STUDIES ON THE SNAIL VECTORS OF BILHARZIASIS MANSONI IN NORTH-EASTERN BRAZIL

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SYNOPSIS

The authors describe the bilharziasis endemic areas in northeastern Brazil, giving the rainfall and general characteristics of the climate. The life-cycles of the two snail vectors-Australorbis glabratus and Tropicorbis centimetralis-in Pernambuco are described. Considerable attention is given to the effects on the snails of the annual drought, which causes many of the habitats to dry up and seriously affects the snail life-cycles and survival patterns. The snails are able to populate habitats that are dry for 5-7 months every year. They survive during the dry season in the protection of debris, vegetation, etc. A. glabratus is more susceptible to infection with Schistosoma mansoni than is T. centimetralis, but the latter is an effective vector, nevertheless, probably because it often occurs in very large numbers. A. glabratus with mature infections die or lose their infections when removed from the water for 20-30 days. Immature parasites are not killed under the same conditions. Infection with S. mansoni injures the snails and may kill them. It also reduces the reproductive capacity of the vectors, but it does not permanently castrate them. The epidemiological significance of these findings and their meaning in terms of snail control are discussed.

Endemic bilharziasis mansoni in north-eastern Brazil is transmitted by Australorbis glabratus and Tropicorbis centimetralis.¹ During the last five years these vectors have been studied intensively in Pernambuco by the staff of the Centro de Pesquisas Aggeu Magalhães (formerly the Instituto

¹ Throughout this paper we shall use the names given above since we believe, with Hubendick (1955), that, until more is known about the phylogeny and anatomy of the various planorbid genera, and agreement is reached as to the taxonomic status of the vectors, confusion will be avoided by the use of names which have until recently been given wide acceptance.

Aggeu Magalhães),² since effective and efficient snail control, and therefore control of the spread of the disease, can be accomplished only when the habits and characteristics of the snails are well understood. Since the studies were made in the vicinity of Recife, the results apply especially to that region. Nevertheless, it is reasonable to believe that in such nearby states as Alagoas, Sergipe and Paraíba similar circumstances prevail and the results are probably applicable in these states too.

Physical Characteristics and Climate of the Region

The State of Pernambuco has three rather distinct regions from the point of view of topography and climate: the coastal zone (zona da mata), a transitional zone (agreste), and the interior zone (sertão).

The coastal zone is low, has heavy tropical vegetation, and is hot and humid. Elevations range from sea level to 300 feet (about 100 m) and the temperature averages about 27°C all the year round, with only small differences between day and night temperatures. The area is cut by numerous small streams and there are numerous temporary pools of standing water in borrow-pits, drainage ditches, filled areas, etc.

The transitional zone, which lies just inland from the coastal zone, is a region of low hills, somewhat less rainfall, lighter vegetation, and better drainage. This region has numerous streams, most of them small, which have great fluctuations in water volume depending on the rainfall. There are some pools, seepage areas, and drainage or irrigation ditches which contain water during part of the year.

The zone of the interior is very extensive. It is essentially a rough, somewhat elevated area which is stony and comparatively barren and is subject to prolonged and intermittent droughts. Except for periods immediately following rains the surface water is limited almost entirely to streams, which vary greatly in volume from time to time.

There is a marked seasonal cycle of rainfall, with a rainy season extending from March or April to July or August. The average monthly rainfall (over 14 years) in the coastal region, as given by Olivier & Barbosa (1955a), is as follows: March: 156 mm; April: 253 mm; May: 374 mm; June: 293 mm; July: 215 mm; and August: 161 mm. During the remainder of the year the average monthly rainfall ranges from 26 mm to 66 mm. As one proceeds inland, the rainfall decreases sharply so that the zone of the interior is relatively dry throughout the year. During the rainy season in the coastal zone and to some extent in the transitional zone, the streams

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are flooded, and there is standing water in all low places. During the dry season the numerous streams become much smaller and may dry up completely, while most of the pools of standing water disappear.

