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STUDY GROUP ON THE ECOLOGY OF INTERMEDIATE SNAIL HOSTS OF BILHARZIASIS

Report

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STUDY GROUP ON THE ECOLOGY OF INTERMEDIATE SNAIL HOSTS OF BILHARZIASIS

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STUDY GROUP ON THE ECOLOGY OF INTERMEDIATE SNAIL HOSTS OF BILHARZIASIS

Report

Bilharziasis [1] ranks with malaria as a communicable disease of man. With more exact knowledge of the habits of the mosquito intermediate hosts, in conjunction with improved insecticides and better methods of treatment, malaria is being brought under control. Progress in the control of bilharziasis has not kept pace and its incidence is on the increase. This has stimulated a search for practical control measures.

The control of the intermediate host appears to be a logical point of attack but it has become apparent, in part indeed from the limited success of this approach, that comparatively little is known about the relationships between the ecology of the habitats of the snails, their life cycles, their habits, and the mechanism of infection. The aim of the Study Group was to consider the available data that would lead to some practical suggestions on control measures ; to make scientists and public health workers aware of the problems involved ; and to stimulate further research in this direction.

1. DISTRIBUTION OF INTERMEDIATE SNAIL HOSTS IN RELATION TO HYDROGEOLOGY

Studies on the ecology of vector snails in all parts of the world have shown that the diversity, abundance and size of fresh-water situations is correlated with the physiography of a region. The more important factors of hydrogeology are :

1. *Slope of the land (orography).* In rugged, mountainous areas, flowing-water (lotic) situations, often of steep gradient, predominate.

[1] By a decision of the International Commission on Zoological Nomenclature (*Opinions and declarations of zoological nomenclature*, 1954, Opinion 226 (Supplement to Opinion 77), vol. 4, pp. 176-200), the generic name of the group to which the human blood flukes belong is *Schistosoma* Weinland, 1858, and not *Bilharzia* Meckel von Hemsbach, 1856, nor yet *Bilharzia* Cobbold, 1859 ; but the same body recommended that the term " bilharziasis " should continue to be used for the diseases which they cause in man. This practice has been followed in the present report.

Non-flowing (lenitic) situations are usually rare unless man-made, as in the case of reservoirs. In flat regions, many lenitic habitats (e.g., marshes, ponds, lakes, etc.) develop. Lotic situations may also be abundant. These are usually of low gradient, and may be associated with lenitic ones in such a way that the distinction between lotic and lenitic becomes very vague.

2. *Soil and bedrock (lithology)*. The kind of regional substrate influences the quality of water and, interrelated with climate (see paragraph 4), may determine in part the orography of a region. For example, limestone areas provide the water with an abundance of calcium, bicarbonate and carbonate ions. These areas are also characterized by the tendency of lotic situations to be underground, and by peculiar lenitic situations, known as limestone sink ponds.

3. *The geological history*. The geological history of an area may account for the kinds of fresh-water situations present, and produce exceptions to the generalities given above. Thus, lenitic habitats may develop in mountain areas (crater lakes; the great lakes of Africa formed by fault zones). Saltatory regional uplift (working with erosion) can convert flat areas into series of terraces, of which only the lowest may contain permanent fresh-water situations (Antilles).

4. *Climate (regional rainfall and temperature)*. Aquatic situations closer to the equator are likely to have less seasonal variation in temperature than those in the temperate zones, but this depends in part on their altitude, which is an aspect of orography. Rainfall cycles, similarly, vary with latitude, but the amount of rainfall and its effect on fresh-water situations are even more profoundly influenced by orography and lithology than is temperature. Thus, areas of high rainfall may adjoin areas of low rainfall, being separated only by a narrow range of mountains. Also, certain substrates (e.g., some limestones, sandstones or serpentines) may be arid, even though receiving a high rainfall, owing to their porous nature.

Consideration of these and similar related phenomena have provided the basis of classification of the fresh-water situations in all major areas where bilharziasis is prevalent. In continental areas, there may be a uniformity of climate, geological history, lithology and orography over tens of thousands of square miles. On small islands, these factors may vary sufficiently within ten miles to provide striking differences in the kinds of fresh-water situations within that distance. While this approach to the ecology of vector snails is useful for generalities of regional scope, it is equally useful to elucidate the ecology of small areas.

There is little possibility of modifying the four factors *per se* which are outlined above to obtain the control of bilharziasis. Yet it should be noted that these same factors have influenced the geography and ecology of man, who has in turn profoundly influenced fresh-water situations by creating new ones (irrigation), modifying existing ones (reservoirs), and destroying others (marsh drainage). This approach is useful for :

(1) determining where and what type of vector control within a given area would be most useful ; and

(2) evaluating the possibility of bilharziasis crossing ecological barriers and becoming established in non-endemic areas.

2. FACTORS CONDITIONING THE HABITAT AND BREEDING CONDITIONS

2.1 Physical factors

2.1.1 *Temperature*

All snails that transmit bilharziasis appear to show a high degree of tolerance to variation in the temperature of their habitat. In general, it may be said that the optimum temperature for these molluscs lies between 22°C and 26°C, that the threshold of favourable temperature is in the neighbourhood of 18°C, and that the maximum is scarcely above 32°C. However, the snails are able to withstand for a considerable period of time both relatively low and relatively high extremes of temperature, ranging from little above freezing point to well above blood heat. They are rapidly destroyed by freezing (with the exception of *Oncomelania nosophora*) and by temperature in the region of 50°C. Snails which are partly dehydrated during hibernation or aestivation are better able to withstand extremes of temperature than are fully active individuals. Specific and racial differentiation exists as regards threshold, optimum and maximum favourable temperatures and also as regards upper and lower lethal temperatures and periods of exposure to those temperatures (see Table I).

Temperature records are largely based on isolated observations at stated times of day ; but water temperatures show great fluctuation, diurnally as well as seasonally, especially in small stagnant bodies of water, and recent observations with recording thermographs have shown that these fluctuations cover a greater range than was previously appreciated, thus further emphasizing the eurythermal nature of these snails.

An important point is the effect of annual range of temperature upon the length of the breeding season. In certain areas, the period of time during which the water is warm enough to permit oviposition, development and growth is only sufficient for the production of one generation. In latitudes where the warm season is longer, several generations may be

TABLE I. RELATIONSHIP BETWEEN SCHISTOSOME VECTORS AND TEMPERATURE *

Species	Lower lethal temperature	Threshold of favourable tempera-ture **	Optimum temperature	Upper limit of favourable tempera-ture **	Upper lethal temperature	Remarks
Bulinus truncatus	0°C	18°C	18–28°C (22–26°C)	28°C	32°C (4 hours) 52°C (few minutes)	Adults
	0°C	18°C	22–28°C	28°C	42°C (4 hours)	Young forms
Austra-lorbis glabratus	0°C	18°C	18–28°C	30°C	42°C (4 hours) 52°C (few minutes)	Adults
	0°C	18°C	20–26°C	30°C	32°C (4 hours)	Young forms
Austra-lorbis glabratus	0°C (12 hours) 7°C (several days)	?	25–28°C	32°C	42°C (2 hours)	Laboratory experi-ments
Oncome-lania nosophora	Survives refrigerator temperature (snails dry) for more than 1 month		20°C (for survival) 26°C (for repro-duction)	Approxi-mately 30°C	32°C (average survival : 3–6 months)	Adults in laboratory habitats kept at tempera-tures indicated
Oncome-lania quadrasi	As above, for 2–4 weeks		26°C		32°C (average survival : 3–6 months)	As above

* It should be noted that unless otherwise stated the figures given above apply to fully adult snails. There is no doubt that, in certain species at any rate, the eggs and young snails show greater susceptibility to temperature changes than the adults, but insufficient information as yet exists upon this point.

** The favourable temperature range is that within which the snails move actively and breed. Outside this range, breeding ceases and the snails become sluggish and seek shelter.

produced, or breeding may even continue all the year round. Thus *Bulinus truncatus* in northern Iraq produces only a single generation annually, while in central and southern Iraq and in Egypt it produces two or more generations each year. *Australorbis glabratus* in north-east Brazil continues to breed all the year round. A similar situation exists with regard to those species of *Oncomelania* which produce only one generation annually in the northern part of their range, but breed all the year round in the warm southern areas.

Strict comparison of the effect of varying temperature upon species of snails from different areas is not yet possible because there has as yet been no standardization of methods of investigation. The depth at which the temperature of the water is taken needs to be recorded in all cases. Thermocouples near the surface usually give a lower reading than mercury bulb thermometers under similar conditions, owing to absorption of radiant heat by the latter. In any case, it is the temperature of the micro-habitat in which the snails live which is important and which has to be measured and not that of the general body of water. In the case of *Oncomelania* spp., the temperature of the soil on the banks is important when the snails leave the water.

