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FACTORS CONDITIONING THE HABITAT OF BILHARZIASIS INTERMEDIATE HOSTS OF THE FAMILY PLANORBIDAE

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SYNOPSIS

In this article, the author examines certain physical, chemical and biological characteristics of water-bodies which make them suitable or unsuitable as habitats for planorbid snails acting as vectors of bilharziasis. The principal conditioning factors appear to be: amount of food available; extent of the growth of aquatic weeds; oxygen content of the water; amount of sunlight able to penetrate the water; strength of the current; nature of the substratum; ionic composition of the water; and presence or absence of parasites and predators. Several of these factors are interdependent. Although there are differences between the various species in their habitat requirements, their ranges of tolerance were found to overlap greatly. The optimum conditions are similar for all species, but extremes are tolerated better by some species than by others. Theoretically, extremes of certain factors should be capable of eliminating snails from a body of water; in practice such extremes rarely occur, and the absence of vectors must be attributed to the combined effect of several factors. Although certain parasites and predators exterminate vectors in the laboratory, the author considers it unlikely that they would do so in nature, as under laboratory conditions the biological balance is disturbed to the disadvantage of the snail. The data available are still too scanty for an exact assessment to be made of the importance of individual environmental factors in controlling the size of vector populations; but this review of present knowledge indicates the lines along which further investigation can be most profitably pursued.

In the survey presented below, an attempt is made to correlate the preference of bilharziasis vectors for particular types of habitat with certain factors in the environment and to discover the ranges of tolerance under which the snails can establish themselves. Only intermediate hosts belonging to the family Planorbidae are considered, and not those that harbour *S. japonicum*. All data are taken from the literature, with special reference to habitats in the Sudan and Egypt, with which the author is most familiar. It will be evident from the report that, although much is already known about the biology of the pulmonates and aquatic snails in general, there is still a great need for detailed investigations into the reactions of the several species of bilharziasis intermediate hosts to various environmental factors and to fluctuations in these factors.

Physical Factors

Altitude

Bilharziasis vectors occur over a wide range of altitude, from sea level to well up in the mountains. I have collected them from Lakes Maryut and Idku near Alexandria, Egypt (approximately sea level), and at about 5000 feet in Jebel Marra in the Western Sudan. Ayad (1956) reports finding *Biomphalaria* spp. and *Bulinus (Bulinus)* spp. at more than 6600 feet in the highlands of Ethiopia, Eritrea, and Yemen. It appears that altitude is not in itself a limiting factor, but that the collective action of other factors at the particular altitude influences the distribution of the vectors. For example, in various parts of Africa, water-bodies at the same high altitude will differ noticeably in water temperature and, consequently, in oxygen tension. Van Someren (1946) believes that at altitudes above 10 000 feet the reduced oxygen tension may be a limiting factor, for *Lymnaea* at least, but in a typical habitat this would tend to be offset by daylight photosynthesis, producing supersaturation.

Temperature

It would seem that temperature has little effect on the distribution of bilharziasis vectors, but does influence their rate of reproduction. To maintain their numbers these snails require a warm season of a few months. The warm season is not only more favourable for reproduction than the cold season, but is also indirectly beneficial to the snails, because during that season there is abundance of microflora (food supply) and of aquatic weeds. The latter provide dissolved oxygen and a suitable surface on which the snails can crawl and deposit their egg masses. The temperature of most water-bodies harbouring these snails is well within their range of tolerance, in spite of marked seasonal and diurnal variations. In general, it appears that the vectors are more tolerant of low temperatures than of high ones.

In a representative Egyptian canal near Qaliub, Hoffman & Zakhary (1954) were able to show that *Bulinus* and *Biomphalaria* were tolerant of a seasonal variation of 18°C in the monthly average. The average water temperature was highest in August (29.6°C) and lowest in January (11.4°C). Daily fluctuations in water temperature were usually somewhat larger in summer than in winter, but were much smaller than the corresponding variations in air temperatures.

In Kenya, near Kabete, van Someren (1946) reported a diurnal variation of 17°C (18.5-35.5°C) in November in a small, clean-water ditch harbouring *Biomphalaria pfeifferi* and the liver-fluke vector, *Lymnaea caillaudi*. In the highland region, *Biomphalaria* and *Lymnaea caillaudi* are capable of withstanding a diurnal variation of as much as 20°C.

In Iraq, Watson (1950) remarked that *Bulinus truncatus* was extremely tolerant of changes in temperature, being able to survive and breed in pools whose temperature rises to almost blood-heat in summer and falls to only a few degrees above freezing point in winter, when thin ice occasionally forms on them. Zakaria (1955), also studying *B. truncatus* in Iraq, reported finding specimens in water with temperatures as high as 33°C and as low as 8°C.

Ayad (1956) stated that in the Eritrean highlands, and near San'a in Yemen, where he collected *Bulinus (Bulinus)* spp. and *Biomphalaria* spp., the water temperature fell well below the freezing point in January.

TABLE I. WATER-TEMPERATURE READINGS IN THE SUDAN (°C)

	Month	8 a.m.	12.30 p.m.	5.30 p.m.
Shambat, Ministry of Agriculture Irrigation Canal [1, 2]	May	25	31	28
	July	20.5	25	22.5
	November	23.5	27	24
Gezira Irrigation Canal, 5 miles south of Wad Medani [1, 2, 3]	April	23.5	28.5	25
	January		24.5	
Sennar Reservoir [2]	April	25	29	26.5
	January	22	25	23.5
Swampy bank of White Nile at Kosti [1, 2, 3, 4]	April	24.5	28	26
	January	22	24.5	23
White Nile at Kosti (open water)	June		28.6	
	October		29.2	
	December		23.4	
White Nile at Malakal [1, 4, 5]	June		27.5	
	December		26	
Bahr-el-Jebel at Shambé [1]	June		28.8	
	December		27	
Bahr-el-Jebel at Bor [4]	June		28.5	
	December		26.5	

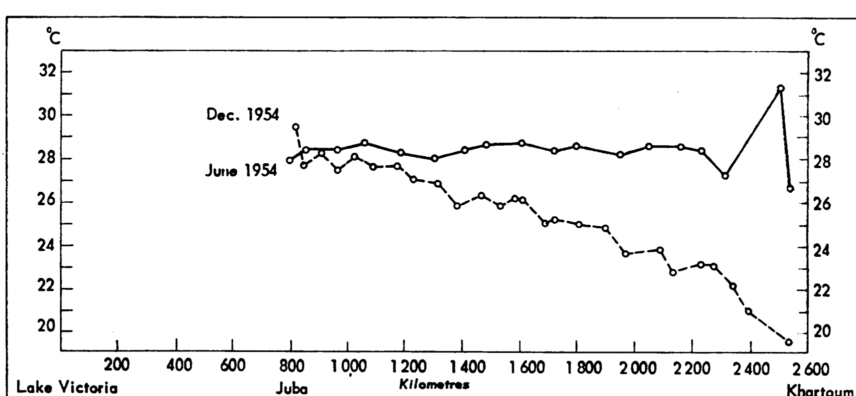
[1] *Bulinus forskalii*
[2] *Bulinus (Bulinus)* sp.
[3] *Biomphalaria rüpellii*
[4] *Bulinus (Physopsis) ugandae*
[5] *Biomphalaria sudanica*

In Sierra Leone, according to Gordon, Davey & Peaston (1934), water temperatures in rivers and streams where *Bulinus (Physopsis) globosus* and *Planorbis* (= *Biomphalaria*) *pfeifferi* occur varies between 18.8°C and 30.2°C. The same authors showed experimentally that the optimum temperature for *Biomphalaria pfeifferi* lies between 27°C and 33°C; raising the temperature to 37° for a few days always resulted in the death of the snails.

In the western Sudan, I have collected *Bulinus (Bulinus)* sp. and *Biomphalaria pfeifferi gaudi* from Jebel Marra, where in December and January the air temperature falls to around freezing point at night and rises considerably in the day-time; I should estimate the diurnal variation to be about 20°C.

It is highly unlikely that temperature is a factor limiting the distribution of bilharziasis vectors, at least in the southern and central Sudan. These snails can easily withstand the range of variation, both seasonal and diurnal, in the various water-bodies examined. Only in small bodies of water would continuous high temperatures reduce the population, through reduction of dissolved oxygen and of the volume of water. In the northern Sudan, temperature does affect the distribution of the vectors, apparently through the high rate of evaporation and eventual drying up of the habitat. Table I shows absolute temperature readings in some localities where vectors were collected by the writer. Temperature readings in June and December in the Bahr-el-Jebel and the White Nile between Juba and Khartoum are shown in Fig. 1. This graph indicates that seasonal variation is slight (about 1.5°C) in the south, but that it increases gradually as one proceeds northward, though still remaining well within the range of tolerance of the vectors (at Khartoum the variation reaches 7°C approximately).

FIG. 1. SEASONAL VARIATION IN WATER TEMPERATURE IN THE BAHR-EL-JEBEL AND WHITE NILE



The above graph was kindly placed at the author's disposal by Dr J. F. Talling.

Sunlight

The effect of sunlight on bilharziasis vectors is an indirect one. The energy obtained from sunlight enables the macrophytic aquatic weeds and the microflora to make use of carbon dioxide, producing carbohydrates and releasing oxygen. Thus sunlight in the snail's habitat means a flourishing of the aquatic weeds, an abundance of microflora (food supply for snails), and a high dissolved-oxygen content. The relation of aquatic weeds and microflora to the snail was referred to in connexion with temperature and will be discussed later in detail (pp. 814 & 815). Sunlight also increases the rate of decomposition of the animal and plant remains on the bottom, so that, instead of fouling the habitat and rendering it unfavourable for snails, they play their usual role in the food cycle, contributing dissolved materials and detritus.

