# Control of the Snail Hosts of Schistosomiasis by Environmental Manipulation A Field and Laboratory Appraisal in the Ibadan Area, Nigeria

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# CONTROL OF THE SNAIL HOSTS OF SCHISTOSOMIASIS BY ENVIRONMENTAL MANIPULATION: A FIELD AND LABORATORY APPRAISAL IN THE IBADAN AREA, NIGERIA

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An account is given of an ecological investigation of freshwater habitats near Ibadan, Nigeria, which was designed to identify and evaluate key factors that might be manipulated to achieve control of the snail hosts of schistosomiasis and fascioliasis. Statistical analyses of data from 24 stations from both lentic and lotic habitats showed that there were statistically significant tendencies for the following snail species to coexist: at the macro-distribution level *Lanistes libycus* and *Bulinus* (*P.*) *globosus*, in lotic habitats, *Lymnaea natalensis*, *Bulinus forskali*, *Biomphalaria pfeifferi* and *Bulinus rohlfsi* in lentic habitats; at the micro-distributional level, *B. rohlfsi*, *B. pfeifferi*, *B. forskali* and *Anisus coretus*.

Several species of aquatic macrophytes, including species that occur at water margins (*Acroceras* and *Commelina* spp.) and those that occur in more persistent aquatic habitats (*Nymphaea* and *Ceratophyllum* spp.) also coexist to a statistically significant extent both with each other and with snail species in the same microhabitats.

However, *Salvinia* proved exceptional as it was negatively associated with four of the snail species. Persistent snail refugia, including areas at stream origins, backwaters and the deeper bays or inlets in lentic habitats, were characterized by the presence of particular macrophyte species. The reasons for the associations between snails and macrophytes are discussed and it is argued that they may be mutualistic.

The snails proved tolerant to a wide range of chemical conditions with the exception of low oxygen concentration. However, the absence of aquatic macrophytes and lentic refugia in head waters and the presence of fast flowing water and high temperatures in shallow water are harmful. Although the indigenous snails, *L. libycus* and *Aplexa waterloti*, proved to be efficient predators on the eggs and juveniles of snail hosts, other laboratory and field evidence appear to preclude the possibility that they may be useful as biological control agents. In contrast, there is evidence that *Melanoides tuberculata* might exclude the snail hosts from eroding substrates in lentic habitats.

The following integrated control measures in lotic habitats are discussed: (*a*) judicious drainage and canalization of marshy areas at stream origins, combined with replacement of key marginal macrophytes; (*b*) dredging and straightening of stream courses; (*c*) replacement of key macrophytes along the banks; (*d*) introduction of *M. tuberculata* if not present. In lentic habitats the following control measures are discussed: (*a*) prevention of immigration of both macrophytes and snails from feeder streams; (*b*) control of subaquatic emergent plant species by using grazing domestic animals or competitor species; (*c*) maximizing wind-generated surface currents to exclude floating plants; (*d*) eradication of submerged rooting plants by herbivorous fish or invertebrates; (*e*) the management of such water bodies as either plankton – herbivorous fish or plankton – herbivorous fish – carnivorous fish systems; (*f*) introduction of efficient, detritivorous non-host molluscs or fish to feed on bottom deposits.

## 1. INTRODUCTION

Schistosomiasis is a debilitating, parasitic disease afflicting more than 200 million people (Hoffman 1979). This disease, which is one of the most prevalent in the world, is continuing to increase (Jordan 1972), particularly in areas of Africa, the Middle East and South America, where water resources are being developed. Of the various strategies that may be used to prevent or reduce the rate of transmission (Hoffman 1979), the methods favoured to date involve the use of drugs to kill the adult parasites and chemicals to control the host snails. Recently the climate of opinion has changed to some extent, and more interest is now being paid to preventive strategies, such as the provision of clean water and latrines, and the development of bioengineering strategies to minimize risks of host snails becoming established in irrigation systems (McMullen 1973; McJunkin 1975; Jenkins 1979).

Unfortunately, little attention has been given to the possibility of applying preventive measures to water bodies in rural areas where intensive transmission may occur as a result of their use by fishermen, farmers, and also by children for recreational purposes. The role of children in transmission cannot be over-emphasized. Thus, according to Jordan (1972), they are mainly responsible for transmission of the disease, and Worthington (1979) states, ‘Personally, I am impressed with the great attraction which water exerts on children in all countries and at all social levels, and it is the children who normally get infected with schistosomiasis for life.’

The work described here is concerned with snail habitats in the Ibadan area of Nigeria, where transmission of schistosomiasis has been known to occur for a long time (Cowper 1959, 1963; Hira 1966, 1968, 1969, 1970; Hira & Müller 1966; Asumu 1975). It has been greatly aided by the recent pioneering work on the ecology and distribution of freshwater snails carried out by Professor F. M. A. Ukoli and his colleagues in Ibadan and other regions of Nigeria (Asumu 1975; Okwuoso 1979; Ndifon 1979; Ukoli & Asumu 1979). The present objectives aim at carrying this work further by identifying and evaluating the key factors that could perhaps be manipulated to control the snail hosts of schistosomiasis.

## 2. General topography and land use in the catchment areas

The sites investigated (figures 1 and 2) are situated on Precambrian–Basement complex rocks, consisting of granite, gneiss, schist and quartz, at an altitude of about 150 m, near Ibadan in the western region of Nigeria (Iloeje 1976). This area is characterized by a mean annual temperature range of only 6 °C; a mean annual rainfall of 123 cm; a dry season of about four months and a mean humidity ranging from over 80% in the morning to about 50–70% in the afternoon. In the absence of direct human interference these environmental conditions support a climax ecosystem of high tropical forest divisible into three storeys. However, much of the high forest in this densely populated area has been destroyed, and the fertile loamy soil is used either for continuous, intensive cultivation or for growing crops on a 12 year rotation.

## 3. Description of the sampling stations

The study area is situated on the outskirts of the capital of Oyo State, Ibadan, which has a population of more than 1000000 people. The locations of the stations investigated and the various molluscan and macrophytic plant species found during the dry season, from January to March 1978, are shown in figures 1 and 2 and tables 1 and 2 respectively. The catchment areas of the various water bodies are used for agricultural, residential, educational and recreational purposes. Most of the sites are located in the ground of the University of Ibadan, including the Botanical Garden (figure 1), but the largest lake studied is in the grounds of the International Institute for Tropical Agriculture (I.I.T.A.) (figure 2).

The accounts of community structure given in subsequent sections are based on thorough searches carried out in approximately 15 m stretches at each of 26 sites (table 1, figures 1 and 2). The habitats investigated have been divided into four classes.

(i) Persistent headwater snail foci, or outbreak areas found in two of the streams (stations M and X). These were characterized by the presence of tall, sub-aquatic plants, which provide shade; macrophytes associated with more persistent aquatic habitats, for example, *Nymphaea* and *Ceratophyllum*; a constant supply of spring water and depositing substrates with fine silt, detritus and epilithic algae.

(ii) Lotic habitats, which were at least temporarily colonized by the snail hosts of *Schistosoma mansoni* and *S. haematobium* (stations C, F, G and O). These were restricted to regions of the Ona river where deep pools, slow reaches or backwaters occurred. One of these, station G, was formed by the construction of a small dam, whereas the others can be attributed to more natural topological features. These habitats are characterized by waterside trees providing shade, sub-aquatic marginal vegetation, mainly Graminae, (for example, *Acroceras*, *Paspalum* spp.),

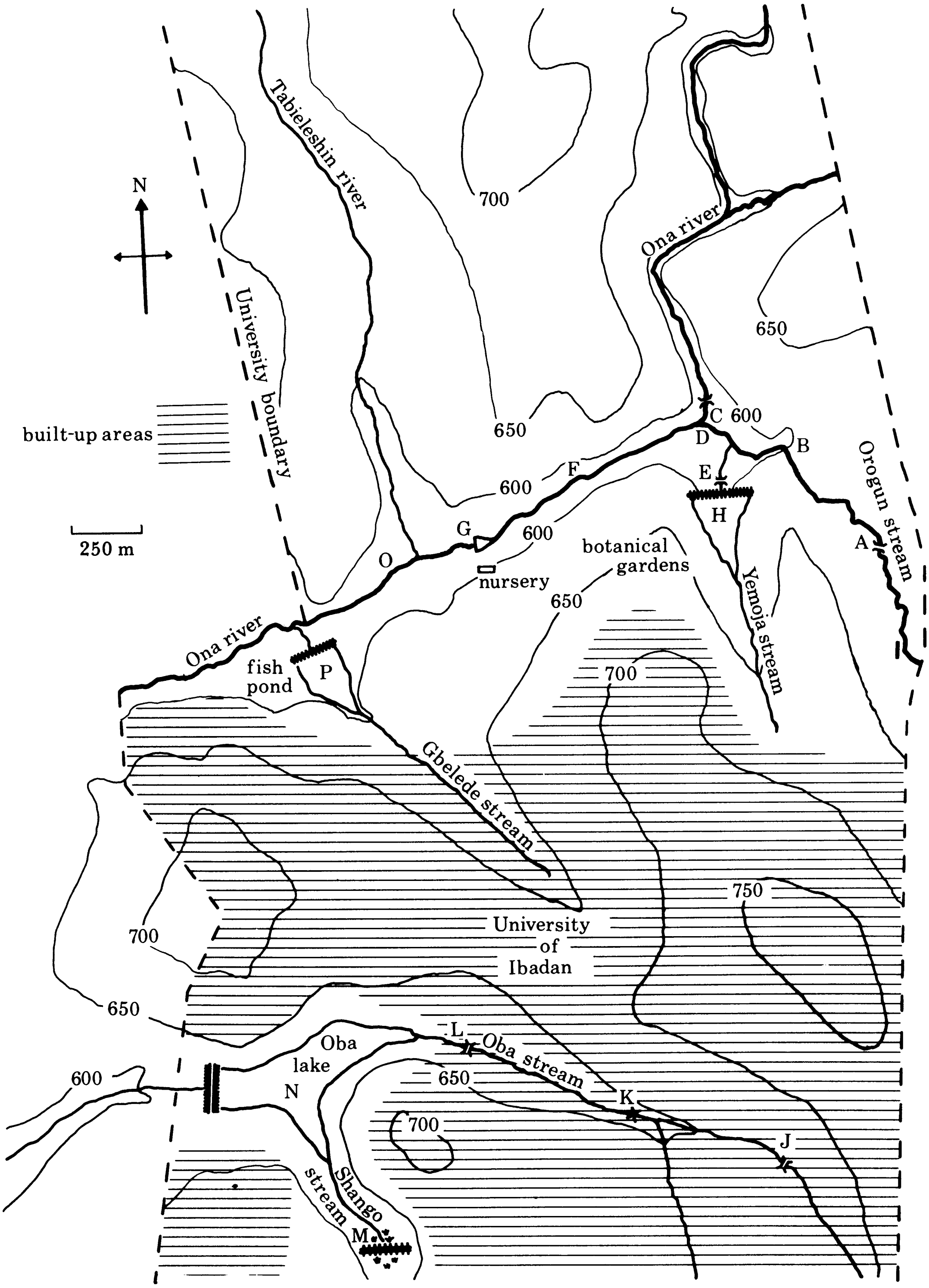

Figure 1. Topographical map of the sampling sites on the University of Ibadan campus.

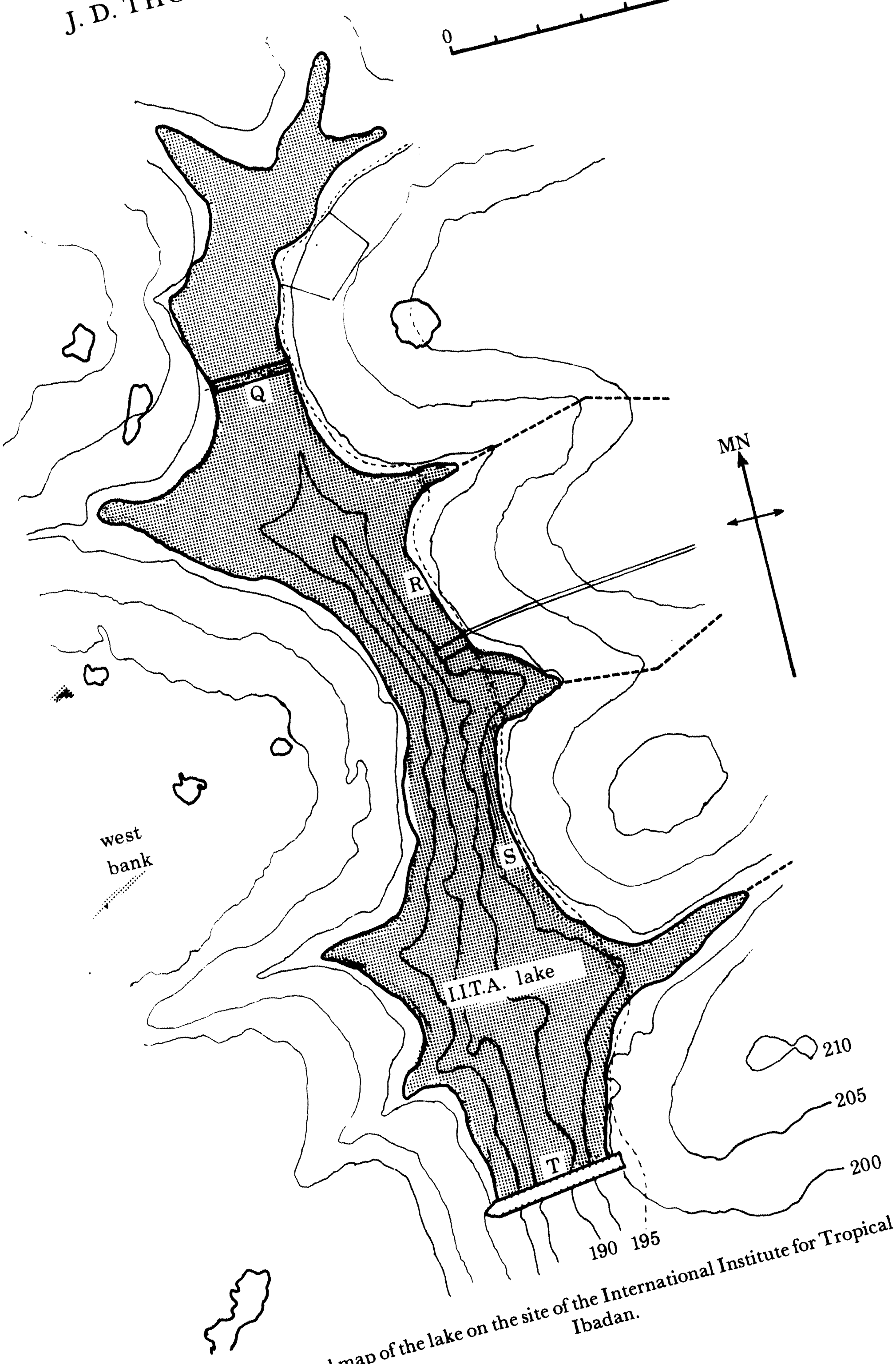

FIGURE 2. Topographical map of the lake on the site of the International Institute for Tropical Agricultu
Ibadan.

### TABLE 1. SNAIL SPECIES ENCOUNTERED AT THE COLLECTING STATIONS NEAR IBADAN

| Stations... | A | B | C | D | E | F | G | H | I | J | M | N | O | P | Q | R | S | T | U | W | X | no. of + stations (% in parentheses) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Biomphalaria pfeifferi* (Krauss) | · | · | + | · | · | + | + | + | · | · | · | + | · | · | · | + | + | + | · | · | · | 8 | (33.3) |
| *Bulinus* (*Physopsis*) *globosus* (Morelet) | · | · | + | · | · | + | + | · | · | · | + | · | + | · | · | · | · | · | · | · | + | 6 | (25.0) |
| *B. rohlfsi* (Clessin) | · | · | · | · | · | · | · | + | · | · | · | + | · | · | · | + | + | + | · | · | · | 5 | (20.8) |
| *B. forskali* (Ehrenberg) | + | · | + | · | · | + | + | + | · | · | · | + | · | · | + | + | + | + | · | · | · | 10 | (41.7) |
| *Melanoides tuberculata* (Müller) | + | + | + | + | + | + | + | + | + | + | + | + | + | · | · | + | + | + | + | + | · | 18 | (75.0) |
| *Aplexa waterloti* Germain | · | · | + | · | + | + | + | · | · | · | + | + | · | + | · | · | · | · | · | · | · | 7 | (29.2) |
| *Lymnaea* (*Radix*) *natalensis* Krauss | · | · | + | · | · | + | + | + | · | · | + | + | · | · | + | + | + | + | · | · | + | 11 | (45.8) |
| *Lanistes libycus* (Morelet) | · | · | + | · | · | + | · | + | · | · | · | · | + | · | · | · | · | · | + | · | · | 5 | (20.8) |
| *Afrogyrus* (*A.*) *coretus* (de Blainville) | · | · | + | · | · | · | + | · | · | · | · | + | · | · | + | + | + | + | · | · | · | 7 | (29.2) |
| *Gyraulus costulatus* (Krauss) | | | | | · | · | · | · | · | · | · | · | + | · | · | · | · | · | · | · | · | 1 | (4.2) |

No snails found in sites K, L or V. Total number of stations visited, 24.

### TABLE 2. AQUATIC AND SUBAQUATIC PLANTS FOUND IN THE STUDY AREA

| | |
|---|---|
| | (*a*) subaquatic plants |
| Gramineae | *Acroceras zizanioides* (Kunth)<br>*Paspalum* spp.<br>*Cynodon dactylon* (Linn.)<br>*Leersia* sp. |
| Commelinaceae | *Commelina* spp. |
| Amaryllidaceae | *Crinum natans* Bak. |
| Onograceae | *Ludwigia* (*Jussiaea*) *leptocarpa* (Nutt) |
| Amaranthaceae | *Alternanthera sessilis* (Linn.) |
| Polygonaceae | *Polygonum lanigerum* R. Br.<br>*P. senegalense* Meisn.<br>*P. salicifolium* Brouss ex Willd. |
| Convolvulaceae | *Convolvulus* sp. |
| Typhaceae | *Typha australis* Schum & Thonn |
| | (*b*) rooting plants with floating leaves |
| Nymphaceae | *Nymphaea lotus* L. |
| | (*c*) submerged non-rooting macrophytes |
| Lentibulariaceae | *Utricularia reflexa* Oliv. |
| Ceratophyllaceae | *Ceratophyllum demersum* L. |
| | (*d*) floating aquatic plants |
| Lemnaceae | *Wolffia arrhiza* (Linn.) Horkel ex Wimm.<br>*Lemna paucicostata* Hegelm ex Engelm.<br>*Spirodela polyrhiza* (Linn.) Schleid. |
| Azollaceae | *Azolla africana* Desv. |
| Salviniaceae | *Salvinia nymphellula* Desv. |
| Avaceae | *Pistia stratiotes* L. |

Nomenclature based on Hutchinson & Dalziel (1954–72) and Alston (1959).

aquatic macrophytes typical of the more persistent water bodies (for example, *Lemna paucicostata*, *Nymphaea lotus*), a rich community of aquatic snails, and a depositing substrate with fine silt, detritus and epilithic algae.