It has been suggested not only that inter-specific differences exist with regard to temperature reactions, but also that geographical races within each species of vector snail may differ as regards favourable and lethal temperatures. Some evidence exists in support of this contention, but more information is necessary before any more definite statement can be made.

2.1.2 *Light intensity*

The opinion has been widely prevalent that snail hosts of bilharziasis are unable to live in complete darkness. However, recent experiments have shown that *Bulinus truncatus* and *Australorbis glabratus* can be maintained and bred in the laboratory in complete darkness over a period of at least five months. Field observations on *Bulinus truncatus* in Egypt, on *Bulinus tropicus* in Rhodesia, and on *Bulinus (Physopsis) africanus* and *Biomphalaria pfeifferi* in South Africa have revealed breeding colonies occurring in covered aqueducts or reservoirs in almost total darkness. In these cases, food materials were probably carried into the habitat by flowing water. The long-term effect of darkness would probably be to reduce the snail populations owing to suppression of the algal growth that provides food for the young forms. It may be, however, that, in the absence of unicellular green algae, other unicellular organisms (such as brown algae, bacteria, protozoa, etc.), fungi, or decomposing organic matter may provide suitable food material for the newly hatched snails. Further observations on this point are desirable.

Under ordinary conditions in nature, certain specific differences in light reactions appear ; thus *Australorbis glabratus* occurs in both exposed and shaded habitats but definitely appears to enjoy direct sunlight. African bulinids and planorbids, on the other hand, appear to prefer lightly shaded habitats and to avoid direct sunlight by hiding under leaves or floating debris. The reactions of *Oncomelania* spp. are similar to those of planorbids and bulinids and, if there is sufficient moisture in the habitat, the avoidance of strong light accounts for a great deal of their activity during the day.

Observations so far made on this point are largely empirical, and further progress will depend upon the carrying out of exact measurements of light intensity and their correlation with the occurrence of the snails.

In assessing the results of any observations on the effects of light upon the snails in natural surroundings, it is necessary to differentiate the effects of light intensity from associated heating effects.

Under natural conditions, sunlight has an important effect on the habitat in ensuring the growth of the flora and fauna which provide the snails with their most suitable food.

The possibility exists that light has an indispensable stimulating action upon the sex glands of the snails and may therefore be essential to continued activity and reproduction among adults and to growth in the case of the embryos, larvae and immature forms. Should this be proved true by further investigation, the long-continued existence of breeding colonies of these snails in total darkness is clearly impossible ; and this would have an important practical bearing upon control, since the covering of irrigation channels and the piping of irrigation water-supplies could be considered as a practical method.

2.1.3 *Water movement*

Water movement in a habitat is beneficial inasmuch as it promotes oxygenation of the medium. It has, however, other effects which may be treated under the following four categories :

1. *Wave action.* Violent wave action is generally deleterious to intermediate hosts of bilharziasis, especially if it takes place upon a steeply shelving shore devoid of water plants. Its effect is normally only of importance in lakes and reservoirs.

2. *Current.* In general, snails that transmit bilharziasis prefer stagnant or slowly running water. Fast running water appears to prevent the establishment of breeding colonies, especially if the water is heavily laden with silt or other suspended particles. Few records exist concerning the limiting speeds of continuous flow, but some evidence is available that *Bulinus truncatus* cannot establish itself where the rate of flow is higher than 15 metres per minute, while *Australorbis glabratus* does not seem to occur in streams with a slope greater than 20 per thousand. Higher rates of flow can be withstood in streams or channels where the current is intermittent ; the longer the intervening periods of stagnations, the higher is the rate of flow which can be borne.

Current velocity in the centre and at the surface are not necessarily indicative of flow conditions at the bottom or sides of a stream or channel where the water is often moving more quietly. The existence of quiet bays and eddies promotes the establishment of the snails in apparently rapidly moving water.

More rapid flow is tolerated when the water is clear than when it is silt laden.

Records of colonies of intermediate snail hosts from apparently fast running water need re-investigation. They may be based on erroneous or misleading observations, especially since figures of current velocity have not been given ; but the possibility also exists that different geographical races of the same species show different resistance to current as a limiting factor.

Marked inter-specific differences in relation to this factor have been noted. Thus *Biomphalaria boissyi* and *Biomphalaria pfeifferi* are less able to establish themselves in rapidly flowing water than *Bulinus truncatus* and *Bulinus (Physopsis) africanus*, which in turn are less able than *Neritina nilotica*.

It has been suggested that larger species and older snails are more readily affected by current velocity than smaller species and younger snails.

The mechanism of the inimical action of current velocity appears to depend in part upon the washing away of the snails, in part upon the inhibition of the growth of water plants, in part upon the removal of substrata, in part upon its restrictive action on the feeding and reproduction of the snails (which may have to remain retracted or attached immobile in order to avoid being swept away), and in part upon the abrasive action of suspended silt.

Current is effective in distributing the snails, which may be carried for long distances. In this way distant habitats may be reached and colonized.

3. *Floods.* Floods appear to be uniformly harmful to snail populations, having all the deleterious effects of rapid current velocity with the addition, in some cases, of a marked drop in temperature which is sufficient to interrupt breeding.

Some individuals usually succeed in surviving the floods by remaining in sheltered spots or by becoming buried in the mud.

The seasonal occurrence of floods has some effect upon seasonal fluctuation in the size of snail populations, since it not only dislodges or destroys many individuals, but also interferes with or entirely prevents breeding.

4. *Turbulence*. Little is yet known about turbulence, but evidence exists that adult snails which transmit bilharziasis can withstand violent turbulence produced by pumps and sluices for limited periods of time and survive to establish themselves in quieter waters further downstream.

The lesser but more continuous form of turbulence produced by the passage of animals or boats through the water appears, in certain instances, to prevent the establishment of breeding colonies of these snails.

2.1.4 *Water-level fluctuation and desiccation*

When stranded on dry land by a falling water level, snails that transmit bilharziasis (especially *Biomphalaria* spp.) make little or no attempt to escape back into the habitat, although their degree of activity would enable them to do so. They are thus exposed to the risk of death by desiccation, by the action of the heat of the sun or by consumption by terrestrial predators (such as land birds, wild rodents, pigs, etc.), which would not normally be able to reach them, and a very large proportion of snails so exposed do, in fact, die. The death-rate depends in part upon the length of exposure, in part upon the rapidity with which the water level falls, in part upon the presence or absence of shade, and in part upon the relative humidity of the atmosphere. Prolonged exposure, rapid fall of water-level, absence of shade and low relative humidity all tend to increase the death-rate and to accelerate death. Rapid and regularly repeated changes of level might be a useful and practical means of controlling aquatic snail hosts in certain types of irrigation channel and reservoir.

Resistance to the lethal effect of desiccation is high in the case of certain strains of snail host species that have been investigated under suitable conditions both in the laboratory and in nature. Survival out of the water for periods of from 3 to 11 months has frequently been achieved under experimental laboratory conditions. In nature, these snails may occur in temporary pools in Africa and South America which dry up for several months during the hot season, obliging the snails to aestivate. Not all individuals survive this dry period, but a sufficient proportion do so to repopulate the habitat when it is once more filled with water.

Desiccation has less effect on adult *Oncomelania* spp. than upon aquatic snails, but affects oviposition, and the eggs which are laid near water-level are very susceptible to drying. Oviposition in these species is stimulated by floods and by a rising water-level. Eggs of other species of snail hosts also show less resistance to desiccation than the adults. As in the case of snails exposed by water-level changes, desiccation may produce no active attempt on the part of some species to escape by burrowing into the mud; but individual snails, in the course of their ordinary movements on a soft substratum, often become partially buried or entirely buried by accident. Evidence exists that deep burial may even be fatal in the case of *Australorbis glabratus*. On account of the resistance shown by, at any rate, a proportion of the snails, desiccation can be used as an effective control measure only under special conditions. Thus, in hot dry climates it is effective in clean cement-lined channels, but only rarely so in mud-lined channels, unless the periods of drought are prolonged in relation to the periods of high water and recur at relatively short intervals. Rapid desiccation is probably more effective than slow desiccation in killing snails. Individual snails may succeed in escaping death if they fall into cracks in the mud or if they are protected by vegetation or debris, which provide them with shade and shelter, where they may survive for prolonged periods until water again reaches them. Desiccation as a means of control is naturally more effective where the subsoil water-level and relative humidity are low; but it is important to realize the existence of microclimatic conditions, whereby the relative humidity in the immediate vicinity of the molluscs may be substantially higher than that in the general atmosphere.