It seems that direct sunlight does not have a harmful effect on the snails. Observations in the field and in the laboratory show that the snails are noticeably active in direct sunlight; egg masses, too, are often seen in direct sunlight, and are apparently unaffected.

Boycott (1936) drew attention to the absence of snails from densely shaded ponds and streams, which have few or no plants and are full of twigs and leaves. Here lack of sunlight and probably also pollution by the debris are the inhibiting factors. Completely shaded forest pools in Bahr-el-Ghazal Province of the Sudan do not harbour bilharziasis vectors.

In exposed water-bodies, however, it seems that partially shaded habitats are preferred by the vectors, although they are also found in completely exposed portions of the same body of water. In the Gezira irrigated area of the Sudan, the majority of canals are almost completely without shade, no trees being grown on the banks. What little shade there is in these canals is provided by the aquatic weeds and by grass growing on the bank, yet it is sufficient for large colonies of snails.

Barlow (1937) also stated that the optimum environment for both *Bulinus truncatus* and *Biomphalaria boissyi* in Egypt was one with both sunshine and shade. Zakaria (1955) found that *Bulinus truncatus* in Iraq was concentrated in the vicinity of willow trees providing a lightly shaded environment.

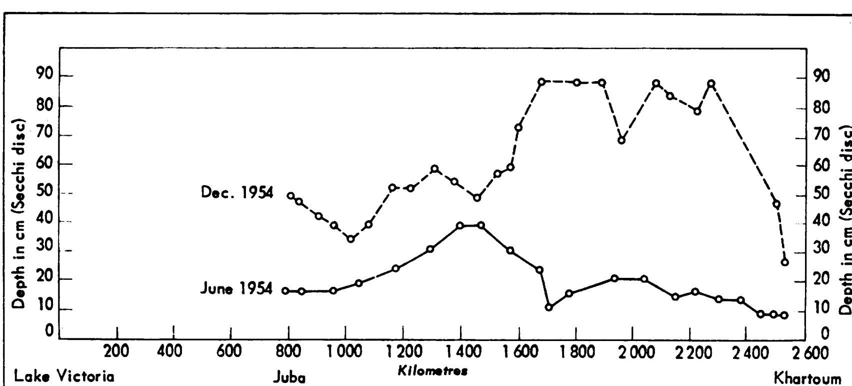
Turbidity

According to Welch (1952), all natural waters exhibit some degree of turbidity, resulting either from a rich growth of plankton or from particulate organic matter in suspension. It is evident that the first type of turbidity is not harmful to snails; on the contrary it indicates an abundance of food in the form of algal members of the plankton which, when it settles, encrusts the submerged surfaces of aquatic weeds and forms a thick film on the bottom and on the banks.

The second factor—particulate organic matter—is the one commonly known to be responsible for rendering waters turbid. If the degree of turbidity is high, such waters are not favourable for bilharziasis vectors. Some authors have regarded clarity of the water as a necessary condition for the presence of freshwater snails (Pilsbry & Bequaert, 1927; Boycott, 1936; Barlow, 1937; van Someren, 1946; Watson, 1950).

Although small quantities of silt do not seem to affect bilharziasis vectors, the Nile flood-water, which contains large amounts of silt eroded from the Abyssinian highlands, is harmful to these snails. It seems to me that this harmful effect is partly a direct one, due to mechanical injury and interference with physiological functions, and partly an indirect one, due to inhibition of the growth of aquatic macroflora and microflora. Silt turbidity obstructs light penetration and thus interferes with the photosynthetic activities of the microflora and the submerged aquatic macroflora (see " Sunlight "). It has been noticed that the vegetative portions of the aquatic weeds in the Gezira canals die down with the arrival of flood-water. These plants do not resume their normal growth until a few months later, when the silt settles. The exact nature of the direct relationship between vectors and silt is still unknown and should be investigated.

FIG. 2. SEASONAL VARIATION IN THE VISIBILITY THROUGH THE WATERS OF THE BAHR-EL-JEBEL AND WHITE NILE



The above graph was kindly placed at the author's disposal by Dr J. F. Talling.

Fig. 2 shows the seasonal variation in the visibility (measured by Secchi disc) through the waters of the Bahr-el-Jebel (Albert Nile) and the White Nile. The low visibility, i.e. high turbidity, in June was probably caused by the flood-water and the accompanying suspended matter and detritus. The readings in December show good visibility in the White Nile at distances of approximately 1700-2300 kilometres from Lake Victoria. Farther north, as far as a point slightly south of Khartoum, there is a high turbidity, apparently caused by vast production of plankton in the vicinity of the Jebel Awliya dam. Similar conclusions were arrived at by Brooks & Rzoska (1954).

Current

For a vector colony to become established, the current should not be strong. Bilharziasis vectors are not normally found at falls, in torrential rivers, on exposed shores of large lakes, or in irrigation canals with very swift flow. Under these conditions the snails are dislodged; a few, however, may be able to survive by attaching themselves to weeds or flotsam, or by sheltering in quiet pools near the bank where the current is less pronounced.

Bilharziasis vectors vary in their tolerance to strong currents, the deciding factor being apparently their ability to cling to a surface. Although some information has been gathered, there is still much to be learned about the relation between water movements and various species of bilharziasis vectors. It seems that *Bulinus (Bulinus)* is better able to withstand swift currents than *Biomphalaria* or even *Bulinus (Physopsis)*. *Bulinus (Bulinus)* has been found in the torrential Blue Nile during flood. The only record of *Biomphalaria* being found in the Blue Nile is in a paper by Archibald (1933). It has not been reported from the Blue Nile since then, nor even from the Sennar reservoir, a fairly lake-like habitat (Markowski, 1953).[1] However, it occurs in Lake Tana, near the outlet of the Blue Nile (Ayad, 1956), and I have found *Biomphalaria rüppellii* in a sheltered habitat in the Dinder River, a tributary of the Blue Nile which is torrential when in flood.[1]

Records in the literature of the occurrence of *Bulinus (Physopsis)* at Roseires and the Gezira are doubtful and it does not seem to establish itself in the Blue Nile, even in sheltered habitats, although it occurs in Lake Tana and the upper reaches of the Blue Nile, 3 kilometres below the outlet from the lake (Ayad, 1956). *Biomphalaria rüppellii*, *B. sudanica* and *Bulinus (Physopsis) ugandae* have been reported from the slowly-flowing White Nile upstream from the Jebel Awliya dam.[1]

The absence of *Biomphalaria* from the Nile at Cairo and the main canals in Lower Egypt, and its presence in the smaller canals and drains of Lower Egypt, are usually explained on the basis of current velocity.

Some observations on the relation between bilharziasis vectors and current velocity have also been made in Iraq. Watson (1950) states that the rapid flow of the water is one of the factors responsible for the absence of *Bulinus truncatus* from the Tigris and Euphrates rivers and their tributaries.

[1] See also article on p. 691.

Zakaria (1955) found that in Iraq a variation in current velocity from 0-15 metres per minute did not affect the distribution of *Bulinus truncatus*.

Permanence and stability

To be suitable as a habitat for bilharziasis intermediate hosts, a water-body should not be subject to sudden fluctuations in level. Such fluctuations are particularly noticeable in certain water-bodies; they hamper the establishment of the snails, and if the snails do become established, keep the population small. The canals of certain pump schemes near Khartoum, which are filled only intermittently from the Nile, contain few snails of *Bulinus (Bulinus)* spp. (probably *Bulinus (Bulinus) truncatus* and *B. forskalii*). The snails are found on weeds in puddles and at the ends of the canals, where the water remains for longer periods. These canals would undoubtedly harbour larger colonies if it were not for the impermanence of their waters. A small, gradual change in water level, however, does not seem to disturb the snails; most of the Gezira canals, which have a diurnal rise and fall of 20-30 cm in water level, do harbour established snail colonies.

One would not expect to find vectors in puddles or small pools that collect after rains in a low rainfall zone (50-300 mm mean annual rainfall). Larger rain pools in the medium rainfall zone (500-1000 mm mean annual rainfall) may harbour bilharziasis vectors, as certain snails are able to survive the dry months by aestivating in sheltered spots, under vegetation, on mud, or in mud crevices. It should also be pointed out here that vectors might be carried to such pools through human or other agency. Tolerance of bilharziasis intermediate hosts to desiccation has been the subject of study by several authors. It has been found that if desiccation takes place gradually, in a habitat where humidity and the level of subsoil water are high, where an adequate growth of weeds is present, and where the dry season is not too long, several snails of a colony are likely to survive until rain or irrigation water arrives again, During the so-called " winter closure " in Egypt, when irrigation canals (except the main ones) are dry for 40-50 days to allow for clearance and repairs, some snails survive until the water is allowed into the canals again (Barlow, 1933, 1935). Barlow & Abdel Azim (1955) reported that 1.5% of *Bulinus* survived a drought period of 12 months on mud in the laboratory, and much larger number survived for shorter periods. The writer collected vectors which had been aestivating out of the water for six weeks on mud and among moist weeds on the west bank of the White Nile at Kosti Bridge, Sudan. When put in water in the laboratory the following percentages revived: 19% of *Biomphalaria sudanica* (37 collected); 10% of *Bulinus forskalii* (10 collected); and 8% of *Bulinus (Physopsis) ugandae* (25 collected). Archibald (1933) found *Bulinus* (presumably *Bulinus (Bulinus)* sp.) in some parts of the Sudan aestivating on mud for 3-4 months until the next rainy season.

Greany (1952), reporting on his observations on the effect of desiccation on vectors in the canals of the Gezira, Sudan, states that a proportion of both *Bulinus* and *Planorbis* (=*Biomphalaria*) snails may survive desiccation for up to 3½ months. After one month, 16.4% of *Bulinus (Bulinus)* sp. tested revived. When the drought had lasted 2 months, 7% of *Bulinus* and 5% of *Biomphalaria* in the same canal revived; while after a 3½ month drought period, 10% of *Bulinus* and 7% of *Biomphalaria* in different canals revived.

