Zeitschrift: Acta Tropica

Herausgeber: Schweizerisches Tropeninstitut (Basel)

Band: 37 (1980)

Heft: 2

Vorwort: Schistosomiasis transmission with particular reference to possible

ecological and biological methods of control: a review

Autor: Jordan, P. / Christie, J.D. / Unrau, G.O.

Nutzungsbedingungen

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. Mehr erfahren

Conditions d'utilisation

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. En savoir plus

Terms of use

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. Find out more

Download PDF: 02.08.2025

ETH-Bibliothek Zürich, E-Periodica, https://www.e-periodica.ch

Schistosomiasis transmission with particular reference to possible ecological and biological methods of control

A review

P. JORDAN¹, J. D. CHRISTIE², G. O. UNRAU³

Key words: schistosomiasis; control; biology; ecology.

Introduction

Schistosomiasis occurs under a wide variety of climatic, geographical, geological and other conditions. The disease is associated with a similarly wide variety of water habitats which can be either natural or man-made.

Man-made habitats are generally thought of in terms of irrigation schemes with their main, primary, secondary and tertiary canals in the irrigated areas and the necessary drainage systems being potential habitats for snail intermediate hosts of schistosome infections. More recently the huge man-made lakes such as Volta and Kariba are becoming important sites of increased transmission. On a smaller scale, dams across seepage areas or small streams or rivers have been built by the thousand in many parts of Africa and South America. These dams are important water sources for millions of people and their domestic animals. While water conservation and irrigation schemes have no doubt been responsible for an increase in schistosomiasis, they have the prime objective of improving living conditions and the economy – unlike the snail-infected borrow pits alongside many necessary new roads in developing countries. These pits can possibly be blamed for the spread of schistosomiasis to some new areas. Other man-made habitats such as water holes, road-side ditches, quarries, blocked drainage ditches and even leaking water taps are contributing to schistosomiasis transmission. In natural and man-made lakes, itinerant fisherman

Correspondence: Dr. P. Jordan, Research and Control Department, Box 93, Castries, St. Lucia, West Indies

¹ MRC staff seconded to Rockefeller Foundation, Research and Control Department, P.O. Box 93, Castries, St. Lucia, West Indies

² Department of Pathology, University of Texas Medical Branch, Galveston, Texas 77550, USA

³ School of Public Health, University of North Carolina, Chapel Hill, North Carolina 27514, USA

and steamer services may also be responsible for the introduction of the infections to new areas (McClelland and Jordan, 1962; Eyakuze et al., 1974). Water in natural habitats can be static as in large or small lakes, ponds, water holes, swamps and marshes, or flowing as in rivers, streams or seepage areas.

Although different snail intermediate hosts of the five species of schistosome commonly affecting man occur in a wide variety of habitats, all endemic areas have a number of common ecological factors necessary for transmission of the infection. These can be summarized: infection in a population with a low level of sanitation and snails susceptible to infection in water used for domestic or occupational purposes.

Schistosomiasis transmission

1. Low levels of sanitation and infection of snails

In areas where schistosomiasis is endemic, sanitation is at a low level. Latrines of one form or another may be in some household compounds but unless properly constructed can be virtually useless. Shallow pits may fill with water in the rainy season and overflow into an aquatic habitat. Even if latrines are well constructed, fly and odor problems may limit their use. Vent pipes (Morgan, 1977a) or water-sealed toilets may alleviate these problems. Children are sometimes not allowed to use latrines as they may soil them, or they do not use them for fear of falling in the pit. However, in developing countries greater efforts are now being made to provide sanitation facilities which are acceptable and appropriate to the society (Oxfam Conference, 1977).

Pit latrines alone may not effectively control schistosomiasis in an area of low level sanitation, but their possible effect on contamination of the environment with schistosome ova can be estimated. The relative index of potential contamination of different age groups takes into account the prevalence and intensity of infection and the population structure. Calculations can be made for populations infected with any of the human schistosomes; the example (Table 1) is taken from an area where *Schistosoma mansoni* is endemic. It is seen that the age groups 5 to 14 years are potentially responsible for 55% of contamination of the environment. As these age groups are generally the first to be reached in government literacy schemes, health education concerning the need for a proper use of latrines may help in reducing the contamination. (A refinement in the above calculation is to allow for difference in hatchability of eggs from persons in different age groups [Upatham et al., 1976]. This modification tends only to emphasize the importance of younger age groups in contaminating the environment.)

The calculations outlined above indicate the relative importance of different age groups in maintaining transmission, and those age groups upon which control efforts should be concentrated in order to reduce contamination.

Table 1. Relative index of potential contamination of different age groups in an S. mansoni infected area of St. Lucia

Age group	Population structure	Prevalence in % (2)	Intensity of infection* (3)	Index of potential contamination** $(1 \times 2 \times 3/100)$	Relative I.P.C. in %
0–4	19.2	25	68	326	5.3
5–9	18.5	61	150	1692	27.7
10–14	14.0	81	149	1689	27.5
15–19	10.0	80	104	830	13.6
20–29	12.3	71	74	646	10.5
30–39	8.0	58	76	352	5.7
40–49	7.7	51	61	239	3.9
50–59	5.0	53	55	145	2.4
60+	5.4	44	87	206	3.4

^{*} Arithmetic mean

While surveys can indicate those age groups and, less satisfactorily with a single stool examination, those individuals who contribute significantly to environmental contamination, little information exists on the relative importance of the routes by which infected faeces enter snail-infested waters. Obvious routes are defaecation directly into water, i.e. from latrines built over rivers or canals, particularly in the Far East; from a bridge over a river (common in St. Lucia); or, more rarely, while swimming or bathing. As observed in St. Lucia and Ethiopia, faeces are frequently found on riverine rocks or on river banks. The greatest amount of contamination is probably from faecal matter deposited behind bushes or in tall grass on river banks and subsequently washed into the stream. Evidence indicates that infection rates of sentinel snails increase with the onset of rains, probably due to wash-in of faeces deposited on the side of the river (Christie and Upatham, 1977). However, longevity of the eggs in stools is decreased by exposure of faeces to direct or indirect sunlight (Maldonado et al., 1949). Although during the dry season faecal matter accumulates adjacent to a river, perhaps only the infected material deposited a short time before the onset and cessation of the rains is important in infection of the snail. At Entebbe, on the shores of Lake Victoria, cattle walked through favorite human defaecation sites, and thus carried human faeces into the lake on their hooves (Prentice, personal communication). The washing of faecally contaminated clothing (Chernin and Antolics, 1973) and the washing of faecally soiled hands probably accounts for snails found infected in the vicinity of leaking community stand pipes. Cleansing of perianal faecal soiling while bathing (Husting, 1965; Prentice et al., 1970) may also add small numbers of schistosome eggs to the water.

^{**} The sum of the age specific I.P.C.'s totals 6125. This number is a measure of the daily egg excretion in 1 ml of faeces from a representative sample of 100 persons of the population. This figure multiplied by 100 approximates to their total daily egg excretion (based on an average daily excretion of 100 g of faeces).

These habits, especially the latter practice common among Moslem males after defaecation, may be important in transmission because of their frequency and non-dependence on the rainy season.

The numerous animal definitive hosts of *Schistosoma japonicum*, and, of less importance, those of *S. mansoni*, add to the contamination of snail habitats with eggs of these worms. Their importance in the transmission model and control of *S. japonicum* has been examined by Hairston (1962).

Contamination of snail habitats with *Schistosoma haematobium* eggs (the excretion of which shows a diurnal pattern [Jordan and Webbe, 1969]) is due essentially to infected persons urinating directly into water. Reasons for this practice may be of interest but are not relevant to the present discussion.

While faecal and urinary contamination are the main source of *S. mansoni* and *S. haematobium* eggs respectively, the finding of these eggs in urine and faeces respectively is not unusual (Blair and Husting, 1965).

In some situations, sewage may be the source of contamination. In Puerto Rico, Rowan (1964a) found 83% of *S. mansoni* eggs were removed by primary sedimentation and decantation and 99.7% by trickling filter and activated sludge plants. In spite of these high rates of egg removal, estimates indicated that over 130 million *S. mansoni* eggs or miracidia per year were discharged from the activated sludge plant investigated. The epidemiological results of this contamination were unknown. Further studies indicated chlorination of effluent to give a 15 minute residual of at least 2.5 mg per liter would remove viable eggs and miracidia (Rowan, 1964b).

Sewage stabilization ponds have been accepted as economical and practical in developing countries. Their potential in the transmission of *S. mansoni* was investigated by Kawata and Kruse (1966) who found that the deep, heavily loaded anaerobic pond will curtail the hatching of eggs and survival of miracidia and *Biomphalaria glabrata*. Aerobic and facultative stabilization ponds are not likely to significantly affect miracidia or snails. However, in field and laboratory trials in Brazil, infection of *B. glabrata* with *S. mansoni* and growth of non-infected snails was lower in water taken from aerobic stabilization ponds than in local tap water (Bunnag et al., 1978). Thus transmission may be reduced in this type of stabilization pond.

Following contamination of water with schistosome eggs, the majority will hatch with emergence of free-living miracidia. The rate of hatch of *S. mansoni* eggs in stools varies, from soft and hard stools respectively, eggs hatch 24 to 48 and 32 to 128 hours after being in water (Upatham, 1972a). The long hatching period of eggs in hard stools is possibly important epidemiologically but perhaps of academic interest as comparatively few heavily infected persons are constipated.

The continuity of the parasite's life cycle depends on these miracidia finding a snail intermediate host to which they are probably "naturally" directed (Chernin, 1974). While searching for such a host, they are liable to ingestion by

fish, carnivorous invertebrates (Chernin and Perlstein, 1971), carnivorous plants (Gibson and Warren, 1970) and to poisoning by molluscicides or other chemicals (soap or natural plant products) or to death by adverse physical conditions. Many workers (DeWitt, 1955; Purnell, 1966a, b; Upatham, 1973a; Prah and James, 1977) have found that the range of temperature and ultraviolet radiation encountered in the field have little effect on infection of snails by miracidia. However, Chu and his colleagues (1966a) pointed out that infection of Bulinus truncatus by S. haematobium in Iran may be decreased during the hot summer and cold winter months. Miracidia may be removed from a habitat by penetration of snails insusceptible to infection (Chernin and Perlstein, 1969; Upatham, 1972b; Upatham and Sturrock, 1973a) which might be a side benefit of biological control using snails as predators or competitors of the intermediate hosts (Frandsen, 1976). An idea of the importance of these factors in reducing infection of snails can be gained by a comparison of results from two experiments performed by Upatham and his colleagues. While 17 to 64% of S. mansoni eggs from stools of infected humans hatched into viable miracidia (Upatham et al., 1976), only 0.15 to 0.60% of eggs from the same source hatched and infected susceptible snails under field conditions (Upatham, 1972c).

In rivers and ravines, infection of snails by miracidia is complicated by the fact that the water containing miracidia is moving past the snail. The exact effect of changes in velocity on infection of hosts by parasites is discussed in a later section; however, two studies should be mentioned. Working with an artificial trough, Webbe (1966a) found that increasing water velocity from 15 cm/sec to 107 cm/sec had little effect on S. mansoni infection rates of Biomphalaria sudanica tanganyicensis. On the other hand, when sentinel B. glabrata were exposed to S. mansoni miracidia in a natural situation, no infections were found when water velocity exceeded 13 cm/sec (Upatham, 1973b). It could be argued that snails exposed over longer periods of time would become infected at greater velocities than this limit. However, there appears to be diminition of snail infection rates as velocity increases in a natural habitat. The question may be academic as most snails found in running-water habitats are located in areas where natural decreases in stream velocity occur. Furthermore, snails are dislodged in streams when water velocity exceeds 33 cm/sec (Jobin and Ippen, 1964).

Finally, a word must be said about the role of "miraxones" (Chernin, 1970) in the meeting of parasite and snail. The majority of miraxonal activity and content in *B. glabrata*-conditioned water appears to be due to magnesium ion (Stibbs et al., 1976; Sponholtz and Short, 1976), of low molecular weight, nitrogen-containing compounds (Wright and Ronald, 1972; MacInnis et al., 1974; Mason and Fripp, 1977). It is hard to envisage a biologically significant role for such a common chemical when balanced against the larger factors which bring parasite and snail into contact.

2. Susceptible snails

Susceptibility of snails to infection varies with species and sometimes within the species. While B. glabrata, Biomphalaria pfeifferi and Biomphalaria alexandrina are the most widespread and probably the most susceptible intermediate hosts of S. mansoni in the New World, sub-Saharan Africa, and the Nile Delta respectively, there are other species which may be of low susceptibility and yet important in transmission in localized areas. Biomphalaria straminea is not very susceptible to S. mansoni and yet is responsible for transmission over wide areas of Brazil (Barbosa, 1962). Some snail species can be infected with only a particular strain of schistosome. In Africa, the *africanus* species-complex (Physopsis sub-genus) of Bulinus is susceptible to a "southern" form of S. haematobium while the truncatus group is invaded by a "northern" strain of the parasite (Berrie, 1970). Particular strains of snails are matched to particular strains of schistosome. Instead of an Oncomelania species, Tricula aperta functions as the intermediate host of the Khong Island form of S. japonicum (Harinasuta et al., 1972) now considered a distinct species, Schistosoma mekongi (Voge et al., 1978). Several strains of *T. aperta* exist with only one of these being infected in nature (Davis et al., 1976).

The basis for compatibility of both snail and parasite is a recognition of "self" by the snail. If the parasite is perceived as foreign by the mollusc, the developing schistosome is walled off by cellular reactions of the host (Basch, 1975, 1976). Research is presently focused on lectin-like substances found in both snail and trematode as a possible means of perception of the parasite as foreign by the intermediate host (Michelson and DuBois, 1977; Yoshino et al., 1977; Yoshino and Cheng, 1978). The search for phenotypic differences which correlate with susceptibility differences at the species and strain level has not been very fruitful. However, one positive result has been the clarification of Bulinus relationships at the species-complex level. The basic haploid number of chromosomes in Bulinus and Biomphalaria, both planorbid snails, is eighteen, while the B. tropicus species complex, which does not include hosts of urinary schistosomiasis, also have the basic planorbid chromosome number (Berrie, 1970). Clearly susceptibility differences in this genus did not arise due to changes in chromosome numbers.

Susceptibility in intermediate hosts and infectivity of the schistosome are both governed by heredity. Apparently susceptibility is governed by a complex of four or more factors with insusceptibility being dominant (Richards and Merritt, 1972), while a given parasite strain may be heterogeneous for infectivity (Richards, 1976). Alteration of susceptibility in snails as a means of transmission control was advocated by Hubendick (1958). Woodruff and Fletcher (unpublished observations) have shown by means of computer simulation that proper selection of snails for insusceptibility followed by introduction of these molluscs into a susceptible field population may cause a change in receptivity of that colony to the parasite in only a few years. However, these simulations

ignore the profound effect of natural catastrophes upon snail populations. Furthermore, prolonged self-breeding to produce refractory snails may reduce genetic variability at other loci. Such a reduction in variability may decrease the ability of the molluscs to adapt to a changing field environment as easily as wild populations of snails (Ayala, 1968).