Recent work has shown that species and strains of snails show great variation in resistance to desiccation. This appears to be a genetical phenomenon. In habitats where desiccation occurs regularly, natural selection has produced genotypes which are highly resistant to dry conditions. In north-east Brazil, it has been shown that mature *Schistosoma mansoni* die out relatively rapidly in aestivating *Australorbis glabratus* under conditions of desiccation; but the immature stages of the parasites may survive in a large proportion of snails, complete their development and give rise to infective cercariae when water returns to the habitat. This phenomenon requires further study, since it is evident that different strains of the vector species may vary in their transmission potential according to their ability to survive drought in the infected condition.

2.1.5 *Depth of water*

In general, the aquatic snails that transmit bilharziasis occur in shallow waters near the shore. Amphibious species may also occur on moist soil, on water plants, or on other surfaces near the water. Under natural conditions, it is rare to find them in depths exceeding 1.5-2 metres. It would appear that this fact is correlated more with conditions of food and shelter for the snails, which are only available near the surface, than with any direct effect of water pressure. The absorption of light by the upper layers of water, especially if these are turbid, limits the occurrence of green algae and of rooted vegetation to the top two metres of most natural habitats of these molluscs; and food and shelter therefore attract the snails to this zone. Experiments with *Bulinus truncatus* and *Australorbis glabratus* have shown that both these species can exist for considerable periods of time at a depth of 10 metres, on the condition that they are artificially provided with food and protected from predators. In any case, species of snails normally living near the bottom in deeper water are of little importance in the transmission of bilharziasis, since schistosome miracidia are positively phototrophic and remain near the surface.

It has been said that the aquatic snail hosts need atmospheric air for respiratory purposes, and since they must therefore come to the surface from time to time to obtain it, they cannot live at any considerable depth. Recent work indicates that the importance of this factor has been exaggerated and that if the oxygen tension is high the pseudo-branch suffices for very long periods to extract oxygen from the water.

The possibility exists that the young snails may be less able to live in deeper water than the adults.

2.2 Chemical factors

2.2.1 *Salinity*

The mineral content of the water has a profound effect upon the snails living therein when limiting values are approached, but within this range there is a wide degree of tolerance. The total amount of dissolved solids (total salinity) of the water is of less importance than the proportions of the constituent salts. Threshold and ceiling values of individual dissolved solids may exist, but they are incompletely understood and, in any case, such limiting values are rarely reached in nature. Considerable differences in tolerance exist between the different species of snail hosts so that what is applicable to one is not necessarily applicable to another species. Thus *Australorbis glabratus* is not inhibited by the sodium chloride content of the water until the concentration reaches 6000 parts per million, whereas *Bulinus truncatus* is seriously incommoded before the value of 4000 parts per million is reached. The ceiling value for young snails is substantially lower than that for adult forms.

A minimal amount of calcium is required by the snails for the formation of the shell, but since the mineral constituents of the shell are extracted from the food or eaten directly, they may be available in sufficient quantities even when present in very low concentration in the water. It has been shown in connexion with land snails that particles of calcium carbonate are transported by amoebocytes from the digestive gland to the mantle. It has also been shown that many species of snails exist quite satisfactorily for long periods in water of which the lime content is less than 10 parts per million.

As regards other mineral salts, it has been found by many workers that the variations which occur in natural habitats are without effect upon the development and life of the snails. However, more needs to be known about the diurnal and seasonal fluctuations in the concentration of mineral salts before any definite statement can be made.

Certain mineral salts, in addition to those, such as the copper salts, which are so well known as to be used as molluscicides, are toxic to the snails. Among these may be mentioned the salts of barium, nickel and zinc, which may produce distress or death. A sublethal concentration of such substances may produce a reversible " distress " phenomenon, whereby the snails appear to suffer from a form of paralysis. Little is known concerning the effect of trace elements upon the life of the snails. A related phenomenon may be the toxicity to the snails of water in newly constructed cement channels.

Sudden rises in chloride content, even though occurring at long intervals of time, may be sufficiently lethal to the eggs or young snails to prevent the establishment of a species in the vicinity of a tidal estuary. Such a situation exists on the banks of the Shatt El-Arab estuary at the head of the Persian Gulf, where, for a considerable distance inland, *Bulinus truncatus* is unknown, owing to periodic rises in the chloride content from the normal 400-800 parts per million to a figure in the neighbourhood of 5000 parts per million for several tides. This phenomenon is due to the fact that low discharge by the river coincides with strong southerly winds from the Persian Gulf and exceptionally high tides which drive salt water far inland. *Bulinus truncatus* is present in abundance further north out of the reach of these saline incursions.

Further work should include investigations into the effect of trace elements upon the snails and into such biochemical problems as the existence and effect of hormones, growth factors and protein decomposition products.

2.2.2 *Ion balance*

In general, concentrations of individual ions are low in waters with only small amounts of dissolved solids and correspondingly high in waters having larger amounts of dissolved solids.

Such investigations as have been carried out appear to show no significant correlation between the calcium-magnesium ratio and the distribution of intermediate snail hosts.

In some situations where *Australorbis glabratus* snails are present, the proportion of the weak acids (bicarbonate and carbonate) to the strong acids (chloride and sulfate) is less than 3 to 1, when these ions are expressed in equivalents per million. In some situations where the snails are not present, this ratio is higher than 4 to 1. A similar relationship may be found to exist in the case of other species of snail hosts.

It has been reported that low concentrations of ions of heavy metals, such as copper and zinc, may be limiting agents in waters having small amounts of dissolved solids; whereas in waters having larger amounts of total dissolved solids similar concentrations of ions of these metals are sometimes without effect.

2.2.3 *Hydrogen-ion concentration*

Field and laboratory observations tend, almost without exception, to indicate that intermediate snail hosts of bilharziasis are tolerant of a wide range of pH in the waters of their habitats.[1] The intermediate hosts have been found (see Table II) in natural bodies of water in which the pH ranges from as low as 4.8 to as high as 9.8, and, within these limits, variation of this factor seems to have no effect on the density of snail host populations. Pronounced specific differences do not appear to exist in regard to this factor. Laboratory experiments have shown that *Bulinus truncatus*, *Biomphalaria adowensis* and *Australorbis glabratus* can be bred between pH 4 and pH 10. *Oncomelania* spp. have been found in waters ranging from 6.2 to 7.8 and on soils ranging from 4.6 to 7.2, and therefore appear to be more restricted than the aquatic species. However, such findings are largely based on isolated observations, and all available evidence points to the existence of great fluctuation in pH in natural bodies of water during 24 hours. Findings based upon continuous field observations over a considerable period of time would be of interest in this connexion. While discussion of pH levels in the occurrence of water snails follows limnological convention, it must be stated that the value of such observations is dubious. The pH is affected by many different environmental factors (occurrence of water plants, chemical composition of the water, etc.), any or all of which may be more important in themselves than the degree of acidity or alkalinity which they produce.

2.3 Pollution

The word pollution has been loosely used to cover a number of different forms of water contamination. It is necessary to state precisely what is meant by pollution in any particular case. For the purposes of this section, forms of pollution may be classified under the following headings:

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[1] Field studies show that the same is true of the pH of the soil in the habitats of *Oncomelania* spp.