Distribution of the Snails

The two species of vector snails have quite characteristic patterns of distribution in north-eastern Brazil. A. glabratus is confined almost exclusively to the coastal zone, where it is found in a wide variety of habitats, including temporary pools, seepage areas, and some of the small streams. T. centimetralis occurs in all three zones. It appears to prefer flowing water although it is found also in borrow-pits, temporary pools, and ditches. The two species are adapted to somewhat different ecological situations and they are almost never found in the same body of water, even though they occur in the same general area.

Life-cycle of the Snails and their Response to Drying

Aside from some earlier fragmentary information, the natural history of the snail vectors of bilharziasis in north-eastern Brazil has been worked out in the last five years.

In permanent bodies of water both A. glabratus and T. centimetralis reproduce throughout the year, but fluctuations in apparent reproductive activity and population density occur without known cause (Olivier & Barbosa, 1955a, 1955b). Their life-span under field conditions is not known exactly, but it is obviously short and is probably not longer than 15, or at the most 18, months.

The snails are prolific and in suitable habitats they grow very rapidly, so that populations depleted for any reason may quickly be replaced. The recovery of A. glabratus populations following depletion by drought has been described by Olivier & Barbosa (1955a). An indication of the rate of growth that may occur in the field may be had from their observation that in 21 days the average diameter of A. glabratus in a small temporary pool in Recife increased from 10.0 mm to 15.4 mm. This represents the addition of one complete whorl to the shell. There was some indication from these studies that the snails may attain a saturation density within 50 days if there is a small nucleus of mature snails in the habitat.

Many of the habitats for the vector snails in north-eastern Brazil are subject to great seasonal changes in water level and some of them are without water for five to seven months out of every year. Obviously the snails living in such habitats must be adapted to long survival without immersion.

It has been known for some time that pulmonate snails can live for a long time out of water. In temperate climates pulmonates may survive in pools that dry up annually (Kolpakov, 1929; Mehl, 1932; Olsen, 1944; Patzer, 1927; Precht, 1939; Shadin, 1926). Similarly, some of the pulmonate schistosome vectors which live in the tropics are also able to survive out of water. Almost as soon as the African schistosome vectors were recognized as such, consideration was given to the reaction of these snails to drying (Leiper, 1918), and as early as 1924 Blacklock & Thompson and Khalil showed experimentally that some of the vectors could live for at least a few days out of water. In 1932 Humphreys noticed that in the Blue Nile Province of the Sudan, Bulinus truncatus lived in an isolated artificial storage pool which was dry for about four months each year. Archibald, in 1933, reported that living Bulinus truncatus were collected from subsoil that had been dry for three to four months.

Considerable interest in the responses of the vectors to drying was aroused by the observations of Barlow (1933, 1935), who reported that both of the Egyptian vectors regularly survived the winter closure of the canals there and that living snails could be collected from the surface of the dried mud during this period. He also noted that the snails made no effort to avoid the consequences of drying by entering the mud and that they could survive even in exposed locations. Furthermore, Barlow observed the vectors in the laboratory and found that some Bulinus truncatus and Biomphalaria boissyi survived out of water for as long as four months; indeed, one specimen of Biomphalaria boissyi lived out of water for 180 days. Later, Barlow & Abdel Azim (1945) kept both species in the laboratory on soil that was moist at first and dried gradually. Under these conditions some Biomphalaria boissyi lived 10 months and some Bulinus truncatus lived 12 months.

More recently, Annecke & Peacock (1951) observed that Bulinus tropicus and Bulinus africanus aestivated in grass tufts and among the roots of grass in habitats that remain without water for many months of the year. They reported raising new colonies from snails collected from a habitat that had been dry for 18 months. They did not observe planorbids (Planorbinae) surviving under these conditions, but they believed that the species could probably do so.

The Schistosoma vectors of the Western Hemisphere are also known to be able to survive out of water. Coutinho, Gouvea & Lucena (1940) found living A. glabratus on the dry soil of temporary pools in Pernambuco, Brazil, and kept them out of water in the laboratory for 60 days. Brumpt (1941) kept A. glabratus from Venezuela out of water for 28 and for 50 days. Scott (1942) collected A. glabratus from a dry Venezuelan pond and kept them in the laboratory at 23°C for three months, at the end of which time one revived when put in water. Luttermoser (1946) remarked that Venezuelan A. glabratus could live out of water for two to three months.