(iii) Lotic habitats where the snail hosts of *S. mansoni* and *S. haematobium* were absent. These are generally characterized by eroding substrates, the absence of aquatic macrophytes, the presence of *Melanoides*, very dense growth of *Pistia* and the absence of suitable snail refugia near the stream source (stations A–E, I–L, U–W).

Table 3. Weather data for the Ibadan I.I.T.A. central station for the period January to December 1978

| | | | mean daily values | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | total rainfall mm | total evaporation mm | wind speed, miles per hour† | solar radiation $\text{s cm}^{-2}\text{ d}^{-1}$ | maximum temperature °C | minimum temperature °C | mean temperature °C | maximum relative humidity, % | minimum relative humidity, % | mean relative humidity, % |
| January | 53.0 | 120.7 | 2.2 | 350.7 | 31.6 | 22.6 | 27.1 | 97 | 43 | 70 |
| February | 0 | 147.7 | 2.4 | 411.6 | 33.2 | 22.2 | 27.7 | 96 | 31 | 64 |
| March | 20.0 | 170.4 | 3.1 | 429.3 | 35.3 | 23.5 | 29.4 | 92 | 28 | 60 |
| April | 94.0 | 191.7 | 3.3 | 441.8 | 33.5 | 23.6 | 28.5 | 93 | 43 | 69 |
| May | 101.3 | 168.8 | 3.1 | 458.2 | 31.5 | 22.7 | 27.1 | 97 | 56 | 77 |
| June | 146.5 | 112.0 | 2.9 | 365.8 | 28.9 | 22.7 | 25.8 | 98 | 67 | 83 |
| July | 94.6 | 97.3 | 2.9 | 308.2 | 27.5 | 22.3 | 24.9 | 96 | 71 | 84 |
| August | 59.5 | 84.4 | 3.4 | 274.7 | 26.7 | 21.1 | 23.9 | 98 | 71 | 82 |
| September | 141.0 | 93.8 | 2.5 | 342.6 | 28.4 | 21.6 | 25.0 | 98 | 66 | 82 |
| October | 207.0 | 126.0 | 2.2 | 412.2 | 29.6 | 22.0 | 25.8 | 98 | 59 | 79 |
| November | 0 | 134.1 | 1.8 | 471.2 | 31.9 | 22.0 | 27.0 | 96 | 42 | 69 |
| December | 0 | 134.5 | 2.1 | 371.6 | 31.8 | 20.4 | 26.1 | 94 | 36 | 65 |

† 1 mile = 1609.344 m.

(iv) Lentic habitats. With the exception of the fish pond (P), which contains *Tilapia*, and station Q in I.I.T.A. lake, lentic, man-made habitats supported rich communities of aquatic snails, including those that serve as hosts for schistosomes (stations H, N, R, S and T). As was the case with the lotic habitats containing the snail host, these are also characterized by the presence of aquatic macrophytes, normally found in more permanent water bodies, and sediments, containing fine silt and detritus.

## 4. Physicochemical factors

### 4.1. *Rainfall and temperature*

Table 3 shows that the main rainy season in 1978 occurred from April to July and the subsidiary or small rains in September to October. This pattern, which is characteristic of this region of West Africa, is caused by the fairly regular northerly and southerly movements of the inter-tropical convergence zones (Thomas & Ratcliffe 1973). As the daily precipitation rates during the wet season are high, exceptionally reaching local values of 254 mm or more, the streams are subjected to spectacular flash flooding. At such times when strongly eroding conditions prevail on the sediments, the conditions become catastrophic for the non-rheophilous elements of the fauna, including the snail hosts of schistosomiasis. It is probable, therefore, that

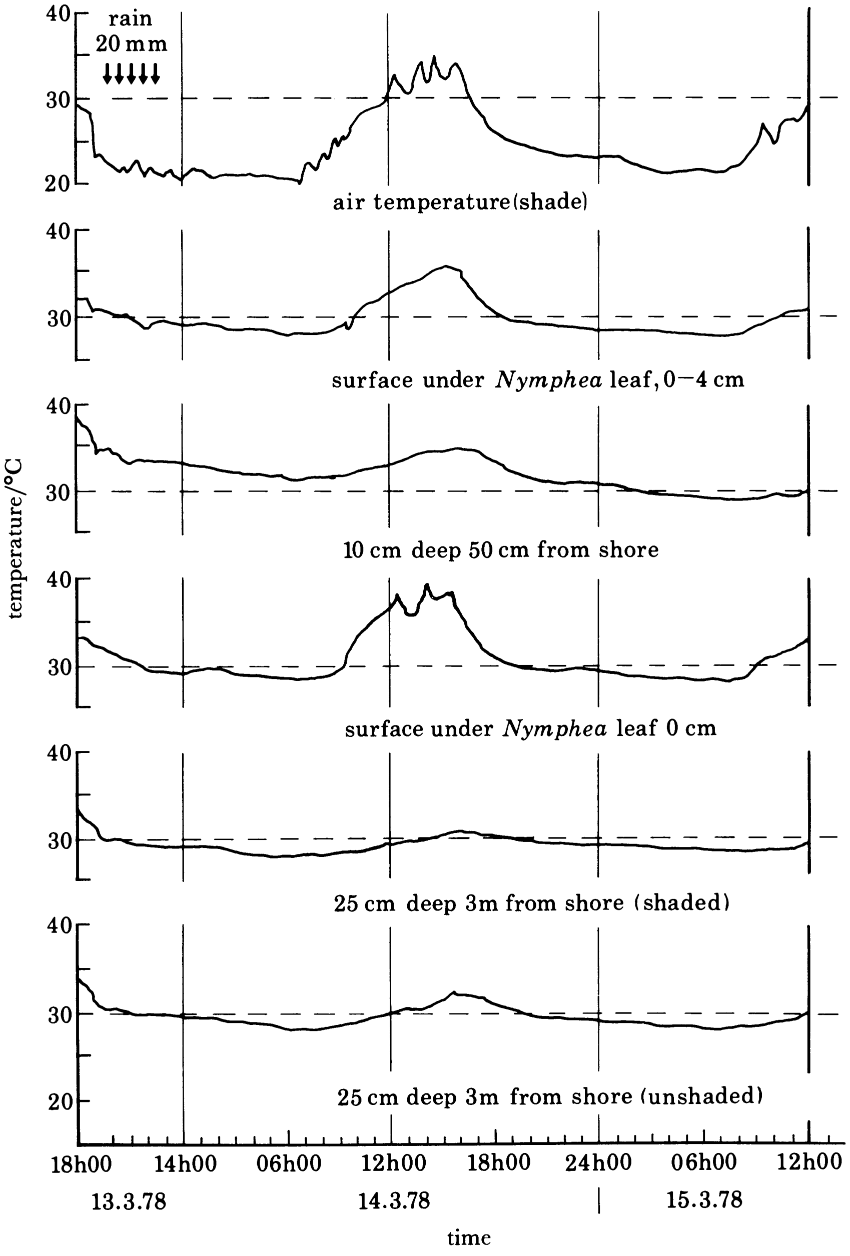

FIGURE 3. Temperatures at various depths in I.I.T.A. lake, taken during March 1978.

they will be scoured from most of the stream sites at this time, with the possible exception of refugia such as marshy areas near the sources or sheltered backwaters.

The mean maximum and minimum temperatures, particularly the latter, vary little during the course of the year (table 3). The lowest mean maximum values occur in the cool–wet and cool–dry season from June to August (26.7–28.9 °C). With the onset of the dry season, temperatures continue to rise until a peak is reached in March or April (33.5–35.3 °C) before the onset of the wet season. Predictably, these annual changes in mean daily air temperature correlate well with those for solar radiation.

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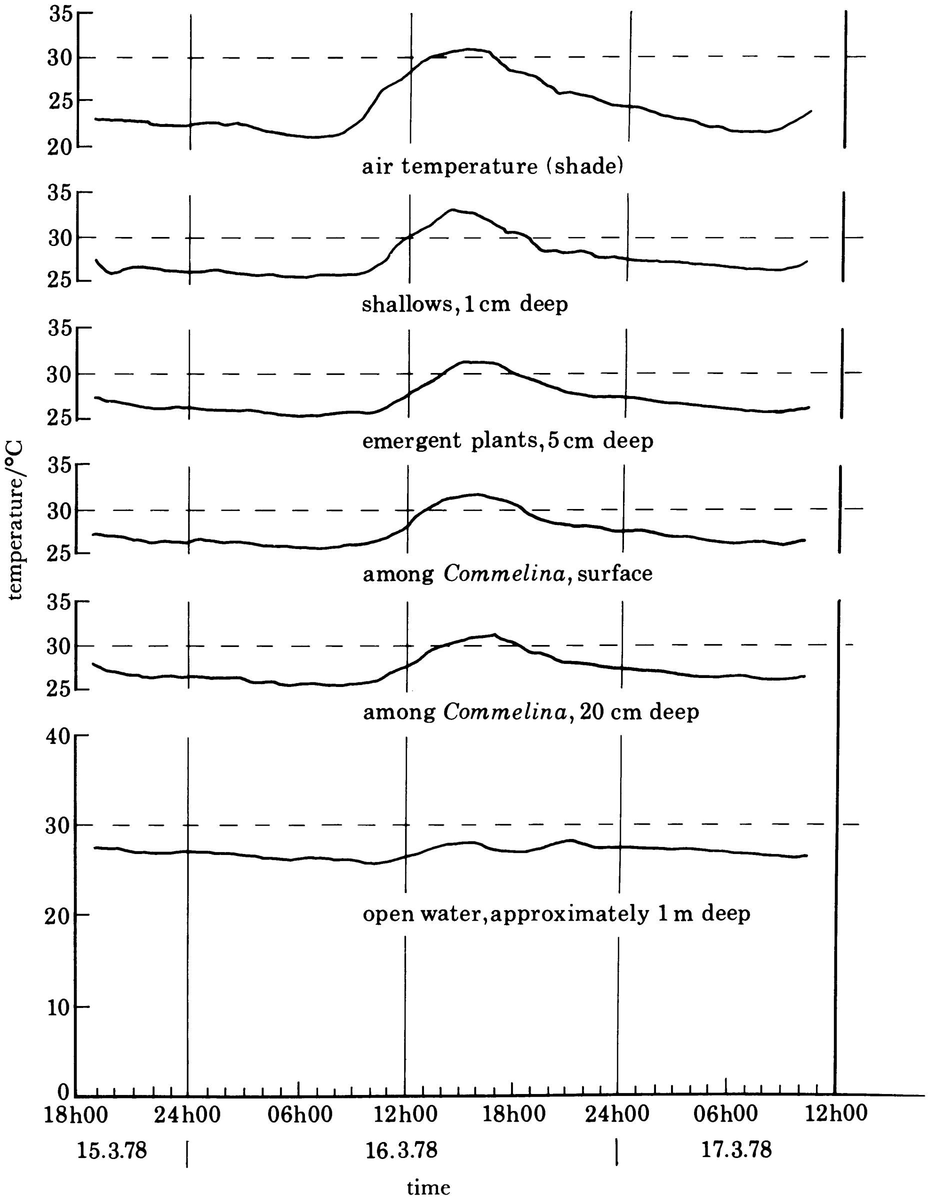

FIGURE 4. Temperatures of various depths in Oba reservoir (station N) during March 1978.

Values for mean temperatures can, however, be deceptive. Towards the end of the dry season in March the daily changes in temperature in the shade can vary from about 20 to 35 °C, or more (figures 3 and 4). Changes in surface-water temperature, even under *Nymphaea* leaves, or among *Commelina*, follow those of the air temperature in the shade very closely. In these microhabitats the temperature increased steeply at approximately 09h00, reaching maximum values at 12h00 to 14h00, and falling to the nocturnal values of 28–29 °C by dusk. The highest water temperatures, ranging from 35 to 40 °C were recorded at the surface at station S. The midday peaks in water temperatures became progressively less with increasing depth, and none is discernible at depths of 1 m or more. It appears that the aquatic macrophytes may give only minimal protection from exposure to high temperature, and that they may even cause the surface water temperature in marginal areas to exceed that of open water, because their damping effects on wind action reduce cooling by surface evaporation.

Inspection of the temperature profile along the E–W transect in I.I.T.A. lake at station S (figure 5) provides support for this hypothesis, as the surface water temperature on the vegetation-protected eastern shore is higher than in the main water body. It can be seen that the lake is thermally stratified, the water below 5 m being isothermal at 23.2 °C. The absence of a well-defined thermocline and an isothermal epilimnion can be attributed to the wind-damping effects of the aquatic macrophytes. These become progressively less dense along the E–W transect.

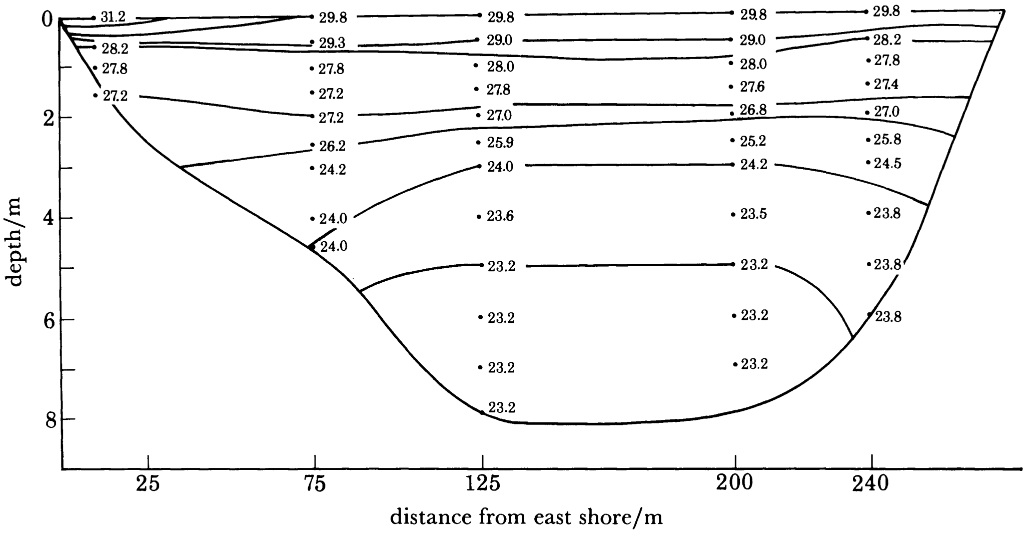

Figure 5. Temperature profile based on observations made in the afternoon between 12h00 and 13h30 along an E–W transect near station S in I.I.T.A. lake (temperatures in °C).

### 4.2. *Water chemistry*

The water chemistry reflects the relatively high fertility status of the parent rock and soils in the Ibadan area (table 4). The conductivity values of 275–610 $\mu\Omega^{-1}$ $cm^{-2}$ fall into the range considered to be mesotrophic or eutrophic (Reid 1961). Many of the chemical parameters fall within the range regarded as being typical of African water bodies placed in class 1 of the Talling & Talling (1965) classification.

(i) The cations conform to a characteristic pattern. Thus, $Na^+$ is the dominant cation, monovalent ions predominate over divalent and the $Ca^{2+}/Mg^{2+}$ ratio varies between 4 and 8.5.

(ii) Bicarbonate is the predominant anion, hence the strong positive correlation between the conductivity and alkalinity values.

(iii) The low concentration of sulphate, corresponding with the small amounts generally present in the soil and sedimentary rocks in Africa (Beauchamp 1953) is another distinctive feature.

(iv) The silica concentrations are relatively high, probably because of its high mobility in the soils.