Snails intermediate hosts occur in a variety of natural habitats where conditions may vary widely. As the intermediate hosts of human schistosomes, with the probable exception of the hydrobiids, are r rather than K specialists, their distribution and population dynamics are probably governed by abiotic rather than biotic factors (Southwood, 1977). Of the possible abiotic influences on populations of schistosome intermediate hosts (Appleton, 1978), temperature and rainfall are the most important. In any endemic region, rainfall influences numbers and temporal distribution of intermediate hosts by its catastrophic effect, while temperature acts as a regulatory force, especially at high latitudes or altitudes, by affecting snail reproduction and growth (Christie and McCullough, in press). However, in any water body, both snails and miracidia may select a micro-environment whose temperature is optimum for survival (Shiff, 1966, 1974).

Rainfall exerts its effects in temporary lentic habitats by causing disappearance of these niches during drought, while, in lotic situations, it causes flushing of the snails during the rainy season and, along with geomorphology, influences stream velocity during the dry season. Numbers of B. glabrata decreased linearly with increasing velocity (Scorza et al., 1961) with an upper limit of 30 cm/sec (Jobin and Ippen, 1964). This upper limit has been attributed to the hydrodynamic drag on the exterior of the snail, but could also be due to prevention of deposition of the detritus on which the snail depends for food (Appleton, 1978). Snails may circumvent the effects of drought by burrowing into the dry mud and aestivating. Though many snails may die under these conditions, sufficient survive to repopulate the habitat when it refills with water. Whether the mollusc survives desiccation or not depends on saturation vapour deficit, length of exposure, snail size, and environmental temperatures (Chu et al., 1967a, b; Sturrock, 1970). Some strains of snails may be more resistant to drought than others (Barbose and Olivier, 1958). This difference may be due to differing abilities to burrow into mud (Chu et al., 1967a, b) and also to part of the population being equipped with apertural lamellae. Possession of apertural lamellae is inherited (Richards, 1963, 1967, 1968) and is probably an adaptive mechanism that ensures that at least part of the population survives the dry season. Snails with developing parasites are also capable of withstanding several months of drought with maturation of the parasite continuing at the onset of the rainy season (Barbosa and Coelho, 1953, 1955; Barbosa and Barbosa, 1958). However, removal of B. glabrata with patent infections from water causes death of the parasite. Since eggs of B. glabrata can tolerate only 1 to 2 hours of desiccation under tropical conditions (Chernin and Adler, 1967), they probably play

little part in repopulating habitats after dry conditions. This limited ability to withstand desiccation may allow transportation of eggs to new habitats by insects, birds, and mammals (Harry and Cumbie, 1956; Pimental et al., 1957) or by man. In St. Lucia, newly dug dasheen gardens may be infected with snails due to transport of eggs and molluscs on dasheen taken from old gardens.

Whenever colonies of snails are depleted by natural "disasters" or mollusciciding, the high intrinsic rate of natural increase plus the monoecious reproduction of planorbid snails guarantee that populations of *Bulinus* and *Biomphalaria* increase rapidly with the return of favorable conditions. Since *Oncomelania* are dioecious, colonies of these molluscs would probably not return as quickly as populations of planorbids would rebound to pre-disaster conditions. While heavy miracidial infections can kill or reduce the fecundity of the intermediate host (Wright, 1966), these changes have little effect on natural populations due to the high r values demonstrated by these snails.

3. Cercarial shedding

Under natural conditions, temperature, light, numbers of infected snails, stream velocity and various natural attenuating mechanisms have the greatest effects on determining numbers of cercariae found at a transmission site (Christie and McCullough, in press). Other factors influencing cercarial densities at locations for human infection include age/size of snail, and numbers and infectivity of miracidia. Besides the changes in infection rates of snails infected by miracidia kept at various temperatures, increasing temperature causes a decrease in time to patency (Gordon et al., 1934; Standen, 1952; Stirewalt, 1954; Foster, 1964). Experiments conducted under semi-natural conditions in Iran, South Africa, and Rhodesia have shown that transmission in natural habitats may be decreased during the coldest months of the year (Pitchford and Visser, 1965; Shattock et al., 1965; Chu et al., 1966; Shiff et al., 1975). On the other hand, a temperature of 35°C almost completely inhibits production of S. mansoni cercariae in B. glabrata (Barbosa, 1962). As increasing temperature probably stimulates utilization of metabolic reserves, less energy is available for penetration, and infectivity is decreased. This statement has been documented in laboratory studies, but the expected change in infectivity occurs only at 30° C or greater (Foster, 1964; DeWitt, 1965; Olivier, 1966; Purnell, 1966a, b).

Cercariae of *S. japonicum* are shed at night, whereas those of *S. mansoni* and *S. haematobium* are released during the hours of daylight; the maximum number probably being in the water at about midday (Jordan and Webbe, 1969). Light seems to be the primary factor in stimulating emergence of the latter two species, with temperature being of lesser importance (McClelland, 1965, 1967). The presence of light acts as a "Zeitgeber" entraining some physiological process of the snail to which the parasite is sensitive (Valle and Alvarenga, 1971). If infected snails are exposed to light, shedding patterns are similar in both *S. haematobium* and *S. mansoni* except that *S. haematobium* larvae are

shed more slowly than those of *S. mansoni* (Schreiber and Schubert, 1949; Sturrock, 1965; McClelland, 1967). In *S. mansoni*, numbers of cercariae reach a peak after three hours with the total number released after five hours, while in *S. haematobium*, the maximum occurs after four hours with the majority of the total larvae shed emitted after seven hours. At seven hours, the total number of larvae released was higher in *S. haematobium* than in *S. mansoni*.

Of prime importance in determining numbers of cercariae present at a transmission site is the number of infected snails nearby. Mean numbers of cercariae emitted per infected snail per day range from less than 50 in the case of *S. japonicum* infecting *O. hupensis quadrasi* to about 1,000 *S. mansoni* cercariae released from *B. glabrata* (Pesigan et al., 1958; Sturrock, 1974; Barbosa et al., 1954). This variation is probably dependent on the size of the snail species as numbers of larvae released increase with growing size of the snail (Christie and McCullough, in press). After the infection in the mollusc becomes patent, the snail usually releases cercariae for the remainder of its life, although cercarial infectivity drops just before the death of the snail (Evans and Stirewalt, 1951).

Between emission by the snail and arrival at the transmission site, numbers of cercariae are affected by stream velocity and attenuation by predation and other factors which may be reflected in the decrease in larval numbers as distance between snail colony and site of human infection increases. If the snail colony and transmission sites are the same and occur in a static water habitat, then maximum numbers of cercariae will occur at noon. If sites are separated by flowing water, then the largest number of larvae may occur in the afternoon at the transmission area due to the time required for stream flow to transport the larvae from snail colony to human infection site (Negron-Aponte and Jobin, 1977; Theron et al., 1977). If there is a pool or obstruction at the transmission area, then larvae may accumulate in significant numbers. Assuming that a constant number of cercariae is released by a snail colony, then as the velocity and consequently volume of water increase, cercarial density in the water flowing by a group of infected molluscs decreases. Infection of humans at the transmission site does not seem to be simply related to stream velocity. As velocity increases, numbers of larvae being swept past a point in a stated unit of time will increase, but time available for penetration will diminish.

Predation by fish, such as guppies, may decrease cercarial numbers significantly especially in static water habitats (Oliver-Gonzalez, 1946; Rowan, 1958; Pellegrino et al., 1966; Knight et al., 1970). Furthermore, cercarial numbers may be reduced by penetration of abnormal "hosts" such as string beans or dead animals (Warren and Peters, 1968) or by capture by carnivorous aquatic plants of the genus *Utricularia* (Gibson and Warren, 1970). Finally, diminution in numbers or infectivity may be due to other causes. Radke and his colleagues (1961) found no reduction in numbers of larvae 610 meters downstream from point of release, while Upatham (1974) could not detect cercariae more than 200 meters from a source. The difference between the two sets of experiments is

that the former were performed in artificial, concrete-lined drains, while the latter took place in a natural stream. Thus, in a natural transmission site, infected snails should be found fairly close to where people are becoming infected. As has been stated earlier, velocity may affect cercarial infectivity by altering time available for penetration. In a stream flowing into Lake Victoria, infection of mice with *S. mansoni* was seasonal, but did not correspond with times at which largest numbers of infected *B. pfeifferi* were found (Webbe, 1965). This difference was attributed to changes in infectivity caused by velocity changes in the stream. Maximal infection rates of mice with *S. mansoni* were found at velocities smaller than, rather than greater than, 1.0 m/sec (Rowan and Gram, 1959; Radke et al., 1961; Webbe, 1966b; Upatham, 1974). The optimum velocity depended on the conditions encountered in each study. Turbulence associated with increasing water flow does not seem to be the major reason that cercarial infectivity decreases above a certain velocity. Upatham (1973c) found that cercariae were still infective to mice after passage over a 30-foot waterfall.

4. Water contact

Domestic reasons for contacting water, common to all endemic areas, include the collection of water for human consumption, for cooking, for clothes and dish washing, for playing by children, and bathing of adults. Table 2 shows the number of observed contacts for different reasons on 105 observation days at 15 sites over a period of 15 months in St. Lucia (Dalton, personal communication). Using this data, Jordan (1972) found a close correlation between water contact and infection rates of males and females (Fig. 1).

In spite of major differences in the socio-economic circumstances of different endemic areas, findings from water contact studies in Egypt (Farooq and Mallah, 1966), Puerto Rico (Jobin and Ruiz-Tiben, 1968), Rhodesia (Husting, 1970), St. Lucia (Dalton, 1976), and Ghana (Dalton and Pole, 1978) are remarkably similar. More women than men were observed engaged in water-related activities in all areas, except Ghana, and children appeared to have more contacts than adults. Some differences in the distribution of contacts does occur, but for each area, the most common contacts are similar (Table 3). The risk of infection from different activities depends on such factors as duration of contact, degree of bodily exposure, and, because of the diurnal pattern of cercarial shedding of *S. mansoni* and *S. haematobium*, time of day. The cercariacidal action of soaps will probably reduce the risk of infection in those activities in which these detergents are used.

The average time for clothes washing contacts varied from 31 minutes in Egypt to 76 minutes in Puerto Rico; St. Lucia was about midway with 59 minutes. In Ghana, domestic water contacts, while the most frequent of water related activity, were of short duration and did not involve laundry activities. Other activities were of similar duration per contact: swimming, 22 minutes in

Table 2. Number of water contacts categorized by age and sex in relation to various activities (St. Lucian data; Dalton, personal communication)

	Age group (years)					Total			
	0–4	5–9	10–14	15–19	20–29	30–39	40-49	50+	=
Males									
W/Carrying	2	57	78	17	6	4	2	5	171
Washing	0	10	22	2	3	4	2	1	44
Bathing	107	109	56	19	19	5	6	15	336
Swimming	120	145	64	9	2	1	0	1	342
Fording	6	69	48	29	43	37	19	57	308
Other	1	3	16	1	0	1	0	1	23
Total males	236	393	294	77	73	52	29	80	1224
% of total contacts	19.2	32.1	23.2	6.2	5.9	4.2	2.3	6.5	
Females									
W/Carrying	10	47	97	88	85	47	22	31	42
Washing	4	47	116	145	160	131	58	57	71
Bathing	98	113	73	67	49	26	18	16	46
Swimming	80	128	59	5	4	1	2	0	27
Fording	22	33	82	88	40	34	40	31	37
Other	3	4	28	13	17	7	3	1	7
Total females	217	373	455	406	355	246	143	136	233
% of total contacts	9.3	15.9	19.5	17.4	15.2	10.5	6.1	5.8	

Egypt and St. Lucia; bathing and playing, 15 and 32 minutes for Puerto Rico compared with 20 minutes for the combined mean for Egypt, 25 minutes for St. Lucia and 16 minutes for recreational activities in Ghana. Bathing and swimming usually involved complete immersion, but playing may encompass paddling with limited surface area in contact with water. Although laundry activities may involve prolonged contact, only limited skin areas are exposed to water. Clothes washing in Egypt starts earlier in the day than it does in St. Lucia; 45% of Egyptian contacts were recorded between 06.00 and 09.00 hours, while 44% of the contacts in the Caribbean were between 11.00 and 14.00 hours.

Some quantitative data relevant to infection of man has been obtained from animal experiments. Thus, exposure of very short duration carries some risk since, even when the skin of hamsters was mechanically dried after only 10 seconds exposure, some *S. japonicum* cercariae were able to penetrate and mature in these rodents (Pan et al., 1954). Similarly, mice exposed to *S. mansoni* cercariae for 60 seconds developed mature adults (Upatham and Sturrock, 1973b), but only when the cercarial concentration was high. Less dense cercarial

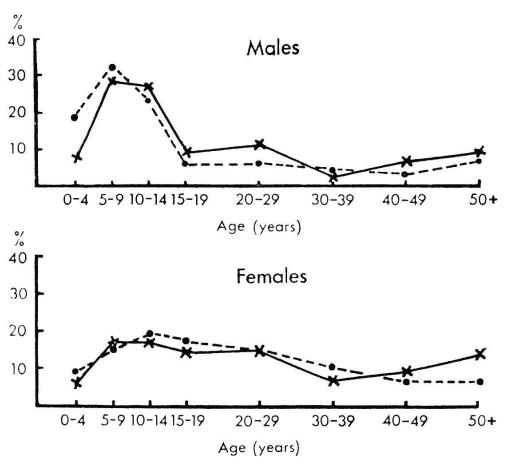


Fig. 1. Correlation between observed water contact and infection with *Schistosoma mansoni*. For each age group and sex, the number of *S. mansoni* positives and water contacts was expressed as a percentage of total number of *S. mansoni* positives (———) and water contacts (------).

Table 3. Most common reasons for water contact in Egypt, St. Lucia, Rhodesia and Ghana

	Egypt	St. Lucia	Rhodesia*	Ghana*
	Washing utensils Washing clothes Bathing and Playing	Washing clothes Bathing Swimming (playing)	Washing dishes Carrying Swimming	Domestic Recreational
% of contacts	57	66	70	58
% of time	76	95	50+	54

^{*} Females only

suspensions decreased penetration and maturation rates in sentinel mice. Warren and Peters (1967) found that death of non-penetrating cercariae occurred on drying skin. However, in hamsters exposed for short periods to *S. japonicum* cercariae with short periods of drying between exposures, there was a greater maturation rate of worms than in infections with a longer, single exposure terminated with immediate drying (Pan et al., 1954). This difference may have been due to rapid penetration by the larvae. Prolonged contact with high

concentrations of cercariae leads to high infection rates and high mean worm burdens in mice. In prolonged exposures, it is not clear as to whether the cercariae which penetrate initially produce a skin reaction limiting further penetration by other larvae (Stirewalt, 1953).

