferred habitats. Fast-flowing water is also not ideal for snail and cercariae survival. Thus, rainfall patterns may result in an increase or decrease of schistosomiasis transmission. The length of dry season has an impact on chances of successful aestivation and only snails capable of adapting to longer drying periods may survive.

Conclusion

Aestivation is an important step in the life of many schistosomiasis-transmitting snails, especially in ephemeral waterbodies. Studies so far have not fully shown how climate change may affect spatial and temporal distribution of these snails. There are contradictory reports on the effect of infectivity to survival of the snails. Climate change is likely to have a profound effect on snail population densities and inevitably transmission. Longer dry periods will negatively impact on survival of snails and may lead to elimination of some vector species. Aestivation capabilities between different species in the context of interspecies competition have not been clearly studied, while aestivation triggers have not been clearly spelt out. However, it has been shown that snails generally prepare themselves for aestivation by altering their physiology, and their survival chances are increased if the waterbodies dry up gradually.

It should be noted that much of the literature on snail aestivation studies is now old. Most of the field studies were carried out from 1930 to 1980. There is a need to revisit some of the studies carried out, especially those done in the 1950s, with a view to filling some of the gaps, given the new information at our disposal, especially in the physiological aspects that have been recently unravelled.

References

Appleton CC. 1977. The influence of temperature on the life-cycle and distribution of *Biomphalaria pfeifferi* (Krauss, 1948) in south-eastern Africa. *International Journal for Parasitology* 7: 335–345.

Appleton CC. 1978. Review of literature on abiotic factors influencing the distribution and life cycles of bilharziasis intermediate host snails. *Malacological Review* 11: 1–25.

Appleton CC, Madsen H. 2012. Human schistosomiasis in wetlands in southern Africa. *Wetlands Ecology and Management* 20: 253–269.

Attwood S. 1999. Genetic variation in *Neotricula aperta*, the snail intermediate host of *Schistosoma mekongi* in the lower Mekong basin. *Journal of Zoology* 249: 153–164.

Badger L, Oyerinde J. 1996. *Schistosoma mansoni*: effect of aestivation on the intra-molluscan stages and the survival rate of infected *Biomphalaria pfeifferi*. *Annals of Tropical Medicine and Parasitology* 90: 617–620.

Badger L, Oyerinde J. 2003. Effect of aestivation of *Biomphalaria pfeifferi* on the survival and infectivity of *Schistosoma mansoni* cercariae. *British Journal of Biomedical Science* 61: 138–141.

Barbosa F. 1956. Some seasonal and climatic factors influencing the life-cycle of *Australorbis glabratus* and *Tropicorbis centimetralis* in north-eastern Brazil. Unpublished report. World Health Organisation, Geneva.

Barbosa F, Barbosa I. 1958. Dormancy during the larval stages of the trematode *Schistosoma mansoni* in snails estivating on the soil of dry natural habitats. *Ecology* 39: 763–764.

Barlow CH. 1933. The effect of the "winter rotation" of water upon snails involved in the spread of schistosomiasis in Egypt, 1930–1931 and 1931–1932. *American Journal of Epidemiology* 17: 724–742.

Barlow CH. 1935. Further studies of the revival, after drying, of the snail hosts of the human schistosomes of Egypt. *American Journal of Epidemiology* 22: 376–391.

Betterton C, Ndifon G, Tan RM. 1988. Schistosomiasis in Kano State, Nigeria. II. Field studies on aestivation in *Bulinus rohlfsi* (Clessin) and *B. globosus* (Morelet) and their susceptibility to local strains of *Schistosoma haematobium* (Bilharz). *Annals of Tropical Medicine and Parasitology* 82: 571–579.

Brown DS. 1980. *Freshwater snails of Africa and their medical importance*. London: Taylor & Francis.

Brown DS. 1994. *Freshwater snails of Africa and their medical importance* (2nd edn). London: Taylor & Francis.

Chandiwana SK, Taylor P. 1990. The rational use of antischistosomal drugs in schistosomiasis control. *Social Science and Medicine* 30: 1131–1138.

Chaumba J, Scoones I, Wolmer W. 2003. From jambanja to planning: the reassertion of technocracy in land reform in south-eastern Zimbabwe? *The Journal of Modern African Studies* 41: 533–554.

Chimbari MJ. 2012. Enhancing schistosomiasis control strategy for Zimbabwe: building on past experiences. *Journal of Parasitology Research* 2012: Article ID 353768 (9 pp).