TABLE II. PH RANGE IN SNAIL HABITATS

Species	pH range	Area
Bulinus truncatus	7.8–8.6	North Africa
Bulinus (Bulinus) sp. *Bulinus forskalii* *Bulinus (Physopsis)* sp. *Biomphalaria ruppellii*	7.1–7.8 8.0 (5.9–6.0) 8.0 7.8–8.0 Diurnal variation in lagoon near Lake No: 8.3–8.7 General pH tolerance of schistosome vectors in Sudan: 6.0–9.0	Sudan
Bulinus spp. and *Biomphalaria* spp. *Bulinus* sp. and *Biomphalaria* sp.	8.6 7.0–8.2	South Africa
Oncomelania sp.	Soil, 4.6–7.2 Water, 6.2–7.8	Philippines
Bulinus truncatus *Bulinus strigosus* *Biomphalaria adowensis* *Australorbis glabratus*	All these species breed in the laboratory between 4.8 and 9.8	Laboratory
Biomphalaria sp. *Bulinus (Bulinus)* sp. *Bulinus (Physopsis)* sp.	6.2–8.9	Rhodesia
Bulinus truncatus	Below 6.3, high mortality Above 7.9, unfavourable	Iraq
Australorbis glabratus	6.0–9.1 (optimum, 7.0–8.0)	Puerto Rico
Tropicorbis paparyensis	6.7–7.6 (5.0 appears to be lethal over long periods)	Brazil
Bulinus (Physopsis) jousseaumei *Bulinus forskalii* *Bulinus guernei* *Bulinus senegalensis* *Biomphalaria gaudi*	6.0–6.7 6.0–7.0 (usually about 6.5) 6.5 6.0–6.5 6.0–6.7	Gambia

(1) Pollution by decaying organic matter :

 (*a*) organic matter of animal origin

 (*b*) organic matter of vegetable origin

(2) Pollution by excrement (faeces and urine) :

 (*a*) human faeces and urine

 (*b*) animal faeces and urine

(3) Pollution by industrial wastes

Pollution by decaying organic matter is a common phenomenon in bodies of fresh water but is markedly more pronounced in the vicinity of human habitations, owing to the casting of animal rubbish (bones, skins, fragments of meat, carcasses, etc.) and plant rubbish (vegetable parings and discards, waste fruit, etc.) into the water. Such pollution is definitely favourable to the occurrence of snails that transmit bilharziasis and appears to provide them with a rich source of additional food material. Certain authors have claimed that there is also a strong positive correlation between the occurrence of these snails and the presence of decaying organic matter of plant origin in natural habitats.

Investigators are almost unanimous in stating that a moderate degree of pollution with human excrement is favourable to the establishment of large populations of snail hosts. It is not known in most cases whether this favourable effect is due to faeces or to urine, since the effects of these two types of excrement can normally not be differentiated, but recent work has shown that in parts of Gambia there is some evidence to show that the pollution of streams by urine alone has a favourable effect on the snail populations. The mechanism of this favourable relationship remains in doubt. It may be that excrement provides one or more growth factors which have a direct effect in stimulating reproduction or development in the snails. On the other hand, it may be that the effect is an indirect one due to the fertilizing action of some elements in the excrement upon the microflora which is suitable for the food of the young snails. A moderate degree of pollution with animal excrement also appears to be favourable in some cases. It may be that a specific relationship exists between the excrement of the definitive host and the growth and development of the intermediate snail host in the case of other species of schistosomes. Some evidence in support of this theory has been found in the case of the *Schistosoma* parasites of wild ducks in North America, in the fact that bovine excrement is favourable to *Bulinus (Physopsis) globosus* (intermediate host of *Schistosoma bovis* in South Africa), and in the fact that the rats that are reservoir hosts of *Schistosoma mansoni* in north-east Brazil defecate in water and that the snail hosts (*Australorbis glabratus*) congregate to feed upon the faeces. Whatever the mechanism may be, there is no doubt that the favourable effect of pollution with human and animal excrement upon the snails results in the development of larger populations of snail hosts in the vicinity of human habitation than elsewhere.

Chemical pollution, coming principally from industrial wastes discharged into reservoirs and streams, appears to be almost uniformly deleterious to the snail hosts, which are generally absent from waters so contaminated.

Knowledge gained so far in this field has been largely based upon casual observations, and future investigations should, where possible, take into account the possibility of utilizing quantitative criteria of pollution. Among methods which have been suggested for this purpose, the following may be mentioned :

1. Measurements of chemical change resulting from pollution

(1) *Oxygen requirement*

(*a*) *Biochemical oxygen demand (BOD)*

This method requires cumbersome field apparatus and is of little value unless the water samples can be delivered to an analytical laboratory within a few hours.

(*b*) *Potassium permanganate reduction*

Titration of 0.1 N solution of potassium permanganate against the water to be investigated provides an estimate of its oxygen content and therefore of the degree of pollution. This method has been criticized but is widely used in connexion with the examination of sea water and is valuable for comparative purposes.

(2) *Chemical analysis of inorganic substances which are increased by some types of pollution*

(*a*) *Chloride content*

This method has been widely used by sewage engineers.

(*b*) *Content of ammonia or other nitrogenous compounds*

These methods are useful because of the implication of proteinoid substances present.

2. Biotic indices

(1) *Gross biotic zonation*

This method consists in observing the sequence of dominant fresh-water organisms proceeding downstream from sources of heavy pollution. (It is likely to be more useful to field workers than methods involving chemical analysis, but its use must be preceded by fundamental limnological investigations, since the fresh-water organisms occurring in the different zones differ in different parts of the world.)

(2) *Plankton identification*

Since the identity of the forms of fresh-water plankton occurring in waters polluted to varying degrees differs markedly, these organisms can be used to indicate the degree of pollution. This method has been described in the report of the Study Group on International Standards of Drinking Water Quality which met in June 1956:[1]

4.6 *Detection of pollution by biological examinations*

The biological examination of water provides a valuable and sensitive means for the rapid detection of pollution of water by sewage, organic wastes and toxic substances. It is particularly adapted to detecting pollution in distribution mains due to cross connexions of polluted water and potable supplies. Numerous techniques have been developed for this purpose. These depend upon the susceptibility of fresh-water plankton to the destructive effects of polluting substances. Most of these organisms are very sensitive indicators of pollution because of the narrow range of pollution concentrations which they can tolerate. Thus, by biological or microscopic examination the degree of pollution may be estimated.

4.6.1 *Procedure*

A sample of 500-1000 ml should be collected, concentrated and examined as soon as possible and without the use of any method of preservation. A count is made, using the established techniques, of the individual uni-cellular organisms, dividing them into two groups:

A = chlorophyll bearing
B = non-chlorophyll bearing

A biological index of pollution (BIP) is then calculated by the following equation:

$$BIP = \frac{B}{A + B} \times 100$$

Values of BIP:	0-8	= clean water
	8-20	= slightly polluted water
	20-60	= polluted water
	60-100	= grossly polluted water

This index is a rapid means of detecting pollution, requiring only a short time to complete. It yields comparable information to that given by the general plate count of bacteria and the several chemical tests for pollution.

2.4 Biological factors

2.4.1 *Natural enemies and predators*

It is doubtful whether natural enemies and predators can ever be in themselves an effective means of control; but, under suitable circumstances, they may be of help in reducing snail populations. In any particular case,

[1] Unpublished working document MH/AS/200.56

it is important to study the possible long-term ecological effects of introducing predatory or competing species into a new area. Laboratory experiments have yielded valuable information about different species of animals which prey upon fresh-water snails, but conditions in nature are frequently different and more needs to be known about the food preferences of predatory species under natural conditions. Among the forms which have been recommended as possibly of value in the control of snails that transmit bilharziasis may be mentioned :

(1) water rats (e.g., *Microtus amphibius*) ;

(2) certain species of ducks (not all species of duck eat snails) ;

(3) turtles (some species feed almost exclusively upon snails in nature) ;

(4) salamanders ;

(5) clawed toads (e.g., *Xenopus* spp.) ;

(6) fish (e.g., *Gambusia* spp., *Lebistes clarias* and *Tilapia massambica*) ;

(7) many species of aquatic insects, including dipterous, lampyrid, dytiscid and odonate larvae as well as adult belostomids ;

(8) crustaceans (e.g., crayfish of the genera *Astacus* and *Cambarus*, fresh-water crabs of the family Potamonidae, ostracods of the genus *Cypridopsis*) ;

(9) carnivorous leeches of various species ;

(10) certain ciliates and other snails, especially species of *Marisa*, *Ampullaria*, *Physa* and *Limnaea*, which sometimes destroy snail-egg masses.

It has to be emphasized that information concerning these matters is largely based upon laboratory experiments, and conditions in nature require further investigation. Ducks have been used experimentally by certain health services in the Philippines as a means of eradicating *Oncomelania* spp. but have been found to be ineffective. In parts of Africa and the West Indies, ducks are extensively bred by the agricultural population, but it is doubtful whether they provide any degree of natural bilharziasis prophylaxis. Further details on the efficacy of ducks for snail control would be of value.

Quantitative investigation into the snail-eating activities of each of these forms is needed. Even in the event that one of them, or some as yet unsuspected species, is found to prey extensively or exclusively upon any species of intermediate snail host, it is by no means certain that its activities will have the effect of permanently reducing the snail population, since interaction between two opposites—predator and prey—may result in continuous periodic fluctuations in the numbers of both species rather than in the complete eradication of the latter.

2.4.2 *Parasites and diseases*

Remarkably little information is available as to the parasites and diseases of snail hosts and their effect upon population numbers. Undoubtedly the snails are affected by epidemic diseases of viral and bacterial origin from time to time, but these matters have been insufficiently investigated. Further work is most desirable in view of the fact that microbiotic agents of destruction are likely to be more specific in their action and therefore more effective than macrobiotic agents.