Pollution

Pollution of a water-body may be brought about by several means: by the dumping of industrial wastes, by sewage in the form of animal or human excrement, by the continual use of the water for washing, when it becomes soapy, or by the accumulation of large quantities of organic matter of vegetable or animal origin.

Refuse from factories pollutes the water and makes it unsuitable for bilharziasis vectors. This industrial waste usually contains large quantities of oils, acids and sawdust and has a high mineral content, far in excess of the limit of tolerance of these animals. Pollution also has an indirect effect on the vectors through harming the vegetation—thus reducing the oxygen supply—and through altering the nature of the bottom.

The refuse of a small cheese factory in a village near Qaliub, Egypt, is dumped into a nearby stream. The part of the stream near the factory does not harbour vectors, because of its polluted waters, whereas farther downstream, where the effect of these wastes diminishes, *Bulinus (Bulinus)* sp. snails were found.

Parts of water-bodies which are used regularly for washing, and where the water becomes soapy, are not usually favourable habitats for bilharziasis vectors. However, the vectors are not uncommon in other sites in the same water-bodies which are not polluted.

The effect of animal and human excrement on bilharziasis intermediate hosts has been reported by several workers. In general, the vectors are abundant near human habitations, which pollute the water with excrement (Mozley, 1944, for *Bulinus globosus* in Southern Rhodesia; Watson, 1950, for *Bulinus truncatus* in Iraq). Some investigators even consider that these snails appear to be a true " mess-mate of man " (Gordon, Davey & Peaston, 1934, for *Bulinus globosus* and *Biomphalaria pfeifferi* in Sierra Leone; Ransford, 1948 for the same species in Nyasaland). Mozley (1944), studying *Bulinus globosus* in Southern Rhodesia, found that, of a total of 384 sites where the snail occurred, 296 were polluted with human excrement. Fouling of the habitat with human excrement is considered by Ransford (1948) to be a requirement for the existence of *Bulinus globosus* in Nyasaland.

It appears, however, that although the vectors thrive better in the presence of animal and human excrement, they do occur in unpolluted habitats as long as their food, mainly in the form of periphyton (see p. 814) is plentiful. Stretches of irrigation canals and drains running through, or in the vicinity of, many villages in the Egyptian delta harbour *Biomphalaria* sp. and *Bulinus (Bulinus)* sp. in the neighbourhood of places used for washing, and also far from these polluted sites, as long as there is adequate food supply. Houseboats on the Nile in El Gezira and Zamalek districts of Cairo pollute the water, which harbours *Bulinus (Bulinus)* sp. in large numbers. The White Nile bank at Kosti is polluted and is a favourable habitat for actual and potential vectors of bilharziasis.[1] Greany (1952) reported that *Bulinus (Bulinus)* sp. and *Biomphalaria* occur not only in polluted parts of canals, close to villages, but are evenly distributed throughout these canals. Similar observations were made by Zakaria (1954), who considers the distribution of *Bulinus truncatus* in Iraq to be related more to food supply and shade than to human and animal pollution.

It has also been observed that excessive pollution is inimical to the existence of these vectors, especially in small, closed water-bodies where the water is not replenished by continuous inflow. A watercourse which is used for sewage disposal by the city of El Mansura, Egypt (on the Damietta branch of the Nile) and is therefore heavily polluted with human excrement, does not harbour *Biomphalaria* or *Bulinus (Bulinus)*, in spite of the abundance of these snails in nearby canals and drains.

Many perennial streams between Kalikuting and Niertiti, in Jebel Marra, in the Western Sudan, harbour *Biomphalaria pfeifferi gaudi* and *Bulinus (Bulinus)* sp.[1] These streams are heavily polluted with human and animal excrement, but their waters are continuously freshened by inflow.

Substratum

In any water-body the substratum is viewed as part of the physical environment which influences the plants and animals living in the water. The soil of the bottom provides the water with certain dissolved elements, particularly calcium and magnesium. The proportion of these elements is low in the waters which flow over granitic rocks or sandstone areas, high in waters flowing over calcareous rocks. A soil of red ironstone (as is found in the south and southwest of the Sudan) is deficient in calcium and other bases, and gives the water above it acidic characteristics.

The type of substratum almost always associated with bilharziasis intermediate hosts is a firm mud bottom, rich in decaying organic matter. This provides support for aquatic plants, a surface on which flourish algae and other micro-organisms on which the snail feeds, and a crawling-surface for the snail. In the Sudan a firm mud bottom is provided by the so-called " black-cotton soil ", common to many parts of the country.

[1] See also article on p. 691.

Such a bottom is rich in calcium carbonate nodules, and the beds of the Gezira canals are also impregnated with sulfates. Clean sand, semi-liquid mud, or a bottom of loose organic matter does not provide a favourable habitat.

The importance of the substratum as a limiting factor has also been emphasized by other investigators. Watson (1950) states that mud rich in decaying organic matter appears to be a usual but not essential characteristic of the habitat of *Bulinus* in Iraq. Pilsbry & Bequaert (1927) observed that *Biomphalaria* and *Bulinus (Physopsis)* in the Belgian Congo prefer shallow ponds in the savannah country or even pools that accumulate in depressions of rocks and are partly filled with aquatic plants, so that the bottom is rich in decaying vegetable matter. In Kenya, van Someren (1946) concluded that a firm, non-flocculent mud bottom favours the occurrence of *Lymnaea caillaudi* and, consequently, of *Biomphalaria pfeifferi*, which is considered to prefer a very similar habitat.

It has been suggested that one means of controlling bilharziasis vectors in countries where they are endemic would be to line the irrigation ditches and drains with concrete. Such watercourses would, indeed, remain free from vectors for some time. It has been noticed, however, that a layer of silt is very likely to be deposited on the bottom and once this occurs it soon supports rooted aquatic vegetation and favours the reintroduction of vectors. *Biomphalaria* and *Bulinus* are present in large numbers in cemented canals in Montaza Palace, Alexandria, Egypt, and also to the east of this palace, where floating vegetation and algal layers on the cement provide a good habitat for these snails. Therefore cementing the canals would not seem to be a very effective control measure.

Chemical Factors

Salinity

There has been considerable variation in the definition of salinity. Some authors measure salinity in terms of the sodium chloride content of the water, others in terms of the amount of " dissolved chlorides ", apparently by analogy with sea water, where the chlorides form most of the dissolved salts (89 %). Inland waters are usually fresh waters, in which the content of chlorides is low. A few types of inland waters, however, do contain large amounts of chlorides.

In dealing with fresh waters it is permissible to use the term " salinity " to mean the total salt content. Moreover, I believe that in the analyses of water in a bilharziasis vector habitat one should consider (a) the total salt content, (b) the amount of each cation and anion present, and (c) the ratio of the harmful ions to the less harmful or beneficial ones. Experimental work has been carried out by some investigators to determine the limit of tolerance of bilharziasis vectors to certain cations and anions and the lethal dose for various species. Further research along these lines is strongly recommended, in order to gain a more complete understanding of the relationship between the dissolved minerals and the vectors. By analysis of certain waters for their mineral content, it may be possible to explain the presence or absence of these snails, if other factors are favourable.

Deschiens (1954) carried out analyses of several water samples, domestic and natural, and compared his results with analyses made in bilharziasis vector habitats by other workers (Vermeil et al. 1952, in Libya; Marill, 1953, in Algeria, and others). From these analyses, and also from experimental work, Deschiens was able to calculate the maximum tolerated concentrations and the lethal concentrations of certain anions and cations for *Australorbis glabratus* and *Bulinus contortus*, as shown in Table II.

TABLE II. MAXIMUM TOLERATED CONCENTRATIONS AND LETHAL CONCENTRATIONS OF ANIONS AND CATIONS FOR CERTAIN BILHARZIASIS VECTORS

	Anions					Cations				
	SO_4 as Na_2SO_4	CO_3 as $NaHCO_3$	Cl as NaCl	NO_2 as $NaNO_2$	NO_3 as $NaNO_3$	Na as NaCl	K as KCl	Ca as $CaSO_4$	Mg as $MgCl_2$	Fe as $FeSO_4$
Bulinus contortus										
Maximum tolerated concentration (p.p.m.)	1350	4000	2123			1374	525	Tolerated well until saturation	510	
Lethal concentration (p.p.m.)	2000	4000	3500	500	1000	4000	1000		2000	
Australorbis glabratus										
Maximum tolerated concentration (p.p.m.)	1350	4000	3641			2359	1047	Tolerated well until saturation	510	140
Lethal concentration (p.p.m.)	2000	4000	6000	500	750	6000	2000		2000	1000

It can be concluded from this table that *Australorbis glabratus* (and probably also species of the genus *Biomphalaria*) has a higher tolerance to Cl as NaCl, than *Bulinus* has. *Bulinus* and *Australorbis* tolerate magnesium less well than sodium or even potassium. On the other hand, the lethal concentration of K is equal to that of Mg in the case of *Australorbis*, and much less in the case of *Bulinus*. Both snails tolerate Ca very well in the form of calcium sulfate, up to saturation of the solution.

The nitrates seem to be better tolerated by both snails than the nitrites; *Bulinus* has a greater resistance than *Australorbis* to the nitrates and equal resistance to the nitrites, in terms of quantity. However, Litalien & Deschiens (1954) state that *Bulinus* has a greater resistance than *Australorbis* to both salts, in the terms of the time required for a lethal concentration to take effect; sodium nitrite and potassium nitrite in concentrations of 1000 parts per million killed *Australorbis* in one day and *Bulinus* in two days, while sodium nitrate and potassium nitrate in the same concentration killed *Australorbis* in 4-5 days and *Bulinus* in 5-6 days.