Chimbari MJ, Madsen H, Ndamba J. 1997. Simulated field trials to evaluate the effect of *Sargochromis codringtoni* and *Tilapia rendalli* on snails in the presence and absence of aquatic plants. *Journal of Applied Ecology* 34: 871–877.

Chimbari MJ, Ndamba J, Madsen H. 1996. Food selection behaviour of potential biological agents to control intermediate host snails of schistosomiasis: *Sargochromis codringtoni* and *Tilapia rendalli*. *Acta Tropica* 61: 191–199.

Chimbari MJ, Shiff C. 2008. A laboratory assessment of the potential molluscicidal potency of *Jatropha curcas* aqueous extracts. *African Journal of Aquatic Science* 33: 269–273.

Chingwena G, Mukaratirwa S, Kristensen, TK, Chimbari M. 2002. Susceptibility of freshwater snails to the amphistome *Calicophoron microbothrium* and the influence of the species on susceptibility of *Bulinus tropicus* to *Schistosoma haematobium* and *Schistosoma mattheei* infections. *Journal of Parasitology* 88: 880–883.

Chu K, Arfaa F, Massoud J. 1967. The survival of *Bulinus truncatus* buried in mud under experimental outdoor conditions. *Annals of Tropical Medicine and Parasitology* 61: 6–10.

de Kock K, Wolmarans C, du Preez L. 2002. Freshwater mollusc diversity in the Kruger National Park: a comparison between a period of prolonged drought and a period of exceptionally high rainfall. *Koedoe* 45: 1–11.

Douglas I, Alam K, Maghenda M, Mcdonnell Y, McLean L, Campbell J. 2008. Unjust waters: climate change, flooding and the urban poor in Africa. *Environment and Urbanization* 20: 187–205.

Engels D, Chitsulo L, Montresor A, Savioli L. 2002. The global

epidemiological situation of schistosomiasis and new approaches to control and research. *Acta Tropica* 82: 139–146.

Esch GW, Gibbons JW, Bourque JE. 1975. An analysis of the relationship between stress and parasitism. *American Midland Naturalist* 93: 339–353.

Eveland L, Ritchie LS. 1972. Infectivity of cercariae of *Schistosoma mansoni* from snails on inadequate diets. *Parasitology* 64: 441–444.

Fenwick A, Rollinson D, Southgate V. 2006. Implementation of human schistosomiasis control: challenges and prospects. *Advances in Parasitology* 61: 567–622.

Gérard C. 2001. Consequences of a drought on freshwater gastropod and trematode communities. *Hydrobiologia* 459: 9–18.

Giraud-Billoud M, Abud MA, Cueto JA, Vega IA, Castro-Vazquez A. 2011. Uric acid deposits and estivation in the invasive apple-snail, *Pomacea canaliculata*. *Comparative Biochemistry and Physiology, Part A* 158: 506–512.

Goll P, Wilkins H. 1984. Field studies on *Bulinus senegalensis* Muller and the transmission of *Schistosoma haematobium* infection in a Gambian community. *Tropenmedizin und Parasitologie* 35: 29–36.

Guppy M. 2004. The biochemistry of metabolic depression: a history of perceptions. *Comparative Biochemistry and Physiology, Part B* 139: 435–442.

Guppy M, Fuery C, Flanigan J. 1994. Biochemical principles of metabolic depression. *Comparative Biochemistry and Physiology, Part B* 109: 175–189.

Guppy M, Withers P. 1999. Metabolic depression in animals: physiological perspectives and biochemical generalizations. *Biological Reviews* 74: 1–40.

Heeg J. 1976. Oxygen consumption and the use of metabolic reserves during starvation and aestivation in *Bulinus* (*Physopsis*) *africanus* (Pulmonata: Planorbidae). *Malacologia* 16: 549–560.

Hira P. 1968. Studies on the capability of the snail transmitting urinary schistosomiasis in western Nigeria to survive dry conditions. *The West African Medical Journal and Nigerian Practitioner* 17: 153–160.

Hong Q, Zhou X, Sun L, Yang G, Huang Y, Yang K. 2002. Impact of global warming on the transmission of schistosomiasis in China I. The hibernation and lethal temperature of *Oncomelania hupensis* in laboratory. *Chinese Journal of Schistosomiasis Control* 14: 192–195.

Hunter WR. 1961. Annual variations in growth and density in natural populations of freshwater snails in the west of Scotland. *Proceedings of the Zoological Society of London* 136: 219–253.

IPCC (Intergovernmental Panel on Climate Change). 2007. Summary for policymakers. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB et al. (eds), *Climate change 2007: the physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change.* Cambridge: Cambridge University Press. pp 1–18.