Recently, it has been reported that the introduction of *Bacillus pinottii* into their habitats results in the death of the snails which transmit bilharziasis. Although it is not yet certain that this bacillus causes epidemic disease among the snails, the results so far achieved should stimulate further search for bacteria and viruses which would produce this effect, thus providing a potent weapon for snail control.

Fungal infections of fresh-water snails have been observed on rare occasions, some species of these parasites attacking the pulmonary cavity and causing death; but such knowledge has yet to be applied to intermediate snail hosts of bilharziasis.

Nothing useful is known about protozoal diseases.

Certain trematode groups (e.g., echinostomes) are more pathogenic for snails than others. They tend to invade the reproductive organs and digestive gland, causing reduced reproductive potential or death. Trematode infections have been tried experimentally in Japan for the control of *Bithynia*, an intermediate host for *Clonorchis sinensis*. This method might be tried out against schistosome infections.

Research into the possibility of other disease-causing organisms affecting these snails should be actively pursued. This is a promising field requiring further investigation. The result of infection of a snail population may not be complete eradication but will probably lead to a marked reduction in numbers.

2.4.3 *Food preferences*

Water snails in general are able to subsist on a variety of different food materials and exercize little apparent choice. The young snails, having as yet a small and feebly developed masticatory apparatus, are obliged to feed upon unicellular organisms or very small soft organic particles. Unicellular green algae appear to be the preferred food of the newly hatched snails. Older snails subsist in part on vegetable matter and in part upon the microflora of their environment. It is rare that water snails attack the healthy tissues of living water-plants, since they seem to prefer partly decayed vegetable matter. In some cases, decaying organic matter of animal origin may be attacked, and this seems to be more common among planorbids than among bulinids. The ability and willingness of the vectors to eat almost any organic material offered to them is largely responsible for the correlation found between human and animal pollution and refuse and numbers of snails.

Specific differences in relation to choice of food do exist. All the vector species are omnivorous, but primarily phytophagous. *Oncomelania* spp. apparently show a preference for food rich in cellulose ; bulinids tend to be fairly strictly herbivorous ; while planorbids eat food of animal origin as readily as they do that of plant origin.

The preference of the snails for vegetable matter which has begun to decay is illustrated by the fact that, while not attracted to fresh palm leaves, they congregate upon and feed on palm leaves which have been submerged for some days and in which decomposition has commenced. There is no evidence that they attack the fresh healthy leaves of water plants, except in the absence of any other source of food.

The feeding habits of various species of intermediate hosts may be important in determining the form in which stomach poisons can be applied. It has been observed, for instance, that *Tropicorbis centrimetralis* tends to feed on the river bed. *Oncomelania* spp. feed on the moist soil above the water-level and on micro-organisms found on living and dead vegetation in the shallow water. Sufficient information is not as yet available concerning feeding habits in general, and further investigation would be valuable.

2.4.4 *Vegetation*

Water plants form a desirable but not an essential feature of the habitat of snail hosts. Bulinids appear to be slightly more dependent than planorbids upon the occurrence of aquatic vegetation, but both types of snails can subsist in its absence provided that other food material is available.

Plants apparently favourable to the aquatic snails include, among many others, *Nympheaceae*, *Potomageton*, *Pistia* and *Myriophyllum*. Broad-leafed plants provide suitable surfaces for the deposition of eggs and for the growth of unicellular green algae which form a favourite food of the snails. There is no doubt that the microflora and fauna on the leaves of these plants are more important to the snails as a source of food than the plants themselves.

Water plants also provide the snails with shelter and protection from intense sunlight and from the mechanical effects of fast current. In habitats exposed to bright sunlight, planorbids and bulinids are generally found sheltering on the underside of the leaves, where the temperature may be two or three degrees lower than in more exposed situations. Oxygen tension may also be higher, especially on the underside of leaves such as those of water-lilies which have no cuticle. The underside of leaves therefore forms a favourite microhabitat.

Oncomelania spp. require emergent vegetation or vegetation growing closely along the bank near the water's edge on account of their amphibious habits. Such plants shade the habitat and their transpiration cools the air and makes the habitat more favourable to snails emerging from the water. Decaying vegetation from water plants assists in the formation of a suitable substratum and provides additional food material for the snails.

In some cases, the translocation of oxygen to the roots of water plants provides water snails with a microhabitat having a high oxygen tension near the bottom. Such snails (e.g., *Bulinus forskalii*) may be found on or close to the roots of plants near the bottom, where they are less likely to become infected by miracidia, which are normally found at the surface. This may explain the fact that *Bulinus forskalii*, also a potential vector, is rarely found infected in nature. A point which requires investigation is the relationship between different species of unicellular algae and the growth of the newly hatched snails. It may be that certain species of algae are more favourable to the growth of the snails than other species. It has been shown that the young snails flourish when supplied with diatoms or Chlorophyceae but dislike Cyanophyceae and die off when these alone are available as food.

Some species of plants have been shown to be antagonistic to the snails; among these may be mentioned *Saponaria*, *Balanites*, *Eucalyptus*, *Tephrosia* and *Schwartzia*. Extracts of some of these plants are actually lethal to certain species of snail hosts.

Further investigation is required, from a botanical as well as from a zoological standpoint, concerning the relationship between different plant species and plant associations in and on the margins of water and the occurrence of various species of water snails therein.

2.5 Breeding conditions

A combination of factors, as yet very imperfectly known, is necessary for successful breeding (i.e., for oviposition, larval existence and youth) of the snail hosts, and is probably of great importance in determining their occurrence and distribution. The habitat of the snails must present this combination of factors (physiological reproductive constants) from time to time if the population is to maintain itself therein. Other factors in the general environment which are apparently correlated with the occurrence or non-occurrence of the snails may actually be of secondary importance. The ability of individual adult snails merely to survive under given ecological conditions is of little value to the species unless the cyclic recurrence of these breeding conditions in the micro-environment is assured.

Oviposition, embryonic development and the life of the young forms of the molluscan intermediate hosts appear to occur, therefore, only within relatively narrow limits of certain environmental factors, which tend to show cyclic recurrence both in nature, in correlation with climatic or seasonal cycles, and in buffered media in the laboratory. Although information on this problem is still very limited, certain of these reproductive constants have been experimentally investigated in the cases, for example, of *Australorbis glabratus* and *Bulinus truncatus*, in particular, as concerns temperature, light intensity, mineral content of the water and food requirements. But further research is needed to investigate these conditions in natural habitats.

3. SEASONAL AND CLIMATIC FACTORS INFLUENCING THE LIFE-CYCLE

Seasonal and climatic factors have a profound effect upon the life-cycle of intermediate snail hosts. It must be emphasized that every habitat shows seasonal variations, which, however, are more pronounced in some cases than in others. Owing to this fact, all ecological studies of the molluscan hosts must be continued over a long period of time in order that the seasonal changes may be accurately assessed. Wherever possible, a number of different localities within any given endemic area should be studied from this point of view because seasonal variations may differ in bodies of water of different types even within a relatively restricted region.

Rainfall cycles are among the more important climatic factors which affect the life of the snails. Flooding due to rainfall is often harmful since it washes the snails away, alters their environment, and sometimes causes a lowering of temperature which is sufficient to interrupt breeding. On the other hand, it may disperse the snails, thus leading to their establishment in habitats where they did not previously occur ; and after the subsidence of the flood waters, it may also bring about the development of highly favourable conditions for breeding. Constant rainfall maintains water-levels, with resulting uniformity of molluscan environmental conditions ; whereas cyclic rainfall leads to cyclic changes in water-levels which are reflected in life-cycle and population changes. The degree of relative humidity of the atmosphere, which has important effects upon the survival of amphibious snails and of aquatic snails deprived of water, is largely regulated by the rainfall. Rainfall also influences the subsoil water, a high level of which is favourable to the snails.

Water-level cycles depend not only upon rainfall but also upon irrigation practices, temperature and evaporation. They are important in the life of the snails for many reasons. They affect oviposition, especially in amphibious species (*Oncomelania* spp.), and have an influence upon the development of snail food. A falling water-level may cause the exposure of the snails, with the result that many of them are destroyed by desiccation or by the attacks of predators or scavengers. A rising water-level, on the other hand, may favour the hatching of the eggs and the development of the young, as in the case of *Oncomelania* spp. In Japan, because of an annual water-level cycle, only one generation of snails that transmit bilharziasis is produced each year. In the Philippines, on the other hand, reproduction is continuous where the water-level is constant or nearly constant ; but in areas in which there is a dry season, the snails do not occur.