Chlorides *

It has been shown in Table II that the maximum tolerated concentration of chlorides as NaCl is 2123 p.p.m. for *Bulinus* and 3641 p.p.m. for *Australorbis.* Watson (1950) reported that the maximum salinity (dissolved chlorides) which had been found in natural habitats of *Bulinus* in Iraq was 1010 p.p.m., and his laboratory experiments showed that adult snails survived in water containing as much as 1500 p.p.m. of dissolved chlorides. Nastasi (1936) stated that *Bulinus contortus* in Libya tolerated 300 p.p.m. of chloride. Lake Kivu, with a salinity of 360 p.p.m. of chloride (Gaud, 1955), harbours *Biomphalaria* and *Bulinus coulboasi* (Schwetz & Dartevelle, 1944). De Azevedo, Cambournac & Pinto (1954), reporting on the chemical composition of waters in southern Mozambique, gave the following figures for NaCl: *Bulinus africanus* habitats, 40-875 p.p.m.; *Biomphalaria pfeifferi* habitats, 30-1215 p.p.m. ; *Pyrgophysa forskalii* habitats, 397-1215 p.p.m.; and in localities where none of these vectors was collected, 70-2862 p.p.m. Helmy (1953) measured the total chloride content of habitats of *Biomphalaria boissyi* in drains leading to the following lakes in the Nile Delta: Lake Borollos, 1240-12 430 p.p.m.; Lake Manzala, 3400-29 990 p.p.m.; Lake Idku, 1000-4110 p.p.m. In habitats where *Biomphalaria* was not found the chloride content was as follows: Nile at Cairo, 32-170 p.p.m.; Lake Karun in Upper Egypt, 3300-12 640 p.p.m.; and occasional samples in Upper Egypt, 1630-9990 p.p.m. Chloride content is not very different in drains in Upper and Lower Egypt, but *Biomphalaria* is present only in the latter. De Andrade (1954) found that the maximum chloride content in planorbid habitats in Brazil was 2562 p.p.m.

Investigators agree that a very high total salt content is lethal to fresh-water snails. It has been noticed, however, especially in coastal areas, that a gradual increase in the salinity of the water is usually tolerated by many individuals of a colony. In Egypt, this phenomenon can be seen very clearly in bilharziasis vectors harboured in marshy areas along the Mediterranean coast and in drains leading to the coastal lakes (Idku, Maryut, Borollos, and Manzala), as these habitats are subject to Mediterranean tides which temporarily increase their salinity. As *Bulinus* is less

* Some of the authors reported their finding in grams/litre or in parts per 100 000; for the sake of uniformity all figures have been converted to p.p.m.

tolerant of salinity than *Biomphalaria*, it is less common in these coastal habitats.

Cations

The following is a discussion of some important cations usually present in vector habitats and their direct and indirect relationship to the vectors. The content of these elements in certain water-bodies of the Sudan is indicated in Table III. The water samples were collected by the writer and their analysis was carried out through the courtesy of the Wellcome Chemical Laboratories, Khartoum.

Calcium. The importance of calcium in shell formation is well known. Moreover, it plays an important role in animal metabolism and helps regulate the permeability of the tissues. It is required by all green plants

TABLE III. ANALYSIS OF SOME WATER-BODIES IN THE SUDAN

	Sennar reservoir [2]	Gezira irrigation canal [1, 2, 4]	Overflow White Nile Kosti [1, 2, 3, 4]	River Atbara [2]	River Rahad	River Dinder [4]
pH	7.1	8.0	8.0	7.8	8.1	7.8
Dionic reading [5]	180	200	340	450	350	330
Total solids dried at 180°C (p.p.m.)	145	160	260	330	250	220
Total hardness ($CaCO_3$ in p.p.m.)	115	100	130	230	200	180
Temporary hardness ($CaCO_3$ p.p.m.)	95	100	130	210	200	180
Excess alkalinity (Na_2CO_3 in p.p.m.)	Nil	15	50	Nil	70	10
Calcium (Ca in p.p.m.)	25	30	25	30	35	30
Magnesium (Mg in p.p.m.)	10	10	15	35	30	25
Other cations (Na in p.p.m.)	10	5.0	30	30	30	5.0
Silicate (SiO_2 in p.p.m.)	40	30	40	50	40	30
Sulfate (SO_4 in p.p.m.)	10	Nil	Nil	30	Nil	Nil
Chloride (Cl in p.p.m.)	15	Nil	5.0	30	Nil	5.0
Nitrate (N in p.p.m.)	Nil	Nil	Nil	Nil	Nil	Nil
Fluoride (F in p.p.m.)	0.35	0.8	0.85	0.5	0.8	0.3
Boron (B in p.p.m.)	Nil	Nil	Nil	Nil	Nil	Nil
Ammoniacal nitrogen (N in p.p.m.)	0.04	Nil	0.2	Nil	Nil	Nil
Albuminoid nitrogen (N in p.p.m.)	Nil	0.14	0.44	0.98	0.3	0.28

[1] *Bulinus forskalii*
[2] *Bulinus (Bulinus)*
[3] *Bulinus (Physopsis)*
[4] *Biomphalaria rüppellii*
[5] The dionic reading (electrical conductivity) is a measure of the total solids (salinity) ; the higher the reading the higher the salinity. The electrical conductivity of water is now considered a better indicator of the toxicity of the water than the concentration of the salts present.

that are beneficial in the vector's habitat. According to Welch (1952) calcium also acts as antidote, reducing the toxic effects of single-salt solutions of sodium and potassium. Calcium is sometimes taken as a measure of the hardness of the water, since the carbonates are mainly combined with calcium and magnesium. Calcium is also present in the form of the sulfate.

Tropical waters, in general, are low in calcium content. Calcium concentration in the White Nile is less than in the Blue Nile. At Khartoum on 7 November 1955 the calcium content of the White Nile was 10 p.p.m., while on the same day the Blue Nile contained 20 p.p.m. Figures as low as 5.7 and 8.5 p.p.m. have been recorded in the open water in the Sudd region of the Sudan, where bilharziasis vectors are known to occur.

The calcium content of the substratum, derived from the exchangeable calcium of the colloidal complex, the calcium carbonate in soil lime, and the calcium silicate in rock fragments, is also important when interpreting analyses of water, especially in dealing with various types of water-bodies. Romeiro & Aguiar (1954), discussing *Australorbis* habitats in Brazil, recommend that the calcium content of the bottom as well as the calcium content of the water should be considered.

It seems that vector snails may even thrive in waters poor in calcium. The calcium content of a particular body of water appears to control only the density of the snail population and whether the shells are thick or fragile.

Magnesium. Magnesium is usually found in association with $CaCO_3$ in soil lime and is a component of the soluble salts in saline soils. Acid substrata are deficient in magnesium. Small quantities of magnesium in the habitat water are necessary for the snail and for the chlorophyll-bearing microflora which form its food supply, but an excess of magnesium is unfavourable to the vectors. Deschiens (1954) reported 510 p.p.m. as the limit of tolerance of *Australorbis* and *Bulinus* to magnesium (see Table II). Thus it comes next to iron in toxicity.

Sodium. Sodium occurs in the water in the form of chloride, sulfate and carbonate. An estimation of the sodium content of the water is important in an evaluation of the quality of the water for snail vectors. Water with a high concentration of Na compared to other cations, especially to calcium, is not favourable to snails. The ratio of cations present in the water is based on the general principle of base exchange: if sodium ions predominate in the water, they will tend to displace the beneficial calcium and less calcium will be absorbed. More research should be carried out on the sodium content of the habitat as a limiting factor for the distribution of bilharziasis intermediate hosts.

Iron. The iron content of inland fresh waters (even those with a high mineral content) is generally small and below the limit of tolerance for bilharziasis vectors. Dechancé & Deschiens (1955) found that the lethal concentration of ferric chloride for *Australorbis* and *Bulinus* is 65 p.p.m. and that of ferric sulfate is 500 p.p.m. In general *Bulinus* (*Bulinus*) is more sensitive than *Australorbis* to iron salts.

Very small amounts of iron are necessary for algal growth. Iron is also concerned in the production of chlorophyll, where it is believed to act as a catalyst only. In the presence of a reduced oxygen tension, iron bacteria in the habitat absorb soluble iron compounds and deposit them again in the form of a red precipitate of ferric hydroxide. Van Someren (1946), in Kenya, observed such a precipitate in several stagnant marshes, and in ponds, streams and ditches which were unfavourable for snails, mosquito larvae, water insects, crustaceans, and worms. A few marshes and ponds with a similar red precipitate, probably of iron compounds, and devoid of any vectors or other aquatic life, were observed by the writer in the southern part of Bahr-el-Ghazal Province of the Sudan.

Silicon. Silicon occurs in fresh water in the form of soluble silicate. It may be present in colloidal form, especially in river waters. Silicon has been associated with diatoms (part of the food supply of vectors) and other organisms that have a siliceous skeleton, because small amounts of its salts are essential in the formation of these shells.

Hardness and alkalinity

It has been indicated on p. 799 that for practical purposes the calcium content of the water may be taken as a measure of hardness, since dissolved calcium salts, together with those of magnesium, are the main compounds producing hardness. One of the difficulties in interpreting water analyses of bilharziasis vector habitats is the use of so many different systems of expressing the alkaline reaction of the water. A uniform terminology should be adopted in order to facilitate the comparison of figures from different habitats and countries. There are certain terms which I feel should be clarified here; the definitions are based on those given by Theroux et al. (1943). Hardness of natural waters is caused by the bicarbonates, sulfates and sometimes the chlorides and nitrates of calcium and magnesium. " Temporary hardness " is caused by the presence of the bicarbonates and is removed by boiling; " permanent hardness " is caused by the sulfates. " Carbonate hardness " is due to the presence of the normal carbonates and bicarbonates, " non-carbonate hardness " to the presence of the sulfates, chlorides, and nitrates. Hardness and alkalinity are always expressed in terms of calcium carbonate ($CaCO_3$).