The effect of water velocity and cercarial density were investigated in experimental flowing water systems where the highest mouse infection rates and *S. mansoni* worm burdens occurred after exposure at velocities ranging between 30 to 40 cm/sec (Radke et al., 1961; Webbe, 1966b). Higher and lower velocities led to reduced worm returns in exposed animals. The number of cercariae used in laboratory and semi-natural field trials are usually far in excess of those found in nature so that in many situations, infection of man probably leads to the development of very few worms.

Domestic contacts vary from day to day and from place to place. Occupational contacts vary from place to place but may involve those individuals working in agriculture, fishing and building (harbor construction, collection of river sand), etc. Other contacts associated with religious activities, sport or hunting will depend on the endemic area and may be seasonal. Among the Hausa, Fulani and Maguzawa of Nigeria, the tenets of Muslim religion, which inhibit public bathing by women, make *S. haematobium* an infection of the male population alone (Pugh and Gilles, 1978). However, Farooq and Mallah (1966) concluded from studies in Egypt that "the human exposure pattern favours the transmission of bilharzia – the peak seasonal and diurnal cycles of infectivity of waters coincide closely with the frequency of and duration of contact and with the period of maximum body exposures".

The domestic water contact pattern, common to the majority of populations exposed to schistosomiasis, determines the infection pattern among children. The typical age-prevalence curve shows the rate increasing to a peak usually in the second decade of life. In highly endemic areas, the peak may occur at an earlier age. The decline in prevalence among the older age groups varies in degree. Differences in the pattern between males and females may reflect variations in their water contact patterns. Variation of intensity with age is similar to prevalence, but the decline in the older age groups is usually greater. Few people have heavy egg burdens; the majority excrete comparatively low numbers of ova. This pattern probably reflects the water contact patterns of the population and the cercarial density in waters at the time of contact and is common to the three main schistosome infections of man.

The changes of prevalence and intensity of infection with age have been said to indicate that some form of immunity exists in adults who, in spite of continued water contact, show a falling rate of infection. This decrease could be due, however, to adults having less water contact than do the younger age groups (Warren, 1973). As other evidence (Memoranda, 1974) supports the concept of immunity to schistosomiasis in humans, the falling indices of infection are probably due to a combination of both factors.

Possible ecological methods of control

In the control of schistosomiasis, the ecologies of three populations are involved – that of the human definitive host and any reservoirs, that of the snail intermediate host, and that of the parasitic worm, in relation to its eggs, to the miracidia, and to the cercariae. Prior to discussing "control" of schistosomiasis, the meaning of the term and its relationship to "eradication" should be clarified.

Control may have the object of limiting the spread of infection, reducing morbidity, or curbing and eventually stopping transmission (eradication). Eradication involves the "ending of transmission and the elimination of the reservoir of infection in the definitive host or hosts in a campaign limited in time and carried out to such a degree of perfection that when it comes to an end there is no resumption of transmission". In contrast, control of transmission implies the reduction of schistosomiasis to a prevalence where it is no longer a major health problem. "Control which has to be maintained by continuous activity carries with it the implication that the program will be unending. In contrast, expenditure on eradication will represent capital investment and not a recurring cost" (Farooq, 1969).

Control of schistosomiasis was and is still frequently thought of in terms of chemically widespread snail control, as the snail intermediate host was considered the weak link in the chain of the life cycle of the parasite. Changing the ecology of snail habitats in the Philippines (Pesigan et al., 1958), reduced transmission of *S. japonicum*, and ecological methods of control are now encouraged, stimulated by those conservationists who felt that the prolonged, and perhaps unending, application of molluscicide would have unacceptable consequences on the aquatic biota, not only in the immediate vicinity of their application, but eventually on marine life.

Other factors are now being appreciated. Snail control may reduce transmission of schistosomiasis, but no other benefit has been reported from this approach, although liver fluke in cattle and sheep may be reduced in a few areas. In contrast, the provision of water to rural communities, normally dependent on a water supply infected with a variety of bacteria and viruses as well as cercariae, has obvious health benefits apart from the prevention of schistosomiasis. Within the past decade the possibility of "mass" treatment, or at least the treatment of all infected persons (selective population chemotherapy) has become a reality. Satisfactory control by a single method, whether snail control, provision of water, or chemotherapy, has been considered unlikely, but control in these terms has not been defined.

The object of control is basically to stop disease. While the effect on health of a few schistosome worms can be considered minimal (perhaps because "measures of health" are as yet insensitive and cannot measure the ill health caused by low numbers of trematodes), heavy infestations lead to schistosomal disease.

Control should thus be concerned with measures to reduce the worm burden in a population to such an extent that schistosomal "disease" does not occur. Although the community worm burden is reflected by egg output and prevalence, the relationship between them and disease is poorly defined. Thus, control schemes aim to lower these indices as far as possible (perhaps below the disease threshold), with increasing control costs and increasing difficulty to decrease low rates further. The achievement of *very* low rates of prevalence and intensity of infection compared with *low* rates may not be economically acceptable as disease rates are likely to be minimally different. With this understanding, different methods of environmental control based on changing the ecology of the definitive and intermediate hosts are suggested in the following pages.

1. Changes in ecology of definitive host

a) Alterations in pattern of water contact

Human contact with water supporting infected snails is one of the prerequisites for continued transmission of schistosomiasis in any endemic area. Therefore, the prevention of this contact should reduce the incidence of new infections, should decrease superinfection in those already parasitized, and, with the gradual spontaneous death of adult worms in the human host, should lower worm burdens and prevalence of infection. Morbidity due to the infection would thus be slowly reduced.

Pitchford (1970) provided safe potable water and simple swimming pools in an area where *S. mansoni* and *S. haematobium* were endemic in South Africa. At the same time, streams containing infected snails were isolated by fencing. While a gradual reduction in prevalence of both infections followed the start of these measures, no comparison area was available for study. In Brazil, Barbosa and his colleagues (1971) also obtained evidence for reduced transmission after the provision of well-water, laundry and showers, and latrines. Bhajan and her colleagues (1978) have shown by multi-factorial regression analysis that the observed decrease in skin test prevalence of *S. mansoni* in Puerto Rico can be correlated best with improved water supply rather than upgraded sewage disposal or increases in education.

In a detailed study in St. Lucia, five villages were provided with individual household water supplies, community washing-laundry units and simple swimming pools (Unrau, 1975; Jordan et al., 1975, 1978). Three experimental water-supply systems were involved and were installed over a period of two years. In Grande Ravine, the settlement first supplied with water in 1970, a drop in the frequency of contact and a 96% reduction in duration of contact occurred at the two main washing sites (Table 4). Between 1970 and 1975 in the five settlements with an experimental water supply, the reduction in prevalence and intensity of infection, as measured by egg output, resulted in a reduction in potential contamination of 68% (Table 5). Sentinel snails (laboratory-bred and

8 Acta Tropica 109

Table 4. Number and duration of water contacts at two sites before and after individual household water supplied in Grande Ravine, St. Lucia (Dalton, personal communication) (from Jordan, 1972)

Age	1969		1970	
	Numbers of contacts	Total time*	Numbers of contacts	Total time*
0-4	48	2.320	3	1
5–9	104	3.299	9	9
10–14	84	2.767	23	31
15–19	71	1.414	5	89
20–29	38	0.953	3	81
30–39	21	0.536	7	6
40–49	2	0.089	5	156
50	7	0.185	11	70
Total	375	11.563	66	443

^{*} Time in minutes

N. B.: Eight days observation, same days of year in 1969 and 1970

exposed in mosquito-net bags in the main river) showed a reduction in the percentage becoming infected from 0.50 to 0.21% (Jordan et al., 1978). This change compares with findings in the comparison area where an increase in the percentage of sentinel snails infected from 0.17 to 0.79% was recorded and all indices of infection increased between 1970 and 1975.

In the comparison area, a Government rural water supply had been installed early in 1969. This supply comprised public stand-pipes at roughly 200-yard intervals along the road. The system had no effect on transmission of schistosomiasis; in fact, incidence increased after installation probably due to changes in climatic conditions. From water contact studies in the area, it was apparent that the stand-pipes were used extensively for collecting water for home use, but washing of clothes, bathing, swimming, playing and fording are still common causes of river contact.

A water supply provided as a control measure against schistosomiasis must furnish adequate water at all times, be reliable, and be conveniently placed for the people it supplies. As an indication of the importance of these factors, one can cite the failure of the experimental water scheme to prevent return of people to their old habits during the drought of 1975, the worst shortage of water in St. Lucia in 34 years. The people of Grande Ravine continued to get some piped water but at a level below their usual requirement of 12 gallons per capita per day, and this lead some inhabitants to return to the rivers. Stool surveys in 1976 showed an increase in incidence due to the occurrence of the drought.

Apart from controlling the transmission of S. mansoni, the provision of

Table 5. Change in prevalence and intensity of infection of *S. mansoni* following introduction of experimental water supplied in St. Lucia (from Jordan et al., 1978)

Age	1970			1975		
	Prevalence in % (1)	Intensity of infection* (2)	Potential contamination (1×2)	Prevalence in % (1)	Intensity of infection* (2)	Potential contamination (1×2)
0-4 5-9 10-14 15-19 20-29 30-39 40-49 50-59 60+ Total potential	16 53 79 78 78 69 69 64	19 34 45 45 38 22 22 18	304 1802 3555 6300 2964 1386 1518 900 1152	7 23 50 60 60 56 40 41	13 17 17 19 23 23 14 14	91 391 850 1140 1380 840 560 574 585
	64	8	1152	39	5	

* Geometric Mean

water has obvious other social and medical benefits. The water system represents a capital asset to the community and provides a much needed requirement of safe water. In the areas of St. Lucia provided with a schistosomiasis control type of water supply, the weight increments of infants have been found to be higher than in areas where people are largely dependent on natural water supplies. Presumably, this change is a result of reduced attacks of gastro-enteritis (Henry, unpublished data).

While water supplies have been shown to be as effective as snail control in reduction of schistosomiasis in St. Lucia, the method should be evaluated in other endemic areas. The method is obviously not applicable to the vast open spaces of Africa or South America with low population densities. Even in those areas, people must obtain household water from somewhere; inexpensive ways. such as protected springs or small diversion weirs, should be used to improve their supplies. In the Cameroun, 15 of 48 village springs were improved by damming the source and then protecting it by building a cover of bamboo and raffia (Isley, 1978). The earthen dam was pierced with a bamboo pipe to provide a tap for the water, and a ditch was built to prevent accumulation of water below the tap. By such simple means, water quality in seven of these fifteen springs improved so as to be potable by WHO standards, while only three of the unimproved sources met such criteria. Villages on major irrigation systems, close to main canals or lakes where water is plentiful, would seem ideal localities for further trials of this control procedure. It must be emphasized that the provision of water alone, without explanation to the public as to the reasons for its provisions and without education at all age levels as to benefits that can be derived from proper usage, may prevent proper fulfillment of the purposes for which water was provided. MacDonald (1965) postulated that if the provision of water supplies reduced the contact people had with contaminated water, a secondary effect might be less contamination by infected excreta, further reducing the chances of transmission. Finally, the supply and proper use of water should theoretically reduce the prevalence of other intestinal helminths such as Ascaris and Trichuris. Regrettably, this reduction has not been observed in St. Lucia.

b) Alterations in defaecation pattern

The basic reasons for transmission of schistosomiasis is the low level of sanitation found in endemic areas with the result that faecal matter and urine containing schistosome eggs get into water containing freshwater snails susceptible to infection. With regard to *S. haematobium*, improved sanitation is unlikely to be effective in controlling transmission. The temptation to urinate in water, especially when bathing, presents a problem which even the best health education is unlikely to overcome. However, health education with a positive approach aimed at encouraging urination *before* swimming rather than "don't urinate while swimming" should be encouraged.

Results of latrine campaigns in Egypt (Scott and Barlow, 1938; Weir et al., 1952) are frequently incorrectly quoted as having shown no effect on *S. mansoni* transmission. In the latter campaign, no stool examinations were reported from the comparison area, and furthermore, examinations were carried out only once in the area where latrines had been installed, and this examination took place before installation of latrines was completed. In the earlier work, stools were obtained annually from populations of both control and comparison areas. On the other hand, only *overall* prevalence among all age groups are given, and, in many cases, the number of persons examined annually varies considerably. In one area, Ibrahim Bey, where the same 171 persons were examined in 1930, 1931, and 1932, prevalence of infection fell from 56 to 42%, suggesting that latrines did reduce transmission.

In the Philippines (Pesigan et al., 1958), latrines were provided, and the *S. japonicum* infection rate fell in nearby snail colonies. At the same time, a rise in infection rate occurred in snails near to other houses not provided with latrines. These results suggest that provision of sanitation facilities can help reduce transmission. Long term effects of this investigation were nullified when a storm destroyed many of the latrine superstructures resulting in disuse of these facilities.

Latrines are notoriously difficult to maintain in a hygienic condition, especially in rural, tropical areas. The most common complaints are bad odor in or near latrines, presence of flies, other insects and rodents, latrines too far from dwelling, lack of privacy, and lack of cleanliness. The latter three items are related to communal latrines in particular, but all of these complaints tend to discourage their use. A large number of methods for the collection and disposal of human excreta are being investigated in order to overcome the shortcomings of the conventional pit latrines. Classifications are almost as numerous as the methods. However, for rural areas, it may be sufficient to consider only whether water is a requirement for the operation.

A variety of water-seal latrines have been developed in the past few years. These units usually require small amounts of water (1–2 litres) to flush and have the advantage of being odor and insect-free. The flushing is accomplished by pouring a small amount of water into the bowl. In some societies, this type may have the disadvantage of blocking when used for disposal of varieties of trash. For this reason, it is best suited for individual household use where better care of the unit can be taken than at communal installations.

In St. Lucia, a water seal unit made of high density plastic has been adapted from a prototype developed in New Zealand and is being evaluated in a community of about 400 households. The unit is molded in two sections consisting of a combined bowl and riser and a connecting S-bend which can either be directed to an offset pit or mounted directly on a concrete slab over the pit. The acceptance of this unit has been very good, and the plastic material makes it easy to keep clean.

The watergate toilet designed in Rhodesia by Morgan (1977b) is another type of water seal unit which uses water very efficiently. This system consists of a squatting plate with a chute, the bottom of which is covered by water held in a pan. The pan is hinged and counter-weighted so that any additional weight in the pan destroys the balance, and the pan tips its contents into the pit. The weight brings back the pan which again fills with water restoring the water seal. The unit requires about two liters of water per flush, and the chute is reasonably large so the problem of blockage does not occur. These units are suitable for public latrines. The few units installed in St. Lucia on a trial basis seem to be working well.