(v) Phosphate concentrations are also relatively high. This is particularly notable in the

TABLE 4. CHEMICAL ANALYSIS OF WATER SAMPLES FROM VARIOUS SITES (ALL VALUES IN MILLIGRAMS PER LITRE UNLESS OTHERWISE STATED)

| station ... | A | C | D | G | H | M | N | P | R |
|---|---|---|---|---|---|---|---|---|---|
| date ... | 10. 2. 78 | 10. 2. 78 | 10. 2. 78 | 10. 2. 78 | 5. 3. 78 | 5. 3. 78 | 5. 3. 78 | 5. 3. 78 | 5. 3. 78 |
| $Ca^{2+}$ | 26.3 | 43.4 | 28.1 | · | 20.4 | · | 38.0 | 28.0 | 33.4 |
| $Cu^{2+}$ | 0.02 | 0 | 0.02 | 0.01 | 0.01 | 0.01 | 0.05 | 0.02 | 0.01 |
| $K^+$ | 8.0 | 12.0 | 9.0 | 8.0 | 8.0 | 13.0 | 11.5 | 23.6 | 10.0 |
| $Mg^{2+}$ | 5.27 | 5.10 | 5.0 |  | 5.12 | · | 5.27 | 4.40 | 5.44 |
| $Na^+$ | 40.0 | 46.0 | 31.0 | 32.0 | 32.5 | 50.0 | 40.0 | 37.5 | 38.0 |
| iron (total) | 0.45 | 0.35 | 0.26 | 0.25 | 0.21 | 1.40 | 1.20 | 0.84 | 0.12 |
| alkalinity |  |  |  |  |  |  |  |  |  |
| phenolphthalein | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| total† | 220 | 250 | 210 | 240 | 100 | 150 | 135 | 90 | 130 |
| hardness† |  |  |  |  |  |  |  |  |  |
| Ca† | 105 | 100 | 100 | 90 | 58 | 125 | 75 | 50 | 85 |
| Mg† | 180 | 180 | 170 | 160 | 105 | 200 | 115 | 75 | 110 |
| total† | 75 | 80 | 70 | 70 | 53 | 75 | 60 | 15 | 25 |
| $CO_2$† | 11 | 12 | 20 | 11 | 10 | 9 | 8 | 12 | 12 |
| $NH_3$ as N | 15.0 | 11.50 | 10.0 | 11.50 | 0.05 | 15.10 | 0.32 | 16.25 | 0.20 |
| ($NH_3$) | 18.30 | 14.03 | 12.20 | 14.03 | 0.06 | 18.42 | 0.39 | 19.82 | 0.24 |
| $NO_2$ as N | · | · | · | · | 0.015 | · | 0.009 | 0.575 | 0.017 |
| ($NO_2^-$) | · | · | · | · | 0.049 | · | 0.030 | 1.897 | 0.056 |
| $NO_3$ as N | 1.2 | 0.2 | 1.7 | 1.5 | 1.4 | 1.3 | 0.8 | 0.9 | 0.4 |
| ($NO_3^-$) | 5.28 | 0.88 | 7.48 | 6.60 | 6.16 | 5.72 | 3.52 | 3.96 | 1.76 |
| $PO_4^{3-}$ (ortho) | 3.50 | 0.70 | 2.60 | 2.0 | 0.13 | 2.10 | 0.48 | 5.0 | 0.12 |
| $SiO_2$ | 18.5 | 15.0 | 19.0 | 13.0 | 17.5 | 13.0 | 12.5 | 2.0 | 16.0 |
| $SO_4^{2-}$ | 5.7 | 6.1 | 7.3 | 7.0 | 4.0 | 10.0 | 0 | 37.0 | 1.0 |
| apparent colour | 65 | 80 | 50 | · | 180 | 150 | 120 | 90 | 60 |
| suspended solids | 15 | 7 | 12 | 9 | 18 | 25 | 17 | 90 | 0 |
| (turbidity (f.t.u.‡) | 70 | 40 | 55 | 60 | 50 | 102 | 27 | 230 | 19 |
| conductivity ($\mu\Omega^{-1}$ $cm^{-2}$) | 580 | 400 | 580 | 550 | 275 | 610 | 370 | 430 | 360 |
| pH | 7.3 | 7.8 | 7.5 | 7.5 | 7.6 | 7.5 | 7.5 | 7.5 | 7.9 |

† All values in milligrams per litre as $CaCO_3$. ‡ Formazin turbidity unit.

streams and fish pond (P), owing to the use of fertilizers in the catchment areas of the former, and to seepage of farm effluent in the latter. Phosphate concentrations are much lower in the lake water and in isolated pools in the Ona river at station C. These differences can be attributed to the higher demands of primary producers in these closed lentic systems.

However, several features of the water chemistry differ from those normally encountered in the African water bodies in class 1 of Talling & Talling (1965).

(i) Calcium levels tend to be relatively high, and in the case of station C they fall within the range of 40–60 mg $l^{-1}$. According to Thomas & Lough (1974) the uptake sites of pulmonate snails become saturated at these concentrations.

(ii) Both the nitrate and ammonia levels are high, the latter being exceptionally so in the stream habitats. The high nitrate concentration is partly attributable to the use of fertilizers in the catchment areas. However, some may also be produced by oxidation of ammonia. It is possible that the latter is produced in large amounts by microbial organisms involved in the decomposition of leaf litter which is continuously imported into the streams. A high rate of decomposition would be favoured by both the temperature and chemical regimes.

However, ammonia values found in the surface waters of the lakes are in accord with those cited by Talling & Talling (1965). These relatively low values of less than 40 μg $l^{-1}$ can be attributed to the dearth of decomposing matter in this zone. Much higher concentrations of organic matter and ammonia occur in the deoxygenated lower layers of stratified eutrophic lakes.

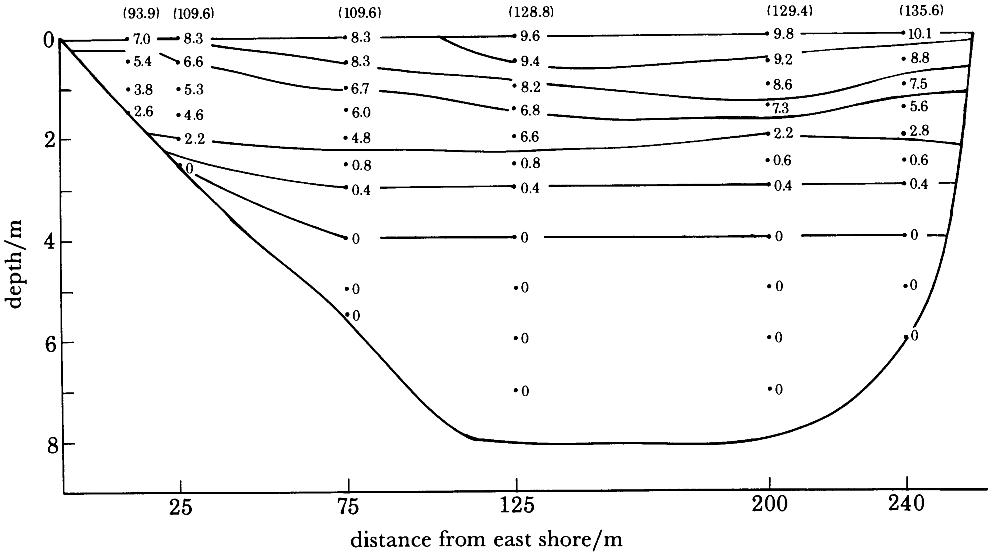

FIGURE 6. Oxygen profile based on observations made in the afternoon between 12h00 and 13h30 along an E–W transect near station S, I.I.T.A. lake. The figures in parentheses are the percentage saturation values for water near the surface (oxygen values in milligrams per litre).

(iii) The iron concentrations are particularly high, especially in the fish pond (P), the Shango Marsh (M) and the Oba lake (N). As ferric iron is almost insoluble in oxygenated water, it is probable that the iron is chelated to humic acid. These acids, derived from autochthonous and allochthonous organic matter, give the water its tea or sherry colour. High concentrations of iron, probably also in chelated form, have been reported in the surface waters of the White Nile after passing through 'Sudd' swamps (Talling 1957).

Several of the stations would appear to have unfavourable chemical regimes for the snails. For example, traces of copper (0.01–0.05 mg $l^{-1}$) were found in all except C (table 4). The conditions at the fish pond (P) appear to be particularly unfavourable, as the values for suspended solids, turbidity, colour and ammonia, are high and oxygen values low (Ndifon 1979). Frequent algal blooms observed in this lake indicate a high level of primary production. It is therefore to be expected that there would be very marked diurnal oxygen pulses, with the water column becoming anoxic at night and the sediments strongly reducing (Thomas & Ratcliffe 1973).

The water column in I.I.T.A. lake is anoxic below a depth of 2.5 m (figure 6) and as the sediments in this zone are strongly reducing, the environment is unfavourable to snails (Asumu 1975). The percentage saturation values of oxygen at the surface increase progressively along the transect from east to west (figure 6). This trend can be attributed to the decrease in the extent to which the air–water interface is covered by the leaves of floating plants such as

*Nymphaea*, *Salvinia* and *Azolla*, as they inhibit primary production by phytoplankton. The water at station V on the Ona river near Eyilele reservoir is also anoxic, being covered by dense growth of *Pistia stratiotes*. The other stations have healthy oxygen regimes (Asumu 1975).

## 5. Distributional patterns of snails in the study area

### 5.1. *Distribution between stations*

Contingency tests (Bailey 1980), based on data collected at 26 stations, reveal that all the statistically significant associations between the snails at this level, are positive ones (table 5, figure 7). These associations fall into two distinct groups. The first consists of *L. libycus*, which is associated with *B.* (*P.*) *globosus*. Both species were found predominantly in lotic habitats and appeared to have similar niche requirements. This is also the case with the second group *B. pfeifferi*, *L. natalensis*, *B. forskali* and *B. rohlfsi*, which are strongly associated with each other. With the exception of *B. rohlfsi*, these species occur in both lotic and lentic habitats.

Certain of the plant species also tend to be strongly associated with each other (table 5, figure 7). In this case there are three distinct groups. The first consists of *Commelina* and *Acroceras* species, which occur on the margins of both lentic and lotic habitats. The second also consists of two species, namely *Nymphaea lotus* and *Ceratophyllum demersum*. These two are good indicators of more persistent aquatic habitats, as they are found predominantly in lentic habitats, or occasionally, in backwaters or pools in streams. The third group, consisting of *Polygonum*, *Wolffia*, *Salvinia* and *Utricularia* species, form part of the marginal plant community in lentic habitats.

There are also strong, statistically significant, positive associations between species of snails and macrophytic plants. These are summarized in table 5 and figure 7. *L. libycus* and *Lemna paucicostata* form a group distinct from the others, as they are found mainly in the sheltered areas such as backwaters, pools and marshy headwater areas of lotic habitats.

### 5.2. *Distribution within stations*

#### 5.2.1. *Snail densities and zonation*

A mark–recapture method (Southwood 1978) involving the use of non-toxic paints as markers, gave values of 51 and 16 $\text{m}^{-2}$ for population densities of *B. pfeifferi* at stations C (isolated pool in Ona stream) and N (Oba reservoir), respectively. The snails at C were associated with subaquatic vegetation (for example, *Acroceras* or *Lemna paucicostata*) and those at station N with detritus. These data support the generalization that beds of aquatic macrophytes tend to support higher densities of snails than bare sediments (Odei 1973).

In the absence of aquatic macrophytes, *B. pfeifferi* shows a marked preference for very shallow water near the shoreline of lentic habitats. This trend is illustrated by data from Oba reservoir (figure 8*a*, *b*). The results from station H are similar, as *B. pfeifferi* was found to occur mainly in shallow water or on the damp soil by the edge of the water, in the NE corner near the dam wall of this reservoir. Population densities of $83 \pm 23.3\ \text{m}^{-2}$ of this species were found in this area, when using 15 $\text{cm}^2$ quadrats. Other species that coexisted with *B. pfeifferi* in this zone, namely *M. tuberculata*, *L. natalensis* and *B. rohlfsi*, occurred at densities of $5.6 \pm 9.35$, $21.6 \pm 4.07$ and $2.4 \pm 1.16\ \text{m}^{-2}$ respectively.

The concentration of these species in the marginal zone is probably partly attributable to the accumulation within it of detritus or neuston carried by wind generated currents. The possibility that this serves as a food source for the snails is supported by observations that snail

TABLE 5. TESTS CARRIED OUT ON DATA COLLECTED FROM 26 COLLECTING SITES $\chi^2$ VALUES OBTAINED FROM $2 \times 2$ CONTINGENCY TESTS

| | *B. pfeifferi* | *B. forskali* | *B. (P.) globosus* | *B. rohlfsi* | *M. tuberculata* | *L. libycus* | *A. waterloti* | *A. coretus* | *G. costulatus* | *L. natalensis* | *Acroceras* | *Commelina* | *Lemna* | *Nymphaea* | *Utricularia* | *Salvinia* | *Wolfia* | *Polygonum* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *B. pfeifferi* | | | | | | | | | | | | | | | | | | |
| *B. forskali* | +4.48† | | | | | | | | | | | | | | | | | |
| *B. (P.) globosus* | +0.44 | −0.39 | | | | | | | | | | | | | | | | |
| *B. rohlfsi* | +4.47† | +6.95‡ | −0.60 | | | | | | | | | | | | | | | |
| *M. tuberculata* | +3.26 | +0.25 | +0.12 | +0.33 | | | | | | | | | | | | | | |
| *L. libycus* | +0.43 | +0.001 | +5.62† | −0.01 | +0.05 | | | | | | | | | | | | | |
| *A. waterloti* | +0.91 | +0.14 | +2.78 | −0.002 | −0.001 | +0.19 | | | | | | | | | | | | |
| *A. coretus* | +0.59 | +2.89 | −0.96 | −1.39 | −0.32 | −0.48 | −0.32 | | | | | | | | | | | |
| *G. costulatus* | −0.81 | −0.06 | +0.43 | −0.63 | +0.81 | +0.11 | −1.18 | −1.51 | | | | | | | | | | |
| *L. natalensis* | +7.17‡ | +12.13§ | +0.82 | +4.10† | +0.58 | +0.33 | −3.31 | +2.34 | +0.03 | | | | | | | | | |
| *Acroceras* | −0.14 | +0.14 | −0.03 | −0.19 | −0.14 | +0.66 | +0.14 | −0.19 | −0.06 | −0.05 | | | | | | | | |
| *Commelina* | −0.11 | −0.66 | +0.86 | −0.03 | +0.11 | +1.00 | −0.11 | −0.18 | +0.28 | −0.17 | +6.51† | | | | | | | |
| *Lemna* | +0.44 | +0.03 | +0.10 | −0.60 | +0.12 | +5.62† | +2.78 | −0.08 | +0.43 | +0.82 | −0.60 | +0.02 | | | | | | |
| *Nymphaea* | +3.52 | +0.14 | +2.78 | +4.47† | +0.78 | +0.43 | +0.001 | +0.59 | +0.18 | +3.07 | −0.25 | +0.11 | +0.44 | | | | | |
| *Utricularia* | +0.002 | +2.60 | −0.17 | +3.77 | +0.002 | −1.02 | −0.002 | +8.97‡ | −0.63 | +5.77† | −0.19 | −0.90 | −0.60 | +1.08 | | | | |
| *Salvinia* | +0.44 | +4.40† | −0.02 | +7.68‡ | +0.12 | −0.32 | −0.12 | +6.94‡ | −0.43 | +7.79‡ | −0.60 | −1.37 | −0.96 | +2.78 | +15.62§ | | | |
| *Wolfia* | +0.002 | +2.60 | −0.02 | +2.53 | +0.002 | −0.60 | −0.002 | +8.97‡ | −0.63 | +5.77† | −0.19 | −0.90 | −0.60 | −1.08 | +15.62§ | +15.62§ | | |
| *Polygonum* | +0.10 | +4.80† | −0.30 | +5.70† | +0.10 | −1.02 | −0.74 | +12.03§ | −0.98 | +3.96† | −1.35 | −0.50 | −0.30 | −2.23 | +11.05§ | +11.05§ | +14.19§ | |
| *Ceratophyllum* | +0.59 | +0.19 | +0.08 | +0.70 | −0.32 | −0.36 | −0.32 | +4.92† | −1.51 | +0.82 | −0.19 | −0.18 | +0.08 | +4.40† | +1.39 | +1.39 | +2.07 | +3.12 |

+, positive associations. −, negative associations. †, ‡, §, $p$ values less than 0.05, 0.01, 0.001 respectively. These values are based on Fisher's exact test, 2-tailed.

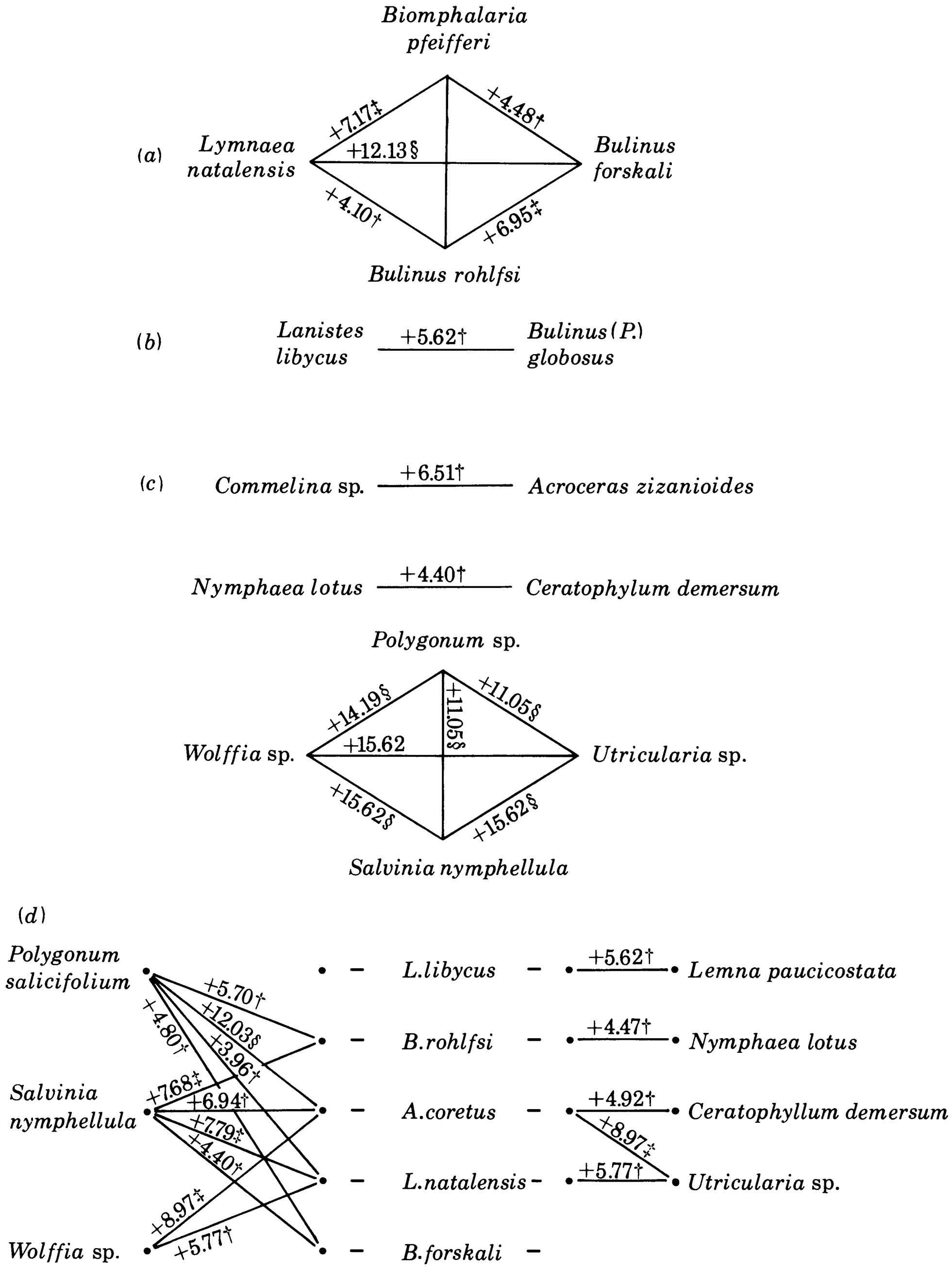

Figure 7. Relationships of biotic components based on contingency tests carried out on data collected from 26 sampling stations. (The $\chi^2$ values are given; levels of significance are indicated thus: †, ‡, §, $p < 0.05$, $< 0.01$ and $< 0.001$, respectively.)

densities tend to be higher on the exposed shores receiving currents generated by the prevailing S or SW winds than on the more sheltered S or SW shores. By using individually marked *B. pfeifferi*, it was observed that although they may move in an apparently random manner, covering distances ranging from 6–66 cm 24 $h^{-1}$ (median 22.4 cm), they continue to remain within this marginal zone. In lotic systems the comparable habitats for snails are backwaters or pools where current borne detritus forms part of the depositing substrate.