Reproductive cycles and population cycles depend not only on rainfall and water level but also on temperature and unknown factors which interact in a way not at present understood. It may be noted, however, that in areas of constant temperature, rainfall and water-level, there are no great cyclic shifts ; small ones may occur, although they are irregular or sporadic. In these areas, reproduction takes place all the year round. In areas where seasonal rainfall, water-level or temperature cycles occur, reproductive and population cycles of snail hosts may be pronounced, particularly as the result of the influence of these factors upon egg-laying. Reproductive and population cycles naturally lead to seasonal fluctuations in the transmission potential of the snails and therefore to the infection risk to man. There is no conclusive evidence for reproductive and population cycles independent of cyclic fluctuation of environmental factors ; but irregular population changes independent of seasonal factors may occur.

As regards oviposition and the egg stage, little evidence is available from South America and Central or South Africa ; but investigations in North Africa and the Middle East have shown that egg deposition by snail hosts is greatest during the warm season of the year, often reaching two peak values, one in early summer and one in late summer. It would appear, therefore, that temperature is the greatest influence in the promotion of egg production, but it must be remembered that some workers believe that in nature seasonal rhythm in oviposition is not only due to temperature but may also be related to the flood season. In the Philippines, where temperatures are fairly constant, oviposition by snails that transmit bilharziasis (*Oncomelania quadrasi*) is influenced by a rise in water-level.

Temperature also affects the hatching time. In North Africa, *Bulinus* eggs require three weeks during the months of December, January and February, whereas during August and September they will hatch in ten days. Marked specific differences exist in relation to egg-laying sites. Thus, *Oncomelania quadrasi* prefers to lay its eggs at or above water-level on a solid substrate, e.g., coconut husk, whereas *Oncomelania nosophora* is more apt to lay eggs in the water and prefers soil as a substrate.

Favourable ecological conditions are most necessary for the young snails during the weeks immediately succeeding hatching. Such snails are less resistant than adult snails to desiccation, to temperature changes and to high concentrations of sodium chloride and other salts. Moreover, they are unable to exist without a microflora consisting of unicellular green algae, diatoms, bacteria and the like. In areas with a pronounced warm season, snails hatched early in the season become mature before the onset of cooler weather, whereas those hatched late in the season do not reach sexual maturity until the following warm season. Vector species which occur in more equable climates do not show seasonal variation of growth to the same extent. In certain species (*Oncomelania quadrasi*), under conditions of year-round even temperatures there is correlation between reproduction rates and rainfall.

The life-span of adult aquatic snail hosts does not normally exceed 12-15 months, whereas the amphibious species have a life-span ranging from 6 months to 3 years. Their behaviour and activities are to some extent affected by seasonal climatic cycles. Some forms aestivate during the warm dry season when the pools in which they live dry up. Other forms hibernate during the cold season, when temperatures fall below the threshold of activity. Conflicting opinions exist with regard to the deliberate burrowing of snails into the mud of drying-up habitats. This phenomenon is considered more likely to occur in nature in the case of bulinids, since it has been observed in the laboratory, than in the case of planorbids or *Oncomelania* spp., in which laboratory evidence suggests that it may not occur. Recent work has shown that at least two different ecological races of *Australorbis glabratus* are to be found in Brazil, which differ markedly in their resistance to desiccation. This fact is probably connected with the seasonal climatic changes in the areas where these forms occur. It may not be out of place to mention here that it has recently been demonstrated for the first time that a diapause in *Schistosoma mansoni* infection of *Australorbis glabratus* exists. If snails of this species are taken out of water less than 20 days after their exposure to infection, development of the infection ceases, to recommence when the snails are restored to water. There is some evidence that approaching aestivation is accompanied by a marked reduction in the size of the sex glands and an increase in the number of glycogen granules in *Bulinus (Physopsis)*.

Fluctuation in adult populations of intermediate snail hosts may thus be due to seasonal temperature changes or to floods (e.g., in the Middle East and North Africa), or to seasonal drought (e.g., in north-east Brazil and eastern, central and southern Africa).

Marked population fluctuation in molluscan hosts, which appears to be independent of seasonal or indeed any other ecological changes, has been reported but requires confirmation.

Population density is affected by many ecological factors which are neither seasonal nor climatic; reference to these has already been made in section 2 (page 5).

Since snail hosts of different species from different geographical areas can be bred successfully under standardized and uniform laboratory conditions, there must be certain basic factors associated with the life-cycle in different habitats.

4. PRESENT KNOWLEDGE OF ECOLOGY AND ITS APPLICATION TO BILHARZIASIS CONTROL MEASURES

4.1 Molluscicides [1]

With present molluscicides, eradication of pulmonate snails that transmit bilharziasis can be achieved without excessive expense in small or static bodies of water such as wells, small ponds, small streams and small irrigated areas unconnected with other bodies of water. Control of the pulmonate vectors, but not eradication, is probably all that can be hoped for or attempted in somewhat larger bodies of water or water systems such as some ponds, lakes, streams and irrigation systems of modest size isolated from other bodies of water. In some areas, it is not now possible even to control the pulmonate vectors economically by the use of molluscicides. Bodies of water in this category include lakes, rivers, large irrigation systems, and swamps. Present knowledge does not permit economical eradication of the snails that transmit oriental bilharziasis in any but very limited areas, and control even is not possible in some of the larger endemic areas.

In cases in which molluscicides are to be employed, ecological knowledge is useful in indicating the chemical of choice and the place, time, method and interval of application. Sufficient ecological knowledge has

[1] The Study Group wishes to recommend that the words " molluscocide " and " molluscacide " should be replaced by the word " molluscicide ", in order to follow etymological precedent and to achieve conformity with the word " insecticide ".

yet to be discovered in the case of most snail hosts, but some information is already available.

Our present knowledge of snail ecology has provided the following useful information concerning snail control by the use of chemical molluscicides :

1. Information concerning the characteristics of the snail life cycles indicates that :

(*a*) it may be most favourable to treat after reflooding of a dried habitat, since reproduction of pulmonate vectors is generally rapid at that time, the population is small and the snails may be immature ;

(*b*) the great reproductive potential of the pulmonate vectors means that treatments may have to be very frequent and that repeated checks at close intervals may have to be made to ensure effective control ;

(*c*) not all current molluscicides kill the eggs at usual concentrations, and repetition of treatment may therefore be necessary ;

(*d*) since *Oncomelania* is more susceptible to molluscicides when it is in its young aquatic phase, treatment should be made when reproduction is active.

2. Information concerning snail habits and characteristics indicates that :

(*a*) in the case of snails resistant to drying, treatment at other than maximum water-level may miss some snails, and stream clearance should not precede treatment since it removes snails from exposure but may not kill them ;

(*b*) in the case of snails not resistant to drying, the water-level at the time of treatment is not so important, and the application may be made before the water has reached its maximum level with a consequent saving of chemical ;

(*c*) burial of snails in soft mud may protect them against some chemical agents ;

(*d*) snails may avoid the action of molluscicide by emerging from the water or penetrating into the mud, and the ecological conditions under which such escape reactions may take place need to be further studied.

3. Information concerning conditions of habitats indicates that :

(*a*) substances in the water may affect the action of the chemical. For example, organic matter binds copper, and silt interferes with the molluscicidal action of both copper and sodium pentachlorophenate ;

(*b*) vegetation and irregular margins may impede the distribution of soluble chemicals ;

(*c*) since flowing water will carry away the chemicals, further amounts will have to be added over a period of time, and the concentration during that period will have to be measured.

In view of the prevailing lack of information concerning the most suitable point in the life-cycle of the snail for the application of molluscicides, attempts have been made to achieve residual application by incorporating the toxic substance in bricks of various materials or by ensuring its impregnation in the bottom mud. Attempts have also been made to achieve the dispersal of insoluble molluscicides in the water, so that they would be consumed by the snails in the course of feeding. Further information is required upon these matters, since tests so far have not shown clear-cut results.

Among substances which have shown themselves to be highly toxic to the snails but at the same time relatively innocuous to man and domestic animals, barium carbonate, which has yet to receive extensive field trials, may be mentioned.

It has also been suggested that the impregnation of palm-leaf traps with molluscicides, or alternatively the impregnation of blocks of molluscicides with extracts of substances attractive to the snails, might be tried.

In general, where the incidence of infection in the snails is low, a moderate reduction in the snail population may be sufficient to effect a substantial measure of control. Where, on the other hand, the incidence of infection in the snails is high, satisfactory control can only be achieved by drastic reduction in the number of molluscs.