Among the numerous devices that exist under the classification of non-water dependent toilets, one of the more attractive is a recent design known as the vented pit privy (Morgan, 1977a). This unit is a modification of the deep pit latrine with features to prevent fly and odor problems. Briefly, the privy consists of a slab with a squatting hole and a second hole (20 cm diameter) to be fitted with a vent pipe not less than 15 cm in diameter. This slab is placed over a pit, and a deliberately small superstructure which admits little light is built on the slab. As a result, the strongest light reaching the pit is from the fly-screened vent which will attract any flies to the opening. Once attracted to the vent, the flies tend to stay in the vent pipe until they die. The other feature is the air circulation created by a temperature differential which removes the odors. An up-draught, aided by sunlight on the vent pipe, lifts the obnoxious gases from the pit. Fresh air replaces the gases in the pit by a down-draught through the squatting hole. By this means, one can build a simple inexpensive unit suitable to individual household ownership.

In areas where night-soil is used as a source of fertilizer, a septic tank for removal of schistosome eggs, such as developed by the Chinese (Chi, 1975), may be constructed for communal use. The tank has three compartments designed to allow sequential sedimentation and filtration of schistosome eggs. Building of such a unit allows use of excreta as fertilizer without the accompanying danger of infection of workers in their fields.

Recently, there has been much discussion about the use of an aerobic "multrum" type of latrine based on biological decomposition (Winblad, 1974). However, most of the data on use of this latrine comes from temperate climates. In tropical climates, these systems have not performed well due to humidity and moisture causing serious odor problems.

The view is often expressed that persons working in their fields will defaecate there for convenience. This statement may well be true, but the concentration of faecal matter will not occur near the villages which are usually the main transmission sites. If everyone used a latrine for alternate bowel movements, faecal contamination would be reduced by 50%, and the number of *S. mansoni* eggs deposited reduced by a similar amount. The effect of this theory has not been investigated, but, in a chemotherapy campaign, where it has been estimat-

ed that contamination was reduced by 63%, no infected wild or sentinel snails were found in the 24 months following the first treatment (Christie and Upatham, 1977). As has been shown in earlier paragraphs of this paper, younger age groups in a population frequently contribute a major proportion of the contamination in an endemic area. Therefore, the construction of adequate and acceptable latrines in schools should be encouraged by public health officials. As with the provision of water supplies, installation of latrines must be accompanied by an extensive and ongoing health education program.

2. Changes in ecology of intermediate host

a) In natural habitats

Drastic changes in the environment are generally required to render a habitat unsuitable for intermediate hosts of schistosomiasis as these snails tolerate a relatively wide range of physical, chemical and biological conditions. It is usually difficult to alter any one of these factors sufficiently to obtain adequate control. However, alteration of one factor may subsequently influence others and achieve the desired effect.

Massive efforts by the Chinese achieved snail control in certain areas by relatively simple engineering methods (Chi, 1975). However, the object of their control efforts, *Oncomelania hupensis hupensis*, is a dioecious mollusc. Even if such massive mobilization of human populations could be achieved in other countries, equivalent results might not be obtained with the snail hosts of *S. mansoni* and *S. haematobium*. As these animals are hermaphroditic and possess a high intrinsic rate of natural increase, complete kill has to be achieved for successful control.

The destruction of the snail habitat is the most complete method of control and is possible in some instances. Reference has been made to borrow-pits which frequently become infested with snails; these pits can be filled with the resulting destruction of that habitat. Similarly, many water-holes used for domestic supplies in Africa could be filled and replaced by properly constructed and protected wells. In some places, marshes and swampy areas can be filled, but these situations are more frequently amenable to drainage. If this change is made, the collector drains may not be a suitable environment for the snails. If snails do become established in the drains, they are more readily treated with molluscicide there than in the original marsh. Hill-side springs frequently give rise to swampy areas. These water sources can be converted into "protected" springs, and when fitted with a tap, can provide a safe water supply. The overflow can be properly channeled so that the seepage area dries.

In laboratory experiments, *B. glabrata* were dislodged with water velocity of 33 cm/sec (Jobin and Ippen, 1964). Therefore, increasing the velocity of a stream may flush snails from their habitats. Such a change can be accomplished

in some situations simply by removing rocks and other obstructions, particularly near the river banks where these obstacles often lead to sluggish water movement and an environment suitable for snails. This environment may be small in area, but such foci can house large snail colonies. Clearing of vegetation and debris (i.e. fallen trees) can increase velocity and render the habitat unfit for snails. Stream speed can be changed also by such measures as channelization, deepening of marginal areas and elimination of contiguous pools. On the other hand, while the general velocity may be high, low flow rate may occur in microfoci where snails can still survive (McJunkin, 1970).

Limited increases in velocity, without flushing snails, may cause more cercariae and miracidia to pass a given point (Rowan and Gram, 1959; Radke et al., 1969) thus leading to greater infection. However, as stated previously, this change will also lead to dilution of cercarial numbers and less contact time between parasite and host. That an increase in velocity may lead to decreased infection of snails is supported by Upatham's (1972c) findings that the infection rate for *B. glabrata* exposed in a static water habitat, was 0.53% while for those exposed in a flowing-water habitat the rate was 0.18%. Both groups of molluscs were exposed to similar numbers of miracidia. Infection of mice by cercariae in different habitats yielded similar findings (Upatham, 1974).

While intermediate snail hosts frequent a variety of habitats, evidence from different endemic areas indicates that colonies often are attracted to organic waste matter (Jordan and Webbe, 1969). The elimination of such material from snail habitats not only reduces the chances of infection but may go some way towards reducing numbers of snail intermediate hosts.

b) In irrigation schemes

In present schemes, opportunities for introducing ecological snail control methods are limited, but room exists for improved maintenance of canals — weeding, clearing, desilting, and restoration of their original cross section. The possibility of improving the distribution system should be investigated — excess seepage should be corrected, foot bridges provided, and adequate drainage should be installed where necessary. The provision of adequate water supplies and laundry and shower units to villages, the construction of latrines, and fencing at selected high risk sites to prevent access to canals should all be considered.

In the Kou Valley of Upper Volta, curb wells and latrines were built as an integral part of settlements of a new rice irrigation scheme (Colette et al., 1977). At the same time, the villages were instructed in simple fundamentals and rules of hygiene. Anyone who habitually violated these rules was expelled from the irrigation scheme. Both parasitological and serological examination of infants to 15-year-olds revealed a decreased prevalence of both *S. mansoni* and *S. haematobium* in those individuals living in the irrigation scheme compared to those people living in traditional villages in the surrounding area.

In designing new irrigation schemes, detailed planning must involve mea-

sures to reduce the risk of establishment of schistosomiasis. Cost estimates should include capital expenditure on anti-schistosomiasis measures as well as recurrent costs. Probably of prime importance is the siting of villages as far from canals as possible. In planning these villages, *adequate* supplies of safe water with sufficient laundry and shower units of appropriate design for local usage should be provided along with simple pools for diversion of children from the canals and latrines for family and community use. Access to nearby canals should be made difficult by the construction of walls, fences or hedges.

The dam and main canals of irrigation schemes are usually well designed and constructed, but water distribution by secondary and tertiary canals and drainage from the fields are frequently given inadequate attention at the planning stage. Attention should be given to these details, and to such items as the elimination of water storage at night in reservoirs or long canals. To this list should be added prevention of excessive seepage leading to water-logged areas, canal lining, closed conduits, effective regulation of water flow, and anti-silt and anti-weed measures. Finally and most importantly, adequate staff should be trained for the efficient running and maintenance of such schemes.

c) In man-made lakes

The creation of man-made lakes within the past decade has introduced a new problem into the control of schistosomiasis. Land inundated by the construction of a dam may previously have been almost waterless with a low density of human population. The impoundment of water can lead to a concentration of people from other areas, and, in tropical regions, some of these people will inevitably be infected with water-borne diseases.

It took only a few years for *Bulinus truncatus rohlfsi* to become established in Lake Volta and for prevalence of *S. haematobium* to increase from less than 5% to 40% in the areas inundated by the lake. Although excessive transmission *may* only be temporary while stabilization of the ecology is taking place (Paperna, 1970; Klumpp and Chu, 1977), continued transmission will occur.

At present, the control of established snail intermediate hosts along the shore line of the vast expanse of water is difficult, if not impossible. In smaller lakes, fluctuation of water levels at frequent intervals may kill snails and their eggs (Jobin and Michelson, 1969; Jobin, 1970). In larger lakes without provision for periodic flushing, prevention of infection of snails might be difficult, but perhaps not impossible, if, in the planning stages, the administrative, legislative, and engineering experts of such schemes are aware of the problem.

Properly planned resettlement villages with water and latrines must be well away from the expected lake shore, perhaps as much as two miles. Fishing will eventually, and necessarily, become a feature of the changed ecological conditions, but legislation could involve the screening of fishermen for schistosome infection. Such screening of persons going to live in new development schemes is already a part of planning in Brazil and Egypt. Access to the lake

shore can be limited, and, in such an area, snail control measures might be possible. The landing of boats at a jetty built out from the shore might help to prevent transmission.

Measures as suggested in the previous paragraph are likely to be considered impossible and wishful thinking, just as has been the ideal of changing the custom of washing in rivers. Such habits can be changed, and since the whole ecology is altering in man-made lakes and irrigation schemes, people may be more acceptable to changes in their way of life. Two aspects of this speculation must be emphasized. The creation of resettlement villages a mile or two from the shore line, even if supplied with a good water distribution system, etc., must be backed by a good maintenance scheme and by health eduction. Secondly, and it must be repeated, these measures aim at *control* of transmission. Complete elimination of transmission is virtually impossible but, as stated earlier, a reduction in the amount of transmission of *infection* can reduce morbidity and the severity of the *disease*.

Apart from suggestions as to legislation, nothing in the way of planning, water supplies, and sanitation in the previous discussion is new. "In the long term, health education, combined with effective sanitation measures, including an efficient excreta disposal system, a safe water supply, and adequate bathing and washing facilities are necessary to prevent continuing transmission of infection. In all water development schemes early advice should be taken and, whenever possible, preventive measures should be built into each project" (Lagler, 1969).

d) Biological control

Biological control of schistosome transmission has focused on the extramammalian phase of the life-cycle. Most attempts at this method of control deal with elimination of the intermediate host, with some efforts directed against the parasite itself, either while it is in the snail or while invading or escaping from that mollusc. Most reports on tests of possible control agents suffer from one or more deficiencies: little or no field evaluation and thus no cost analysis; inability to realize that any control method has its limitations; no exploration of those limitations either in the laboratory or field; and lack of good controls.

The harmful effects of parasites, predators, and competitors on snail intermediate hosts have been well documented (Michelson, 1957; Wright, 1968; Andrade, 1971; Berg, 1973; Ferguson, 1977). Various protozoons, fungi, bacteria, and nematodes have been isolated from planorbid snails. As of yet, no viruses have been found in medically important molluscs (Malek and Cheng, 1974). Furthermore, until recently (Hansen, 1976; Bayne et al., 1978), no molluscan cell lines existed for the culture of viruses once they had been isolated from a source. The organisms which have been found in snails have been commensals, or, at best, opportunistic pathogens and have not, with one exception, been evaluated in field tests. That one exception, *Bacillus pinottii*, was shown by

Venezuelan workers (Texera and Scorza, 1954) and scientists working in Egypt (Dias and Dawood, 1955) to kill B. glabrata. However, Tripp (1961) showed that Dias' strain of B. pinottii was non-pathogenic to a laboratory strain of B. glabrata. Besides lack of field evaluation, some problems are inherent in the use of parasites as biological control agents. First and most obvious is the task of elucidating the life cycle and subsequent laboratory maintenance of the agent. Second is the possible danger to humans caused by using parasites as control agents. The discovery of Naegleria fowleri with its associated pathogenic effects makes evaluation of vertebrate pathogenicity of possible amoebic control agents a necessity. Recently, an insect picornavirus, which has been mentioned as a possible viral insecticide (Smith, 1976), has been shown to elicit naturally occurring antibodies in man. Assuming that a parasite is pathogenic to snails under laboratory conditions, there is also the fact that snails are poikilotherms which means that parasite development in these animals may be greatly dependent on environmental temperatures. This relationship is shown very clearly by the increased maturation times and decreased sporocyst numbers of S. mansoni in B. glabrata maintained at suboptimum temperatures (Upatham, 1973a) and by the changes in pathogenicity of Hexamita sp. in the oyster, Crassostrea virginica, with changing environmental temperatures (Scheltema, 1962). Next is the possibility that pathogenicity observed in a laboratory experiment may not be associated with the organism that one is testing but may be due to an interaction between that organism and other species already present in the laboratory strain of snails. Other problems associated with parasites as biological control agents will be discussed in a later section on echinostome antagonism.

While almost every class of animal has been represented in the list of predators of medically important molluscs (Ferguson, 1977), only three groups, ampullarid snails, larvae of sciomyzid flies, and malacophagous fish, have undergone any degree of field evaluation. Of the ampullarids, Marisa cornuarietis has been used most successfully for biological control; indeed that snail is employed as an integral part of schistosomiasis control programs in Puerto Rico and several other Caribbean islands. As Marisa browses over vegetation, it consumes all stages of Biomphalaria and Bulinus with which it comes in contact (Demian and Lutfy, 1965a, b, 1966). Cost-effectiveness studies show that treatment of a particular habitat with Marisa is cheaper than using molluscicides (Ruiz-Tiben et al., 1969; Jobin and Berrios-Duran, 1970; Jobin et al., 1970; Jobin et al., 1977). However this predator seems to have been used only in ponds and reservoirs where its effectiveness may be diminished by large quantities of aquatic vegetation. In addition, while Marisa has been shown to be very effective in killing snails, no evidence exists that it has had any effect on transmission of schistosomiasis of Puerto Rico as the important transmission sites are in running water and not in static habitats such as ponds.

In Brazil, laboratory tests indicated that *Pomacea australis* was similar to *Marisa* in its ability to destroy *Biomphalaria* (Paulinyi and Paulini, 1972).

However, in St. Lucia, field tests of *P. glauca* as a control agent revealed no changes in numbers of *B. glabrata* compared to numbers found in untreated areas (Prentice, personal communication). Furthermore, the ampullarids are voracious herbivores, and though this voracity may aid in clearing habitats of plants which may nourish and shelter planorbids, it indicates a potential for economic damage. The fact that *Marisa* can damage rice seedlings (Ortiz-Torres, 1962) and that *P. lineata* is an important rice pest in Surinam (Dinther, 1956) argues against introduction of these snails into areas without consideration of their potential for agricultural damage. Also disquieting is the fact that although *Marisa* has been used as a biological control agent for many years, few detailed investigations of its ecological niche and life requirements have been made. This lack of information may make introduction and success of *Marisa* in new habitats a hit-or-miss affair.