When aquatic macrophytes encroached far into I.I.T.A. lake as at sites Q and R the snails followed suit. Their vertical zonation in beds of vegetation at these stations was investigated by using a Freshwater Biological Association (F.B.A.) net with a surface area of 484 cm². Figure 9, which gives the mean number of the various snail species collected in 50 sweeps of 2 m at the surface, in midwater (0.5 m) and at the bottom (1 m) showed that, with the exception of *M. tuberculata*, all the snail species are restricted to the upper 50 cm zone of the water column.

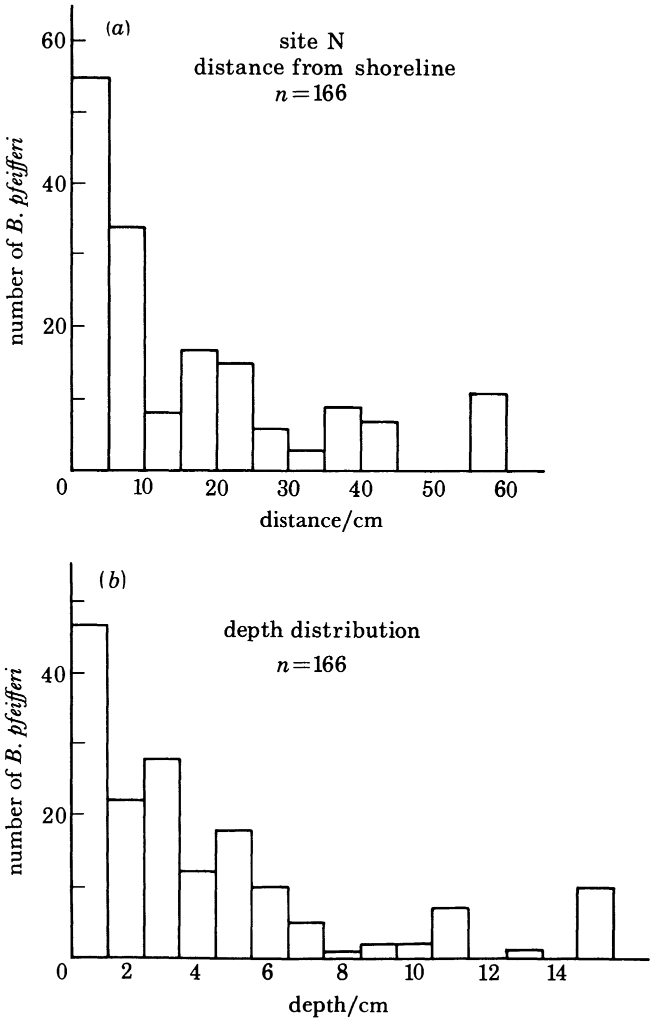

FIGURE 8. Relation between numbers of *B. pfeifferi* and (*a*) distance from the shore line (*b*) depth of water in centimetres in Oba reservoir (station N).

Population densities of snails in the vegetation beds in I.I.T.A. lake were estimated by sampling units of habitats with a 100 cm × 300 cm² steel cylinder. When the lower edge of the cylinder was pushed into the sediment it served as an effective seal, thus making it possible to evacuate all its contents including water, plants, snails and sediment to a depth of 1 cm. The contents of the aspirator were then sieved and both plants and snails removed by hand. The 200 samples collected at stations R and S gave values for population densities of 8.17 ± 1.94, 10.33 ± 1.64, 68.03 ± 2.48, 15.17 ± 2.14, 1.83 ± 0.54 and 10.33 ± 2.10 $\mathrm{m}^{-2}$ for *B. pfeifferi*, *B.*

*rohlfsi*, *B. forskali*, *A. coretus*, *L. natalensis* and *M. tuberculata* respectively. However, much higher densities of up to 9800 $m^{-2}$ of *M. tuberculata* were found in the Ona stream at stations D and O.

### 5.2.2 *Distribution in relation to macrophytes*

Contingency tests 2 × 2, were used to quantify the relationships between snails and plants at stations H (Botanical Garden Pond), R and S (I.I.T.A. lake). The results obtained were as follows:

(i) Station H (Botanical Garden Pond)

The data (table 6) are based on 1500 5 × 5 cm contiguous quadrats taken near the SW shoreline by the dam wall. The presence or absence of the following was noted in each quadrat:

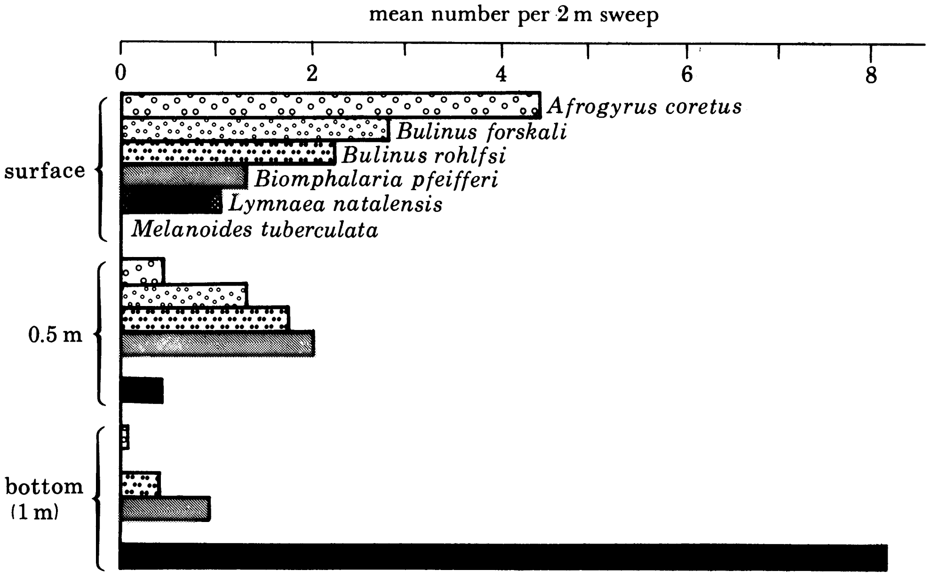

FIGURE 9. The mean number of snails collected in 50 2 m length sweeps at various depths in I.I.T.A. lake.

*B. pfeifferi*, *B. rohlfsi*, *L. natalensis*, *M. tuberculata*, *Cyperus* sp., *Jussiaea* sp., *Cynodon dactylon*, *Paspalum* sp., *Commelina* sp. detritus and rock with its epilithic algae. The results of the 2 × 2 contingency tests (Bailey 1980) show that *B. pfeifferi* and *L. natalensis* were positively associated ($p < 0.05$) with detritus and negatively associated with rocky substrate ($p < 0.05$). However, *B. pfeifferi* and *L. natalensis* showed different microhabitat preferences for plants as they were found to be positively related with *Commelina* sp. and *Cynodon dactylon* respectively ($p < 0.05$ in both cases). Neither *B. rohlfsi* nor *M. tuberculata* showed any statistically significant associations with the environmental components.

(ii) Stations R and S. (I.I.T.A. lake)

The data given in tables 7 and 9 and figure 10 are based on the 200, 300 $cm^2$ samples taken with the steel cylinder. 2 × 2 contingency tests were used to test for statistically significant negative or positive associations between the species. There were several significant positive associations. Thus, *A. coretus*, *B. forskali* and *B. pfeifferi* were all positively associated with *Nymphaea lotus* ($p < 0.001$, $p < 0.001$ and $p < 0.05$, respectively) and *A. coretus* and *B. pfeifferi* were both positively associated with *Lemna paucicostata* ($p < 0.001$ in both cases). Three species, namely *B. forskali*, *B. pfeifferi* and *B. rohlfsi*, were positively associated with *Ceratophyllum demersum*

TABLE 6. THE RESULTS OF $2\times 2$ CONTINGENCY TESTS BASED ON A TOTAL OF 1500 $5\times 5$ cm QUADRATS TAKEN AT THE WESTERN END OF THE DAM WALL AT STATION H

| | substrates | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | *Cyperus* | *Ludwigia* sp. | *Cynodon dactylon* | *Paspalum* | *Commelina* | Detritus | Bare rock | Snail species |
| O | 0 | 0 | 3 | 3 | 54 | 165 | 156 | *Biomphalaria pfeifferi* |
| | | −† | | | +† | +† | −† | |
| E | 2.50 | 4.99 | 3.74 | 4.37 | 24.34 | 86.11 | 198.43 | |
| O | 0 | 0 | 0 | 0 | 0 | 5 | 9 | *Bulinus rohlfsi* |
| E | 0.07 | 0.14 | 0.11 | 0.126 | 0.70 | 2.48 | 5.72 | |
| O | 0 | 0 | 15 | 3 | 9 | 33 | 36 | *Lymnaea natalensis* |
| | | | +† | | | +† | −† | |
| E | 0.65 | 1.30 | 0.97 | 1.13 | 6.32 | 22.36 | 51.52 | |
| O | 0 | 0 | 0 | 0 | 0 | 6 | 6 | *Melanoides tuberculata* |
| E | 0.17 | 0.34 | 0.25 | 0.29 | 1.64 | 5.80 | 13.36 | |

O, observed values; E, values expected by chance.

† Significant difference ($p < 0.05$) between observed and expected values using chi-squared and Yate's correction where appropriate.

TABLE 7. $\chi^2$ VALUES OBTAINED FROM $2\times 2$ CONTINGENCY TESTS CARRIED OUT ON 200 SAMPLES COLLECTED WITH THE AID OF THE VACUUM PUMP APPARATUS AT STATION R AND S AT I.I.T.A. LAKE

| snail species | | | | | | |
|---|---|---|---|---|---|---|
| *Afrogyrus coretus* | *Bulinus forskali* | *Biomphalaria pfeifferi* | *Bulinus rohlfsi* | *Lymnaea natalensis* | *Melanoides tuberculata* | plant species |
| 2.62 | 0.75 | 1.85 | 2.34 | 0.63 | 7.02 (−‡) | *Azolla* |
| 4.88 (−†) | 11.09 (+§) | 9.89 (+‡) | 7.67 (+‡) | 2.44 | 4.22 (−†) | *Ceratophyllum demersum* |
| 3.90 (+†) | 0.00 | 0.10 | 3.90 (+†) | 0.73 | 0.29 | *Commelina* |
| 3.61 (−†) | 0 | 0.08 | 1.06 | 0.20 | 1.06 | filamentous green algae |
| 11.30 (−§) | 1.20 | 20.83 (+§) | 2.24 | 0.32 | 2.24 | *Lemna paucicostata* |
| 137.81 (+§) | 14.64 (+§) | 4.95 (+§) | 3.79 | 1.48 | 6.59 (+†) | *Nymphaea lotus* |
| 2.71 | 0.11 | 0.21 | 0.06 | 0.44 | 3.03 | *Polygonum lanigerum* |
| 1.08 | 0 | 0 | 0 | 0.11 | 4.81 (+†) | *Polygonum salicifolium* |
| 0.02 | 1.27 | 0.10 | 0.29 | 0.73 | 0.51 | *Polygonum senegalense* |
| 12.26 (−§) | 4.91 (−‡) | 11.18 (−§) | 5.98 (−†) | 0.17 | 0.75 | *Salvinia* |
| 0.33 | 0.05 | 0.09 | 0.02 | 0.04 | 4.30 (−†) | *Utricularia reflexa* |
| 0.68 | 0.01 | 0.91 | 0.00 | 0.36 | 0.94 | *Wolffia* |

+, positive associations; −, negative associations.

†, ‡, §, $p < 0.05$, $< 0.01$, $< 0.001$, respectively.

($p < 0.001$, $p < 0.01$ and $p < 0.01$, respectively). The only species found to be significantly positively associated with *Commelina* was *B. rohlfsi* ($p < 0.05$). *M. tuberculata* was unique in being the only species to be positively associated with *Polygonum salicifolium*.

There were also several significant negative associations between species of macrophytes and snails. Thus four species, namely *A. coretus*, *B. forskali*, *B. pfeifferi* and *B. rohlfsi*, were negatively associated with *Salvinia nymphellula* ($p < 0.001$, $p < 0.01$, $p < 0.001$, and $p < 0.05$ respectively).

Table 8. Contingency tests carried out on data based on 200 samples collected from sites R, S, with the aid of a vacuum pump apparatus

| | *Afrogyrus coretus* | *Bulinus forskali* | *Biomphalaria pfeifferi* | *Bulinus rohlfsi* | *Lymnaea natalensis* | *Melanoides tuberculata* | |
|---|---|---|---|---|---|---|---|
| *Afrogyrus coretus* | 91 | 56 | 29 | 36 | 7 | 31 | O |
| | | 44.59 | 22.29 | 28.21 | 5.01 | 28.21 | E |
| *Bulinus forskali* | (10.50) | 98 | 31 | 39 | 4 | 30 | O |
| | +‡ | | 24.01 | 30.38 | 5.39 | 30.38 | E |
| *Biomphalaria pfeifferi* | (4.90) | (5.29) | 49 | 22 | 2 | 16 | O |
| | +† | +† | | 15.19 | 2.70 | 15.19 | E |
| *Bulinus rohlfsi* | (5.72) | (6.95) | (5.86) | 62 | 2 | 15 | O |
| | +† | +‡ | +† | | 3.41 | 19.22 | E |
| *Lymnaea natalensis* | (0.87) | (0.30) | (0.02) | (0.37) | 11 | 1 | O |
| | | | | | | 3.41 | E |
| *Melanoides tuberculata* | (0.73) | (0.01) | (0.08) | (1.95) | (1.64) | 64 | O |
| | $\chi^2$ | $\chi^2$ | $\chi^2$ | $\chi^2$ | $\chi^2$ | | |

Total number of each species along diagonal.
O, observed values; E, values expected by chance.
−, negative associations; +, positive associations.
† = $p < 0.05$
‡ = $p < 0.01$
§ = $p < 0.001$
$\chi^2$, using Yate's correction where appropriate in parentheses.

*A. coretus* was negatively associated with *Ceratophyllum demersum*, *Lemna paucicostata* and filamentous algae and *M. tuberculata* with species of *Azolla*, *Ceratophyllum* and *Utricularia* ($p < 0.01$, $p < 0.001$, $p < 0.05$, respectively). *L. natalensis* was unique in showing neither positive nor negative associations with any of the plant species.

### 5.2.3. *Distribution of snail species in relation to each other in I.I.T.A. lake*

The results of 2 × 2 contingency tests on the various snail species collected in the 200, 300 $cm^2$ samples are given in table 8. These show that there are significant positive associations between *A. coretus* and *B. forskali* ($p < 0.01$), *B. pfeifferi* and *B. rohlfsi* ($p < 0.05$), *B. forskali* and *B. pfeifferi* ($p < 0.05$), *A. coretus* and *B. pfeifferi* ($p < 0.05$), *B. forskali* and *B. rohlfsi* ($p < 0.01$) and *A. coretus* and *B. rohlfsi* ($p < 0.05$).

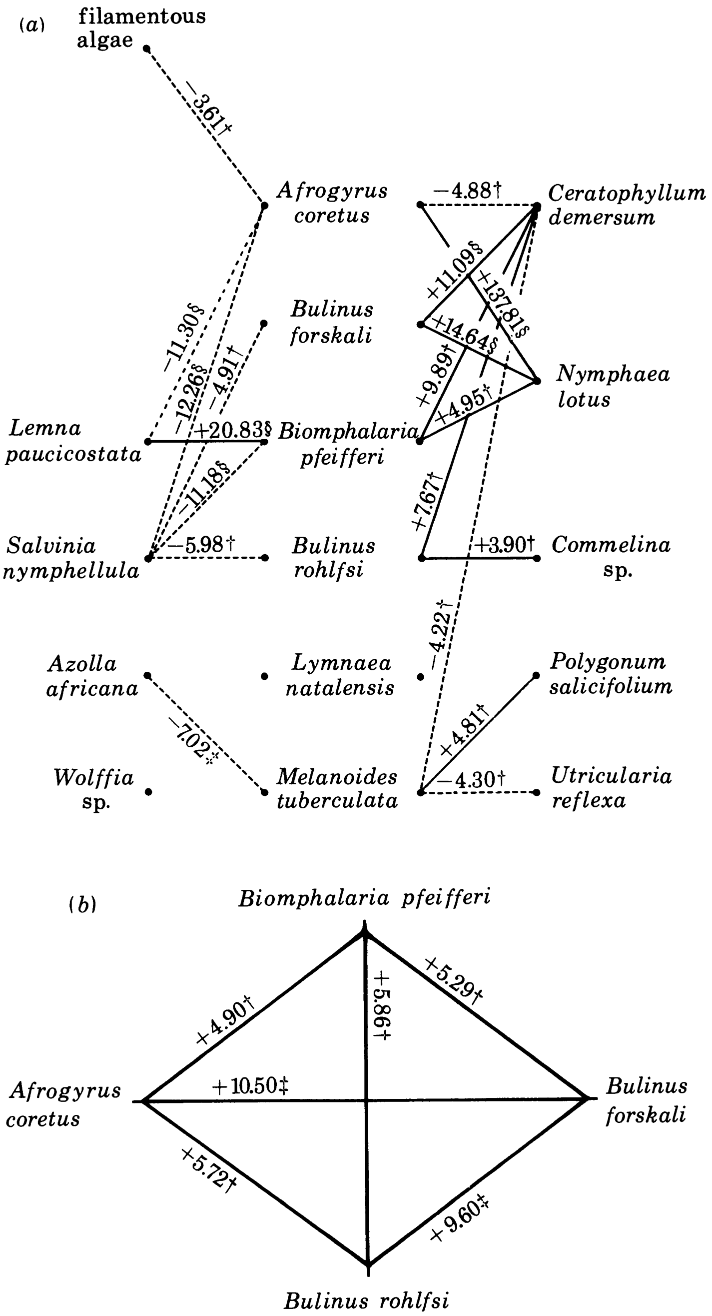

FIGURE 10. Relationships between the biotic components based on 200 samples taken from I.I.T.A. lake with a vacuum pump apparatus. The $\chi^2$ values are given, the levels of significance are indicated thus: †, ‡, §, $p < 0.05$ $< 0.01$ and $< 0.001$, respectively.