It appears that bilharziasis vectors are tolerant of a wide range of hardness. The only association observed was that in waters of very low hardness the number of individuals was reduced and the shells became relatively thin.

Deschiens (1954) found experimentally that *Bulinus truncatus* and *Australorbis glabratus* showed good tolerance to hardness to the point of $CaSO_4$ saturation (Table II). This apparently refers to permanent hardness as defined above. Van Someren (1946) reports finding *Lymnaea caillaudi* (the liver fluke vector) and *Biomphalaria pfeifferi* in Kenya in water with a hardness range of 8-200 p.p.m. of $CaCO_3$. The hardness of certain Sudan waters is shown in Table III.

In river waters, such as the Nile, the term " alkalinity ", used by other authors, is actually a measure of the bicarbonate content, since this is the main anion present. The following are alkalinity figures in p.p.m. for certain Sudan waters: White Nile (10^{-4}N), 26; Sennar Reservoir, 19; Gezira Canal, 20; River Dinder, 36. Dr J. F. Talling, formerly of the University of Khartoum, has kindly provided me with some additional figures for the Bahr-el-Jebel: main river at Bor, 23.4; swamp at Bor, 27.6; Sudd region, 105 km south of Lake No, 30.0. De Azevedo, Cambournac & Pinto (1954) expressed their analyses of Mozambique waters in terms of phenolphthalein alkalinity (indicating the normal carbonates) and methyl orange alkalinity (mainly bicarbonates) as shown in Table IV.

TABLE IV. ALKALINITIES OF DIFFERENT SNAIL HABITATS IN MOZAMBIQUE

Waters containing:	Alkalinity in p.p.m.	
	Phenolphthalein	Methyl orange
Bulinus africanus	0-14	14-260
Biomphalaria pfeifferi	0-12	38-230
Bulinus forskalii	0	58-100
None of above vectors	0-16	26-458

For Lake Kivu (surface water at Burkawu) high alkalinity figures (carbonate: 132 p.p.m., bicarbonate: 634.4 p.p.m.) have been reported by Gastellier and Jadin (cited in Deschiens, 1954). Delmotte and Jadin (also cited in Deschiens, 1954) give the figures for Kabono Bay, Lake Kivu as carbonate: 29.4 p.p.m., bicarbonate: 990.7 p.p.m.

Hydrogen ion concentration

The more one investigates habitats of bilharziasis vectors and the more one considers the pH readings recorded by other workers, the more evident it becomes that hydrogen ion concentration is rarely a factor limiting the distribution of the snails. It is necessary to be very circumspect in correlating pH measurements with vector distribution. Actually, the combined effects of other factors correlated with pH (alkali reserve, carbon dioxide content, sunlight, photosynthesis with its active removal of CO_2 and the production of O_2, and the character of the substratum) are more important than pH alone. Welch (1952) also explains how pH is dependent on these factors.

About thirty years ago, biologists attached great importance to pH, probably because of its physiological and ecological implications, and because it is easily measured in the field. From a study of the habitats of freshwater molluscs of Great Britain, Boycott (1936) concluded that pH is not a major factor in snail distribution and that it is chiefly of value as a means of distinguishing quickly between alkaline and acid waters in the field. Both Boycott (1936) and van Someren (1946), who studied *Lymnaea* and *Biomphalaria pfeifferi* habitats in Kenya, report that water in any particular habitat may vary quite widely in pH from hour to hour during the day.

Allee et al. (1949), after consideration of various environmental factors which affect organisms in fresh waters, concluded that pH is of real, though limited, importance.

Bilharziasis vectors appear to tolerate a wide range of pH—generally speaking, from 6.0 to 9.0. Figures on either side of this range have been reported in some cases, however.

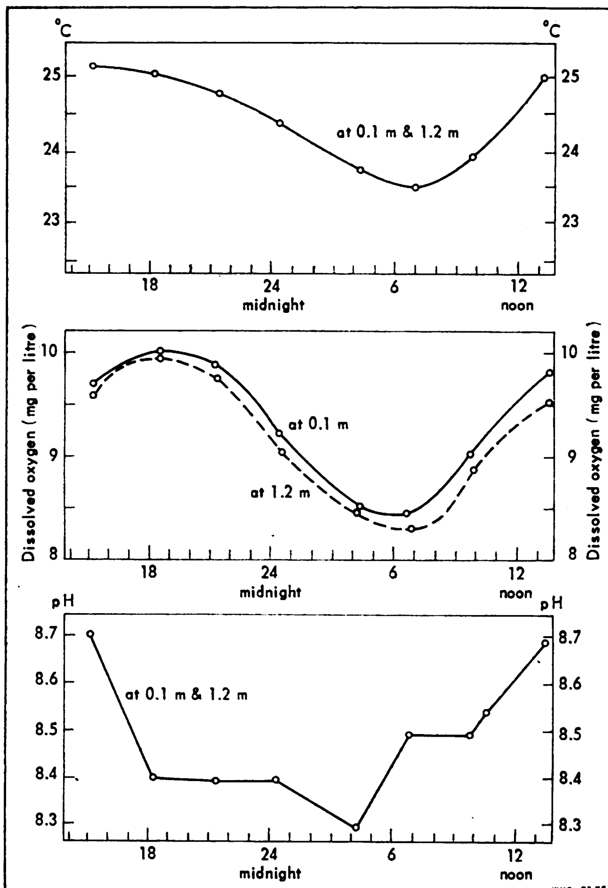
De Azevedo, Cambournac & Pinto (1954) recorded the following pH ranges in Mozambique: *Bulinus africanus* habitats: 6.0-8.2; *Biomphalaria pfeifferi* habitats: 6.0-8.2; *Bulinus forskalii* habitats: 6.6-7.2; places where none of these snails were found: 5.8-8.4. In the Distrito Federal area of Brazil, however, de Andrade (1954) encountered planorbid snails in the range pH 4.0-9.0.

Bulinus (Bulinus) sp. was found in waters with a pH range of 7.1-8.0 in Fezzan (Vermeil et al. 1952), while Marill (1953) reported the same snail from waters with a pH range of 7.2-8.8 in Algeria. Ganzin (cited in Deschiens, 1954) reported a pH range of 5.49-6.82 for *Planorbis* (= *Biomphalaria*) in French Equatorial Africa. The surface water in Lake Kivu was reported by Gastellier and Jadin (cited in Deschiens, 1954) to have a pH of 9.2. Experimentally, Deschiens (1954) found that both *Bulinus (Bulinus) truncatus* and *Australorbis glabratus* can tolerate a pH range of 4.5-10.0.

Gillet & Wolfs (1954), reporting on bilharziasis in the Belgian Congo, gave a pH range of 6.8-9.2 in *Biomphalaria* and *Bulinus* habitats (not including the large lakes); *Bulinus forskalii* was also found in waters with a range of 5.9-6.0. For the great lakes (Albert, Kivu, and Tanganyika, where vectors also occur) the same authors report a definitely alkaline range of 8.2-9.2.

In some Sudan waters where vectors were collected, the pH varied between 6.6 and 8.2. In the ironstone region of the south-west, and in certain parts of the Sudd region, one would expect a pH of less than 6.6, well within the acidic range. It is intended in future investigations to examine more samples from various types of water-bodies in order to determine their pH and other factors.

FIG. 3. DIURNAL VARIATION IN WATER TEMPERATURE, DISSOLVED OXYGEN CONTENT AND HYDROGEN ION CONCENTRATION IN A LAGOON 60 KM SOUTH OF LAKE NO, BAHR-EL-JEBEL



The above graphs were kindly placed at the author's disposal by Dr J. F. Talling.

The diurnal variation in pH in a lagoon 60 km south of Lake No (see Fig. 3) was from 8.3 to 8.7. This is not much when compared with the considerable diurnal variation reported by some other investigators. Diurnal variation supports the contention that it is not safe to relate the distribution of bilharziasis vectors to a particular range of pH values. Moreover, it is surprising to note that some of the authors referred to above found vectors in acid waters with a pH as low as 5.8 and even 4.0. At 5.8 the deposition of lime becomes theoretically impossible. It is puzzling, therefore, that the snails are able to extract enough lime from these waters for their shells.

Dissolved oxygen

Snail vectors of bilharziasis, being pulmonates, are provided with a lung which enables them to make use of atmospheric oxygen for their respiratory requirements when they ascend to the surface. This pulmonary respiration can take place only if a thin film of water covers the surface of the lung (for gaseous exchange). Anatomical examination shows that the snails also possess a pseudobranch which is embraced by the mantle collar. This structure represents an outgrowth from the respiratory wall, is highly vascular and functions like a gill, providing the animal with dissolved oxygen from the water when it remains submerged. Although the snails possess lungs, it seems that they depend more on oxygen dissolved in the water than on atmospheric oxygen.

It is evident, therefore, that the oxygen content of the water is very important in conditioning the habitat of these snails. Dissolved oxygen should be adequate and should not fall to the suffocation limit. A low concentration of oxygen, even if not immediately fatal to the snail, reduces its movements and thus impairs feeding and reproduction. Water obtains oxygen partly from the atmosphere, but mainly from oxygen-producing plants. Oxygen is lost from the water as a result of the respiration of living organisms and the oxidation of organic matter and of dead bodies.

In certain habitats in the Sudan where snails were collected, dissolved oxygen averaged 4.7-7 p.p.m. However, in habitats where algae are abundant and where aquatic weeds are present in moderate numbers, but not dense enough to stop light penetration, supersaturation of the habitat, due to photosynthetic activities, is noticed. In such habitats a diurnal oxygen pulse exists. Figure 3 shows measurements taken in a lagoon in the Bahr-el-Jebel, 60 miles south of Lake No (a *Bulinus* habitat), where oxygen tension at a depth of 0.1 metres reaches a peak of 10 p.p.m. in the late afternoon and is at a minimum of 8.5 p.p.m. near dawn. A similar diurnal oxygen pulse was found by van Someren (1946) in a ditch near Kabete, Kenya, which harbours a fairly large population of *Biomphalaria pfeifferi*. At the lower end of the ditch the peak of the oxygen tension (11.4 p.p.m.) was at 2 p.m., and the minimum (8.5 p.p.m.) at 8 a.m. Therefore, in spite of the rise in temperature in the afternoon, supersaturation values in excess of 200% may be reached.