Aquatic larvae of sciomyzid flies have shown an ability to kill and feed on medically important molluscs (Berg, 1964). Although the larvae can attack Bulinus and Biomphalaria, they seem unable to kill Oncomelania possibly because of the operculum which offers some degree of protection against predation (Neff, 1964). However, Sucharit et al. (1976) showed that although larvae of Sepedon spangleri preferred non-operculate snails as prey, they would also consume operculate snails. In these authors' opinions, it was not whether the snail was operculate or non-operculate that mattered, but whether the prey's natural habitat was suitable for the larvae of the fly. For operculate snails, Japanese workers (Ferguson, 1977) have reported that aquatic larvae of fireflies are predators. In Swaziland, firefly larvae have been seen preying on Lymnaea natalensis and Bulinus sp. (Brown, personal communication). One possible advantage to the use of sciomyzid fly larvae is that the biology and ecology of the many species have been extensively studied, and therefore, reasons for success or failure in field trials can be formulated with some degree of realism. However, in the few field trials to date, sciomyzid larvae proved unsuccessful in attacking lymnaeid intermediate hosts of fascioliasis (Boray, 1964; Duran, 1975). Clearly, this method of control needs further extensive field trials.

Drastic reductions in snail densities have been obtained with the use of mollusc-eating fish in certain habitats. Such a series of trials was conducted in Kenya, where dams were stocked with Astatoreochromis alluadi (Pellegr.). Over a prolonged period, impressive reductions in numbers of Biomphalaria were obtained in ponds containing this fish (McMahon et al., 1977). However, this fish has been found in ponds which also contain thriving populations of B. pfeifferi (Webbe, 1961). Perhaps the central point is that a malacophagous fish may do very well in laboratory trials in eliminating a particular snail but, in nature, that fish will be offered a large variety of organisms as food and may even control another animal which acts as a check against the mollusc one wishes to control. For example, in the laboratory, redear sunfish (Leponis microlophus) eats Lymnaea and Physa as a large part of its diet; examination of fish from a

natural habitat shows that snails constitute only a small percentage of food consumed by the sunfish (Carothers and Allison, 1966). Even assuming that a fish which is strictly malacophagous in its food preferences can be found, it must be remembered that the fish will eventually be limited by the disappearance of its prey. The chances of finding any predator which is broad enough in its food preferences to switch to other molluscs when low snail numbers prevail yet is specific enough in eating habits to be able to devour snails in numbers large enough to affect schistosome transmission seem slim indeed.

Perhaps more hope should be placed in biological control based on competition by snails which are similar in their niche requirements to medically important molluscs. In a swampy area outside Recife, Brazil, *B. straminea* displaced *B. glabrata* over a period of four years (Barbosa, 1973). Barbosa speculated that either the lessened susceptibility to *S. mansoni* infection or a greater ability to resist desiccation of *B. straminea* compared to *B. glabrata* may have been responsible for the change. A neutral observer might say that any number of unknown factors were responsible for displacement of the one species by the other.

Helisoma sp. have been mentioned as possible competitors of Bulinus and Biomphalaria. In the only detailed field study to date, Rasmussen (1974) claimed that H. duryi controlled B. pfeifferi in drainage ditches in a sugar estate near Mwanza, Tanzania. However, a careful inspection of the data reveals that controls were inadequate for the experiment. Furthermore, the drainage ditches containing the different treatments were connected by main ditches allowing cross contamination of the drainage ditches. In Puerto Rico, Ferguson (1977) reported that B. glabrata was replaced by H. duryi in ponds supplied with dense algal mats, but did not give details of these field trials. In St. Lucia, H. duryi was found to eliminate B. glabrata in a series of trials conducted in semi-natural banana drains. The time required for elimination varied depending on rainfall, temperature and initial numbers of H. duryi present (Christie et al., in manuscript). Reasons for this replacement include excretion of a chemical by H. duryi which inhibited egg-laying and hatching by B. glabrata (Abdallah and Nasr, 1973; Christie et al., in manuscript). The presence of H. duryi may also cause increased mortality of *Biomphalaria* sp. and *B. truncatus* (Ayad et al., 1970; Abdallah and Nasr, 1973). However, a differential reproductive response of B. glabrata and H. duryi to environmental temperatures may actually play the major role in replacement of the former species by the latter (Christie et al., in manuscript).

In aquaria in which crowding produced inhibited reproduction and growth of *B. glabrata*, larger quantities of minerals and organic matter were found than in water taken straight from the tap (Chernin and Michelson, 1957). Wright (1960) suggested that the substance responsible for crowding was an excretory product of snails which could be removed from water by passage through activated charcoal. An organic ester was isolated from water of a pool

in which inhibition of growth of B. sudanica tanganyicensis occurred (Berrie, 1968). This ester was capable of inhibiting growth in laboratory colonies of snails (Berrie and Visser, 1963). Levy and his colleagues (1973) claimed to have isolated a proteinaceous excretory product of both B. glabrata and Ferissia which inhibits population growth of the former snail. Thomas and his co-workers have isolated a series of factors which affect growth and reproduction of B. glabrata. Acceleration of growth and natality were produced by compounds which included chemicals in the molecular weight range 500-104, low concentrations of ammonia, substances found in snail faeces, and cellulases of snail origin. With the exception of indole acetic acid (a plant hormone) and the chemical found in snail faeces, the rest of the substances were produced by the snails themselves (Thomas, 1973; Thomas and Aram, 1974; Thomas and Benjamin, 1974a, b; Thomas et al., 1975b; Thomas et al., 1974b, 1975a). Negative effects on growth and reproduction were produced by depletion of calcium, plant inhibitory factors and high concentrations of ammonia (Thomas, 1973; Thomas et al., 1974a; Thomas and Lough, 1974; Thomas et al., 1975c; Thomas et al., 1976). Finally, Brazilian workers have isolated a substance which has been partially purified by activated charcoal passage, deionization, and lypholization (Coelho et al., 1977). This chemical isolated from B. glabrata culture can inhibit respiration of snails, the extent of inhibition depending on the amount of substance added to aquarium water. The question now is whether or not the H. duryi excretory product is one of these products discussed in the previous sentences? More importantly, is the substance a product of *H. duryi* specifically, or is it a chemical such as ammonia common to all pulmonate snails? If the chemical is excreted only by H. duryi, then inhibition of reproduction of medically important molluscs by this compound is the primary method of control. If the substance is a common excretory product of all snails, then some other mechanism such as differential reproductive responses of B. glabrata and H. duryi is the primary method of control. If the latter statement is true, then research should focus on finding competitors whose niche requirements offer a chance of these snails being able to eliminate schistosome intermediate hosts in the appropriate situation.

Perhaps the most important aspect of *Helisoma* as a control agent is that its use may be limited to certain field situations. *H. duryi* cannot withstand the high velocities that *Biomphalaria* encounters in a stream or river (Prentice, personal communication). This difference may be due to the heavier weight of *H. duryi* and may be offset by the smaller size at onset of egg-laying (Christie, in manuscript). More to the point is that introduction of the snail into certain habitats in Puerto Rico and St. Lucia failed utterly to control *B. glabrata*. Whether this failure is due to these sites being unsuitable or is due to *Biomphalaria* having filled a particular niche preventing introduction of an ecological homologue is unknown. All this doubt points to the need for further field and laboratory studies of *H. duryi* and its niche requirement compared to those of *B. glabrata*.

The other snail that has been mentioned as a possible control agent for Biomphalaria is Thiara (= Melanoides = Tarebia). Whether this snail is a competitor or predator of Biomphalaria is unknown; indeed whether the snail really has any effect on B. glabrata is a moot point as the replacement of that snail by T. granifera in Puerto Rico may have been due to environmental changes. What is certain is that the conical shape of Thiara is better adapted to running water than the helical shape of Biomphalaria (Ferguson, 1977) allowing for a quicker repopulation by the larger number of survivors of the former snail after flushing of a stream containing both species. Faster repopulation by Thiara may also be helped by the fact that this prosobranch is either parthenogenetic or only mates when extremely young and is also ovoviviparous which may give that mollusc a higher intrinsic rate of increase than the schistosome intermediate hosts possess.

If *Thiara* proves to be a good control agent for schistosome-bearing snails in laboratory evaluations, research should then focus on a related species, *Brotia*, which shares the same life history strategies and morphological characteristics but is not a host of *Paragonimus westermani* as *Thiara* is.

Another problem with this snail is that it can eliminate indigenous mollusc species (Murray, 1970). With the increasing emphasis on protection of unique species of organisms, this could have adverse effects on public acceptance of control efforts.

The last method to be used as a control agent for snails is the planting of vegetation whose products may be toxic to snails. The literature abounds with the use of local plants, or extracts therefrom, as molluscicides – *Phytolacca dodecandra* (Endod) is the most outstanding example of this endeavor (Lemma et al., 1978). In Uganda, the molluscicidal properties of *Phytolacca* have long been known, but the plant has not been used in snail control because of its local reputation as an abortifacient (Prentice, personal communication). *Eucalyptus* sp. may be used for drying marshy snail habitats; additionally; the leaves of the tree are toxic to snails, and the timber may be commercially valuable. The use of toxin-producing algae (Gentile, 1971; Schantz, 1971; Shilo, 1971) to control both snails and other plants deserves a closer look.

Biological control against the extra-mammalian phases of the schistosome life-cycle has focused on three methods: decrease in genetic susceptibility of the snail host which has been discussed earlier; attack on sporocysts by echinostomes or microsporidians; and decoy of miracidia by insusceptible snails.

Laboratory analysis of the efficacy of echinostome antagonism toward schistosome sporocysts as a biological control measure has been well documented by Lim and Heyneman (1972). The actions of echinostomes on schistosome sporocysts can either be direct, the rediae ingest the larvae, or indirect, the echinostome rediae or sporocysts inhibit schistosome development. In two field trials which took place in a tin-mining pool, seeding of some areas of the pool with eggs of *Echinostoma malayanum* helped reduce *Schistosoma spindale* infec-

tion rates in these sections (Lie et al., 1970, 1971). However, in both trials, transmission of *Nosema eurytremae* from *E. malayanum* to *S. spindale* may have contributed to this control and also to death of the host snail.

This finding lead to interest in control of medically important molluscs and schistosome larvae by microsporidians. Control of snails with microsporidians seems remote for two reasons. So far only three microsporidians have been found in the molluscs of importance (Richards and Sheffield, 1970; Basch and Di Conza, 1973; Bayne et al., 1975). Only in one of these three cases has the parasite been assigned an identity. In addition, fairly narrow host specificity may exist; *Plisotphora husseyi* will only infect members of the family Physidae (Michelson, 1963). Microsporidians may do more damage as parasites of those trematode larvae which infect medically important molluscs. The species of *Nosema* found so far in trematodes will infect more than one species of trematode which, in turn, may infect several species of snail (Cort et al., 1960a; Canning and Basch, 1968; Higby and Canning, 1975). In this manner, the microsporidians may be able to be disseminated by non-human trematodes through populations of medically important molluscs.

In stepping from the laboratory to the field, there are several constraints which limit the usefulness of echinostome or microsporidian antagonism. Little information exists on laboratory maintenance of the Microsporea. In addition, many of the echinostomes have fairly exotic definitive hosts although Ribeiroia marini guadeloupensis can be maintained in the laboratory rat (Nassi, 1978). The dynamics of the infection process would also seem to limit the usefulness of either of these methods. In the E. malayanum field trials which were not costed, daily seeding with 300 to 5,000 eggs for eleven months was needed to attain success in a fairly circumscribed area. A low infection rate of trematodes with Nosema sp. in the field has been attributed to development of resistance by the parasite (Cort et al., 1960b). More probably, various environmental factors caused a low hatching and infection rate of the microsporidian spores. Even at sites of high transmission, snail infection rates in St. Lucia are on the order of 1 to 20%. Even assuming that an infection rate of 20% can be attained with echinostomes or microsporidians, this level would probably not reduce cercarial densities sufficiently to decrease transmission of schistosomes.

The use of insusceptible animals as passive sponges, trappers, or poisoners of miracidia was advocated as a result of laboratory studies by Chernin and his colleagues (Michelson, 1964; Chernin, 1968; Chernin and Perlstein, 1969). On the basis of body surface area, *Physa marmarota* was the most efficient passive "miracidial sponge" of the animals found naturally associated with St. Lucian *B. glabrata* (Upatham, 1972a; Upatham and Sturrock, 1973a). In the *Fasciola hepatica-Lymnaea truncatula* system, filter-feeding prosobranches and bivalves and predatory *Daphnia pulex* removed miracidia from water (Christensen et al., 1976, 1977; Nansen et al., 1976). Toxic secretions of planarians did not affect miracidia of *F. hepatica* (Christensen et al., 1977), unlike the situation found

with *S. mansoni* miracidia (Chernin and Perlstein, 1969; Glaudel and Etges, 1973). However, diminution of miracidial numbers by insusceptible organisms would probably only work with those organisms which are predators or competitors of medically important snails. Addition of other animals to any particular habitat would not achieve any lasting results as the carrying capacity of that environment for the particular species would probably be exceeded by the addition of more numbers of that group.

Interestingly, *Physa acuta* has been documented as a competitor of *B. truncatus* and *B. alexandrina* (El-Hassan, 1974) and, therefore, may be useful as a passive "sponge". Besides competing with medically important snails, *H. duryi* has been shown to reduce cercarial shedding in infected molluscs (Frandsen, 1976; Frandsen and Christensen, 1977). Not only does *H. duryi* act as a decoy for *S. mansoni* miracidia, but its excretions may also affect them in some manner (Etges et al., 1975). In addition, some evidence indicates that the presence of *H. duryi* may inhibit intramolluscan development of *S. mansoni*, but that effect may simply be due to crowding (Coles, 1973).

In conclusion, this section of the review has focused on biological control against the background of environmental factors which may affect schistosome transmission. If the prospects of large-scale biological control seem gloomy, and if possible biological control mechanisms have been omitted from discussion, then these faults are deliberate. Emphasis has been placed on systems which may work in the field and not on organisms which may play a natural regulatory role of some sort but could not possibly be used to control medically important snails. The gloominess of the prospects for biological control is due to past tendencies to over-emphasize the ease of and results that could be attained by this method. Frequently overlooked is that the limitations of the environmental aspects of transmission *must* dominate the thinking of anyone involved in field aspects of control. If these considerations are kept in mind, then an idea of time scale, of needs in terms of future research, and of expenses involved in such research may help biological control do its intended job – limitation of schistosomiasis transmission.

Acknowledgments are made to Dr. P. Dalton for permission to quote unpublished data on water contact studies, to the British Medical Bulletin for permission to reproduce Figure 1 and Table 4, to the James W. McLaughlin Fellowship Fund for providing financial support to J. D. C. during the preparation of this review, and to Mr. G. Barnish for help in preparation of Figure 1.

9 Acta Tropica 125

Abdallah A., Nasr T.: *Helisoma H. duryi* as a means of biological control of schistosomiasis vector snails. J. Egypt. med. Ass. *56*, 514–520 (1973).