## 6. FOOD OF *B. PFEIFFERI*

The crops of *B. pfeifferi* from I.I.T.A. lake were examined. The major portion, by volume, of the diet consisted of diatoms, including species of *Nitschia*, *Pinnularia*, *Amphora*, *Frustulia* and *Cymbella*, which were probably scraped from macrophytes by the radulae of the snails. Other major components included amorphous material, mainly detritus and bacteria, blue-green and green algae, pollen grains and small seeds, macrophyte fragments including those of *Lemna* and

*Salvinia*, and sand particles. Rather surprisingly it was found that the latter made up 30% of the total volume. Although *B. pfeifferi* is strongly associated with macrophytes it only used them as food to a very small extent. The absence of filamentous algae in the diet may be owing to their paucity in the flora at this time.

## 7. EXPERIMENTS TO EVALUATE SOME OF THE ENVIRONMENTAL FACTORS THAT MAY INFLUENCE THE DISTRIBUTION AND ABUNDANCE OF THE SNAIL HOSTS OF SCHISTOSOMIASIS WITH PARTICULAR REFERENCE TO THOSE THAT MIGHT BE MANIPULATED TO EXCLUDE OR CONTROL THEM

The environmental factors that may influence the distribution and abundance of snails have been discussed by Thomas (1973). They include physicochemical factors such as water chemistry, temperature, solar radiation, water currents, detritus and associated bacteria, as well as potentially inimical factors such as other species of snails acting as competitors, predators and also parasites and pathogens. Any hypotheses concerning key factors that could perhaps be manipulated to exclude or control the snails, should be based on field observations and then tested under experimental conditions. In the present investigation three such hypotheses were tested and are discussed below.

### 7.1. *Water chemistry, possible presence of toxic chemicals*

*B. pfeifferi*, *L. natalensis* and *B. globosus* were absent from the Orogun stream above its confluence with the Ona, although common in the latter. As the two streams were physically similar it was postulated that the absence of these snail species from the Orogun might be owing to the presence of toxic chemical factors, which were either diluted or neutralized by the input from the Ona stream.

To test this, various water samples were assayed, using *B. pfeifferi* and *Helisoma duryi* ($4.5 \pm 0.15$ and $6.25 \pm 1.5$ mm in shell diameter respectively). The assay snails were kept individually in glass beakers, containing 200 ml of the test medium and fed with one 2 $\text{cm}^2$ disc of boiled lettuce every 2 d. The media were changed every 3 d. Each treatment was replicated ten times. Growth, survival and natality rates were measured at weekly intervals, and after the second week the numbers of juvenile recruits noted. The shell diameters of the snails were measured along a line passing through the outer lip of the aperture and the centre of the spire. The diameters were then converted to mass in milligrams using a regression formula derived from a sample of 50 snails. This made it possible to calculate the specific growth rate: $(W_n - W_0) . 100/W_0(t_n - t_0)$, where $W_0$ = initial growth rate in milligrams at time $t_0$ and $W_n$ = mass in milligrams at time $t_n$ (days).

The results (table 9) show that there were no significant differences between the growth and natality rates of the assay snails kept in water obtained from the Orogun and Ona streams. However, the water from the Ona further downstream at station O was particularly favourable as the mean growth rate of *B. pfeifferi* cultured in it was significantly higher ($p < 0.05$) than that of snails in water obtained higher upstream at station F. There was no evidence that factors toxic to the snails were present in any of the water samples tested.

### 7.2. *Aquatic macrophytes*

Aquatic macrophytes can be classified on the basis of whether interactions between them and the snail are positive or negative.

#### 7.2.1. *Plants that induce positive effects*

These may be ranked on the basis of their ability to attract snails, arrest their movement, initiate feeding behaviour, stimulate continuous feeding, and induce rapid somatic and reproductive growth.

TABLE 9. THE RESULTS OF BIOASSAY EXPERIMENTS CARRIED OUT ON VARIOUS WATER SAMPLES

| | After 1 week | | | |
|---|---|---|---|---|
| source of water | mean specific growth rate† ± s.e. | % mortality | mean number of egg masses per snail | after 2 weeks: mean number of juveniles per snail |
| | assay snail: *B. pfeifferi* | | | |
| water from A | 3.51 ± 0.60 | 20 | 1.13 ± 0.37 | 4.13 ± 1.34 |
| water from C | 4.01 ± 1.13 | 30 | 1.29 ± 0.40 | 4.86 ± 1.82 |
| water from F | 3.54 ± 0.41 | 20 | 1.0 ± 0.42 | 4.0 ± 1.40 |
| water from I.I.T.A lake | 3.89 ± 0.36 | 10 | 1.55 ± 0.50 | 4.78 ± 1.42 |
| water from O | 7.59 ± 1.86 | 30 | 1.13 ± 0.30 | 3.88 ± 1.11 |
| water from H | 5.06 ± 1.10 | 20 | 1.0 ± 0.35 | 5.0 ± 1.75 |
| | assay snail: *Helisoma duryi* | | | |
| water from C | 3.04 ± 0.33 | 20 | 2.25 ± 0.55 | 11.50 ± 3.91 |
| water from H | 3.59 ± 0.43 | 10 | 1.89 ± 0.46 | 10.33 ± 2.85 |
| water from I.I.T.A. lake | 2.89 ± 0.97 | 10 | 2.67 ± 0.50 | 13.33 ± 3.41 |

† See text.

#### 7.2.2. *Plants that induce negative effects*

These may be ranked on the basis of their ability to produce allomones, which repel snails, inhibit feeding activity, growth, reproduction and perhaps cause mortality.

Laboratory experiments were, therefore, carried out to ascertain the extent to which aquatic macrophytes coexisting with the snail species could be classified on these bases. The snails were maintained individually in 200 ml of water from station H, and provided with approximately 20 mg dry mass of various species of aquatic and sub-aquatic plants (table 10). Lettuce discs of the same mass were used as controls. Each treatment was replicated ten times. The wet masses of various plant species that were required to give the correct dry mass equivalents are given in table 10. The amount of plant material left in each replicate at the end of each week was weighed and replaced with fresh material.

The water was replaced every three or four days. The shell diameter of each snail was measured at weekly intervals for up to three weeks and their masses calculated, as described in the previous experiment. The number of eggs and neonate snails were also counted at the same time.

The results (table 11) reveal that only two macrophytes, namely *Lemna paucicostata* and *Salvinia nymphellula*, are readily consumed by *B. pfeifferi* while their tissues were still living. The other species are relatively non-ingestible. However, after the tissues of *Nymphaea lotus* had been killed by boiling, the dead decaying tissue became much more palatable. These results suggest that detritus is likely to be an important food source for this snail. *Helisoma duryi*, of the same size range as *B. pfeifferi*, tend to ingest much higher percentages of every plant species although the order of preferences is very similar. For *B. pfeifferi* this is as follows: *L. paucicostata* > lettuce > *N. lotus* (boiled) > *S. nymphellula* > *C. demersum* > *A. africana* > *U. reflexa* > *N. lotus* > *P. stratiotes* > *A. zizanioides*.

Table 10. Amounts of plant materal supplied per week

| plant species | dry/wet mass ratio | desired dry mass mg | wet mass provided mg |
|---|---|---|---|
| lettuce (boiled) | 0.061 | 20 | 328 |
| *Acroceras zizanioides* | 0.190 | 20 | 105 |
| *Azolla africana* | 0.162 | 20 | 124 |
| *Ceratophyllum demersum* | 0.100 | 20 | 200 |
| *Lemna paucicostata* | 0.073 | 20 | 274 |
| *Nymphaea lotus* | 0.175 | 20 | 114 |
| *Nymphaea* (boiled) | 0.139 | 20 | 144 |
| *Pistia stratiotes* | 0.051 | 20 | 392 |
| *Salvinia nymphellula* | 0.086 | 20 | 233 |
| *Urticularia reflexa* | 0.081 | 20 | 247 |

Table 11. Percentage plant material consumed per week

| plant species | *B. pfeifferi* | *Helisoma duryi* |
|---|---|---|
| | $\bar{x}$ s.e. | $\bar{x}$ s.e. |
| lettuce (boiled) | 76.02 ± 1.34 | 97.53 ± 0.81 |
| *Acroceras zizanioides* | 1.09 ± 0.16 | 1.97 ± 0.22 |
| *Azolla africana* | 7.04 ± 0.18 | 12.14 ± 0.28 |
| *Ceratophyllum demersum* | 9.13 ± 0.15 | 18.13 ± 0.16 |
| *Lemna paucicostata* | 83.23 ± 1.06 | 92.24 ± 0.71 |
| *Nymphaea lotus* | 4.06 ± 0.22 | 19.15 ± 0.19 |
| *N. lotus* (boiled) | 63.44 ± 1.24 | 97.09 ± 0.54 |
| *Pistia stratiotes* | 3.06 ± 0.20 | 8.03 ± 0.09 |
| *Salvinia nymphellula* | 33.16 ± 0.85 | 48.49 ± 0.56 |
| *Urticularia reflexa* | 6.04 ± 0.17 | 9.13 ± 0.15 |

As might be expected, there is a good correlation between the ingestibility of the plants and the growth rates achieved by the snails in the various treatments (table 12). None of the aquatic plants tested produced factors that were toxic to the snails.

### 7.3. *Other snail species*

Several authorities have advocated using snail species, such as *Helisoma duryi*, *Marisa cornuarietis* and *Physa* species as agents for the biological control of the snail host of schistosomiasis (Oliver-Gonzales *et al.* 1956; Ferguson *et al.* 1968; El Hassan 1974; Jobin *et al.* 1970; Frandsen & Madsen 1979; Madsen & Frandsen 1979). In the present investigation attention was focused on indigenous species such as *M. tuberculata*, *L. libycus* and *A. waterloti*. Their potential was evaluated by using the replacement model (De Wit 1971) as this is probably the most cost-effective method.

### 7.3.1. *Replacement series experiments involving B. pfeifferi and L. libycus*

The experimental arrangements are summarized in table 13. The snails were kept in glass beakers containing 600 ml of water obtained from station H. Washed sand and gravel from site 0 was used to cover the bottom of each beaker to a depth of 2 cm. The water was changed twice weekly. During the first week the snails were provided with rations of four 4 cm$^2$ discs of *N. lotus* and 20 fronds of *Lemna* per beaker every 3 d, and subsequently with four 4 cm$^2$ discs of lettuce per beaker every 2 d. Egg masses were counted at weekly intervals and surviving adults and juveniles every two weeks.

TABLE 12. MEAN SPECIFIC GROWTH RATES ($\bar{x}$)† (AND STANDARD ERRORS) ACHIEVED BY *BIOMPHALARIA PFEIFFERI* AND *HELISOMA DURYI* IN FEEDING EXPERIMENT

| plant species | *B. pfeifferi* | *Helisoma* |
|---|---|---|
| | $\bar{x}$ s.e. | $\bar{x}$ s.e. |
| lettuce (boiled) | 4.43 ± 0.82 | 4.60 ± 0.76 |
| *Acroceras zizanioides* | −1.27 ± 0.92 | −1.30 ± 0.32 |
| *Azolla* | −0.18 ± 0.46 | 0.16 ± 0.24 |
| *Ceratophyllum demersum* | 0.06 ± 0.22 | 0.42 ± 0.10 |
| *Lemna paucicostata* | 5.10 ± 0.98 | 4.98 ± 0.62 |
| *Nymphaea lotus* | 0.71 ± 0.15 | 1.02 ± 0.19 |
| *N. lotus* (boiled) | 3.76 ± 0.83 | 5.36 ± 0.79 |
| *Pistia stratiotes* | −0.63 ± 0.51 | 0.69 ± 0.45 |
| *Salvinia nymphellula* | 2.44 ± 0.23 | 2.87 ± 0.38 |
| *Urticularia reflexa* | −0.39 ± 0.11 | −0.43 ± 0.27 |

† See text.

TABLE 13. THE EXPERIMENTAL ARRANGEMENT FOR THE DISPLACEMENT SERIES EXPERIMENTS INVOLVING *L. LIBYCUS* AND *B. PFEIFFERI*

| treatment | A | B | C | D | E | snails from sites |
|---|---|---|---|---|---|---|
| number of *B. pfeifferi* per beaker | 4 | 3 | 2 | 1 | 0 | N |
| number of *L. libycus* per beaker | 0 | 1 | 2 | 3 | 4 | F |

Five replicates per treatment.

The results (table 14) show that although *B. pfeifferi* suffered a high mortality in all the cultures, there were no statistically significant differences between the mortalities in treatments B, C, D and the control A, at any time. *L. libycus* also suffered a high mortality. However, in this case, the mortalities in the mixed cultures C and D were significantly higher than in the control E, possibly owing to inter-species competition.

*B. pfeifferi* in mixed cultures produced significantly fewer eggs and juveniles than in monocultures (table 15). This treatment effect is probably due to predation by *L. libycus*. None of the *L. libycus* produced eggs during the course of the experiment. The reasons for this are not known, but it is possible that the experimental conditions may not have been suitable for this species to oviposit.

### 7.3.2. *Replacement series experiments involving B. pfeifferi and A. waterloti*

The experimental arrangements are summarized in table 16. The snails in each treatment were kept in 500 ml beakers containing 320 ml of water from station H. This was changed every

Table 14. The mean percentage mortality of the snails in the various treatments

| | | week 1 | 2 | 4 | 6 |
|---|---|---|---|---|---|
| A | 4 *B. pfeifferi* | 30 | 45 | 60 | 60 |
| B | 3 *B. pfeifferi* | 6.7 | 51.3 | 51.3 | 51.3 |
| | 1 *L. libycus* | 0 | 0 | 0 | 0 |
| C | 2 *B. pfeifferi* | 40 | 40 | 60 | 60 |
| | 2 *L. libycus* | 20 | 20 | 20 | 20 |
| D | 1 *B. pfeifferi* | 20 | 80 | 100 | 100 |
| | 3 *L. libycus* | 13.3 | 20 | 26.7 | 26.7 |
| E | 4 *L. libycus* | 0 | 5 | 5 | 5 |

For *B. pfeifferi* there is no significant difference between treatments (*t* test).

For *L. libycus* the mortality in treatments C and D is significantly higher ($p < 0.05$ on *t* test) than in treatments E or B.

Table 15. The number of egg masses (e.m.) and juvenile snails (j.s.) found in the various treatments

| | | week 1 | | 2 | | 4 | | 6 | |
|---|---|---|---|---|---|---|---|---|---|
| treatment | | e.m. | j.s. | e.m. | j.s. | e.m. | j.s. | e.m. | j.s. |
| A | 4 *B. pfeifferi* | 28 | 0 | 54 | 36 | 19 | 385 | 8 | 466 |
| B | 3 *B. pfeifferi* | 4 | 0 | 1 | 0 | 2 | 5 | 1 | 15 |
| | 1 *L. libycus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| C | 2 *B. pfeifferi* | 7 | 0 | 8 | 30 | 0 | 24 | 0 | 17 |
| | 2 *L. libycus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| D | 1 *B. pfeifferi* | 3 | 0 | 0 | 2 | 0 | 6 | 0 | 5 |
| | 3 *L. libycus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| E | 4 *L. libycus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

The figures are the totals for all five replicates in each treatment.

Treatment A is significantly different ($p < 0.01$) from B, C and D for both egg masses and juveniles.

Table 16. The experimental arrangement for the displacement series experiments involving *B. pfeifferi* and *A. waterloti*

| treatment | A | B | C | D | E | site obtained from |
|---|---|---|---|---|---|---|
| number of *B. pfeifferi* per beaker | 8 | 6 | 4 | 2 | 0 | N |
| number of *A. waterloti* per beaker | 0 | 2 | 4 | 6 | 8 | P |

Five replicates per treatment.

3 d. The snails in each replicate were fed on two 4 cm$^2$ discs of *N. lotus* and 20 leaves of *L. paucicostata* every three days for the first week and subsequently on one 4 cm$^2$ lettuce disc per snail every two days. The egg masses were counted each week and the number of surviving adults and juveniles every two weeks.

The results (table 17) show that *B. pfeifferi* suffered high mortalities in all the treatments. However, there were no statistically significant treatment effects. In contrast, the presence of *A. waterloti* in mixed cultures caused statistically significant decreases ($p < 0.05$) in both the number of egg masses and juveniles produced by *B. pfeifferi*. This effect is probably owing to

Table 17. The percentage mortality resulting from the treatments described in table 16

| treatment | | week 1 | 2 | 4 | 6 |
|---|---|---|---|---|---|
| A | *B. pfeifferi* | 75 | 77.5 | 77.5 | 77.5 |
| B | 6 *B. pfeifferi* | 83.3 | 86.7 | 90 | 90 |
| | 2 *A. waterloti* | 20 | 30 | 40 | 50 |
| C | 4 *B. pfeifferi* | 65 | 90 | 90 | 90 |
| | 4 *A. waterloti* | 10 | 10 | 20 | 40 |
| D | 2 *B. pfeifferi* | 100 | 100 | 100 | 100 |
| | 6 *A. waterloti* | 0 | 30 | 40 | 53.3 |
| *E* | 8 *A. waterloti* | 20 | 60 | 82.5 | 87.5 |

There were no significant differences between treatments.

Table 18. The number of egg masses (e.m.) and juvenile snails (j.s.) in the various treatments described in table 16

| | | week 1 | | 2 | | 4 | | 6 | |
|---|---|---|---|---|---|---|---|---|---|
| treatment | | e.m. | j.s. | e.m. | j.s. | e.m. | j.s. | e.m. | j.s. |
| A | 8 *B. pfeifferi* | 5 | 0 | 19 | 53 | 5 | 205 | 3 | 231 |
| B | 6 *B. pfeifferi* | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| | 2 *A. waterloti* | 4 | 0 | 4 | 15 | 3 | 42 | 4 | 79 |
| C | 4 *B. pfeifferi* | 2 | 0 | 0 | 11 | 0 | 7 | 0 | 5 |
| | 4 *A. waterloti* | 5 | 0 | 1 | 23 | 0 | 31 | 1 | 29 |
| D | 2 *B. pfeifferi* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 6 *A. waterloti* | 2 | 0 | 0 | 18 | 2 | 20 | 1 | 45 |
| E | 8 *A. waterloti* | 3 | 0 | 2 | 2 | 3 | 8 | 0 | 23 |

A is significantly different ($p < 0.05$) from B, C and D for *Aplexa waterloti*.
B is significantly different from E in terms of juveniles per adult snail ($p < 0.05$).