In view of the importance of oxygen tension in habitats of bilharziasis vectors, some attention has been given to the study of the physiology of the respiration of snails, both aerobic and anaerobic. Von Brand, Nolan

& Mann (1948) demonstrated the wide range of oxygen tension through which *Australorbis glabratus* maintained a steady rate of oxygen consumption. Some work has also been done on the resistance to anaerobic conditions shown by various species of snails, including planorbids, and it was found that they had a higher resistance than lymnaeids and physoid snails (von Brand, Baernstein & Mehlman, 1950). The products of such respiration, in the case of freshwater snails, especially the bilharziasis vector *Australorbis glabratus*, were investigated by Mehlman & von Brand (1951). Such studies to determine the tolerance of snails to lack of oxygen should be extended to include all species, and investigations should be carried out to determine the oxygen suffocation limits of these vectors, i.e. the lowest dissolved oxygen tension at which each species can survive. More research is also needed on the effect of oxygen tension on vector-parasite relationships. Olivier, von Brand & Mehlman (1952) were able to show that, under anaerobic conditions, *Australorbis glabratus* infected with *S. mansoni* ceased to shed cercariae or only shed them in very small numbers, and that infected snails were less able to withstand anaerobic conditions than were uninfected ones.

There is another point worth investigating in the case of bilharziasis intermediate hosts: it has been observed in the field that in some habitats with a dense growth of algae and of macrophytic aquatic weeds, where supersaturation with oxygen would be expected during daylight hours, only a few snails and other aquatic animals occur. It has been suggested, in the case of animals other than snails, that the presence of " nascent oxygen " is the toxic factor responsible for the reduction in population; this might also be true for snails.

Biological Factors

Certain associate animals and plants which exert an influence on bilharziasis intermediate hosts constitute the biological factors in their environment. These factors seem to play an important part in conditioning the habitat of the snails. The associate animals include the commensals, the symbionts, the predators and the parasites; the associate plants consist of aquatic weeds and microflora.

The commensals and symbionts play a part in the food cycle of the habitat because when they die they disintegrate and contribute directly to the detritus and dissolved nutritive material in the water. The organisms that most closely affect the vectors, however, are the predators, parasites, aquatic weeds, and microflora.

Several vertebrates and invertebrates attack bilharziasis intermediate hosts and other molluscs; their defenceless condition and slow movement make them easy prey for many associate organisms, as well as for organisms that visit the habitat only occasionally. Bilharziasis intermediate hosts harbour both ectoparasites and endoparasites. The latter, especially, often affect the snails, both mechanically and physiologically, to an extent that has led some workers to advocate the use of parasitic organisms not harmful to man or domestic animals as a means of biological control. The effectiveness of certain predators or parasites in controlling populations of bilharziasis vectors under laboratory conditions has been tested in the last few years with successful results. Whether these organisms can exterminate the vectors or limit their distribution under natural conditions will only be known for certain when a sufficient number of field observations and statistical data have been collected. It is most likely, however, that predators and parasites would only limit the abundance of the vectors and would be unable to exterminate them under natural conditions, as there are several biological mechanisms which operate to insure the equilibrium and stability of the community. When a predator, such as a fish or a crab, or a parasite, such as a leech, is brought together with a vector under the artificial conditions of the laboratory, the biological balance is disturbed to the disadvantage of the mollusc. Under these conditions there is sometimes an absence of natural ecological contact, and usually an absence of other sources of food which the predator would have eaten by preference in nature. It is thus difficult to know whether organisms which prey on snails effectively in the laboratory offer a practical method for biological control of bilharziasis vectors in their natural habitats.

Parasites

Viruses, bacteria and fungi

Experience gained in rearing bilharziasis vectors or in working with them in the field has led some investigators to suspect the existence of certain micro-organisms which are responsible for the premature death of the snails, especially when other factors seem favourable. These micro-organisms must, therefore, be considered able to limit the abundance of the vectors in certain habitats, if not to cause their complete disappearance. Cowper (1946) noticed that the presence of a certain fungus, *Catenaria*, caused the death of his snails. Standen (1951) found that the use of meat extracts as food for *Australorbis glabratus* caused the death of the snails, because the extracts spread in the water of the aquaria and soon set up undesirable bacterial activity. When rearing the snails *Biomphalaria boissyi* and *Bulinus truncatus* in laboratory cultures, I have observed that an abundant growth of a fungus belonging to the *fungi imperfecti* killed the snails in the aquaria (Abdel Malek, 1952). The vegetative mycelia of the fungus grew and multiplied rapidly, covering the shells of the snails and eventually surrounding the apertures. The fungus also covered the leaves of the aquatic plant *Vallisneria* and the walls of the aquarium.

McMullen called attention to the possible value of bacteria, fungi, and viruses for biological control of bilharziasis vectors (WHO Expert Committee on Bilharziasis, 1953). Since then, some additional knowledge has been gained of the bacteria which infect snails in nature, and which have been used in attempts to find a biological method of snail control. Cruz & Dias (1953) described *Bacillus pinotti*, a natural parasite of aquatic snails in Brazil. Later, Dias (1954a and 1954b) isolated the bacterium—which he called for convenience BET (bacilo de esporo terminal)—from *Australorbis glabratus*, and reported that cultures, preferably in peptone solution, had been successfully applied to a number of water bodies, killing *A. glabratus* and *A. nigricans*. Morphologically similar bacilli have been isolated from *A. glabratus* in Venezuela by Texera & Vicente (1954) and from *Biomphalaria boissyi* in Egypt by Dias & Dawood (1955).

From these findings it is evident that when conditions in a certain habitat are favourable to the propagation of the pathogenic bacteria which already exist there, they become an important limiting factor. It has been shown that epidemic haemorrhage, from which the vectors sometimes suffer in nature, is caused by bacterial infection.

Research along these lines should be encouraged with the aim of finding other pathogenic micro-organisms which affect snails in their natural habitats. An unusually high mortality among young snails may also be due to some sort of virus or bacterium. The significance of micro-organisms in relation to " infant mortality " should be investigated.

Digenetic trematodes

These trematodes are probably the most important organisms that parasitize bilharziasis vectors. Their larval stages—miracidia, sporocysts, rediae and cercariae—all cause injurious effects to their snail hosts.

Research workers who rear bilharziasis intermediate hosts in the laboratory have observed that infected snails die sooner than uninfected ones; and snails naturally infected with trematodes (including schistosomes) do not live as long as uninfected ones when brought into the laboratory.

The damage which these parasites cause to aquatic snails in general is usually mechanical and physiological, sometimes even morphological. Mechanical damage takes place when the larval stages migrate through the various tissues to reach the distal organs of the snail. The motile daughter sporocysts and the motile and voracious rediae also inflict considerable damage. Physiological effects are caused by the consumption by the larvae of digested food materials, the amount of which depends on whether the infection is light or heavy, and by the accumulation of large amounts of toxic waste products excreted by the parasite (Faust, 1920; Hurst, 1927; von Brand & Files, 1947; Abdel Malek, 1952). Some authors (Hurst, 1927; Wesenberg-Lund, 1934; Rothschild, 1936, 1941a, 1941b; Porter, 1938) claim that they have observed changes in size, colour, shape of the tentacles and foot, and structure of the shell, which have enabled them to distinguish the infected snails from the uninfected ones.

However, it seems that digenetic trematodes differ in the extent of the damage they cause, and in the effect this damage has on the life span of the intermediate host. Some cause little or no effect on the host; others are very destructive. It can be stated, in general, that the trematodes which have a redial stage in their life cycle are more injurious than others to aquatic snails.

Hurst (1927) stated that the ovotestis was absent in *Physa occidentalis* heavily infected with *Echinostoma revolutum*, and Pratt & Barton (1941) made a similar observation in *Stagnicola emarginata angulata* infected with rediae of *Plagiorchis muris*. Rediae of *Cercaria himasthla* ate the gonads of *Littorina littorea*, while sporocysts of *C. emasculans* and *C. littorinae* produced less destruction in the same snail (Rees, 1936). Parasitization of the snail *Helisoma corpulentum* Say from Lake Itasca, Minnesota, USA, with *Petasiger chandleri* (Abdel Malek), 1952, *Clinostomum marginatum* Rudolphi, and *Uvulifer ambloplitis* (=*Crassiphiala amblophitis*, Hughes, 1927) caused a great reduction in the glycogen stored in the digestive gland and considerable mechanical damage to many organs (Abdel Malek, 1952). In the case of the echinostome *Petasiger chandleri*, whose rediae possess a relatively long gut, there was a considerable reduction in the number of tubules of the digestive gland; in one section there were only 27 tubules, with 141 rediae. Moreover, no less than 95% of the acini of the ovotestis were occupied by rediae and the reproductive structures were either digested completely or in a degenerate condition. On the other hand, infection with *Uvulifer ambloplitis* did not involve or damage the ovotestis; the sporocysts of this trematode could not invade the acini, but were found in the connective tissue between them. Other organs, such as the prostate, kidney, heart, and connective tissue in general, were affected by all three trematodes.

Bayer (1954) observed that *Bulinus africanus*, *Biomphalaria pfeifferi*, and *Bulinus tropicus* near Durban harboured a large variety of larval trematodes. He noted that such infections caused great damage to the digestive gland, the ovotestis and other tissues of the snail, and that parasitized snails died much sooner than uninfected ones under identical conditions.