Lancastre F, Vianey-Liaud M, Coutris G, Bolognini-Treney J. 1989. Resistance to desiccation of *Biomphalaria glabrata* adults by polyinfection of schistosomiasis. *Memórias do Instituto Oswaldo* 84: 205–212.

Makura O, Kristensen T. 1991. National freshwater survey of Zimbabwe. In: Meierbrook C (ed.), *Proceedings of the Tenth International Malacology Congress,* Tübingen 27 August–2 September 1989. Tübingen: Unitas Malacologica. pp 227–232.

Martens WJ, Jetten TH, Focks DA. 1997. Sensitivity of malaria, schistosomiasis and dengue to global warming. *Climatic Change* 35: 145–156.

Mas-Coma S, Valero M, Bargues M. 2008. Effects of climate change on animal and zoonotic helminthiases. *Revue Scientifique et Technique* 27: 443–457.

Mas-Coma S, Valero MA, Bargues MD. 2009a. Climate change effects on trematodiases, with emphasis on zoonotic fascioliasis and schistosomiasis. *Veterinary Parasitology* 163: 264–280.

Mas-Coma S, Valero M, Bargues MD. 2009b. *Fasciola*, lymnaeids and human fascioliasis, with a global overview on disease transmission, epidemiology, evolutionary genetics, molecular epidemiology and control. *Advances in Parasitology* 69: 41–146.

McCarthy JJ, Canziani OF, Leary NA, Dokken DJ, White KS (eds). 2001. *Climate change 2001: impacts, adaptation, and vulnerability. Contribution of Working Group II to the third assessment report of the Intergovernmental Panel on Climate Change.* Cambridge: Cambridge University Press.

McCreesh N, Booth M. 2013. Challenges in predicting the effects of climate change on *Schistosoma mansoni* and *Schistosoma haematobium* transmission potential. *Trends in Parasitology* 29: 548–555.

McCullough FS. 1992. The role of molluscicides in schistosomiasis control. Unpublished document WHO/SCHIST/92.107. Division of Control of Tropical Diseases, World Health Organization, Geneva.

Morand S, Manning S, Woolhouse M. 1996. Parasite-host coevolution and geographic patterns of parasite infectivity and host susceptibility. *Proceedings of the Royal Society of London, Series B* 263: 119–128.

Morgan J, Dejong R, Snyder S, Mkoji G, Loker E. 2001. *Schistosoma mansoni* and *Biomphalaria*: past history and future trends. *Parasitology* 123: 211–228.

Moyo N. 1995. The biology of *Sargochromis codringtoni* in Lake Kariba. PhD thesis, University of Zimbabwe, Zimbabwe.

Ndlela B, Chimbari MJ, Madsen H. 2007. Interactions between *Bulinus globosus* and *B. tropicus* (Gastropoda: Planorbidae) in a pond experiment in Zimbabwe. *African Journal of Aquatic Science* 32: 13–16.

Ohlweiler F, Kawano T. 2001. Effects of the desiccation on *Biomphalaria tenagophila* (Orbigny, 1835) (Mollusca) infected by *Schistosoma mansoni* Sambon, 1907. *Memórias do Instituto Oswaldo Cruz* 96: 737–739.

Olivier L. 1956. The location of the schistosome vectors, *Australorbis glabratus* and *Tropicorbis centimetralis*, on and in the soil on dry natural habitats. *The Journal of Parasitology* 42: 81–85.

Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE (eds). 2007. *Climate Change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the fourth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.

Secor SM, Lignot JH. 2010. Morphological plasticity of vertebrate aestivation. In: Navas AN, Carvalho JE (eds), *Aestivation*. Berlin: Springer. pp 183–208.

Senghor B, Diaw OT, Doucoure S, Seye M., Talla I, Diallo A, Sokhna C. 2015. Study of the snail intermediate hosts of urogenital schistosomiasis in Niakhar, region of Fatick, West central Senegal. *Parasites and Vectors* 8: 410 (8 pp).

Simoonga C, Utzinger J, Brooker S, Vounatsou P, Appleton C, Stensgaard AS et al. 2009. Remote sensing, geographical information system and spatial analysis for schistosomiasis epidemiology and ecology in Africa. *Parasitology* 136: 1683–1693.

Smithers S. 1956. On the ecology of schistosome vectors in the Gambia, with evidence of their role in transmission. *Transactions of the Royal Society of Tropical Medicine and Hygiene* 50: 354–365.