Andrade R. M. de: Notes on laboratory and field observations regarding planorbid competitiors and predators: Protozoans, Crustaceans, and Mollusks. Rev. bras. Malar. 23, 193–194 (1971).

Appleton C₁C₂: Review of literature on abiotic factors influencing the distribution and life cycles of bilharziasis intermediate host snails. Malacol. Rev. 11, 1–26 (1978).

- Ayad N., Mousa A. H., Ishak M. M., Yousif F., Zaghleul S.: A preliminary study on biological control of the snail intermediate hosts of schistosomiasis in U.A.R. by *Helisoma duryi* snails. Hydrobiologia *35*, 196–202 (1970).
- Ayala F. J.: Genotype, environment, and population numbers. Science 162, 1453–1459 (1968).
- Barbosa F. S.: Aspects of the ecology of the intermediate hosts of *Schistosoma mansoni* interfering with the transmission of Bilharziasis in northeastern Brazil. In: CIBA Foundation Symposium on Bilharziasis (ed. by G.E.W. Wolstenholme and M. O'Connor), p. 23–35. J. and A. Churchill Ltd., London 1962.
- Barbosa F. S.: Possible competitive displacement and evidence of hybridization between two Brazilian species of planorbid snails. Malacologia 14, 401–408 (1973).
- Barbosa F. S., Barbosa I.: Dormancy during the larval stages of the trematode *Schistosoma mansoni* estivating on the soil of natural habitats. Ecology *39*, 763 (1958).
- Barbosa F. S., Coelho M. V.: Acao da desseçação sôbre as fases larvarias intracaramujo de *Schisto-soma mansoni* em *Australorbis glabratus*. Publcoes avuls. Inst. Aggeu Magalhães 2, 159–162 (1953).
- Barbosa F. S., Coelho M. V.: Comportamento das formas larvarias de *Schistosoma mansoni* em *Australorbis glabratus* (Mollusca Planorbidae), sujeitos a estivação. Publicoes avuls. Inst. Aggeu Magalhães 4, 51–60 (1955).
- Barbosa F. S., Coelho M. V., Dobbin J. E.: Qualidades de vector dos hospedeiros de *S. mansoni* no Nordeste do Brasil. II. Duração da infestação e eliminação de cercarias em *A. glabratus*. Publicoes avuls. Inst. Aggeu Magalhães 3, 79–92 (1954).
- Barbosa F. S., Olivier L.: Studies on the snail vectors of Bilharziasis mansoni in northeastern Brazil. Bull. Wld Hlth Org. 18, 895–908 (1958).
- Barbosa F. S., Pinto R., Souza C. A.: Control of Schistosomiasis mansoni in a small northeast Brazilian community. Trans. roy. Soc. trop. Med. Hyg. 65, 206–213 (1971).
- Basch P. F.: An interpretation of snail-trematode infection rates: specificity based on concordance of compatible phenotypes. Int. J. Parasit. 5, 449–452 (1975).
- Basch P. F.: Intermediate host specificity in Schistosoma mansoni. Exp. Parasit. 39, 150–169 (1976).
- Basch P. F., DiConza J. J.: Primary cultures of embryonic cells from the snail *Biomphalaria glabra-ta*. Amer. J. trop. Med. Hyg. 22, 805–813 (1973).
- Bayne C. J., Owczarzak A., Allen J. R.: Molluscan (*Biomphalaria*) cell line: serology, karyotype, behavioral, and enzyme electrophoretic characterization. J. Invert. Path. *32*, 35–39 (1978).
- Bayne C. J., Owczarzak A., Noonan W. E.: In vitro cultivation of cells and a microsporidian parasite of *Biomphalaria glabrata* (Pulmonata: Basommatophora). Ann. N.Y. Acad. Sci. 266, 513–527 (1975).
- Berg C. O.: Snail control in trematode diseases: the possible value of sciomyzid larvae, snail-killing Diptera. In: Advances in Parasitology, Vol. 2 (ed. by B. Dawes), p. 259–309. Academic Press, London/New York 1964.
- Berg C. O.: Biological control of snail-borne diseases: a review. Exp. Parasit. 33, 318–330 (1973).
- Berrie A. D.: Prolonged inhibition of growth in a natural population of the freshwater snail, *Biomphalaria sudanica tanganyicensis* (Smith) in Uganda. Ann. trop. Med. Parasit. 62, 45–51 (1968).
- Berrie A. D.: Snail problems in African schistosomiasis. In: Advances in Parasitology, Vol. 8 (ed. by B. Dawes) p. 43–96. Academic Press, London/New York 1970.
- Berrie A. D., Visser S. A.: Investigations of a growth-inhibiting substance affecting a natural population of freshwater snails. Physiol. Zool. 35, 167–173 (1963).
- Bhajan M. B., Martinez V., Ruiz-Tiben E., Jobin W. R.: Socioeconomic changes and reduction in prevalence of schistosomiasis in Puerto Rico. Bol. Asoc. med. P. Rico 70, 106–112 (1978).
- Blair D. M., Husting E. L.: The routes of schistosome egg passage from the human body. Centr. Afr. J. Med. 11, 243–254 (1965).
- Boray J. C.: Studies on the ecology of *Lymnaea tomentosa*, the intermediate host of *Fasciola hepatica*. Aust. J. Zool. 12, 217–230 (1964).
- Bunnag T., Freitas J. R. de., Scott J. G.: Sewage stabilization pond: the effects on *Schistosoma mansoni* transmission. S. E. Asian J. trop. Med. publ. Hlth. 9, 41–47 (1978).

- Canning E. U., Basch P. F.: *Perezia helminthorum* sp. nov., a microsporidian hyperparasite of trematode larvae from Malaysian snails. Parasitology *58*, 341–347 (1968).
- Carothers J. L., Allison R.: Control of snails by the red-ear (shellcracker) sunfish. Fish. Rep. FAO No. 44, 339–406 (1968).
- Chernin E.: Interference with the capacity of *Schistosoma mansoni* miracidia to infect the molluscan host. J. Parasit. *54*, 509–516 (1968).
- Chernin E.: Behavioral responses of miracidia of *Schistosoma mansoni* and other trematodes to substances emitted by snails. J. Parasit. *56*, 287–296 (1970).
- Chernin E.: Some host-finding attributes of *Schistosoma mansoni* miracidia. Amer. J. trop. Med. Hyg. 23, 320–327 (1974).
- Chernin E., Adler V. L.: Effects of desiccation on eggs of *Australorbis glabratus*. Ann. trop. Med. Parasit. 61, 11–14 (1967).
- Chernin E., Antolics V. M.: Laboratory transmission of *Schistosoma mansoni* to snails via fomites. J. Parasit. *59*, 589–591 (1973).
- Chernin E., Michelson E. H.: Studies on the biological control of schistosome-bearing snails. III. The effects of population density on growth and fecundity in *Australorbis glabratus*. Amer. J. Hyg. 65, 57–70 (1957).
- Chernin E., Perlstein J. M.: Further studies on interference with the host-finding capacity of *Schistosoma mansoni* miracidia. J. Parasit. 55, 500–508 (1969).
- Chernin E., Perlstein J. M.: Protection of snails against miracidia of *Schistosoma mansoni* by various aquatic invertebrates. J. Parasit. *57*, 217–219 (1971).
- Chi L. W.: Mass control of *Oncomelania hupensis hupensis* snail vector for schistosomiasis in the People's Republic of China. Veliger 18, 95–98 (1975).
- Christensen N. O., Nansen P., Frandsen F.: Molluscs interfering with the capacity of *Fasciola hepatica* miracidia to infect *Lymnaea truncatula*. Parasitology 73, 161–167 (1976).
- Christensen N. O., Nansen P., Frandsen F.: Interference with *Fasciola hepatica* snail finding by various aquatic organisms. Parasitology 74, 285–290 (1977).
- Christie J. D., McCullough F. S.: A review of factors determining the temporal and spatial dynamics of human *Schistosoma* transmission. Acta trop. (Basel) (in press).
- Christie J. D., Upatham E. S.: Control of *Schistosoma mansoni* transmission by chemotherapy in St. Lucia. II. Biological results. Amer. J. trop. Med. Hyg. 26, 894–898 (1977).
- Chu K. Y., Arfaa F., Massoud J.: The survival of *Bulinus truncatus* buried in mud under experimental outdoor conditions. Ann. trop. Med. Parasit. 61, 6–10 (1967a).
- Chu K. Y., Bijan J., Massoud J.: The ability of *Bulinus truncatus*, *Biomphalaria alexandrina* and *Lymnaea gedrosiana* to survive out of water in the laboratory. Ann. trop. Med. Parasit. 61, 1–5 (1967b).
- Chu K. Y., Massoud J., Sabbaghian J.: Host-parasite relationship of *Bulinus truncatus* and *Schisto-soma haematobium* in Iran. 3. Effect of water temperature on the ability of miracidia to infect snails. Bull. Wld Hlth Org. 34, 131–133 (1966a).
- Chu K. Y., Massoud J., Sabbaghian H.: Host-parasite relationship of *Bulinus truncatus* and *Schisto-soma haematobium* in Iran. 4. Effect of month of infection on cercarial incubation periods of *S. haematobium* and *S. bovis.* Bull. Wld Hlth Org. 34, 135–140 (1966b).
- Coelho P. M. Z., Figueiredo Y. P., Pellegrino J., Melo G. R.: *Biomphalaria glabrata*: the crowding effect related to aquarium water components. J. Parasit. 63, 284 (1977).
- Coles G. C.: The effect of diet and crowding on the shedding of *Schistosoma mansoni* cercariae by *Biomphalaria glabrata*. Ann. trop. Med. Parasit. 67, 419–423 (1973).
- Colette J., Garrigue G., Sellin B.: Efficacité des règles d'hygiène dans la prophylaxie des schistosomiases. Etude parasitologique, sérologique et épidémiologique d'une zone rizicole Africaine à haut risque d'extension bilharzienne. Méd. trop. 37, 521–528 (1977).
- Cort W. W., Hussey K. L., Ameel D. J.: Studies on a microsporidian hyperparasite of strigeoid trematodes. I. Prevalence and effect on the parasitized larval trematodes. J. Parasit. 46, 317–326 (1960a).

- Cort W. W., Hussey K. L., Ameel D. J.: Studies on a microsporidian hyperparasite of strigeoid trematodes. II. Experimental transmission. J. Parasit. 46, 327–336 (1960b).
- Dalton P. R.: A sociological approach to the control of *Schistosoma mansoni* in St. Lucia. Bull. Wld Hlth Org. *54*, 581–595 (1976).
- Dalton P. R., Pole D.: Water-contact patterns in relation to *Schistosoma haematobium* infection. Bull. Wld Hlth Org. *56*, 417–426 (1978).
- Davis G. M., Kitikoon V., Temcharoen P.: Monograph on "Lithoglyphopsis" aperta, the snail host of Mekong River schistosomiasis. Malacologia 15, 241–288 (1976).
- Demian E. S., Lutfy R. G.: Predatory activity of *Marisa cornuarietis* against *Biomphalaria alexandrina* under laboratory conditions. Ann. trop. Med. Parasit. *59*, 337–339 (1965a).
- Demian E. S., Lutfy R. G.: Predatory activity of *Marisa cornarietis* against *Bulinus (Bulinus)* truncatus, the transmitter of urinary schistosomiasis. Ann. trop. Med. Parasit. 59, 331–336 (1965b).
- Demian E. S., Lutfy R. G.: Factors affecting the predation of *Marisa cornuarietis* on *Bulinus* (Bulinus) truncatus, Biomphalaria alexandrina, and Lymnaea caillaudi. Oikos 17, 212–230 (1966).
- DeWitt W. H.: Influence of temperature on penetration of snail hosts by *Schistosoma mansoni* miracidia. Exp. Parasit. 4, 271–276 (1955).
- DeWitt W. H.: Effects of temperature on penetration of mice by cercariae *Schistosoma mansoni*. Amer. J. trop. Med. Hyg. 14, 579–580 (1965).
- Dias E., Dawood M. M.: Preliminary trials on the biological snail control with *Bacillus pinottii* in Egypt. Mem. Inst. Osw. Cruz 53, 13–29 (1955).
- Dinther J. B. M. van: Control of *Pomacea (Ampullaria)* snails in rice fields. Bull. Landb. Proefstn. Surinam *68*, 1–20 (1956).
- Duran E.: Biology of the predator-prey relationship between *Fasciola hepatica* snail vectors and *Sepedon caerulea* marsh flies (Diptera Sciomyzidae). M. S. Thesis, University of Puerto Rico Library 1975.
- El-Hassan A. A.: *Helisoma tenue* and *Physa acuta* snails as biological means of control against *Bulinus truncatus* and *Biomphalaria alexandrina*, snail intermediate hosts of schistosomiasis in Egypt. Proc. Third Int. Congr. Parasit. München, p. 1597–1598 (1974).
- Etges F. J., Carter O. S., Webbe G.: Behavioral and developmental physiology of schistosome larvae as related to their molluscan hosts. Ann. N.Y. Acad. Sci. 266, 480–496 (1975).
- Evans A. S., Stirewalt M. A.: Variations in infectivity of cercariae of *Schistosoma mansoni*. Exp. Parasit. 1, 19–33 (1951).
- Eyakuze V. M., Dallas A. B. C., Baalawy S. S., Mtoi R. S.: The role of steamers and itinerant fishermen in the dissemination of *Schistosoma mansoni* to the western shore of Lake Victoria. E. Afr. J. med. Res. 1, 47–52 (1974).
- Farooq M.: Pre-control investigations in bilharziasis. J. trop. Med. Hyg. 72, 14–18 (1969).
- Farooq M., Mallah M. B.: The behavioural patterns of social and religious water-contact activities in the Egypt-49 bilharziasis project area. Bull. Wld Hlth Org. *35*, 377–387 (1966).
- Ferguson F. F.: The role of biological agents in the control of schistosome-bearing snails. U.S. Dept. of Health, Education and Welfare Public Health Service, CDC/Atlanta 1977.
- Foster R.: The effect of temperature on the development of *Schistosoma mansoni* Sambon 1907 in the intermediate host. J. trop. Med. Hyg. 67, 289–292 (1964).
- Frandsen F.: The suppression, by *Helisoma duryi*, of the cercarial production of *Schistosoma mansoni*-infected *Biomphalaria pfeifferi*. Bull. Wld Hlth Org. 53, 385–390 (1976).
- Frandsen F., Christensen N. O.: Effect of *Helisoma duryi* on the survival, growth, and cercarial production of *Schistosoma mansoni*-infected *Biomphalaria glabrata*. Bull. Wld Hlth Org. 55, 577–580 (1977).
- Gentile J. H.: Blue-green and green algal toxins. In: Microbial Toxins, Vol. 7 (ed. by S. Kadis, A. Ciegler and S. Ajl), p. 27–66. Academic Press, London/New York 1971.
- Gibson M., Warren K. S.: Capture of *Schistosoma mansoni* miracidia and cercariae by carnivorous vascular plants of the genus *Utricularia*. Bull. Wld Hlth Org. 42, 833–835 (1970).