The effects of parasitization by the trematode *Schistosoma* have also received the attention of several investigators. These effects can be summarized as follows:

(i) Infection with *Schistosoma* affects the life span of the snail, usually causing premature death. Manson-Bahr & Fairley (1920) in Egypt, Gordon, Davey & Peaston (1934) in Sierra Leone, and Porter (1938) in South Africa noted a higher death-rate among infected vectors than among uninfected ones. Barbosa, Coelho & Dobbin (1954) in Brazil also demonstrated that infection of *Australorbis glabratus* with *S. mansoni* resulted in almost all cases in the death of the snails within a period varying from 1 day to 5 months.

(ii) Infection with *Schistosoma* renders the vectors less tolerant of desiccation. This is, no doubt, an important limiting factor in the spread of the disease, especially in habitats which naturally dry up for a few months every year, or in irrigation canals which are emptied for certain periods (see also p. 792). The snails that can withstand the drought and act as the seed for the next season are mostly, if not all, uninfected ones. Barlow (1935) noted that the winter closure in Egypt (usually lasting 40-50 days) resulted in a decrease in the relative numbers of infected snails (*Biomphalaria boissyi* and *Bulinus truncatus*). Brumpt (1941) stated that *Australorbis glabratus* infected with *S. mansoni* were less resistant to desiccation. In Brazil a great deal of research has been carried out in the last three years on the tolerance of *A. glabratus* to desiccation, and it has been confirmed that infected snails are much less resistant to drought than uninfected ones. Barbosa & Coelho (1953) observed that sporocysts and cercariae degenerate on the 20th day of desiccation. A more detailed study was later carried out by Olivier, Barbosa & Coelho (1954), who found that the effect of desiccation was apparent during the first 20-30 days, but thereafter deaths among infected snails were no more frequent than among the uninfected.

(iii) Infection with *Schistosoma* affects the reproductive capacity of the snail. Coelho (1954) observed a significant reduction in the number of egg masses and eggs laid by specimens of *A. glabratus* infected with *S. mansoni*, when compared with those uninfected. From histological studies of *Biomphalaria boissyi*, I have observed that there is a reduction in the number of ova in each acinus of the ovotestis in specimens infected with *S. mansoni*. It appears that the infection does not cause mechanical damage to the acini; evidently the sporocysts cannot invade the acini, but are always found in the interacinal connective tissue (Abdel Malek, 1955). The infection probably interferes with physiological processes, the effect being to prevent the acini producing as many ova as are normally produced in uninfected snails under similar conditions.

(iv) The parasite consumes stored polysaccharides. Von Brand & Files (1947) found that infection of *A. glabratus* with *S. mansoni* resulted in a considerable reduction in the polysaccharide content of the snail, though it did not interfere seriously with the storage of fat. By the help of histochemical tests, I have also observed a great reduction in the glycogen content of *Biomphalaria boissyi* infected with *S. mansoni*.

Leeches

That leeches are natural parasites of aquatic molluscs was reported many years ago. Harding (1910) mentioned two members of the family Glossosiphonidae (= Clepsinidae) as common in lakes, ponds, ditches and sluggish streams in the British Isles. The first, *Glossosiphonia complanata*, Linnaeus, 1758, is chiefly parisitic on *Lymnaea* and *Planorbis*, but also attacks other freshwater molluscs and the larvae of *Chironomus*. The second leech, *Helobdella stagnalis*, Linnaeus, 1758, is largely parasitic upon gastropods, but also preys upon a variety of other hosts. Whitehead (cited in Boycott, 1936) also claims that gastropods are the natural food of the above two leeches. Pilsbry & Bequaert (1927) described the habits of leeches of the genus *Glossiphonia* (presumably *Glossosiphonia*), which live on snails, especially *Lymnaea*, and considered it probable that most other leeches also attack molluscs at times.

In aquaria, Krull (1931) and Boycott (1936) have found leeches to be extremely destructive. Chernin, Michelson & Augustine (1956) showed that the growth of a population of *Australorbis glabratus* was effectively controlled by the leech *Helobdella fusca*, under laboratory conditions.

In many water-bodies in the northern United States and in the Sudan, I have observed leeches parasitic on planorbid snails. From one to three leeches were seen near the snail's aperture, between the mantle and the shell, and often inside the pulmonary cavity, which they reached through the pneumostome. These leeches left the snail when it was placed under an anaesthetic.

The part that leeches play in conditioning the habitat of vectors in nature is still obscure and many more field observations are needed. However, if the leeches are abundant, they probably reduce the number of snails.

Other parasites

Cooke (1913) points out that certain nematode worms (Rhabditis) inhabit the intestine and salivary glands of some land snails and slugs; this might apply to aquatic snails as well. I have myself observed that certain oligochaete worms parasitize planorbids in a number of water-bodies in northern Michigan. Pilsbry & Bequaert (1927) referred to investigations made by Lundbeck (1923) on certain small European muscid flies of the family Sciomyzidae, whose larvae or pupae occur in *Lymnaea* and *Planorbis*. Schwetz (cited by Gillet & Wolfs, 1954) noticed larvae of Lampyridae (Coleoptera) in some planorbids in Irumu and Lake Albert in the Belgian Congo.

Predators

Crabs and crayfishes

Lagrange & Fain (cited in Gillet & Wolfs, 1954) noted the molluscophagous role of the crabs *Potamonautes didieri* and *P. lirrangensis*. Crabs belonging to the genus *Potamonautes* and crayfishes of the genus *Astacus* and *Cambarus* proved to be important predators on bilharziasis vectors under laboratory conditions, although the crabs were not as efficient as the crayfishes (Deschiens, Dechancé & Vermeil, 1955; Deschiens & Lamy, 1955). The crayfishes used in the experiments were tropical American species, while the crabs occur in North Africa from Egypt to Morocco.

Insects

Certain aquatic coleoptera, particularly those belonging to the family Dytiscidae, have been stated to prey on aquatic snails, especially on the egg-masses and young snails (Taylor, 1894; Cooke, 1913; Pilsbry & Bequaert, 1927; Boycott, 1936).

Snails

Several examples are to be found in the literature of a mollusc preying on another mollusc, and a new one has recently been added. Oliver-González, Bauman & Benenson (1956) associated the disappearance of *Australorbis glabratus* from a stream in Puerto Rico with the recent introduction of the operculate snail, *Marisa cornuarietis*. This snail is voracious; it ingests the eggs of *Australorbis* and causes a great depletion in the common food supply. The authors considered that it might have played an important role in the death of the bilharziasis vector. Chernin, Michelson & Augustine (1956) arrived at similar conclusions as the result of laboratory studies and noticed that *Marisa* ingests the eggs and the newly-hatched *Australorbis*. The operculate snails *Pila* spp. and *Lanistes* spp., belonging to the same family as *Marisa* (family Pilidae (= Ampullaridae)), are of common occurrence in the Nile valley and other parts of Africa. It is of interest to note that *Pila* and *Lanistes* are among the associate molluscs of bilharziasis vectors, and in the Sudan *Pila* especially reaches a very large size. Although I believe that these operculates play little or no part in limiting the distribution of the vectors in this part of the world, I would advocate more field observations to settle this point definitely.

Fishes

Molluscs have long been known to form a substantial part of the food of fish, and certain species of aquatic snails have been discovered for the first time in the stomach contents of fish. Taylor (1894) and Cooke (1913) mentioned several species of fish, mainly European and American, which feed on snails. Hey (1946) recommended *Gambusia affinis*, the European tench *Tinca vulgaris*, and the African lungfish *Protopterus*, which are known to prey on aquatic snails, for bilharzia control in South Africa. It was also stated by Oliver-González (1946) that the guppy, *Lebistes reticulatus*, eats the egg-masses of *Australorbis glabratus*. De Bont & De Bont Hers (1952) reported on the good molluscophagous capacity of certain local fish in the Belgian Congo, especially the cichlid *Serranochromis* sp.

(presumably *S. macrocephala*), the stomach of which usually contains various species of molluscs, especially planorbids. This fish generally eats a larger number of snails in ponds than it does in rivers. *Chrysichthys mabusi* is a siluroid which the above authors have also found to feed on snails in the Belgian Congo. Six species of the cichlid genus *Haplochromis* include molluscs in their diet (Greenwood, 1954); three of them feed exclusively on molluscs in the adult stage, but when young, they also eat insects. All the species are present in Lake Victoria; *H. ishmaeli* is also found in Lake Edward, and *H. humilior* in the Victoria Nile.

Amphibians

Many frogs and toads have been described as preying on snails in England (Taylor, 1894), in North America (Needham, 1905), and in the Belgian Congo (Pilsbry & Bequaert, 1927; Lagrange & Fain, cited in Gillet & Wolfs, 1954).

Birds

Aquatic birds are also among the predators of molluscs, which form a major portion of their diet. However, Chapin (cited in Pilsbry & Bequaert, 1927), who examined the stomach contents of some Congo birds, states that molluscs do not seem to furnish an abundant source of food for the aquatic birds of that part of Africa. The following birds only were listed as having eaten molluscs: the open-bill stork (*Anastomus lamelligerus*), wood rail (*Himantornis haematopus*), finfoot (*Podica senegalensis*), certain species of duck (*Pteronetta hartlaubi*), ring plover (*Charadrius hiaticula*), green sandpiper and lily-trotter (*Actophilus africanus*). In the Sudan, the writer observed some open-bill storks flying with *Pila* sp. (presumably *Pila ovata*) or *Lanistes* sp. (presumably *Lanistes carinatus*) in Bahr-el-Ghazal Province. Stomach contents of a stilt (*Himantopus himantopus*, Linnaeus) contained almost complete shells of *Bulinus forskalii*, *Bulinus* (*Physopsis*) *ugandae* and *Gyraulus* sp., besides a number of insects. Ducks kept at certain hafirs (man-made pits) and fish-ponds in the Sudan might have been responsible for the reduction of the snail population in those water-bodies. Gillet (cited in Gillet & Wolfs, 1954) doubts the efficacy of ducks as predators, however, since he came across abundant colonies of molluscs in habitats which are regularly visited by certain species of duck.