Table 19. The experimental arrangement for the displacement series experiments involving *B. pfeifferi* and *Melanoides tuberculata*

| treatment | A | B | C | D | E | Sites snails obtained from |
|---|---|---|---|---|---|---|
| number of *B. pfeifferi* per beaker | 8 | 6 | 4 | 2 | 0 | N |
| number of *M. tuberculata* per beaker | 0 | 2 | 4 | 6 | 8 | O |

Five replicates per treatment.

predation by *A. waterloti*. There is evidence that *A. waterloti* had benefited from this predation as they produced more eggs and juveniles in the mixed cultures than in the monoculture controls. The differences between the number of juveniles produced by *A. waterloti* in treatments E and B were in fact, statistically significant ($p < 0.05$).

### 7.3.3. *Replacement series experiments involving B. pfeifferi and M. tuberculata*

The experimental arrangement is summarized in table 19. The snails in each replicate were kept in 500 ml beakers containing 320 ml of water obtained from site H. A washed mixture of sand and gravel from site O was placed in each beaker to a depth of 1 cm. The water was changed twice weekly. During the first week the snails in each replicate were provided with two 4 $cm^2$ discs of *N. lotus* and 20 leaves of *L. paucicostata*. From the second week onwards they were given one 4 $cm^2$ lettuce disc per snail every 2 d.

Analyses of the data presented in table 20 show that the mortality suffered by *B. pfeifferi* in monocultures is significantly higher ($p < 0.05$) than in mixed cultures. However, there are no significant differences between treatments B, C and D. Neither were there significant differences in the number of eggs or juveniles produced by *B. pfeifferi* or in the number of juveniles produced by *M. tuberculata* in the various treatments (table 21). It should be noted, however, that as the plant food was provided at the surface in these experiments it would, therefore, be relatively inaccessible to *M. tuberculata*. As this experiment only shows what the outcome of interactions might be in lentic systems similar tests should also be carried out in running water.

Table 20. The percentage mortality resulting from the treatment described in table 19

| | week | | | |
|---|---|---|---|---|
| treatment | 1 | 2 | 4 | 6 |
| A 8 *B. pfeifferi* | 60 | 90 | 90 | 90 |
| B 6. *B. pfeifferi* | 36.7 | 53.3 | 53.3 | 56.7 |
| 2 *M. tuberculata* | 0 | 0 | 0 | 0 |
| C 4 *B. pfeifferi* | 30 | 40 | 40 | 45 |
| 4 *M. tuberculata* | 0 | 0 | 0 | 0 |
| D 2 *B. pfeifferi* | 30 | 30 | 30 | 30 |
| 6 *M. tuberculata* | 0 | 0 | 0 | 0 |
| E 8 *M. tuberculata* | 0 | 0 | 0 | 0 |

Mortality of *B. pfeifferi* in A is significantly different from B, C and D ($p < 0.05$) but there is no significant difference between B, C and D.

Table 21. The number of egg masses (e.m.) and young (j.s.) produced in the various treatments described in table 19

| | week | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | | 2 | | 4 | | 6 | |
| treatment | e.m. | j.s. | e.m. | j.s. | e.m. | j.s. | e.m. | j.s. |
| A 8 *B. pfeifferi* | 3 | 0 | 13 | 39 | 6 | 117 | 5 | 141 |
| B 6 *B. pfeifferi* | 13 | 0 | 11 | 27 | 6 | 96 | 2 | 111 |
| 2 *M. tuberculata* | – | 0 | – | 2 | – | 7 | – | 10 |
| C 4 *B. pfeifferi* | 9 | 0 | 4 | 12 | 2 | 43 | 0 | 32 |
| 4 *M. tuberculata* | – | 0 | – | 3 | – | 20 | – | 27 |
| D 2 *B. pfeifferi* | 4 | 0 | 6 | 6 | 2 | 34 | 1 | 39 |
| 6 *M. tuberculata* | – | 0 | – | 5 | – | 21 | – | 31 |
| E 8 *M. tuberculata* | – | 0 | – | 11 | – | 59 | – | 75 |

Total results for all five replicates.
As *Melanoides* is viviparous no egg masses were produced.

## 8. Discussion

Factors that may influence the distribution and abundance of the snails are first considered separately and then in a holistic context. Finally, the factors that might be manipulated to achieve control in the study area are evaluated, and a provisional programme for assessing their effectiveness under field conditions is outlined.

### 8.1. *Ecologically important factors considered separately*

#### 8.1.1. *Temperature*

This is a major factor influencing the distribution of the snail hosts of schistosomiasis in Africa (Appleton 1978). Circumstantial evidence, based on field observation, suggests that high temperatures over long periods are detrimental to the snail hosts. Thus, *B. pfeifferi* is found more commonly in the cooler waters at higher altitudes in Kenya (Teesdale 1962), South Africa (van Eeden & Combrinck 1966) and Nigeria (Ndifon 1979). Appleton (1976) showed that there was a significant inverse relationship between the fecundity of this species and temperature, and that it was absent from habitats with more than 120–179 degree-hours higher than 27 °C per week. Similarly, Chu *et al.* (1968) noted that the population density of *B. truncatus* declined after temperatures had risen to 38 °C in the afternoons and Hira (1966) attributed the enhanced reproductive rate of *B. forskali* in the wet season to a decrease in temperature. This hypothesis is supported by laboratory work. Thus the optimal '*r*' value for *Bulinus* (*P.*) *globosus* (Shiff 1964), *B. pfeifferi* (Sevilla 1965; Sturrock 1966; Shiff & Garnett 1967), *B. glabrata* (Sevilla 1965; Sturrock & Sturrock 1972), and *B. alexandria* (Sevilla 1965) occurred at 25 °C. There is general agreement that temperatures above the optimum are more harmful to the mechanisms controlling reproductive physiology than to those influencing general metabolism and growth (Shiff 1964; Michelson 1961*b*; van der Schalie & Berry 1973).

The behavioural responses to temperature by snails have been little studied. Chernin (1967) showed that *B. glabrata* had a preference for 27–30 °C in a temperature gradient of 12–33 °C and Appleton (1978) has suggested that the diurnal changes in temperature may be partly responsible for the diurnal migration shown by several species of aquatic pulmonates.

The present observations suggest that the temperatures in exposed, shallow marginal waters may at times be detrimental and even lethal to snails such as *B. pfeifferi*. However, this hypothesis requires testing by field experimentation designed to elucidate the effects of varying water depth and the degree of exposure to direct sunlight. The results of such experiments would have practical application to the design of irrigation channels and other water systems.

#### 8.1.2. *Light*

There is laboratory evidence that *B. truncatus* and other species of planorbid snails avoid strong light and prefer shaded areas (Boettger 1944; Zakaria 1955). There are also several anecdotal accounts that this might be the case under field conditions (Gerber 1952; Hira 1966; Asumu 1975; Ndifon 1979). Ndifon (1979) attempted to quantify the effects of variation in light intensity or shade on the distribution of snails in SW Nigeria and found that *B.* (*P.*) *globosus* and *M. tuberculata* occurred most frequently in habitats exposed to 26–50 % of direct sunlight. The corresponding figures for other species were as follows: *B. pfeifferi* and *L. natalensis*, 76–100 %; *A. waterloti*, *L. libycus* and *G. costulatus*, 0–25 %. Under field conditions it is not, of course, possible to distinguish between the effects of direct solar radiation and temperature.

Light may either affect the snails' physiology directly or indirectly by its influence on photosynthetic activity of water plants. For example, red light may cause avoidance behaviour (Boettger 1944), or a reduction in egg production (Joy 1971). Direct sunlight may also have a lethal effect on some species. Thus, juveniles of *Physa inarmorata* died after exposure to direct sunlight for only 6 h over a 3 d period (Rankin & Harrison 1979). It would be valuable to know the spectral component responsible for this lethal effect. The ultraviolet component may be important, as recent experiments in this laboratory have shown that albino *B. glabrata* in an inverted position on the surface film, died after exposure to approximately 1.6 $\mathrm{J\ m^{-2}\ min^{-1}}$ of u.v. irradiation (source of u.v. radiation: Phillips TUV 15 Watt, 57415P/40; the intensity was measured with a Latarjet no. 272 meter). In view of the potential application of the findings, further experimentation is required.

### 8.1.3. *Water chemistry*

Although differences occur in the water chemistry at the various stations, it seems unlikely that, with the exception of oxygen, these are responsible for the differences in the distributional patterns of the snails for the following reasons. First, it seems unlikely that there is a lack of any of the biologically important ions in the water bodies analysed. Calcium and iron are among the most important ions for the snails because they are components of the shell and haemoglobin respectively. There is a great deal of circumstantial evidence that $Ca^{2+}$ can influence the distribution and abundance of snails (Boycott 1936; Macan 1950; Hunter 1961; Harrison & Shiff 1966; Harrison *et al.* 1970; Williams 1970*a*, *b*; Ökland 1969; Ndifon 1979). Some species are, however, more tolerant of low calcium concentrations in the medium than others, possibly because they can acquire it in a more concentrated form from plants (van der Borght & van Puymbroeck 1966). However, the calcium concentrations in the various stations investigated in the present study (20.4–43.4 $\mathrm{mg\ l^{-1}}$) are likely to be optimal or suboptimal for snail growth (Thomas *et al.* 1974). Iron, probably chelated to humic or fulvic acids, as the water was oxygenated, was also present in measurable amounts (0.12–1.20 $\mathrm{mg\ l^{-1}}$). Both iron and calcium can be taken up actively from the medium by the snails at rates that are proportional to their growth rates (Gazzinelli *et al.* 1970; Thomas & Lough 1974).

Secondly, the distributional evidence and the results of the bioassay tests, indicate that none of the chemical components is likely to be harmful to the snails. Of the chemical species identified in the water samples, $Mg^{2+}$, $Cu^{2+}$ and ammonia (as $NH_3$) are potentially harmful to snails if present above critical thresholds. The magnesium ion is important because it can compete with calcium for uptake sites. However, from the evidence given by Harrison *et al.* (1966) it is unlikely to be harmful in the water bodies studied as the $Ca^{2+}/Mg^{2+}$ ratios varied from 4 to 8.5. Copper is also unlikely to be toxic at the concentrations found (Ritchie 1973). The snails were found in some streams with surprisingly high concentrations of ammonia (up to 16.25 $\mathrm{mg\ l^{-1}}$). However, this was not completely unexpected, as Thomas *et al.* (1976) have shown that *B. glabrata* can tolerate ammonia concentrations as high as 25 $\mathrm{mg\ l^{-1}}$ provided the pH is close to neutral. At this pH the ammonia exists largely as the non-toxic, $NH_4^+$, form.

It can be hypothesized that snails have become tolerant to ammonia as a result of natural selection, as it is a major excretory product, which can occur in the blood of some snails at concentrations as high as 7–20 $\mathrm{\mu g\ ml^{-1}}$ (Speeg & Campbell 1969). The detritivorous snails also have to tolerate high ammonia concentrations in the vicinity of their food as it is a major component of microbial decomposition (Patience *et al.* 1983). It is possible that some snail species, particularly those that are not highly detritivorous, may have a relatively low level of tolerance to exogenous ammonia. *B. rohlfsi* may fall into this category. It would be of interest, therefore, to ascertain whether its absence from the Ibadan streams was owing to high ammonia concentrations. Fish and other freshwater species are much less tolerant to ammonia than snails. For example, Ball (1967) gives $LD_{50}$ values of 0.29 and 0.41 mg $l^{-1}$ ammonia (N) for some fish species.

Thirdly, the possibility that many snail species were absent from the Orogun stream owing to the presence of toxic organic substances has been disproved by bioassay experiments. It is more likely that it is due to lack of refugia such as headwater marshes or associated lentic habitats in this stream system. The present results provide support for the generalization that aquatic pulmonate snails have a wide range of tolerance to chemical factors (Appleton 1978; Ndifon 1979). This is not unexpected because these snails have evolved in aquatic systems, which are liable to rapid changes in chemical composition.

However, one chemical factor that may limit the distribution of snails is a low level of dissolved oxygen. For example, Asumu (1975) found snails absent from habitats where oxygen levels were below 1.3% saturation and Ndifon (1979) found that all the snail species, with the exception of *L. libycus* were absent from habitats with oxygen concentrations of 0–10%. These findings may explain the absence of snails from I.I.T.A. lake at depths greater than 3 m and from the fish pond (P). The only snail species, *A. waterloti*, found in the latter was confined to moist sediments shaded by *A. zizanioides* on the water's edge. In conclusion it can be stated that although the snail hosts of schistosomiasis have a wide range of tolerance to most chemical factors they are susceptible to anoxic conditions. This observation suggests that the transformation of water bodies into eutrophic plankton-based fishponds might provide one useful strategy for excluding the snail hosts.

### 8.1.4. *Water flow*

Flow rate is a major factor in influencing the distribution of the snail hosts of schistosomiasis (Appleton 1978). It is known that they have a strong preference for lentic habitats and when occurring in lotic habitats, show marked preferences for slow or non-flowing regions, such as pools, backwaters or slack water near banks, colonized by subaquatic plants such as *Commelina* or *Acroceras*. The present results agree with those of Dowdeswell (1983), Watson (1950), McCullough & Duke (1954), Ayad (1956), Teesdale (1962), Odei (1961, 1964), W.H.O. (1965); Hira (1966), Hira & Müller (1966), Asumu (1975) and Ukoli & Asumu (1979).

Several quantitative attempts have been made to correlate the distribution of snails to stream velocity (Scorza *et al.* 1961; Appleton 1978; Ndifon 1979). Although the values given are based on measurements made in the mainstream rather than in microhabitats where the snails occur, they do give an indication of the status of streams as suitable snail habitats. Scorza *et al.* (1961) demonstrated a significant linear relationship between the densities of *B. glabrata* and current velocities up to the limit of 30 cm $s^{-1}$. This value is in agreement with that for African species such as *B. pfeifferi* (Appleton 1978). This generalization also receives support from the work of Ndifon (1979), as he found that both *B. pfeifferi* and *B. forskali* were absent from lotic habitats with current speeds greater than 30 cm $s^{-1}$. *B. forskali*, *B. pfeifferi*, *M. tuberculata* and *G. costulatus* occurred most frequently in habitats with a current velocity of 0–10 cm $s^{-1}$. In contrast, both *L. libycus* and *L. natalensis* were more tolerant of fast flowing water and were found in habitats with main stream current speeds of 30–60 cm $s^{-1}$. However, *B. rohlfsi*, as in the present investigation, was never found in lotic habitats. Had these observations been available before the construction of the Volta Lake, the importance of *B. rohlfsi* as the major snail host in such habitats could have been predicted.

The following hypotheses can be advanced to explain why host snails of schistosomiasis are not commonly found in flowing water. First, they would have to expend a great deal of energy to maintain their station. Some species, such as *L. natalensis*, *B. globosus* and *L. libycus*, have a hemistreamlined shape and are better adapted than *Biomphalaria* species for life in flowing water. This might explain why they were classed as typical stream species by Ndifon (1979). Secondly, flowing water may have a detrimental effect on their physiology. Thus the growth rate of *B. glabrata* in flowing water was significantly less than in controls kept in closed systems (Thomas *et al.* 1975), possibly owing to the loss of growth factors released by the snails. Thirdly, snail food, such as detritus and epiphytic algae on macrophytic plants, tends not to occur in fast flowing waters, but in depositing sediments in pools or backwaters, where the water velocity is normally close to zero. Fourthly, fine sand or silt particles, which are important components of the snails gizzard, do not occur in the eroding substrates in flowing water. These particles are used by the snails to triturate the food before it is taken up by the hepatopancreas for intracellular digestion.

The behavioural repertoire of these snails would tend to ensure that they would remain only as temporary members of any truly lotic community. Thus it is well known that snails such as *B. glabrata* exhibit positive rheotoxis when in currents (Radke & Ritchie 1961; Paulini 1963; Bousfield 1978). It is to be expected, therefore, that this high level of activity would tend to bring them into non-flowing habitats where they would encounter the arresting influences of detritus and food organisms.

In contrast, prosobranch snails belonging to the families Hydrobiidae and Thiaridae (Melaniidae) are morphologically better adapted for life in currents. Thus, *Potamopyrgus jenkinsi*, *Pyrgophorus parvalus* and *M. tuberculata* are hemistreamlined and able to feed on fine particulate organic drift brought down by currents in lotic habitats. In this connection, their gregarious habitats may assist feeding by facilitating the deposition of drift. Wind generated currents in lentic habitats may also assist in concentrating detritus for such snails along the shore-line of lakes.

Heavy flooding in the wet season is likely to eliminate populations of the snail hosts in most of the stream habitats at this time. However, recolonization can probably occur rapidly from the refugia already described.

### 8.1.5. *Sediment types*

Snails were generally found on depositing substrate consisting of fine silt, mud and detritus, in both lotic and lentic habitats. Such habitats are generally colonized by aquatic macrophytes. These observations are in accord with those of other workers, including Walton (1918), Blacklock & Thompson (1924), Walton & Wright (1926), Malek (1958, 1972), Watson (1958), Frank (1964), McCullough (1964), Hira (1966), Combrinck & van Eeden (1969) and Richard & Frank (1966). In contrast, eroded sediments consisting of coarse gravel and stones, in running water, are more favourable habitats for prosobranchs such as *M. tuberculata* than for pulmonate snails.

### 8.1.6. *Absence of water owing to seasonal drying*

During the dry season there was a marked decrease in the surface areas of both lotic and lentic habitats, leaving extensive drawdown areas. Flow patterns in the stream may also become disrupted, leaving a series of isolated pools, as in the Ona stream. The snails stranded in the draw-down areas are vulnerable to predation by species of aquatic birds, including waders (Thomas 1966). However, some may survive for long periods by aestivating in sediment, detritus or vegetation. The presence of subaquatic plants, such as *Acroceras*, *Commelina*, and stranded aquatic plants, such as *Pistia*, *Salvinia* or *Azolla*, may greatly increase the probability of snail survival (Appleton 1978). The permanent water systems, identified by biotic indicators such as *Nymphaea* and *Ceratophyllum*, are also vitally important for snail survival in the dry season.

### 8.1.7. *Aquatic and subaquatic macrophytes*

The present results show that the pulmonate snails are positively associated with both subaquatic and aquatic macrophytes or decaying plant material, at macro- and micro-distributional levels. Some of these, such as *Acroceras zizanioides*, *Commelina* sp. and *Nymphaea lotus*, are, therefore, good biotic indicators for certain snail species.