Recently, the survival of the Brazilian snail vectors out of water has received considerable attention. Barbosa & Dobbin (1952) observed that A. glabratus could survive out of water in the field for seven months. Olivier (1956a, 1956b) and Olivier & Barbosa (1954, 1955a, 1955b, 1956) have carried out extensive studies on the survival of the vector snails both in the field and in the laboratory. They found that in north-eastern Brazil both A. glabratus and T. centimetralis populate pools which are without water for five to seven months every year. As the pools dry, the snails are left stranded at the soil surface, where they may lie fully exposed, in depressions, in vegetable debris, or among the stems and surface roots of persistent vegetation. The exposed snails usually die or are consumed by other animals soon after the habitat dries, but the more protected snails may persist until the water returns. However, usually only a very small proportion of the previous population survives. The survivors may be of any size. With the return of the water, the snails grow, reproduce, and rapidly repopulate the pools. In 50 to 60 days after flooding of the pools the populations may reach maximum density. During the dry period the snails retract into their shells. As they retract some of the snails secrete fine membranes across the shell opening which may help them to resist water loss.

Snails from habitats that dry up annually were brought into the laboratory, where it was found that they could live out of water for many months, either in moist clay jars or on dry soil in wooden boxes. In controlled experiments in which the snails were kept at known relative humidities ranging from 0-5% to 96%, it was found that weight loss and survival of the snails were dependent on the relative humidity. Loss of weight with time always increased as the humidity was decreased and death was much more rapid at low relative humidities. All 10 snails in one group survived for 30 days at 0-5% relative humidity. Some snails lived until their weight was as low as 47-50% of the original weight, but they usually died when their weight approached 60% of the original.

It is important to note that although both species of vectors from temporary bodies of water in Pernambuco State are able to survive out of water for long periods, the same species living in other localities may not be as tolerant of this condition. Olivier (1956b) showed that snails from permanent bodies of water were less tolerant of drying than those from temporary pools and that A. glabratus from permanent bodies of water in Bahia State would survive for only a short time if removed from the water.

Long survival out of water under natural conditions does not necessarily imply that the snails are subject to severe desiccation or to high temperatures. On the contrary, the snails that survive the long dry season in Pernambuco are probably those that are protected from both excessive drying and high tropical temperatures. The eggs of the snails do not survive drying for any significant period of time.

No clear evidence has been presented to support the view that the snails penetrate deep into the soil to escape unfavourable conditions, although some workers have believed that this could occur.

Barbosa & Dobbin (1952) suggested that A. glabratus possibly survived the dry season in the mud. There is no question that the Brazilian schistosome vectors go down to the bottom of the pools where they are commonly seen browsing in the soft mud. Under laboratory conditions this habit is observed also. Veloso (1953) observed in Minas Gerais that A. glabratus was in the habit of laying eggs on the roots of aquatic plants (Tradescantia virginiana) in the mud. A similar observation was made in Recife by Coelho (unpublished data).

The finding of snails buried in mud does not mean that the snails dig their way down into it, since they may be buried accidentally.

The observations of Olivier & Barbosa (1955a, 1955b) indicate that the snails do not necessarily penetrate the soil to avoid the rigours of the dry season. These authors found living snails at the soil surface in vegetation and among plant debris throughout the dry season and they concluded that such locations provide enough protection against the dry season.

In laboratory experiments Olivier & Barbosa (1956) found that A. glabratus did not enter the soil when the water level fell and that if these snails were buried in water-saturated mud they soon died. This observation was confirmed by Perlowagora-Szumlewicz & Dias (1955).