Mammals

Although certain mammals, like the musk-rat, rat and otter, have been reported to feed on molluscs in Europe and America, Pilsbry & Bequaert (1927) believe that, in Africa, perhaps only otters select fluviatile molluscs as a preferred type of food.

Aquatic weeds

It is a well-known fact that the presence of aquatic vegetation is advantageous to organisms living in the water, because it increases the amount of dissolved oxygen and consumes carbon dioxide. The effects of these plants on the animal life of water-bodies are listed by Welch (1952).

The broad-leafed vegetation provides a particularly suitable surface where the snail can crawl and deposit its egg masses. Food is also provided for the snail in the form of the brownish-green layer, the periphyton (see p. 814), which encrusts the submerged parts of the plant.

Water-plants are an important factor in the habitat of bilharziasis snail vectors; they affect the number of snails, but are not essential for their occurrence. In other words, the presence of vegetation makes the habitat more favourable for subsistence and breeding, but snails also occur in smaller numbers in the absence of these weeds. Boycott (1936), who made a statistical study of concurrences between snails and plants, arrived at the conclusion that the snails can get along quite well without the plants and that there is no essential biological connexion between them.

It seems that a heavy growth of aquatic plants, especially in small swamps or pools that have no inflow, renders the habitat unsuitable for the vectors. This is due to stagnation of the water and to the abundance of humus and decaying vegetable matter, which occurs both in colloidal suspension, and also settles out and changes the nature of the bottom. Conditions of this type are found in some areas of the swampy Sudd region of the Sudan, where there is a large island, the central area of which harbours only few vectors, while on the outskirts, near the open water, vectors occur in larger numbers.

Aquatic plants may be either free-floating or anchored to the mud. Some beach plants which invade the water from the banks are also used by the snails, especially in the absence of true aquatic vegetation.

In the canals of the Gezira irrigated area of the Sudan, the following plants were reported by Andrews (1945):

Aquatic free-floating: *Spirogyra decima*, *S. maxima*, *S. crassa*.

Aquatic, anchored to the mud: *Potamogeton perfoliatus*, *P. nodosus*, *P. crispus*, *P. pectinatus*, *Chara globularis*, *Ottelia alismoides*, *Polygonum glabrum*, *Jucellus* sp., *Ceratophyllum demersum*, *Najas pectinata*, *Nitella batrachosperma*, *Vallisneria aethiopica*, *Zannichellia palustris*, and *Typha angustifolia*.

Of the plants that invade the canals from the banks, the most important genera are: *Panicum*, *Echinochloa*, *Cyperus*, *Vossia*, *Phragmites*.

In the irrigation canals in Egypt, Simpson (1932) reported the following plants:

Aquatic, free-floating: *Eichornia crassipes* and *Pistia stratiotes*.

Anchored to the mud: *Ceratophyllum demersum*, *Nymphaea caerulea*, *Nymphaea lotus*, and the same species of *Potamogeton* found in the Gezira canals and listed above.

There are also a number of plants invading the canals from the banks, the most important of which belong to the genera *Agrostis*, *Cyperus*, *Echinochloa*, *Phragmites*, *Polygonum* and *Typha*.

It is interesting to note that *Pistia stratiotes*, the " water lettuce ", and *Nymphaea* spp., " the water lilies ", are abundant in the White and Blue Niles, in the Sennar Reservoir, and are common in Egypt, but do not occur in the Gezira.

The White Nile contains more species of aquatic plants than are found in the Blue Nile and the Gezira, since the White Nile is a relatively slow-flowing non-silt-carrying river.

Microflora and food supply

It is self-evident that food is a factor conditioning the habitat of any organism. The food of bilharziasis vectors is largely vegetal, consisting of microflora which form the main constituent of the slimy layer encrusting the submerged plants, and commonly known as periphyton. These microflora multiply rapidly to form a scummy layer on the submerged stems and leaves of plants, on the under-surface of floating leaves, on the bottom mud, on stones, on gravel and on any flotsam. Young (1945) defined periphyton as the assemblage of organisms growing on free surfaces of objects submerged in water, and covering them with a slimy greenish-brown coat. The organisms composing the periphyton belong to several plant and animal phyla, and thus certain microscopic sedentary animals are sometimes also taken in by the snail in the process of ingesting the microflora.

Scrapings of periphyton on stems and leaves of plants in the White Nile at Kosti, on which plentiful and active vectors were crawling, consisted mainly of the following: [1]

Myxophycae (blue-green algae): *Anabaena*, *Anabaenopsis*, *Lyngbya*, and *Oscillatoria*.

Bacillariaceae (diatoms): *Synedra*, *Bacillaria*, *Gomphonema*, *Melosira*, *Nitzschia*, and *Navicula*.

Chlorophyceae (green algae): *Spirogyra*, *Scenedesmus*, *Ankistrodesmus*, *Chlorella*, *Dictyosphaerium*, *Chlamydomonas*, *Arthrodesmus*, and *Cosmarium* (the last two are desmids).

Bacteria: *Spirochaetes*

Protozoa: *Difflugia*, and ciliates

Bryozoa (unidentified)

[1] This is only a partial list :the organisms were identified only as to genus.

Most of these components of the periphyton were present, in fragments or complete, among sand granules in the stomach contents of two *Biomphalaria sudanica* and two *Bulinus (Physopsis) ugandae*.

It is noticed both in the field and in the laboratory that bilharziasis intermediate hosts will eat decaying aquatic plants, although they would not eat the same species when green. Boycott (1936) does not believe that either planorbids or lymnaeids would eat green leaves of the aquarium plants Vallisneria and Nymphaea, as has been claimed by some authors. In the laboratory Standen (1949) found that raw apple-parings and tomato were taken reluctantly by *Biomphalaria boissyi* and *Bulinus truncatus*. I have found that the same vectors raised in aquaria ate lettuce leaves, especially when partly decayed, and dead maple leaves which had previously been soaked in water for a long time. They also ate wheat cereal cooked with milk and agar and supplied on cork floats (Abdel Malek, 1950), as advocated by Noland & Carriker (1946) for *Lymnaea stagnalis*. Watson (1950) in Iraq, observed *Bulinus truncatus* to feed, under natural conditions, on the leaves, twigs and bark of eucalyptus, leaves and twigs of oleander, and leaves of palm, apricot and mulberry.

It was apparent from examination of the contents of the digestive tract of some of these vectors, that they have no preference for any particular species of microflora. As long as the green and blue-green algae and diatoms are represented in the diet, the food supply appears to be suitable for these snails. It should be noted that a diet of this type is found in the majority of habitats, whether they contain well-established colonies or only a few individuals. Consequently, it is not the type of diet but its quantitative composition which is important in conditioning the habitat of the vectors. Both the density of the snail population and the size of the individuals are directly correlated with the amount of food available and probably also with a few other factors, e.g., volume of water. As there is a seasonal fluctuation in the quantity of microflora, one would expect the density of the snail population to vary seasonally also. Scantiness of food supply results in stunted snails. This phenomenon is evident when snails are raised in the laboratory under congested conditions; and dwarfed snails are also met with in natural stocks.

RÉSUMÉ

L'auteur a cherché les raisons de la préférence que montrent certains vecteurs de la bilharziose, au Soudan et en Egypte, dans le choix de leur habitat. Son étude porte sur la littérature concernant les Planorbidés, hôtes intermédiaires des schistosomes, à l'exception de *S. japonicum*.

L'altitude n'a d'importance qu'en corrélation avec d'autres facteurs. La température n'affecte que peu la répartition. Malgré une grande tolérance aux variations saisonnières et diurnes, les mollusques ne se reproduisent activement qu'en saison chaude. Le rayonne-

ment solaire active la croissance des plantes et de la microflore favorables aux mollusques. L'opacité de l'eau est gênante. Les habitats ombreux sont préférés. Des colonies de mollusques ne peuvent prospérer dans de forts courants d'eau ou dans des canaux qui ne sont remplis que temporairement. La dessiccation est fatale. Certains mollusques survivent cependant lorsque le sous-sol ou des herbes leur assurent un minimum d'humidité et une protection contre le soleil. Les eaux usées sont nocives, mais une légère pollution excrémentielle peut être favorable. Un substrat de boue ferme contenant des matières organiniques en décomposition est indispensable. Des sables propres, des rochers, de la boue liquide ne sont pas favorables. La tolérance — par ordre décroissant — de *Bulinus contortus* et de *Planorbis (Australorbis) glabratus* pour anions et cations est la suivante: carbonates, chlorures, sulfates, nitrates, nitrites; calcium, sodium, potassium, magnésium, fer. La présence de bactéries ferrugineuses est peu favorable. Le pH toléré s'étend entre 4 et 9, l'optimum étant 6,5-8,5. Dans les eaux très douces, on trouve des populations peu abondantes et les coquilles des mollusques restent minces. Les mollusques, bien que pulmonés, dépendent plus étroitement de l'oxygène dissous dans l'eau que de l'oxygène atmosphérique. Les conditions qui entraînent la multiplication des bactéries pathogènes, des champignons et peut-être des virus sont nuisibles aux mollusques. L'infection par les schistosomes cause leur mort prématurée, les rend plus sensibles à la dessiccation, réduit la production des œufs, diminue la réserve en polysaccharides. Les mollusques sont victimes de prédateurs qui ne semblent pourtant pas les exterminer, dans les conditions naturelles, contrairement à ce que l'on observe en laboratoire. Ils se nourissent d'algues vertes ou bleues et de diatomées. En aquarium, ils mangent, entre autres aliments, des feuilles de salade partiellement décomposées, des feuilles d'érable mortes et du blé cuit. La quantité de nourriture détermine en partie la densité de la population et la taille des mollusques.

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