Souza CPD. 1995. Molluscicide control of snail vectors of schistosomiasis. *Memórias do Instituto Oswaldo Cruz* 90: 165–168.

Steinmann P, Keiser J, Bos R, Tanner M, Utzinger J. 2006. Schistosomiasis and water resources development: systematic review, meta-analysis, and estimates of people at risk. *The Lancet, Infectious Diseases* 6: 411–425.

Stensgaard AS, Utzinger J, Vounatsou P, Hürlimann E, Schur N,

Saarnak CF et al. 2013. Large-scale determinants of intestinal schistosomiasis and intermediate host snail distribution across Africa: does climate matter? *Acta Tropica* 128: 378–390.

Storey KB. 2002. Life in the slow lane: molecular mechanisms of aestivation. *Comparative Biochemistry and Physiology, Part A* 133: 733–754.

Storey KB, Storey JM. 2012. Aestivation: signaling and hypometabolism. *The Journal of Experimental Biology* 215: 1425–1433.

Studer A, Thieltges D, Poulin R. 2010. Parasites and global warming: net effects of temperature on an intertidal host-parasite system. *Marine Ecology Progress Series* 415: 11–22.

Sturrock R. 1966. The influence of temperature on the biology of *Biomphalaria pfeifferi* (Krauss), an intermediate host of *Schistosoma mansoni*. *Annals of Tropical Medicine and Parasitology* 60: 100–105.

Thomson AJ, Chimbari MJ, Chandiwana SK, Ndlela B, Chitsiko RJ. 1996. Control of schistosomiasis: a practical guide for irrigation development. Overseas Development Assistance Technical Report OD/TN 78. HR Wallingford.

Utzinger J, Raso G, Brooker S, De Savigny D, Tanner M, Ørnbjerg N et al. 2009. Schistosomiasis and neglected tropical diseases: towards integrated and sustainable control and a word of caution. *Parasitology* 136: 1859–1874.

Vera C, Bremond P, Labbo R, Mouchet F, Sellin E, Boulanger D et al. 1995. Seasonal fluctuations in population densites [*sic*] of *Bulinus senegalensis* and *B. truncatus* (Planorbidae) in temporary pools in a focus of *Schistosoma haematobium* in Niger: implications for control. *Journal of Molluscan Studies* 61: 79–88.

Vörösmarty CJ, Green P, Salisbury J, Lammers RB. 2000. Global water resources: vulnerability from climate change and population growth. *Science* 289: 284–288.

Webbe G. 1962. The transmission of *Schistosoma haematobium* in an area of Lake Province, Tanganyika. *Bulletin of the World Health Organization* 27: 59–85.

White MM, Fried B, Sherma J. 2006. Determination of the effects of estivation and starvation on neutral lipids and phospholipids in *Biomphalaria glabrata* (NMRI Strain) and *Helisoma trivolvis* (Colorado Strain) snails by quantitative high performance thin layer chromatography-densitometry. *Journal of Liquid Chromatography and Related Technologies* 29: 2167–2180.

White MM, Fried B, Sherma J. 2007. Effects of aestivation and starvation on the neutral lipid and phospholipid content of *Biomphalaria glabrata* infected with *Schistosoma mansoni*. *Journal of Parasitology* 93: 1–3.

Whitwam RE, Storey KB. 1991. Regulation of phosphofructokinase during estivation and anoxia in the land snail, *Otala lactea*. *Physiological Zoology* 64: 595–610.

WHO. 2006. *Preventive chemotherapy in human helminthiasis. Coordinated use of anthelminthic drugs in control interventions: a manual for health professionals and programme managers*. Geneva: World Health Organization.

Withers PC, Cooper CE. 2010. Metabolic depression: a historical perspective. In: Navas CA, Carvalho JE (eds), *Aestivation: molecular and physiological aspects.* Progress in Molecular and Subcellular Biology 49. Springer. pp 1–23.

Woolhouse M, Taylor P. 1990. Survival rates of *Bulinus globosus* during aestivation. *Annals of Tropical Medicine and Parasitology* 84: 293–294.

Yuan Y, Xu XJ, Dong HF, Jiang MS, Zhu HG. 2005. Transmission control of *Schistosomiasis japonica*: implementation and evaluation of different snail control interventions. *Acta Tropica* 96: 191–197.

Zhou XN, Yang GJ, Yang K, Wang XH, Hong QB, Sun LP, Utzinger J. 2008. Potential impact of climate change on schistosomiasis transmission in China. *American Journal of Tropical Medicine and Hygiene* 78: 188–194.