Magalhães Neto (1953) conducted experiments on the physiology of desiccation and demonstrated that in A. glabratus the oxygen consumption dropped to a very low level when the snails were submitted simultaneously to desiccation and to starvation. The glycogen content of the digestive gland, stomach, and ovo-testis of the snails dropped to less than 50% after 15 days' desiccation and, at the end of the experiment (75 days), it was reduced to 10-15%. In the foot of the snails the glycogen loss was much less pronounced (Magalhães & Almeida, 1956).

Von Brand, McMahon & Nolan (1957) found that with decreasing humidity there was a progressively rapid decline in survival time, weight, and oxygen consumption. The decrease in oxygen consumption was largely due to desiccation, but at high humidities starvation was a factor.

The effects of temperature upon A. glabratus were also studied. Twelve hours' freezing was lethal for all snails out of a group of 100, but they withstood 7°C for several days. The optimum temperature seems to lie between 25°C and 28°C. Between 32°C and 42°C the snails moved slowly. The thermal death-point of A. glabratus was determined as 42°C for two hours. There is some evidence that A. glabratus is better able to resist the effects of high temperature when kept out of water. For example, 45°C for one hour killed 93 of 100 snails which were kept in water but only 5 of 100 snails which had been out of water for 30 days. Moreover, 40 (68%) out

of 59 snails kept out of water in the laboratory for 112 days remained alive when submitted to 45°C for one hour.

Vector Capabilities and Transmission

A number of studies has been made in north-eastern Brazil which give information as to the ability of the two vectors there to harbour and transmit bilharziasis mansoni. Most of the observations have been made on A. glabratus, largely because it is the more efficient vector and so more readily provides material for study.

Susceptibility to infection

It has been shown that strains of Schistosoma mansoni from different endemic areas do not infect geographic strains of the vectors with equal success. Thus, for instance, S. mansoni from Puerto Rico will readily infect A. glabratus from Puerto Rico, but may infect A. glabratus from other endemic areas less readily or not at all (Files & Cram, 1949). Files (1951) suggested that incompatibilities between the vector and the parasite may be due to variations both in the vector and in the parasite. Newton (1953) showed that susceptibility to infection with S. mansoni in A. glabratus is a heritable character and that several genetic factors are probably involved. MacQuay (1953) was unable to increase the low susceptibility of T. havanensis to S. mansoni by selection of susceptible snails.

Under experimental conditions A. glabratus is much more susceptible to infection with S. mansoni than is T. centimetralis. In one experiment Barbosa & Coelho (1954) found that 57.4% of A. glabratus could be infected while only 6.3% of T. centimetralis took the infection. Barbosa & Coelho (1956) produced evidence that A. glabratus is also a much more efficient vector in the field. Out of 7579 A. glabratus examined over a period of one year from two localities, 844 (11.1%) were infected with S. mansoni, while only 45 (0.02%) of 185 039 T. centimetralis from 17 other localities were infected during the same period. The snails were all collected in localities where approximately 50% of the people were known to be infected.

Experiments conducted by Barbosa & Coelho (1956) have shown that the miracidia of S. mansoni penetrate successfully into both vectors. The miracidia enter through any of the exposed parts of the snail but there is a preference for the base of the tentacles, the foot, and the mantle collar. Histological sections made during the first few days after penetration of the miracidia revealed that the host reactions were substantially different in the two species. After 24 hours the sporocysts usually looked the same in both hosts, but some sporocysts in T. centimetralis had a slight cellular reaction about them while the sporocysts in A. glabratus excited no reaction.

When the sections from exposed *T. centimetralis* were examined 2, 3, 4, 5, and 6 days after infection, most of the sporocysts were degenerate and were surrounded by an extensive cellular reaction. Reactions of that type were seen very seldom in *A. glabratus*. The cellular reactions were very similar to those seen by Newton (1952) and Barbosa & Coelho (1955b) in *A. glabratus*, and by Brooks (1953) in *T. havanensis*.

Population density and transmission

Fluctuations in snail population density can be of major importance in the transmission of bilharziasis mansoni. It appears likely that *T. centimetralis* may not be effective in transmitting infection unless it is in high density, since, under apparently favourable conditions for infection, only a very small proportion of the snails are infected. On the other hand, relatively few *A. glabratus* are probably capable of transmitting the infection effectively.