The subaquatic plants, which grow in the ecotone zone, are important to the snails. The micro-distributional studies revealed statistically significant positive associations between both *B. pfeifferi* and *L. natalensis*, and the subaquatic plants, *Commelina* sp., *Cynodon dactylon* and detritus along the margin at station H. *B. rohlfsi* was also significantly associated with *Commelina* sp. in I.I.T.A. lake. These results are in agreement with those of other malacologists in West Africa. Thus, Gordon *et al.* (1934) observed that *B. pfeifferi* was associated with *Acrocerus zizanioides* and *Eleocharis fistulosa* in Sierra Leone. Hira (1966) working in the Ibadan area, found that *B.* (*P.*) *globosus* was associated with *A. zizanioides*, *Commelina* sp. and *Alternanthera nodiflorum*, *B. pfeifferi* with *A. sessilis*, *Commelina* sp. and *A. zizanioides* and *B. forskali* with *A. nodiflorum*. Subaquatic plants including *Acroceras* sp., *Commelina* sp., *A. sessilis*, *Polygonum salicifolium* and *Coix lacrymajobi* were found to be good biotic indicators of snail habitat in NW Nigeria by Ndifon (1979). This author found statistically significant positive associations between the following species: *B. globosus* with *Commelina* sp.; *B. forskali* with *Paspalum* sp. and *A. sessilis*; *B. pfeifferi* with *Commelina* sp., *A. zizanioides* and *Paspalum* sp.; and *B. rohlfsi* with *A. sessilis*.

Statistically significant positive associations were found in the present study between the following species of aquatic macrophytes and snails; *Nymphaea lotus* with *A. coretus* and *B. forskali*; *Lemna paucicostata* and both *A. coretus* and *B. pfeifferi*; *Ceratophyllum demersum* and both *B. rohlfsi* and *B. forskali*. These results are in general accord with those obtained by other workers in West Africa. Thus McCullough (1956) noted the tendency for both *B. forskali* and *B. sericinus* to be associated with *Nymphaea* and *Ceratophyllum* in Ghana. Statistically significant positive associations were demonstrated between both *Bulinus truncatus* and *Biomphalaria alexandrina* and the plant species *Potamogeton crispus*, *Eichornia crassipes* and *Polygonum serulatum* by Dazo *et al.* (1966) in Egypt. The strong tendency for *B. rohlfsi* to be associated with *Ceratophyllum demersum* in the Volta Lake has been noted by Paperna (1969*a*, *b*), Odei (1972, 1973); Chu & Vanderberg (1976) and Klumpp & Chu (1977). These last authors stress the role of the emergent, subaquatic plant *Polygonum* sp. in providing shelter for *Ceratophyllum*, thus protecting it from the action of wind generated currents. Petr (1968) and Obeng (1969) found that *B. rohlfsi* and *B. forskali* also occurred on *Pistia stratiotes*. Both *Pistia* and *Ceratophyllum* may well be important agents for dispersing snails as they are readily carried by currents in both lentic and lotic habitats. In the roadside habitats investigated by Ndifon (1979), relatively few species of aquatic macrophytes were present. However, he was able to demonstrate statistically significant associations between *B. forskali* and *Lemna paucicostata*, and also between *B.* (*P.*) *globosus* and filamentous algae. The results of the present investigation indicate that the snails were usually found adhering to the plants. This was obligatory in the deeper water in I.I.T.A. lake, as the water column was anoxic at depths below 3 m. These results are in accord with those of other workers. Thus Paperna (1969*b*) found that the order of preference of *B. rohlfsi* for substrates in Lake Volta was as follows: *Ceratophyllum* > *Pistia* > *Scirpus* > sediments. These preferences were quantified by Odei (1972, 1973). He estimated that only 3.4% of the snails occurred on the bottom sediments, compared with 60.9 and 35.7% on living and dead plant material respectively. Ndifon (1979) also observed that *B. rohlfsi*, *B. pfeifferi* and *B. forskali* were usually found on plant material and rarely on bottom sediments, and that *B. globosus* was the snail most commonly found on bottom sediments.

Significant negative associations between aquatic macrophytes and snails were also found in the present investigation. These were between *Salvinia nymphellula* and four snail species: *B. forskali*, *B. pfeifferi*, *B. rohlfsi* and *A. coretus*; and between *Azolla*, *Ceratophyllum*, *Utricularia* and *M. tuberculata*. *L. natalensis* was exceptional, as it showed neither significant positive nor negative associations with plants in I.I.T.A. lake. It seems capable of existing in very dense beds of floating plants such as *Salvinia* and *Pistia*, unlike other snail species. There are other anecdotal accounts of negative associations between snails and aquatic macrophytes. For example, McCullough (1957) and Teesdale (1962) found that *B.* (*P.*) *globosus* tended not to occur in very dense beds of either *Azolla* or *Nymphaea*.

The causative mechanisms responsible for these positive and negative associations have yet to be elucidated. It can be argued that it would be selectively advantageous for the aquatic plants to produce allelopathic substances, capable of acting as repellants or toxicants, for protection against ingestion by the snails. If such substances do exist it might explain the negative associations. However, this hypothesis is not supported by the feeding experiments as there was no evidence of any plant producing allelopathic factors. In fact all were eaten by the assay snails to some extent. For example, *Salvinia*, was a good food source for the assay snails in the laboratory although four snail species were found to be negatively associated with it in I.I.T.A. lake.

It is, therefore, necessary to seek an alternative explanation for the negative associations between snails and floating plants such as *Salvinia* and *Pistia*. One possibility is that snail survival is impaired by the difficulty they might encounter in gaining access to the air–water interface to replenish their air supply when these plants are tightly packed. This would also prevent photosynthesis in the water column underneath. As a result dissolved oxygen and food resources, such as submerged macrophytes and detritus would not be available. Support for this hypothesis is provided by observations that show that the water column underneath beds of floating plants, such as *Pistia*, can be anoxic (Thomas & Ratcliffe 1973). *L. natalensis* survives under these conditions by being amphibious and subsisting on decaying leaves of the floating plants.

Another apparent negative association between *A. coretus* and *Ceratophyllum* can be explained in terms of the very strong affinity shown by this snail to *Nymphaea*. However, in the present state of our knowledge, the negative associations between *Melanoides* and certain plant species cannot be explained. The possibility that it might be caused by allelopathic substances in the decaying remains of these plants is perhaps worthy of investigation.

As positive relationships between pulmonate snails and macrophytes predominate over negative ones, it is necessary to seek explanations for this interesting observation. The most obvious is that snails occur on the plants because the plants are being used as a food source. However, two observations militate against this. Firstly, the results of the laboratory feeding experiments indicate that with the exception of *Lemna*, and to a lesser extent *Salvinia*, the aquatic macrophytes are relatively unpalatable and an inadequate food source for the snails. Secondly macrophytes are relatively unimportant components in the dietaries of *B. pfeifferi* and other snail hosts in nature (McCullough & Duke 1954; Malek 1958; Ndifon 1979).

The reasons for the low ingestibility of most of the macrophytes to the snails have yet to be elucidated. The possibility that it may be owing to their hard texture is supported by the work of Ndifon (1979) as he found that when macrophytes were the only food source for *B.* (*P.*) *globosus*, the snails lost large numbers of radula teeth. It is therefore possible that it might not be cost effective for them to feed on living macrophytes. The low ingestibility might also be owing to the presence or absence of chemical factors, which act as feeding inhibitors or incitants respectively. However, the results of the feeding experiment rule out the involvement of toxic allelopathic factors. In contrast the subaquatic plant *Alternanthera sessilis* does contain chemicals that are toxic to snails (Ndifon 1979). However, this mode of defence may have evolved as a result of selective pressures resulting from attacks by terrestrial insects.

It appears, therefore, that the relationships between pulmonate snails and aquatic macrophytes may differ from those involving terrestrial plants and herbivores, as in the latter case chemical defence mechanisms appear to be of paramount importance. In contrast, it is probable that the relationships between snails and their aquatic macrophytes is essentially symbiotic (table 21). The present results provide some support for this model. First, it has been shown that, with the exception of *Lemna*, the snails consume epiphytic organisms such as desmids, diatoms, rotifers, etc., in preference to macrophyte tissue. This observation is supported by the earlier work of Malek (1958), McCullough & Duke (1954), Ndifon (1979). The snails, therefore, perform the role of cleaning symbionts, and in their absence epiphytic organisms could perhaps overwhelm the macrophytes.

Secondly, the detritivorous habits of the snails could benefit the plants in several ways. Thus, the removal of dead tissues could reduce the probability of disease organisms becoming established in living tissues. Detritivores can also accelerate the turnover rate of essential minerals and thus increase their availability to the plant (Wallwork 1970). The present observations indicate that detritus is an important food source for the snails thus confirming observations of other workers (Boettger 1944; Malek 1958; McCullogh & Duke 1954; Calow 1973, 1974; Ndifon 1979). In this connection it is of interest that boiled *Nymphaea* leaves, which serve as a good substrate for bacteria and therefore resemble detritus, are readily eaten by *B. pfeifferi* whereas the living plant is relatively unpalatable.

Macrophytes also benefit snails by providing them with shelter against inimical factors including radiation, high temperature, currents and by inducing depositing conditions where detritus and fine silt may accumulate. Subaquatic macrophytes may play a key role in this connection, particularly in temporary habitats. The hypotheses, in table 22, require testing under experimental conditions.

The hypothesis that removal of macrophytes from snail habitats would be followed by a reduction in snail densities does not appear to have been tested under rigorous experimental conditions although there are some supporting anecdotal accounts (Saliternik & Witenberg 1959; Asumu 1975). Conversely, an increase in macrophyte population should be followed by an increase in snail density. This is supported by some qualitative evidence (Gerber 1952; Saliternik & Witenberg 1959; Paperna 1969*b*; Chu & Vanderberg 1976). It must not be overlooked that the quality as well as quantity of food is important. Thus, Eisenberg (1966, 1970) showed that the addition of high quality plant food in the form of spinach was followed by a dramatic increase in growth and reproduction by *Lymnaea elodes*.

TABLE 22. SOME OF THE BENEFITS THAT BOTH PULMONATE SNAILS AND MACROPHYTES MAY DERIVE FROM COEXISTENCE

| | benefits to plants | benefits to snails |
|---|---|---|
| 1. | Snails clean them of epiphytes, damaged or decaying parts and potentially harmful pathogens that may feed on these. | Plants protect snails from inimical factors, for example, strong light, high temperatures, water currents, allow access to air–water interface and oviposition sites. |
| 2. | Faeces, dead snails, released nutrients. | Serve as food source. |
| 3. | Exogenous factors released by snails may benefit plants, for example, ammonia, carbon dioxide. | Exogenous factors released by plants. may benefit snails, for example, $O_2$ during the day, exogenous factors enhance growth rates of snails. |
| 4. | Removal of exogenous plant factors by snails may benefit plants for example, $O_2$ which may induce photorespiration. | Removal of exogenous snail factors by plants may benefit snails, for example, ammonia may be toxic to snails (see Thomas (1982)). |

### 8.1.8. *Other snail species*

Both *A. waterloti* and *L. libycus* were efficient predators on the eggs and juveniles of *B. pfeifferi*. In this respect they resemble other snail species such as *Marisa cornuarietis* (Demian & Lufty 1965, 1966; Léon 1975), *Pomacea* sp. (Paulinyi & Paulini 1972) and *Helisoma duryi* (Frandsen & Madsen 1979), which have been advocated as agents for the control of the snail hosts of schistosomiasis. However, the following evidence makes it unlikely that these two species could be used for the biological control in the study area. First, the results of the laboratory experiments appear to show that they are weak competitors. Thus, *L. libycus* suffered higher mortalities in the mixed cultures than in the monocultures.

Secondly, the distributional evidence suggests that neither of these two species could exclude any of the snail hosts. On the contrary, *L. libycus* and *B.* (*P.*) *globosus* tend to coexist, as the present results are indicative of strong significant positive, rather than negative, associations. This is also the case with *B. pfeifferi*, *B. forskali* and *B. rohlfsi* at both macro- and micro-distributional levels. It would be interesting to elucidate the mechanisms that permit these snail associations when their microhabitat preferences are so similar. The most likely explanations, which require verification, are that it is either because their feeding niches do not overlap or alternatively because numbers are kept in check by inimical forces, such as predators, parasites or physicochemical factors. The possibility that they may derive mutual benefit from coexistence is also worthy of investigation, as there is laboratory evidence that this might be the case with some species of pulmonate snails (Madsen 1982).

Thirdly, both *L. libycus* and *A. waterloti* have a more restricted distribution than schistosome-bearing snails. Thus *L. libycus* is only commonly found on muddy substrates in marshy areas, at stream origins or in shaded woodland streams. *A. waterloti* is also patchily distributed and found in abundance only in marginal habitats with rich deposits of organic matter shaded by luxurious growths of subaquatic plants.

It can be concluded, therefore, that the present results provide no evidence that any of the snail species are being excluded as a result of interspecies competition under field conditions, as all significant associations were positive at both micro- and macro-distributional levels. Earlier anecdotal accounts of apparent mutual competitive exclusion involving *B.* (*P.*) *globosus* and *A. waterloti* (McCullough 1957) and also *Bulinus ugandae* and *Biomphalaria sudanica* (Berrie 1964) require quantification and experimental verification.

Rather surprisingly the presence of *M. tuberculata* in the displacement experiments, increased the survival rate of *B. pfeifferi*. Although the causative mechanism has not been elucidated, the possibility that *M. tuberculata* may benefit *B. pfeifferi* by removing factors toxic to it from its faeces, or decaying plant material on the substrate by ingestion, is worthy of exploration. Alternatively *M. tuberculata* may release factors into the medium that benefit *B. pfeifferi*. This possibility is supported by the observation that some pulmonate snails release factors into the medium that enhance the growths of conspecifics (Thomas & Aram 1974; Scheerboom & Geldof 1978) and other species (Madsen 1982).

The conditions of the displacement experiments involving *B. pfeifferi* and *M. tuberculata* resemble those found in lentic habitats. In these *M. tuberculata* occurs mainly on the substrate, whereas the snail hosts occur above them on macrophytic plants. However, in the absence of macrophytes any snails present would be forced to coexist on the sediments. Other displacement experiments should, therefore, be undertaken, to ascertain whether *M. tuberculata* could compete successfully with the snail hosts of schistosomiasis in such habitats.

The following observations favour the possibility that *M. tuberculata* might exclude or control the snail hosts of schistosomiasis in lotic habitats particularly if these could be altered by the engineering measures described below. First, it is very widely distributed in both lotic and lentic habitats. Thus it scored the highest percentage occurrence of any snail in the study area. Ndifon (1979) also found that it was the most abundant snail in SW Nigeria. Secondly, it occurs at very high densities (nearly 10000 $m^{-2}$) in eroding stream habitats. The only other species coexisting with it in such habitats were tubiculous chironomids and tubificid worms.

### 8.2. *The holistic view and integrated control*

Two important generalizations can be made from the present study. First, persistent populations of snails occur in certain restricted foci. Secondly, in the other parts of the study area the snails are discontinuously distributed in both space and time.

These observations are encouraging for two main reasons. First, they suggest that successful long-term control, or even exclusion of the snail hosts, might be achieved by concentrating control effort in the stable foci. If, as suspected, these foci provide the immigrants for the more temporary 'r' populations in the less favourable habitats, this strategy could be more cost-effective in the long term than focal control directed at disease transmission sites.

Secondly, snails might be either eliminated or controlled by manipulating some of the key factors that influence their distribution and abundance. These factors, which were considered separately in the previous section, can be classified into those that may act as either density legislative or density governing factors (Nicholson 1958). Density legislative factors are usually physicochemical in nature, such as temperature, light, certain chemical species and currents, which can determine whether a species can exist in a particular location or not. Density governing factors, on the other hand, are biological in nature and act in a density-dependent manner to maintain the snail populations below a critical threshold. When considering possible manipulative measures for control, priority should be given to those that act in a density legislative manner, thus excluding snails, as there is evidence that the critical density below which transmission cannot take place is very low indeed (McCullough 1956; Duke & Moore 1976*a*, *b*, *c*).

Field experiments are needed to evaluate the effects of particular manipulations. Although ideally each one should be considered separately, reasons are given below for believing that successful eradication or control is more likely to be achieved by integrated control, involving two or more simultaneous perturbations. To facilitate discussion and future planning, lotic and lentic systems are considered separately.

### 8.2.1. *Lotic habitats*

The more persistent snail foci are located in the small pools and swampy ground associated with stream origins (for example, Gbelede and Shango). In such habitats populations can persist in stable equilibrium, perhaps because the following niche requirements are satisfied. First, the water supply is continuous although at a velocity close to zero throughout the year. The low velocity is made possible by the small volume of water involved, the gentle gradient and the buffering effect of aquatic and sub-aquatic vegetation. Secondly, the prolific growth of emergent macrophytes provide protection from the effects of solar radiation. Thirdly, the spring waters are likely to be at a lower temperature than the more exposed water bodies. Fourthly, the conditions favour the deposition of fine silt and detritus. Fifthly, macrophytes provide the snails indirectly with a source of food in the form of epiphytic algae and detritus. Sixthly, the presence of humic or fulvic acids in such habitats would chelate iron, thus increasing its availability to the snails. Finally, the spring-fed stream is less likely to dry up at the source than elsewhere along its length.

These persistent snail habitats can be identified by the presence of biotic indicators, such as the aquatic plants *Nymphaea lotus* and *Ceratophyllum demersum* or by emergent, subaquatic plants, such as species of *Polygonum*, *Typha* and *Crinum*. The coexistence of several snail species, such as *B.* (*P.*) *globosus L. natalensis*, *B. forskali*, *B. pfeifferi* and *L. libycus* is also indicative of favourable conditions.

The snail refugia found in the present study area resemble those described for *B. glabrata* by Sturrock (1973, 1974) and McKillop & Harrison (1980). According to these authors, the marshes and elevated spring ponds associated with the headwaters of rivers serve as permanent reservoirs exporting *B. glabrata* into the streams, low level marshes and banana drains where transmission of the disease occurs. In contrast, populations of *B. glabrata* in the streams are denuded by heavy seasonal spates, whereas those in low level marshes and banana drains are decimated by drought in the dry seasons. They consider that without constant immigration from the permanent reservoirs the populations in the lowland habitats would die out. Rowan (1959), Milward de Andrade (1962) and one of the present authors (J.D.T.) found that headwater marshes and pools act as refugia for *Biomphalaria* species in Puerto Rico, the state of Minas-Gerais, Brazil, and in the Adwa area of Ethiopia respectively.