- Glaudel R. J., Etges F. J.: Toxic effects of freshwater Turbellarians on *Schistosoma* cercariae. J. Parasit. *59*, 74–76 (1973).
- Gordon R. M., Davy T. J., Peaston H.: The transmission of bilharziasis in Sierra Leone with an account of the life cycle of the schistosomes concerned, *S. mansoni* and *S. haematobium*. Ann. trop. Med. Parasit. 28, 323–418 (1934).
- Hairston N. G.: Population ecology and epidemiological problems. In: Bilharziasis. Ciba Foundation Symposium (ed. by G. E. W. Wolstenholme and M. O'Connor), p. 36–62. J. and A. Churchill Ltd., London 1962.
- Hansen E.: A cell line from embryos of *Biomphalaria glabrata* (Pulmonata): establishment and characteristics. In: Invertebrate Tissue Culture. Research Applications (ed. by K. Maramorosch), p. 75–99. Academic Press, London/New York 1976.
- Harinasuta C., Sornmani S., Kitikoon V., Schneider C. R., Pathammavong O.: Infection of aquatic hydrobiid snails and animals with *Schistosoma japonicum*-like parasites from Khong Island, southern Laos. Trans. roy. Soc. trop. Med. Hyg. 65, 184–185 (1972).
- Harry H. W., Cumbie B. G.: Stream gradient as a criterion of lotic habitats suitable for *Australorbis glabratus* in Puerto Rico. Amer. J. trop. Med. Hyg. 5, 921–928 (1956).
- Higby G. C., Canning E. U.: The effects of *Nosema eurytremae* (Protozoa, Microsporida) on the larval stages of *Fasciola hepatica*. Trans. roy. Soc. trop. Med. Hyg. 69, 16 (1975).
- Hubendick B.: A possible method of schistosome-vector control by competition between resistant and susceptible strains. Bull. Wld Hlth Org. 18, 1113–1116 (1958).
- Husting E. L.: A probable method of transmission of *Schistosoma mansoni*. Centr. Afr. J. Med. 11, 330–331 (1965).
- Husting E. L.: Sociological patterns and their influence on the transmission of bilharziasis. Centr. Afr. J. Med. 16, 5–10 (1970).
- Isley R. B.: Assainissement des sources d'eau par des moyens locaux: une contribution a la recherche d'une technologie "appropriée". Ann. Soc. belge Méd. trop. 58, 140–156 (1978).
- Jobin W. R.: Control of *Biomphalaria glabrata* in a small reservoir by fluctuation of the water level. Amer. J. trop. Med. Hyg. 19, 1049–1054 (1970).
- Jobin W. R., Berrios-Duran L. A.: Cost of harvesting and spreading *Marisa cornuarietis* for biological control of *Biomphalaria glabrata* in Aibonito, Puerto Rico. Bull. Wld Hlth Org. 42, 177–179 (1970).
- Jobin W. R., Brown R. A., Velez S. P., Ferguson F. F.: Biological control of *Biomphalaria glabrata* in major reservoirs of Puerto Rico. Amer. J. trop. Med. Hyg. 26, 1018–1024 (1977).
- Jobin W. R., Ferguson F. F., Palmer J. R.: Control of schistosomiasis in Guayama and Arroyo, Puerto Rico. Bull. Wld Hlth Org. 42, 151–156 (1970).
- Jobin W. R., Ippen A. T.: Ecological design of irrigation canals for snail control. Science *145*, 1324–1326 (1964).
- Jobin W. R., Michelson E. H.: Operation of irrigation reservoirs for snail control. Amer. J. trop. Med. Hyg. 19, 657–664 (1969).
- Jobin W. R., Ruiz-Tiben E.: Bilharzia and patterns of human contact with water in Puerto Rico. Bol. Asoc. méd. P. Rico 60, 279–284 (1968).
- Jordan P.: Epidemiology and control of schistosomiasis. Brit. med. Bull. 28, 55–59 (1972).
- Jordan P., Bartholomew R. K., Unrau G. O., Upatham E. S., Grist E., Christie J. D.: Further observations from St. Lucia on control of *Schistosoma mansoni* transmission by provision of domestic water supplies. Bull. Wld Hlth Org. *56*, 965–973 (1978).
- Jordan P., Webbe G.: Human Schistosomiasis. Heinemann Medical Books, London 1969.
- Jordan P., Woodstock L., Unrau G. O., Cook J. A.: Control of *Schistosoma mansoni* transmission by provision of domestic water supplies. Bull. Wld Hlth Org. 52, 9–20 (1975).
- Kawata K., Kruse C. W.: The effect of sewage stabilization ponds on the eggs and miracidia of *Schistosoma mansoni*. Amer. J. trop. Med. Hyg. 15, 896–901 (1966).
- Klumpp R. K., Chu K. Y.: Ecological studies of *Bulinus rohlfsi*, the intermediate host of *Schistoso-ma haematobium* in the Volta Lake. Bull. Wld Hlth Org. 55, 715–730 (1977).

- Knight W. B., Ritchie L. S., Liard F., Chiriboga J.: Cercariophagic activity of guppy fish (*Liebistes reticulata*) using cercariae labelled with radioselenium (75 Se). Amer. J. trop. Med. Hyg. 19, 620–625 (1970).
- Lagler K. F.: Man-made lakes: planning and development. Food and Agriculture Organization of the United Nations, p. 23. Rome 1969.
- Lemma A., Goll P., Duncan I., Mazengia B.: Control of schistosomiasis by the use of endod in Adwa Ethiopia: results of a 5-year study. Proc. Inter. Conf. Schisto. Cairo, p. 415–436 (1978).
- Levy M. G., Tunis M., Isseroff J.: Population control in snails by natural inhibitors. Nature (Lond.) 241, 65–66 (1973).
- Lie K. J., Kwo E. H., Owyang C. K.: A field trial to test the possible control of *Schistosoma spindale* by means of interspecific trematode antagonism. S. E. Asian J. trop. Med. publ. Hlth *1*, 19–28 (1970).
- Lie K. J., Kwo E. H., Owyang C. K.: Further field trial to control *Schistosoma spindale* by trematode antagonism. S. E. Asian J. trop. Med. publ. Hlth *2*, 237–243 (1971).
- Lim H. K., Heyneman D.: Intramolluscan inter-trematode antagonism: a review of factors influencing the host-parasite system and its possible role in biological control. In: Advances in Parasitology, Vol. 10 (ed. by B. Dawes), p. 191–268. Academic Press, London/New York 1972.
- Macdonald G.: The dynamics of helminth infections, with special reference to schistosomes. Trans. roy. Soc. trop. Med. Hyg. *59*, 489–506 (1965).
- MacInnis A. J., Bethel W. M., Cornford E. M.: Identification of chemical of snail origin that attract *Schistosoma mansoni* miracidia. Nature (Lond.) 248, 361–363 (1974).
- Maldonado J. F., Acosta-Matienzo J., Thillet C. J.: Biological studies on the miracidium of *Schisto-soma mansoni*. Part 2. Behavior of the unhatched miracidium in undiluted stools under diverse environmental conditions. Puerto Rico J. publ. Hlth trop. Med. 25, 153–174 (1949).
- Malek E. A., Cheng T. C.: Medical and economic malacology. Academic Press, London/New York 1974.
- Mason P. R., Fripp P. J.: Chemical stimulation of *Schistosoma mansoni* miracidial activity. Z. Parasitenk. 53, 287–296 (1977).
- McClelland W. F. J.: The production of cercariae by *Schistosoma mansoni* and *S. haematobium* and methods of estimating the numbers of cercariae in suspension. Bull. Wld Hlth Org. 33, 270–276 (1965).
- McClelland W. F. J.: Production of *Schistosoma haematobium* and *Schistosoma mansoni* cercariae in Tanzania. Exp. Parasit. 20, 205–218 (1967).
- McClelland W. F. J., Jordan P.: Schistosomiasis at Bukoba, Tanganyika, on Lake Victoria. Ann. trop. Med. Parasit. *56*, 396–400 (1962).
- McJunkin F. E.: Engineering measures for control of schistosomiasis. A report to the Agency for International Development. Washington, D.C. 1970.
- McMahon J. P., Highton R. B., Marshall T. F. de C; Studies on biological control of intermediate hosts of schistosomiasis in Western Kenya. Env. Conserv. 4; 285–289 (1977).
- Memoranda: Immunology of schistosomiasis. Bull. Wld Hlth Org. 51, 553–595 (1974).
- Michelson E. J.: Studies on the biological control of schistosome-bearing snails. Predators and parasites of freshwater molluscs: a review of the literature. Parasitology 47; 413–426 (1957).
- Michelson E. H.: *Plistophora husseyi* sp. n., a micro sporidian parasite of aquatic pulmonate snails. J. Insect. Path. *5*, 28–38 (1963).
- Michelson E. H.: The protective action of *Chaetogaster limnaei* on snails exposed to *Schistosoma mansoni*. J. Parasit. 50, 441–444 (1964).
- Michelson E. H., DuBois L.: Agglutinins and lysins in the molluscan family Planorbidae: a survey of hemolymph, egg-masses, and albumen-gland extracts. Biol. Bull. 153, 219–227 (1977).
- Morgan P. R.: The pit latrine-revived. Centr. Afr. J. Med. 23, 1–4 (1977a).
- Morgan P. R.: Recent developments in environmental sanitation and their role in the prevention of bilharziasis. Centr. Afr. J. Med. 23 (suppl.), 11–15 (1977b).
- Murray H. D.: Discussion of Dr. Taylor's Paper (Western freshwater mollusks). Malacologia 10, 33–34 (1970).

- Nansen P., Frandsen F., Christensen N. O.: A study on snail location by *Fasciola hepatica* using radio-isotopically labelled miracidia. Parasitology 72, 163–171 (1976).
- Nassi H.: Données sur le cycle biologique de *Ribeiroia marini guadeloupensis* new ssp., trématode stérilisant *Biomphalaria glabrata* en Guadeloupe. Acta trop. (Basel) 35, 41–56 (1978).
- Neff S. E.: Snail-killing sciomyzid flies: application in biological control. Verh. int. Verein. theor. angew. Limnol. *15*, 933–939 (1964).
- Negron-Aponte H., Jobin W. R.: Guidelines for spacing and timing of samples to detect populations of *Schistosoma mansoni* cercariae in the field. Int. J. Parasit. 7, 123–126 (1977).
- Oliver-Gonzalez J.: The possible role of the guppy, *Lebistes reticulatus*, on the biological control of schistosomiasis mansoni. Science 104, 605 (1946).
- Olivier L. J.: Infectivity of Schistosoma mansoni cercariae. J. trop. Med. Hyg. 15, 875-881 (1966).
- Ortiz-Torres E.: Damage caused by the snail, *Marisa cornuarietis*, to young rice seedlings in Puerto Rico. J. Agric. Univ. P. Rico 46, 241 (1962).
- Oxfam Conference: Sanitation in developing countries (ed. by Arnold Pacey). John Wiley and Sons, Chichester/New York/Brisbane/Toronto 1978.
- Pan C. T., Williams R. R., Ritchie L. S.: The penetration-time for cercariae of *Schistosoma japonicum*. Amer. J. trop. Med. Hyg. *3*, 136–138 (1954).
- Paperna I.: Study of an outbreak of schistosomiasis in the newly formed Volta Lake in Ghana. Z. Tropenmed. Parasit. 21, 411–425 (1970).
- Paulinyi H. M., Paulini E.: Laboratory observations on the biological control of *Biomphalaria glabrata* by a species of Pomacea (Ampullariidae). Bull. Wld Hlth Org. 46, 243–247 (1972).
- Pellegrino J., Demaria M., Demoura M. F.: Observations on the predatory activity of *Lebistes reticulatus* (Peter, 1859) on cercariae of *Schistosoma mansoni*. Amer. J. trop. Med. Hyg. 15, 337–341 (1966).
- Pessigan T. P., Hairston N. G., Jauregui J. J., Garcia E. G., Santos A. T., Santos B. C., Besa A. A.: Studies on *Schistosoma japonicum* infection in the Philippines. 2. The molluscan host. Bull. Wld Hlth Org. *18*, 481–578 (1958).
- Pimentel D., White P. C. Jr., Ildefonso V.: Vagility of *Australorbis glabratus*, the snail intermediate host of *Schistosoma mansoni* in Puerto Rico. Amer. J. trop. Med. Hyg. 6, 576–580 (1957).
- Pitchford R. J.: Control of bilharziasis by rural management. Centr. Afr. J. Med. 23, (suppl.) 31–33 (1970).
- Pitchford R. J., Visser P. S.: Some further observations on schistosome transmission in the Eastern Transvaal. Bull. Wld Hlth Org. 32, 83–104 (1965).
- Prah S. K., James C.: The influence of physical factors on the survival and infectivity of miracidia of *Schistosoma mansoni* and *S. haematobium*. I. Effect of temperature and ultra-violet light. J. Helminth. *51*, 73–85 (1977).
- Prentice M. A., Panesar T. S., Coles G. C.: Transmission of *Schistosoma mansoni* in a large body of water. Ann. trop. Med. Parasit. *64*, 339–348 (1970).
- Pugh R. N. H., Gilles H. M.: Malumfashi endemic diseases research project. III. Urinary schistosomiasis: a longitudinal study. Ann. trop. Med. Parasit. 72, 471–482 (1978).
- Purnell R. E.: Host parasite relationships in schistosomiasis. I. The effect of temperature on the infection of *Biomphalaria sudanica tanganycensis* with *Schistosoma mansoni* cercariae. Ann. trop. Med. Parasit. 60, 90–93 (1966a).
- Purnell R. E.: Host-parasite relationships in schistosomiasis. III. The effect of temperature on the survival of *Schistosoma mansoni* miracidia and on the survival and infectivity of *Schistosoma mansoni* cercariae. Ann. trop. Med. Parasit. 60, 182–186 (1966b).
- Radke M. G., Ritchie L. S., Rowan W. B.: Effects of water velocities on worm burdens of animals exposed to *Schistosoma mansoni* cercariae released under laboratory and field conditions. Exp. Parasit. 11, 323–331 (1961).
- Rasmussen O.: *Helisoma duryi* in biological control of bilharziasis. Danish Bilharziasis Laboratory, Charlottenlund, Denmark 1974.
- Richards C. S.: Apertural lamellae, epiphragms, and aestivation of planorbid mollusks. Amer. J. trop. Med. Hyg. 12, 254–263 (1963).