Before one can adequately study transmission potential in the field one needs to be able to measure snail population densities with some reliability. Unfortunately, there is no reliable and yet practical method for doing this. However, *relative* population densities can be determined with some accuracy (Olivier & Schneiderman, 1956), and such data can be very useful in the study of transmission and population dynamics.

Effect of infections on the snails

It has been shown in work with S. mansoni infections in A. glabratus that, in the laboratory, infected snails are often killed as a result of the infection. The snails usually die within five months after infection, but mortality is greatest in A. glabratus and T. centimetralis during the development of the secondary sporocysts in the digestive gland and in the first days after shedding of the cercariae begins (Barbosa & Coelho, 1954). It has also been noted that infected snails appear to be much more likely to react unfavourably to adverse environmental conditions and to molluscicides (Paulini & Pellegrino, 1957).

Although controlled studies have not been made in the field, it is reasonable to surmise that infection also causes death of snails under natural conditions.

It also has been noted that snails infected with *S. mansoni* may lose their infections when held under routine laboratory culture conditions (Barbosa, Coelho & Dobbin, 1954; Gordon, Davey & Peaston, 1934; Lagrange & Scheecqmans, 1950; Stirewalt, 1954). It is not known whether loss of the infection is due to resistance acquired by the host or exhaustion of the reproductive capabilities of the parasite. Snails which lose their infection in this way may be reinfected by exposing them to miracidia (Barbosa & Coelho, 1955b).

Barbosa & Coelho (1953, 1955a) and Olivier, Barbosa & Coelho (1954) have demonstrated that, when A. glabratus with fully developed infections are removed from the water and held in a moist environment, a large proportion of the snails die within 20-30 days and all the surviving snails are free of infection. Barbosa & Coelho (1955a) presented evidence that this loss of infection occurs only when the infection is mature. When 402 snails harbouring mature infections were kept out of water for 21-60 days, 122 survived and all were free of infection. On the other hand, if the snails are taken from the water when the infection is incompletely developed quite a different phenomenon occurs. When infected snails were removed from the water within the first 25 days after exposure, they retained their infections even though some of them were kept out of the water for 90 days. On replacement in the water the snails became active again and developed normal infections. From this experiment one may conclude that a partially developed infection is arrested while the snail is out of the water and that development is resumed when the snail is returned to the water. The time interval between the penetration of the miracidia and the removal of the snails from the water added to the time interval between the replacement of the snails in the water and the shedding of the first cercariae averaged about 31 days. This corresponds to the average length of time usually required for development of the infection when the snail is kept in water continuously at the same temperature.

Desiccated snails have also been found to harbour immature infections under field conditions. This finding suggests the probability that, in the field, immature infections are carried over in the snails from one wet season to the next.

Effect of infection on snail reproduction

Several authors have observed sporocysts of *S. mansoni* in the ovotestis of *A. glabratus* and Brumpt (1941) observed that infected snails laid fewer eggs. On the other hand, Marcuzzi (1950) was unable to find any important changes in the reproductive system of infected snails. Coelho (1954) showed that although complete castration did not occur the infection was responsible for a significant reduction in the number of egg-masses and in the number of eggs produced by infected snails. When infected snails lost their infections, egg-laying was always resumed. Examination of heavily infected snails always revealed the sexual cells to be reduced in number, but functionally active. Most of the eggs from infected snails failed to develop and the mortality of the "new-born" snails was high during the first ten days. Thirty days after hatching, however, snails from both infected and uninfected groups were of normal size, and so it appears that, if snails from infected parents survive the first critical days, their development is no longer affected.