In the case of *Oncomelania* spp., the immature snails are more susceptible to the action of molluscicides than are either the eggs or the adults. The breeding season of *Oncomelania nosophora* in Japan is limited. These two facts have led to effective molluscicidal techniques that drastically reduce populations of this species. The use of residual molluscicides is particularly important in control measures against the adults of *Oncomelania* spp., because their habits remove them from time to time from the influence of molluscicides dissolved in water. The application of insoluble molluscicides to the banks of infested streams and pools is, perhaps, more effective against the adult snails than the use of soluble molluscicides.

Much remains to be learned about the complex relationships existing between molluscicides, the snails and the environment. In particular, the following problems require further investigation :

(1) The role and fate of the molluscicides in the environment, including their physiological effect in killing the snails.

(2) The influence of temperature, sunlight and other ecological factors on the lethal effect of molluscicides. It has been shown, for instance, that ionized copper is more effective in waters having small amounts of dissolved solids.

(3) The residual effect of molluscicides and the ways in which this may be further developed as a means of application ; the development of new and more effective types of molluscicides.

(4) The determination of optimum time and concentration of molluscicides for different strains of intermediate host species.

(5) The exact stages in the life-cycle of the different snail species at which the application of molluscicides is most effective ; and the effect of molluscicides on the different stages in the life-cycle.

(6) The development of resistance to molluscicides. This phenomenon has not yet been reported, but owing to the effects that modern insecticides have produced in malaria mosquitos, the possibility that it will occur should not be overlooked.

(7) The effect of molluscicides on other organisms, especially human beings, domestic stock, fish and crop plants.

(8) The possible use of supplementary substances to increase economically the efficacy of molluscicides.

(9) The effect of other substances dissolved in the water on the action of molluscicides.

(10) The determination, in any particular case, of the degree of reduction of the snail population which is necessary to achieve control.

4.2 Sanitation measures

The avoidance of pollution of any type of running or standing water with excrement or rubbish would lead to a great reduction in the population of the snail hosts. Provision of latrines and of adequate waste disposal facilities are obviously an essential measure, but if this is to be effective the facilities must be used.

The filling in or draining of all unnecessary bodies of water and the prevention of the accumulation of standing pools in sections of irrigation channels and drains would also go far towards reducing the snail population. With controlled bodies of water such as irrigation canals and large public reservoirs, it is desirable and perhaps possible to limit human access. Alternative supplies of safe water for domestic purposes must be provided whenever such limitation is practised.

Bathing pools, separate from any other bodies of water, preferably cement lined and filled with clean chlorinated water, would justify the expense of their establishment by saving the cost of treating infected children. In hot climates children must bathe, and unless provided with safe bathing places they will naturally use infested channels and other bodies of water.

4.3 Irrigation engineering control measures

Observations on the establishment of breeding colonies of bulinid and planorbid snails in irrigation systems in various parts of the world have led to the development of some engineering control measures which may be expected to limit or reduce the snail populations. Among these may be mentioned the following.

4.3.1 *Rapid flow in channels*

A continuous average water velocity of 20-25 metres or more per minute reduces the likelihood of the establishment of breeding colonies of aquatic snail hosts in clean open canals, or may eliminate them entirely.

4.3.2 *Clearance of weeds*

The maintenance of irrigation channels and drains of all types completely free from aquatic vegetation discourages the establishment of snail colonies.

4.3.3 *Drying-out*

Complete drying-out of irrigation channels especially if carried out at frequent intervals, may not succeed in destroying individual snails but so interferes with the life and reproduction of colonies that they become reduced in number and, if the periods of drought are either sufficiently frequent or sufficiently prolonged, may eliminate them entirely. The latter statement is particularly true in the case of lined canals. It is for this reason that terminal distributory channels in the Tigris-Euphrates valley are almost always snail-free. In different climatic regions, experimental research is needed to determine the most suitable frequency and periodicity of such an operation.

4.3.4 *Covering of channels or piping of irrigation water*

Colonies of snails that transmit bilharziasis do not maintain themselves permanently in covered channels or, in particular, in irrigation water-supply pipes, although a few experimental observations to the contrary have been reported. It is true that the water emerges from the pipes through hydrants in the channels for distribution in the fields or gardens, but within a few hours or a day at most, it is absorbed into the earth or evaporates and thus no time is available for snails to establish themselves in the distributory channels. Irrigation rotations rarely permit such frequent running of water into these channels that permanent pools remain at any point. Gardens and small fields in the area of Heliopolis in Egypt and in the Masbah-Hindiyah suburb of Baghdad are supplied with irrigation water in this way and are entirely snail-free, although *Bulinus truncatus* colonies are abundant in adjacent areas supplied by open earth channels.

4.3.5 *Safe canal crossings*

The floor of culvert heads is generally at a lower level than that of the supply pipe or discharge channel and therefore these conduits frequently contain permanent stagnant water, thus forming suitable snail foci. The construction of culvert heads with a floor on the same level as, or slightly above, that of the discharge channel would eliminate such habitats, particularly if the floor is constructed of cement. Consideration might also be given to the construction of silt basins with a gravel bottom, in order to prevent the retention of standing water after canals are dried out.

4.3.6 *Drainage of irrigation canals*

Provision should be made for the complete removal of water from all channels of any irrigation system, if necessary section by section, in order that cleaning operations may be carried out efficiently, and because the drainage reduces the snail population and may be particularly lethal to the young snails.

4.3.7 *Beds of irrigation canals*

Irrigation channels of all types should be so constructed that their beds form a continuous gradient without depressions. At no point along their length should water be allowed to accumulate so that snails can develop during periods, when the canals are not in use.

4.3.8 *Screens over irrigation intakes*

Screens over irrigation intakes have not been found to be effective in preventing the ingress of snail hosts to the channels. A very fine mesh is required on account of the small size of the very young snails (which may be as small as 0.5 mm) and thus the screens rapidly become clogged with debris and interfere with the flow of irrigation water. In any case, snails readily gain access to more distal points of the system by such methods of dissemination as their transport in mud adhering to the feet of human beings, the bodies of waterbirds or water buffalos, the roots of trees in course of transplantation, etc.

4.3.9 *Lining of irrigation canals*

There is sufficient evidence to show that the lining of irrigation canals contributes effectively to the creating of an environment unsuitable for snail populations. Only hard surface linings (such as concrete, brick and masonry) need be considered, however. The lining used should be as smooth as possible and free from cracks from which aquatic vegetation might emerge. It is also desirable that the sides of lined canals be as steep as possible in order to maintain a uniform flow across the channel, and to reduce to a minimum shallow places most favourable to the snails. The lining of irrigation channels has proved to be an effective way of controlling *Oncomelania nosophora*.

4.3.10 *Drainage channels*

Drainage channels would be less likely to support breeding populations of molluscan hosts if the drainage flow (which, usually, is relatively small) were concentrated in lined inverts laid with a uniform gradient. This would discourage the growth of rooted water plants at the bottom and make cleaning an easy matter.

4.4 Water management

The effect of stream control on populations of bulinids and planorbids varies according to circumstances. In some instances the canalization of a stream for drainage purposes may lead to reduction or elimination of its normal snail populations. On the other hand, such canalization may lead to the introduction of the snails into swimming pools or other bodies of water from which they were formerly absent. Each local situation requires study before control measures of this sort can be taken.

The widening, deepening and straightening of streams for navigation purposes is generally beneficial inasmuch as it leads to the elimination of many favourable snail habitats and to the reduction of snail populations.

The effect of the construction of dams for flood control, for the development of hydro-electric power, and for the storage of water for domestic and irrigation purposes, varies according to circumstances also. It may lead to the flooding out of a series of favourable habitats and thus to the elimination of breeding pools of the snails; on the other hand, it may lead to the formation of large reservoirs around the margins of which favourable snail habitats develop. Where, as is the case sometimes in Iraq, flood-control projects are leading to the elimination of swamps formerly heavily infested with snails and to the conversion of marshy land into fields, the effect is highly beneficial.

In certain parts of south central Africa the construction of dams for the purpose of soil conservation has led to the formation of favourable new habitats.

In the case of the *Oncomelania* spp., the same principles apply, but the changing of water flow is on a much smaller scale. The repeated temporary damming of the small streams in order to catch fish, the water-buffalo wallows, and the use of small dams to divert water to the rice fields, are examples. These and similar diversions force the water away from any defined channel, soften the stream bed, make the flow more sluggish, and encourage the growth of semi-aquatic grasses and other plants which further impede the water flow. This vicious circle produces ideal habitats for *Oncomelania*.

4.5 Modification of fishing and farming practices

Fishing and farming practices in some places have a profound effect on the occurrence of intermediate snail hosts, but it is not easy to modify them in such a way as to achieve any appropriate measure of control.