- Richards C. S.: Estivation of *Biomphalaria glabrata* (Basommatophora: Planorbidae). Associated characteristics and relation to infection with *Schistosoma mansoni*. Amer. J. trop. Med. Hyg. *16*, 797–802 (1967).
- Richards C. S.: Aestivation of *Biomphalaria glabrata* (Basommatophora: Planorbidae): genetic studies. Malacologia 7, 109–116 (1968).
- Richards C. S.: Variations in infectivity for *Biomphalaria glabrata* in strains of *Schistosoma mansoni* from the same geographical area. Bull. Wld Hlth Org. *54*, 706–707 (1976).
- Richards C. S., Merritt J. W. Jr.: Genetic factors in the susceptibility of juvenile *Biomphalaria* glabrata to Schistosoma mansoni infection. Amer. J. trop. Med. Hyg. 21, 425–434 (1972).
- Richards C. S., Sheffield H. G.: Unique host relations and ultra-structure of an new microsporidian of the genus *Coccospora* infecting *Biomphalaria glabrata*. Proc. Fourth International Colloquium on Insect Pathology, p. 439–452 (1970).
- Rowan W. B.: Daily periodicity of *Schistosoma mansoni* cercariae in Puerto Rican waters. Amer. J. trop. Med. Hyg. 7, 374–381 (1958).
- Rowan W. B.: Sewage treatment and schistosome eggs. Amer. J. trop. Med. Hyg. 13, 630–634 (1964a).
- Rowan W. B.: Schistosomiasis and the chlorination of sewage effluent. Amer. J. trop. Med. Hyg. 13, 577–581 (1964b).
- Rowan W. B., Gram A. L.: Relation of water velocity to *Schistosoma mansoni* infection in mice. Amer. J. trop. Med. Hyg. 8, 630–634 (1959).
- Ruiz-Tiben E., Palmer J. R., Ferguson F. F.: Biological control of *Biomphalaria glabrata* by *Marisa cornuarietis* in irrigation ponds in Puerto Rico. Bull. Wld Hlth Org. 41, 329–333 (1969).
- Schantz E. J.: The dinoflagellate poisons. In: Microbial Toxins, Vol. 7 (ed. by S. Kadis, A. Ciegler, and S. Ajl), p. 3–26. Academic Press, London/New York 1971.
- Scheltema R. S.: The relationship between the flagellate Protozoon *Hexamita* and the oyster *Crassostrea virginica* J. Parasit. 48, 137–141 (1962).
- Schreiber F. G., Schubert M.: Experimental infection of the snail *Australorbis glabratus* with the trematode *Schistosoma mansoni* and the production of cercariae. J. Parasit. 35, 91–100 (1949).
- Scorza J. V., Silva J., Gonzales L., Machado R.: Stream velocity as a gradient in *Australorbis glabrata* (Say, 1818). Z. Tropenmed. Parasit. 12, 191–196 (1961).
- Scott J. A., Barlow C. H.: Limitations to the control of helminth parasites in Egypt by means of treatment and sanitation. Amer. J. Hyg. 27, 619–648 (1938).
- Shattock M. S., Fraser R. J., Garnett P. A.: Seasonal variations of cercarial output from *Biomphalaria pfeifferi* and Bulinus (Physopsis) globosus in Southern Rhodesia. Bull. Wld Hlth Org. 33, 276–278 (1965).
- Shiff C. J.: The influence of temperature on the vertical movement of *Bulinus (Physopsis) globosus* in the laboratory and in the field. S. Afr. J. Sci. 62, 210–214 (1966).
- Shiff C. J.: Seasonal factors influencing the location of *Bulinus (Physopsis) globosus* by miracidia of *Schistosoma haematobium* in nature. J. Parasit. 60, 578–583 (1974).
- Shiff C. J., Evans A., Yiannakis C., Eardley M.: Seasonal influence on the production of *Schistosoma haematobium* and *S. mansoni* cercariae in Rhodesia. Int. J. Parasit. 5, 119–123 (1975).
- Shilo M.: Toxins of Chrysophyceae. In: Microbial Toxins, Vol. 7 (ed. by S. Kadis, A. Ciegler, and S. Ajl), p. 67–106. Academic Press, London/New York 1971.
- Smith K. M.: Virus-Insect Relationships. Longman Group Ltd., Harlow, Essex 1976.
- Southwood T. R. E.: Habitat, the templet for ecological strategies? J. anim. Ecol. 46, 337–365 (1977).
- Sponholtz G. M., Short R. B.: *Schistosoma mansoni* miracidia: stimulation by calcium and magnesium. J. Parasit. 62, 155–157 (1976).
- Standen O. D.: Experimental infection of *Australorbis glabratus* with *Schistosoma mansoni*. I. Individual and mass infection of snail, and the relationship of infection to temperature and season. Ann. trop. Med. Parasit. 46, 48–53 (1952).
- Stibbs J. J. E., Chernin E., Ward S., Karnovsky M. L.: Magnesium emitted by snails alters the swimming behaviour of *Schistosoma mansoni* miracidia. Nature (Lond.) 260, 702–703 (1976).

- Stirewalt M. A.: The influence of previous infection of mice with *Schistosoma mansoni* on a challenging infection with the homologous parasite. Amer. J. trop. Med. Hyg. 2, 867–882 (1953).
- Stirewalt M. A.: Effect of snail maintenance temperatures on development of *Schistosoma mansoni*. Exp. Parasit. *3*, 504–516 (1954).
- Sturrock R. F.: Studies on the biology of *Biomphalaria angulosa* Mandahl-Barth and on its ability to act as an intermediate host of *Schistosoma mansoni*. Ann. trop. Med. Parasit. 59, 1–9 (1965).
- Sturrock R. F.: An investigation of some factors influencing the survival of St. Lucian *Biomphalaria* glabrata deprived of water. Ann. trop. Med. Parasit. 64, 365–371 (1970).
- Sturrock R. F.: Problems associated with mollusciciding natural habitats. In: Molluscicides in Schistosomiasis Control (ed. by T. C. Cheng), p. 51–66. Academic Press, London/New York 1974.
- Sucharit S., Chandavimol Y., Sornmani S.: Biology of the snail-killing fly, *Sepedon spangleri* Beaver (Diptera: Sciomyzidae). II. Ability of the larvae to kill snails of medical importance in Thailand. S. E. Asian J. trop. Med. publ. Hlth 7, 581–585 (1976).
- Texera D. A., Scorza J. V.: Investigaciones sobre una forma bacteriana parecida al *Bacillus pinottii* hallada en Venezuela con accion patogena sobre el *Australorbis glabratus*. Say. Arch. venez. Pat. trop. 2, 235–242 (1954).
- Theron A., Pointier J. P., Combes C.: Recherches sur les facteurs responsables des densités de cercaires de *Schistosoma mansoni* en Guadeloupe. Ann. Parasit. hum. comp. 52, 421–433 (1977).
- Thomas J. D.: Schistosomiasis and the control of molluscan hosts of human schistosomes with particular reference to possible self-regulatory mechanisms. In: Advances in Parasitology, Vol. 11 (ed. by B. Dawes), p. 307–394. Academic Press, London/New York 1973.
- Thomas J. D., Aram R. H.: The chemical ecology of *Biomphalaria glabrata* (Say): the effects of media homotypically conditioned by adult snails on the growth of juveniles. J. exp. Zool. 190, 329–340 (1974).
- Thomas J. D., Benjamin M.: The effects of population density on growth and reproduction of *Biomphalaria glabrata* (Say) (Gasteropoda: Pulmonata). J. anim. Ecol. 43, 31–50 (1974a).
- Thomas J. D., Benjamin M.: Effects of numbers, biomass and conditioning time on the growth and natality rates of *Biomphalaria glabrata* (Say) the snail host of *Schistosoma mansoni* Sambon. J. anim. Ecol. 11, 823–840 (1974b).
- Thomas J. D., Benjamin M., Lough A., Aram R. H.: The effects of calcium in the external environment on the growth and natality rates of *Biomphalaria glabrata* (Say). J. anim. Ecol. 43, 839–860 (1974a).
- Thomas J. D., Goldsworthy G. J., Aram R. H.: Studies on the chemical ecology of snails: the effect of chemical conditioning by adult snails on the growth of juvenile snails. J. anim. Ecol. 44, 1–27 (1975a).
- Thomas J. D., Goldsworthy G. J., Benjamin M.: Chemical conditioning of the environment by the freshwater pulmonate snails (*Biomphalaria glabrata*) and its effect on growth and natality rates. J. Zool. (Lond.) 172, 443–467 (1974b).
- Thomas J. D., Goldsworthy G. J., Benjamin M.: Studies on the chemical ecology of *Biomphalaria glabrata*: the effects of chemical conditioning by the snails kept at various densities on their growth and metabolism. J. Zool. (Lond.) 175, 421–437 (1975b).
- Thomas J. D., Lough A.: The effects of external calcium concentration on the rate of uptake of this ion by *Biomphalaria glabrata* (Say). J. anim. Ecol. 43, 861–871 (1974).
- Thomas J. D., Lough A. S., Lodge R. W.: The chemical ecology of *Biomphalaria glabrata* (Say) the snail host *Schistosoma mansoni* Sambon: the search for factors in media conditioned by snails which inhibit their growth and reproduction. J. appl. Ecol. 12, 421–436 (1975c).
- Thomas J. D., Powles M., Lodge R.: The chemical ecology of *Biomphalaria glabrata*: the effects of ammonia on the growth rate of juvenile snails. Biol. Bull. 151, 386–397 (1976).
- Tripp M. R.: Is *Bacillus pinottii* pathogenic for *Australorbis glabratus?* J. Parasit. 47, 464 (1961).
- Unrau G. O.: Individual household water supplies as a control measure against *Schistosoma mansoni*. Bull. Wld Hlth Org. 52, 1–8 (1975).

- Upatham E. S.: Rapidity and duration of hatching of St. Lucian *Schistosoma mansoni* eggs in outdoor habitats. J. Helminth. 46, 271–276 (1972a).
- Upatham E. S.: Interference by unsusceptible aquatic animals with the capacity of the miracidia of *Schistosoma mansoni* Sambon to infect *Biomphalbria glabrata* (Say) under field-simulated conditions in St. Lucia. J. Helminth. 46, 277–283 (1972b).
- Upatham E. S.: Studies on the hatching of *Schistosoma mansoni* eggs in standing-water and running-water habitats in St. Lucia, West Indies. S. E. Asian J. trop. Med. publ. Hlth *3*, 600–604 (1972c).
- Upatham E. S.: The effect of water temperature on the penetration and development of St. Lucian *Schistosoma mansoni* miracidia in local *Biomphalaria glabrata*. S. E. Asian J. trop. Med. publ. Hlth 4, 367–370 (1973a).
- Upatham E. S.: Location of *Biomphalaria glabrata* (Say) by miracidia of *Schistosoma mansoni* Sambon in natural standing and running waters on the West Indian island of St. Lucia. Int. J. Parasit. *3*, 289–297 (1973b).
- Upatham E. S.: Effect of a waterfall on the infectivity of St. Lucian *Schistosoma mansoni* cercariae. Trans. roy. Soc. trop. Med. Hyg. 67, 884–885 (1973c).
- Upatham E. S.: Dispersion of St. Lucian *Schistosoma mansoni* cercariae in natural standing and running waters determined by cercaria counts and mouse exposure. Ann. trop. Med. Parasit. 68, 343–352 (1974).
- Upatham E. S., Sturrock R. F.: Field investigations on the effect of other aquatic animals on the infection of *Biomphalaria glabrata* by *Schistosoma mansoni* miracidia. J. Parasit. 59, 448–453 (1973a).
- Upatham E. S., Sturrock R. F.: Studies on the effects of cercarial concentration and length of exposure on the infection of mice by *Schistosoma mansoni*. Parasitology 67, 219–228 (1973b).
- Upatham E. S., Sturrock R. F., Cook J. A.: Studies on the hatchability of *Schistosoma mansoni* eggs from a naturally infected human community on St. Lucia, West Indies. Parasitology 73, 253–264 (1976).
- Valle J. P., Alvarenga N.: Rito circadiano de emergencia de cercarias (Schistosoma mansoni-Biomphalaria glabrata). Rev. brasil. Biol. 31, 53-63 (1971).
- Voge M., Bruckner D., Bruce J.: *Schistosoma mekongi* n. sp. from man and animals compared with four geographic strains of *Schistosoma japonicum*. J. Parasit. *64*, 577–584 (1978).
- Warren K. S.: Regulation of the prevalence and intensity of schistosomiasis in man: immunology or ecology? J. infect. Dis. 27, 595–609 (1973).
- Warren K. S., Peters P. A.: Quantitative aspects of exposure time and cercarial dispersion on penetration and maturation of *Schistosoma mansoni* in mice. Ann. trop. Med. Parasit. *61*, 294–301 (1967).
- Warren K. S., Peters P. A.: Cercariae of *Schistosoma mansoni* and plants: attempts to penetrate *Phaseolus vulgaris* and *Hedychium coronarium* produces a cercaricide. Nature (Lond). 217, 647–648 (1968).
- Webbe G.: Laboratory and field trials of a new molluscicide, Bayer 73, in Tanganyika. Bull. Wld Hlth Org. 25, 525–531 (1961).
- Webbe G.: Transmission of bilharziasis. 2. Production of cercariae. Bull. Wld Hlth Org. 33, 155–162 (1965).
- Webbe G.: The effect of water velocities on the infection of *Biomphalaria sudanica tanganyicensis* exposed to different numbers of *Schistosoma mansoni* miracidia. Ann. trop. Med. Parasit. 60, 85–89 (1966a).
- Webbe G.: The effect of water velocities on the infection of animals exposed to *Schistosoma manso-ni* cercariae. Ann. trop. Med. Parasit. 60, 78–84 (1966b).
- Weir J., Wasif I. M., Faroq Rizk H., Attia S. M., Abdel Kader M.: An evaluation of health and sanitation in Egyptian villages. J. Egypt. Publ. Hlth Ass. 27, 55–122 (1952).
- Winblad U.: Evaluation of waste disposal systems for urban low income communities in Africa. Community Hlth 5, 296–302 (1974).

- Wright C. A.: The crowding phenomenon in laboratory colonies of freshwater snails. Ann. trop. Med. Parasit. 54, 224–232 (1960).
- Wright C. A.: The pathogenesis of helminths in the molluscs. Helminth. Abstr. 35, 207–224 (1966).
- Wright C. A.: Some views on biological control of trematode diseases. Trans. roy. Soc. trop. Med. Hyg. 62, 320–324 (1968).
- Wright D. G. S., Ronald K.: Effects of amino acids and light on the behavior of miracidia of *Schisto-somatium douthitti* (Cort 1914). Canad. J. Zool. 50, 855–860 (1972).
- Yoshino T. P., Cheng T. C.: Snail host-like antigens associated with the surface membranes of *Schistosoma mansoni* miracidia. J. Parasit. *64*, 752–754 (1978).
- Yoshino T. P., Cheng T. C., Renwrantz L. R.: Lectin and human blood group determinants of *Schistosoma mansoni:* alteration following *in vitro* transformation of miracidium to mother sporocyst. J. Parasit. 63, 818–824 (1977).