Factors affecting cercarial production and shedding

The shedding of cercariae of S. mansoni from infected snails has been studied by many authors, including Faust & Hoffman (1934), Giovannola (1936), Kuntz (1947), Schreiber & Schubert (1949), and Stirewalt (1954). In all these papers light intensity and temperature were shown to be important factors in regulating the time and number of cercariae shed. Barbosa, Coelho & Dobbin (1954) made an extensive study of the shedding of the cercariae of S. mansoni from A. glabratus in Pernambuco. They found that in the laboratory the cercariae emerged in a marked daily cycle, most of them being liberated between 11 a.m. and 5 p.m. Only small numbers were liberated at other times of the day. It is interesting in this connexion that Luttermoser (1955) was able to reverse the pattern of cercarial emergence by reversing the light cycle. He was also able to cause emergence of cercariae during the early morning hours by suitable regulation of the light cycle.

According to Barbosa, Coelho & Dobbin (1954), infected A. glabratus liberated an average of 4598 cercariae daily during the period the infection lasted. Some snails liberated a total of over half a million cercariae if the infection lasted more than four months. One snail shed 17 600 cercariae in one day. When readings were made every day, the shedding of cercariae was greatest in the fifth week and there was a marked decrease in the number of cercariae shed after the fifth week.

Shedding was inhibited at temperatures below 13°C and above 41°C. The most favourable temperatures for shedding are in the range of 19 to 37°C.

Coelho & Barbosa (1956) found that, in the laboratory, the duration of S. mansoni infections in T. centimetralis was usually very short. Most of the snails died within the first days after shedding began and the majority died within 10 days, although one infected snail lived 91 days. The snails liberated an average of 415 cercariae per day. "Self-cure" seemed to be much more frequent with this species than with A. glabratus.

Comments and Conclusions

A. glabratus and T. centimetralis, the two vectors of bilharziasis mansoni in north-eastern Brazil, are able to maintain themselves in a wide variety of habitats. One of the most important limiting factors in their environment is the seasonal rainfall cycle, which produces an annual drought with the disappearance of water from many of the habitats. A large proportion of the snails die during this dry season as a direct or indirect consequence of lack of water. Some snails survive the dry season in persistent bodies of water. Others are able to survive in dried habitats provided they are protected by debris, vegetation, or a shallow covering of soil, where they can

avoid high temperatures and excessive drying and where they will not be found readily by scavenging animals. The considerable reproductive capacity of the snails makes it possible for them rapidly to repopulate the habitats when the water returns.

When the water in the habitats recedes, the snails are unable to avoid drying by seeking shelter or by burrowing actively into the mud. However, they may at times be covered by a shallow layer of soil, since they browse in the very soft mud and may be covered accidentally as the habitat dries up. It is not known how important this factor may be in relation to the ability of the snails to survive the dry season.

Since survival of snails out of water is obviously dependent upon the humidity of the micro-environment and the ambient temperature, detailed observations should be made on these points when field studies are conducted. The exact locations of the snails should also be recorded, since this may determine whether they survive. For instance, snails exposed for even a few hours a day to the sun will probably be killed in a short time. Other snails, only a few inches away, may survive for many months when protected by vegetation or debris. Such shelter apparently affords a higher relative humidity, lower temperature, and less variable conditions, all of which probably favour the survival of the snails. The location of the snails with reference to the soil surface should also be noted carefully. Detailed information concerning environmental factors must be obtained before adequate evaluation can be made concerning the ability of snails to resist drying. Similar data are needed in comparing the behaviour of the snails in different areas.

Control measures must take into account the possibility that snails outside the water may still be alive. Temporary bodies of water may serve as habitats, although transmission in these habitats may be interrupted frequently. The snails in such temporary bodies of water may be washed into and reinfest permanent bodies of water previously treated with molluscicides.

The clearance of streams or ditches before treatment with molluscicides can result in the transfer of snails to the banks along with mud and debris. In such a location the snails are out of reach of chemicals applied to the water. Those that are buried in the mud and debris may even be out of reach of chemicals applied to the banks. On the other hand, clearance of vegetation from the banks of irrigation ditches, after they are drained and dry, may be beneficial, since it may expose the snails to the sun and to predators.

Closure of irrigation ditches can result in the destruction of very many snails, even though it will probably not kill all of them.