In Iraq, winter crops, consisting chiefly of wheat and barley, are not associated with snail-infested streams, since during the growing season the snails are hibernating or relatively inactive, while during the fallow season, when the weather is warm and the snails are active, the irrigation canals are dry. Summer crops, consisting chiefly of rice and dates, are, on the other hand, associated with heavy snail infestation of irrigation channels, since they are grown at the time of year when the snails are active. It would, however, be manifestly impossible to convert all the agricultural land to winter crops.

Recent work has shown that experimental modification of the method of rice culture in the Philippines can lead to substantial reductions in populations of *Oncomelania* spp. In most of the endemic areas in the Philippines, rice is usually planted during the wetter portion of the year. The tall vegetation in a swampy area is trampled into the soil by water buffalo and the rice is planted in the resulting quagmire. After planting there is no cultivation. Only the heads of the rice are cut off when it is harvested and the tangle of rice stalks, sedges, etc., remain on the swampy plots.

During the initial cultivation the snail populations are markedly reduced, but the environment soon becomes suitable for the snail, and repopulation takes place quickly. The land is often left fallow for a year or two and the environment remains quite favourable for the snail during this period. Rice production under such conditions is relatively low.

Rice culture methods used in more productive areas have been tried in test plots in Leyte. These methods include drainage and irrigation with well established dikes, cultivation during the growing period, the drainage and drying of the plots when the grain is ripe, and the cutting of the stalks a few inches above the ground and their removal for threshing. Such plots produced about twice as much rice as the control plots. The snail population was reduced by about 80% in the experimental plots. Also, if irrigation water is available and fertilizer is used the plots can be kept under almost continual cultivation. Under such a regimen, two or three crops can be obtained per year, rather than one crop every one to three years.

Under certain circumstances wet rice cultivation may lead to an increase in molluscan host populations owing to the creating of extensive, favourable habitats. Such a state of affairs may be altered by the encouragement of upland rice cultivation.

Fish farming is being increasingly advocated in Africa as a means of increasing the protein-intake of the indigenous population. The ecology of fish ponds is such that they become ideal breeding places for aquatic snails, since among the requirements for the successful propagation of fish are shallow water, adequate vegetation—macro and micro—and periodic fertilization with animal manures. The danger inherent in situations of this description is such that precautions must be taken to prevent human pollution of these ponds. On the other hand, it has been found in Leyte that the conversion of a swamp habitat into a fish pond greatly reduces the *Oncomelania quadrasi* population.

5. QUANTITATIVE METHODS FOR THE MEASUREMENT OF THE DENSITY OF MOLLUSC POPULATIONS DURING SURVEYS AND FOR THE EVALUATION OF RESULTS OF CONTROL METHODS

The study of the ecology of any species requires many lines of attack. Among these are geographic and local distribution, breeding habits, food requirements, causes of death, movements and methods of dispersal. Some knowledge of the size and structure of the population is desirable, and this becomes essential in a study of a species that is to be subjected to control efforts. Moreover, a study of the population dynamics must frequently be used as an indirect approach to some of the other problems listed.

With few, if any, exceptions, the study of a population requires the examination of a sample, since the entire population is too large to come under complete scrutiny. The selection of the method or methods to be used in obtaining the sample is of the utmost importance, because the picture of the population is distorted if the sample is not representative.

An ideal sampling method should (*a*) reveal population density (or total population) accurately; (*b*) include all sizes of snails from all positions in the habitat; (*c*) create minimum disturbance in the habitat; (*d*) not deplete the snail population, and (*e*) require only simple equipment.

The nature of the information required will determine, in part, the degree of refinement of the method to be used. Critical population studies require a better method than observation of gross population shifts.

A variety of methods has been used. Each method has its inherent advantages and weaknesses; each is applicable to certain habitat situations. Estimates of relative population density are more readily made and almost as useful as estimates of total population. All depend on human factors and each requires care, discrimination and, above all, long practice. None of these methods is ideal.

Methods for sampling used or proposed are as follows:

		Advantage	*Disadvantage*
1.	Estimation (judgement of density of visible population)	Easy, fast	Low reliability
2.	Count of snails collected per unit of time	Easy, fast; fair accuracy on repetition by same collector; little habitat disturbance	Requires well-trained and careful collectors
3.	Count per unit area:	Fast, easy, accurate	Does not get snails in mud or soil
	(*a*) from mud or soil surface only	Adapted to use with amphibious snails	Difficult with vegetation present
	(*b*) exhaustive (collection of every snail by removal of a block of the habitat)	Accurate, reveals total population	Very time-consuming, not usable in many habitats; destroys a part of the habitat; not usable with low densities
4.	Proportional (by the mark-and-release method)	Untried with the snail hosts	
5.	Palm-leaf traps	Easy, fast	Detects snails at low density; hard to standardize
6.	Count per dip, using a standard net, sieve or scoop	Rapid, easy	

Collecting devices required:

(*a*) scoop net or dip net (metal frame with cloth or wire-net cover)
(*b*) metal sieve
(*c*) bottom sampling device
(*d*) weed sampling device
(*e*) palm-leaf trap

NOTE: Writers should record (1) the method they used; (2) their evaluation of the method; (3) whether the snails were returned to the habitat; and (4) the degree to which the habitat was disturbed.

6. SUGGESTIONS FOR FURTHER STUDIES IN ECOLOGY AND PHYSIOLOGY IN RELATION TO CONTROL METHODS

The efficiency of control measures taken against molluscan hosts depends to a considerable extent on a knowledge of the species' ecology. There is no doubt that precise information on the living conditions of snails, with particular reference to the various stages of development (egg-laying, hatching, and the life of the young), will make it possible to contemplate practical and efficient means of control.

The development of ecological research has now reached a point at which extensive field studies can no longer be efficiently carried out by individuals, and co-operation between specialists in different scientific disciplines is desirable. Co-operation of this nature would naturally vary according to the nature of the problems to be investigated and the area of the world in which this co-operation is to take place. This co-operation may have to be international in nature, as few countries can themselves provide all the experts considered desirable. Among such specialists the following may be mentioned:

(1) an epidemiologist with wide experience in the whole field of bilharzia research;

(2) a malacologist interested in and with experience of ecological as well as taxonomic problems;

(3) a botanist having special interest in and knowledge of aquatic plants;

(4) a parasitologist having a zoological background;

(5) a limnologist;

(6) a chemist able to undertake any necessary analyses of water, soil or plants;

(7) a biochemist with experience in physiological chemistry, able to undertake the investigation of problems connected with the growth and physiology of the snails ;

(8) a specialist in problems of water management, with some background of public health knowledge.

Laboratory and field research must be conducted simultaneously. The points which call most urgently for study are as follows :

(1) the natural history of the snail hosts in a variety of types of natural habitats, emphasis being placed on life history, growth, development, reproduction and population dynamics ;

(2) comparison of the ecology of favourable and unfavourable situations with the purpose of explaining the distribution of the snails and learning how habitats may be made unfavourable for them ;

(3) the biotope and climax associations of the marginal zones between areas where urinary bilharziasis is predominant and areas where intestinal bilharziasis is predominant (e.g., in Ubangi Shari, Madagascar, and other territories) ;

(4) the development of new chemical molluscicides :

(*a*) having residual action ;

(*b*) based upon elements known to be inimical to snails in minute quantities, e.g., copper, nickel, zinc ;

(*c*) as insoluble toxic compounds, incorporating substances attractive to snails.

Among the particular problems which also require investigation may be mentioned the following :

(1) bacteriological research towards the development of epidemic diseases of snails and possibly of aquatic ferments unsuitable to snails ;

(2) investigation of the introduction of zoophytic associations unfavourable to snails ;

(3) adaptability of schistosome miracidia to new intermediate hosts ;

(4) physiological uptake of individual ions (use of radioactive isotopes) ;

(5) taxonomic work related to ecology (hybridization) ;

(6) feeding habits, with reference to stomach poisons ;

(7) movement of snail populations in streams (use of radioactive tracers) ;

(8) research on seasonal and regional variations in the life-cycle to determine the optimum time for molluscicidal treatment.

Finally, ecological knowledge might be applied by the conducting of pilot water-management experiments in areas where bilharziasis is hyperendemic ; for example, the study and development of systems of lined and unlined channels and of covered conduits on limited areas cultivated and submitted to a system of rotation and drainage, with whatever other installations are considered most satisfactory, accompanied by engineering economic analysis of methods considered and by quantitative observations of the snail fauna. Comparisons should be made with control areas and conclusions should be drawn only after the experiments have lasted a sufficiently long period of time.

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