Where the snails have the capacity to survive out of water, water-level fluctuations are unfavourable from the point of view of snail control because snails may be stranded when the water level falls. Under such conditions,

it is advantageous to apply molluscicides during periods of high water levels.

In the habitats that never dry, fluctuations due to unknown causes were observed in the size and density of the snail population. Perhaps disease is a cause of some population crises. Also, heavy rains during the rainy season disturb the population by carrying the snails downstream. In some streams, after heavy rain, it is difficult to find snails even after a careful search.

Another interesting aspect of snail biology is the question of differences among geographic races. Snails of the same species found in different areas may behave in different ways owing to genetic as well as to seasonal and climatic factors.

The epidemiology of bilharziasis is correlated with a number of factors and among these the snail-parasite relationship is of considerable importance. For example, it has been demonstrated that under the climatic conditions in north-eastern Brazil, mature infections in the snail are lost during aestivation in the dry season, when the snails are subject to varying degrees of desiccation. Immature infections may persist, however, and thus carry over the infection into the next rainy season.

RÉSUMÉ

La biologie des mollusques Australorbis glabratus et Tropicorbis centimetralis qui entretiennent l'endémie bilharzienne dans le nord-est du Brésil a été étudiée au cours des cinq dernières années, dans la région de Recife plus particulièrement. Dans les collections d'eau permanentes, ces deux mollusques se reproduisent toute l'année. Leur durée de vie est de 15-18 mois. Ils sont prolifiques et réparent rapidement les brèches que certaines conditions défavorables, telle que la sécheresse, peuvent creuser dans leurs collectivités. A partir d'un petit noyau de mollusques à maturité sexuelle, une population peut se reconstituer en 50 jours. De nombreux habitats de ces mollusques sont exposés à des fluctuations saisonnières du niveau des eaux, et parfois sont à sec pendant 5-7 mois de l'année. Certains mollusques paraissent s'adapter à ces conditions puisqu'ils survivent à la sécheresse, protégés de la dessiccation totale par des débris ou des végétaux. Lors d'études sur la résistance des mollusques à la sécheresse, il faut tenir compte de l'humidité et de la température du micro-milieu. La localisation exacte des mollusques doit être précisée, car il suffit de quelques herbes ou de minimes détritus pour assurer au mollusque la protection qui lui permettra de survivre plusieurs mois. Les mesures de lutte doivent donc tenir compte du fait que les mollusques émergés peuvent subsister. Ceux qui persistent dans les collections d'eau temporairement asséchées peuvent, lors des crues, être entraînés dans des eaux permanentes qui ont été traitées par des molluscicides et les réinfester. Lors du désherbage, des mollusques peuvent être déposés sur les bords des canaux et ruisseaux et échapper ainsi aux substances ajoutées à l'eau pour les détruire; certains d'entre eux, au contraire, exposés au soleil, y succombent rapidement. Dans les habitats qui ne sont jamais à sec, des fluctuations de la population des mollusques ont été constatées, dont on ignore les causes. Les grandes pluies bouleversent l'équilibre des populations en entraînant les mollusques vers l'aval, de façon qu'il est parfois difficile de trouver des mollusques dans certains cours d'eau. Il existe des races géographiques de mollusques. Des exemplaires de la même

espèce, récoltés dans des régions différentes, peuvent présenter des variations de comportement dus à des facteurs génétiques, ou sous la dépendance des saisons et du climat.

L'épidémiologie de la bilharziose est déterminée par de nombreux facteurs, parmi lesquels la relation parasite-mollusque est d'importance primordiale. C'est ainsi, par exemple, que, dans les conditions climatiques régnant dans le nord-est du Brésil, le parasite arrivé à maturité dans le corps du mollusque au moment de la sécheresse, disparaît chez les mollusques soumis à des degrés variables de dessiccation au cours de la saison sèche. Au contraire, le parasite immature persiste dans le corps de son hôte et peut poursuivre son développement au retour de l'humidité. L'infection peut ainsi subsister d'une saison des pluies à la suivante, à la faveur des parasites immatures en vie latente dans le corps des mollusques survivant à la sécheresse.

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