Other economically important species such as *Locusta migratoria migratoria* R. & F. and the red locust *Nomadacris septemfasciata* resemble the snail hosts of schistosomiasis in having relatively small outbreak areas from which they disperse into very extensive invasion areas. Locust swarms are dispersed by wind, whereas the snails are carried by water currents. While locust dispersion mechanisms have been widely studied because of their relevance to the development of control strategies (Uvarov 1966), analogous aspects of snail biology have been neglected.

Along their lengths, lotic systems show increasing heterogeneity and various water types such as pools, backwaters, riffles and fast reaches become more clearly defined although their relative sizes will be determined mainly by topology and climate. The present results indicate that riffles and fast reaches are unfavourable habitats for snail hosts. In contrast, backwaters and pools are more favourable albeit often temporary habitats, because they allow deposition of silt, detritus and colonization by macrophytic plants. Such habitats are also advantageous to the enactment of the life cycle of trematode parasites of freshwater fish (Thomas 1964) and man, as their larvae are typically planktonic.

Although most pools or backwaters provide only inadequate protection to the snail hosts from the effect of floods in the wet season, some lotic systems do have natural features which may serve as more persistent snail refugia. For example, Appleton (1975) and Appleton & Stiles (1976) found that the presence of exposed granite or basalt rocks on the river bed allowed formation of permanent pools that provide adequate shelter in time of flood. In contrast snails were absent, or only occurred temporarily in river beds consisting of unstable soft rock or alluvial sand.

Unfortunately, by damming streams and rivers and constructing irrigation channels, man has greatly increased the availability of persistent refugia for pulmonate snails. This is illustrated by examples from the Kruger National Park, South Africa, and in the state of Minas-Gerais Brazil, where snails are very difficult to find in natural habitats, but are common in areas where man has constructed dams or watering places (Frank 1964; Freitas 1976). As snail populations in these natural habitats may be regulated and maintained at very low levels by biological agents, a search for the latter could, therefore, be rewarding. Such an approach has been responsible for the identification of successful agents to control exotic weeds and pests, such as the cactus, *Opuntia*, and the cotton cushion scale insect *Icerya*, which had become separated from their natural control agents by the action of man (Krebs 1972).

Organic pollution in man-made aquatic habitats can often benefit snails. For example, Ndifon (1979) found that snails, such as *B.* (*P.*) *globosus*, *B. forskali*, *M. tuberculata*, *B. pfeifferi*, *A. waterloti* and *G. costulatus* occurred more commonly in habitats that were obviously polluted by man. However, *B. rohlfsi* was an exception to this rule.

On this basis, streams devoid of refugia, particularly at their origins, would be unfavourable to snails. This is probably why *B.* (*P.*) *globosus* and *B. pfeifferi* are absent from the Orogun stream. In contrast, the Ona river, which has several small man-made lakes along its length, has large populations of the snail hosts along its entire course. The intermittent nature of this stream caused by the upstream dams may benefit the snails, as the permanent, isolated deep pools serve as ideal habitats during the dry season. Furthermore, the dams dampen the effects of flooding during the wet season.

### 8.2.2. *Lentic habitats*

The snails in these habitats are generally restricted to marginal areas in association with communities of either aquatic or subaquatic plants. As these water bodies are subjected to considerable seasonal fluctuations in volume, the snails may become stranded in the extensive draw-down zones during the dry season. The role of vegetation in providing protection for predators at this time has already been discussed in §8.1.6. The vegetation also protects the snails from the harmful effects of solar radiation and high temperature (Hira & Müller 1966) and by maintaining a high level of humidity in the microhabitat of the snails. The latter is a major factor in determining the survival rate of aestivating pulmonate snails such as *B. glabrata* (Sturrock 1970). Arfaa (1975) and Choudhry (1974) have also stressed that vegetation is an important factor in allowing survival of molluscs such as *B. abyssinicus* and *B. pfeifferi* in seasonal irrigation systems. When conditions are favourable the snail hosts of schistosomiasis may aestivate successfully for long periods of up to five to eight months for *Bulinus nasutus* and *B.* (*P.*) *globosus* (Webbe & Msangi 1958), and six to seven months for *B. senegalensis* (Smithers 1956). However, according to Brown (1980) *B.* (*P.*) *globosus*, *L. natalensis* and *B. pfeifferi* are only moderately good aestivators compared with some other species.

Snail survival is also possible in the more persistent lotic habitats, identified by the presence of aquatic macrophytes, such as *Nymphaea lotus* and *Ceratophyllum demsersum*, as well as in deep bays and inlets in lentic systems. The latter are often deepened by man to provide mooring sites for canoes.

During the wet season aestivating snails, and also those from refugia, may rapidly recolonize the marginal habitats. Immigrant snails may be carried by floating plants such as *Pistia*, *Salvinia* and *Azolla* from the refugia in the feeder streams. These floating plants like the snail population in temporary habitats, have become adapted to an 'r' strategy. In lotic habitats they tend to predominate in areas sheltered from wind because of their vulnerability to wind generated currents in more exposed habitats. Here they tend to be replaced by *Ceratophyllum* and *Nymphaea*. Although plants such as *Ceratophyllum* are well adapted to exploit such exposed sites, as they are rootless and, therefore, readily transported by water currents, they do require other emergent plants such as *Polygonum* spp. and *Nymphaea lotus* for anchorage. As these conditions are particularly unfavourable to species of submerged rooting aquatic plants, it is not surprising that they are poorly represented by comparison with water bodies in the temperate zone.

### 8.3. *Factors that might be perturbed simultaneously to achieve control in lotic systems including irrigation channels*

#### 8.3.1. *Judicious drainage and canalization combined with selective removal of key subaquatic and aquatic vegetation in outbreak areas at or near the sources of streams.*

Possible approaches are discussed by W.H.O. (1965), Pesigan *et al.* (1958*a*, *b*), Pesigan & Hairston (1961) and Hairston *et al.* (1975). According to McJunkin (1975) the costs of such operations are remarkably low. In the present system the prime objectives should be the exclusion of tall subaquatic plants, which provide shade for the snails, and their substitution by recumbent plant species such as *Paspalum notatum* after judicious drainage and canalization. Such measures should make the habitats unsuitable for *Pistia*, *Ceratophyllum*, *Salvinia*, etc., and thus make it less likely that the downstream lentic habitats would be invaded by these undesirable plants and associated snails. However, some of the measures proposed by McJunkin (1975) could well be in conflict with the need to conserve water and wetland habitats. It is clear, therefore, that in order to achieve a satisfactory compromise it would be necessary to undertake carefully designed pilot experiments, in collaboration with surface engineers, before deciding on the most cost-effective methods to be used.

### 8.3.2. *Elimination of pools and backwaters further downstream*

This could be achieved by dredging and straightening stream or river courses as far as possible, thus making them swifter and more uniform with a predominantly eroding substrate of coarse gravel and pebbles. Such conditions are unfavourable to the snail hosts and associated organisms for the reasons given.

### 8.3.3. *Replacement of ecologically undesirable subaquatic vegetation along stream margins*

Species of *Acroceras* and *Commelina* are among the most undesirable subaquatic plants from the point of view of snail control, as not only do they provide shade, but they also encroach into the water, thus providing substrates for the snails to adhere to. McJunkin (1975) suggested that the removal of waterside shrubs and trees would make conditions unfavourable for such aquatic plants. However, the implementation of this proposal would clearly meet with resistance from those concerned with land use, as it would make the banks vulnerable to erosion. One possible compromise, worthy of experimentation, would be the planting of *Paspalum notatum* along the banks, as this species was used successfully by Thomas & Compston (1980) to stabilize margins of a man-made lake in the Lagos area. The reasons for its success were as follows: first, it is able to grow well, even on a nutrient-poor soil, because it possesses nitrogen-fixing symbionts in its roots. Secondly, individual plants are able to colonize new ground rapidly by producing new rhizomes. Thirdly, its recumbent form allows it to cover most of the ground surface and smother competitors such as *Acroceras* and *Commelina*. It would be a much better alternative than the latter plants as it is less prone to encroach into the water and its recumbent growth form would provide little or no shade. The removal of waterside trees could be counter-productive for the following reasons. First, the dense canopy could have an adverse effect on *Acroceras* and *Commelina* by impeding light. Secondly, the decomposition of allochthonous leaves in the water could result in low oxygen and high ammonia concentrations that might help to exclude the snail hosts.

### 8.3.4. *Introduction of M. tuberculata, if absent*

The above manipulations should create conditions that would favour *Melanoides* for these reasons.

(i) Their hemistreamlined form is better adapted to running water than that of pulmonate snails, particularly planorbids. According to Appleton (1978) they can tolerate currents of at least 30 cm $s^{-1}$. As a result they may be found in rivers like the Awash, which is inhospitable for most other molluscs owing to its eroding substrates and irregular flow (Kloos & Lemma 1974).

(ii) They feed on fine, particulate, organic drift that becomes trapped in the gravel.

(iii) Their crepuscular and nocturnal feeding habits protect them from predators or harmful radiation during the day (Beeston & Morgan 1979).

(iv) As they are parthenogenetic and viviparous, the young are better able to withstand currents than the neonates of pulmonate snails.

According to Lévêque (1967) *M. tuberculata* has a very high biotic potential and in some regions of Lake Chad the production rate was 141 g $m^{-2}$ $a^{-1}$. Thus when conditions are favourable, as they already are in some stretches of the Ona river, their population density can become very high (up to 9804 $m^{-2}$). As there is very little space available for other species it is likely that they would exclude the snail hosts.

There is circumstantial evidence that other species of prosobranch snails may exclude pulmonate snails from eroding type substrates. For example, Lévêque (1967) and Brown (1974) observed that when prosobranchs such as *Bellamya unicolor* and *Cleopatra bulimoides* were present in very large numbers in Lake Chad, pulmonate snails were rarely encountered. *Potamopyrgus jenkinsi* (Smith) also seems to be a successful competitor in stream habitats. Thus Léger & Léger (1974) found that after this species had invaded lotic habitats in Corsica in 1961, pulmonate snails, especially *B. truncatus*, became much less common. *Pyrgophorus parvalus* is a prominent member of the riffle community in St Lucia (McKillop & Harrison 1980) and it is possible that the engineering manipulations described above could be used to aid exclusion of *B. glabrata* from this island.

There are, however, two reasons why these proposals should be treated with some caution. Firstly, *M. tuberculata* is a suspected, but not proven, host of *Paragonimus westermani*, the human lung fluke (Brown 1980). Secondly, the altered environmental conditions might be favourable for *Simulium damnosum*, the vector of *Onchocerca volvulus*. However, it is probable that very high densities of *M. tuberculata* would also exclude *Simulium*. Of course, these questions can only be resolved by experimentation.

### 8.4. *Factors that could be perturbed simultaneously to control the snail hosts in lentic habitats*

#### 8.4.1. *Removal or control of subaquatic and aquatic vegetation*

The close relationship between snails and aquatic macrophytes has been demonstrated previously.

The possible strategies for control or regulation of plants that are prerequisites for control of the snails are discussed below.

(*a*) *Control of subaquatic vegetation in the draw-down area and along water margins.* This may be achieved either by mechanical cutting or by using grazing animals as advocated by Little (1975). Thomas (1966) and Thomas & Ratcliffe (1973) have described how farm animals and seed ants proved effective in controlling the growth of subaquatic vegetation in the draw-down areas of Nungua Lake in Ghana. According to Gillet *et al.* (1960) this strategy caused a decline in snail populations along the shore of Lake Kivu. There are two major reasons why this manipulation could be harmful to pulmonate snails. First, it deprives them of shelter from inimical forces and of food resources such as detritus and epiphytic algae. The consequent lack of shelter for aestivating snails during the dry season could be particularly crucial. Secondly, removal of emergent subaquatic plants makes floating plants, such as *Pistia*, *Salvinia* and *Lemna* species, which are also important to the snails, very vulnerable to beaching by wind action.

(*b*) *Control of floating plants by preventing immigration from feeder streams.* Attempts have been made to prevent floating plants entering Oba reservoir by constructing strong metal grids to act as filters across the stream. However, this method proved relatively ineffective as both debris and floating plants brought down by floods tend to block the system and hence bypass it.

When feasible, a better method is to exclude streams and to maintain a constant water level by ground-water flow (Thomas & Compston 1980).

In the present study area the best approach would be to use the methods already advocated by Thomas & Compston (1980) for lotic habitats.

(*c*) *Control of floating plants by wind-generated currents.* The wind, although relatively weak in the tropics, can generate effective surface currents, mainly directed towards the NE or E by the prevailing winds. The wind energy can be maximized by (i) constructing lakes with their longitudinal axes in the same direction as the prevailing wind; (ii) avoiding indentations such as bays or inlets, which serve as refugia, and trees or shrubs which obstruct wind; (iii) stabilizing soil along the shoreline and in the catchment area to prevent sheet or gully erosion and the development of small inlets; (iv) the slope in the boundary zone between land and water should be gentle (for example, 1 in 20) to allow the wind generated current to beach-floating and non-floating plants, such as *Ceratophyllum* and *Utricularia*; (v) the foreshore should be kept clear of emergent subaquatic plants; (vi) facilities for lowering the water level should also be provided if possible. Lanoix (1958); McMullen (1962, 1963); Jobin (1970*a*); Jobin & Michelson (1969) and Lantz *et al.* (1967) have reported successful vegetation control by using a draw-down.

(*d*) *Control of floating plants by removal of rooting aquatic plants, such as Nymphaea lotus*. This can be achieved by mechanical or biological means. These plants are more difficult to remove mechanically when they occur in the deep water. Control by reduction in water volume or chemical control is not always feasible, as man-made lakes are used as sources of potable water. However, mechanical cutting using the 'Water Warrior' (John Wilder Engineering, Wallingford, Oxford, U.K.) has been partially successful against *Nymphaea* in I.I.T.A. lake.

Possible agents for the biological control of aquatic plants include herbivorous fish, such as *Tilapia mossambica* P., *Tilapia melanopleura* Dumeril, *Tilapia nilotica* L., the grass carp, *Ctenopharyngodon idella*, the common carp *Cyprinus carpio* L., the goramy *Osphronemus gorami* Lae and the towe *Puntius javonicus* B (Bennett 1971; 1974; Stott 1974). Whenever possible indigenous fish, adapted for existence in these water bodies, should be given preference. One of these, *Tilapia zilli* var. *guineensis*, is a particularly good choice, as although it feeds readily on several species of macrophytes, it can also survive on alternative food, such as planktonic organisms and insect larvae when there is a dearth of macrophytes. Other fish species that might be considered are *Alestes macrolepidotus* C & V, *Alestes dentex* L., *Alestes nurse Rüppell*, and *Distichodus rostratus*, Günther, as they feed on aquatic plants including subaquatic Graminae (Imevbore & Bakare 1970).

Invertebrate herbivores that might be used include snails such as *Pila africana* (Martens), *Marisa cornuarietis* L. and *Pomacea caniculata* Lamer (Bennett 1974). The effectiveness of *Marisa* as a herbivore may help to explain its apparent success in excluding *B. glabrata* from certain lakes in Puerto Rico (McMullen 1973).

Other invertebrate species that might be used as control agents are the chrysomelid beetle, *Galerucella nymphaea* L., which feeds on the waterlily; the chrysomelid beetle, *Agascicles hygrophila* (Selman and Vogt), which feeds on *Alternanthera*; and the acridid grasshopper, *Paulinia acuminata* De Geer; the weevil, *Cyrtobagous singularis* Hulst; and the moth *Samea multiplicalis* Guenee, which feed on *Salvinia* species (Bennett 1974). It has been suggested that an aphid transmitted virus is an important factor in contributing to the annual die back of *Pistia stratiotes* in Nigeria (Pettet & Pettet 1970). The possibility of using this pathogen and others for the control of aquatic weeds deserves serious consideration. Another possible agent is a leaf burrowing chironomid which attacks *Nymphaea lotus*.

In addition to fish, other potential vertebrate control agents are domestic or wild duck, coots, the coypu (*Myocaster coypus* Molina) and the manatees (*Trichechus* sp.) (Holm *et al.* 1968; Bennett, 1971, 1974; Little 1975). Introduction of the coypu or manatee to control the weeds in the lake in the study area must be ruled out, for the reasons given by Bennett (1974). Conservation of birds such as the white-faced duck *Dendrocygna viduata* (L), the spur-winged goose *Plectropterus gambiensis gambiensis* L., several species of waders and gallinules already frequenting the area should be encouraged, and their impact on aquatic macrophytes and the snail hosts studied.

Possible methods for harvesting and using the aquatic macrophytes as a resource should be explored. Such plants could be used as a source of food for man or domestic animals. Alternatively they could be broken down into compost or for mulching.

### 8.4.2. *Control by introduction of competitor species*

The present results indicate that neither *L. libycus* nor *A. waterloti* could compete against the snail hosts of schistosomiasis in a lentic habitat. However, the possibility that *M. tuberculata* might succeed, in the absence of macrophytic vegetation, is worth exploring. Two other species that have been introduced into Africa, namely *Marisa cornuarietis* and *Helisoma duryi* appear to have many of the attributes needed for successful snail control. The following experimental observations indicate that *Marisa* has considerable potential. (i) It has a much broader niche than *B. glabrata* both in terms of food items and physicochemical parameters. (ii) Its functional response to varying food densities overlaps that of *B. glabrata*. (iii) The replacement series experiments based on the de Wit model indicate that it is a better competitor than *B. glabrata* (Léon 1975). (iv) It is an efficient predator on the eggs and juveniles of *B. glabrata* (Demian & Lufty 1965, 1966; Léon 1975). There is also good experimental evidence from laboratory studies that *Helisoma duryi* resembles *Marisa* in all these respects (Tait 1982; Frandsen & Madsen 1979). Results of field trials for both *Marisa* (Jobin 1970*b*; Jobin & Berrios-Duran 1970; Jobin *et al.* 1973; Demian & Kamel 1973) and *Helisoma* (Abdallah & Nasr 1973; Ayad *et al.* 1973; Rasmussen 1974) have also been encouraging. However, more extensive, statistically viable and rigorously controlled experiments are necessary under field conditions before any final conclusion can be drawn.

There are, unfortunately, potential problems in using these species. (i) There is some evidence that *Marisa* may damage plants such as rice grown under irrigation (Ferguson 1977). Studies on the environmental impact of this species are, therefore, needed before introduction, as recommended by McCullough (1981). (ii) The niches of *Marisa* and *Helisoma* may not completely overlap those of the snail hosts. There is evidence, for example, that small floating plants such as *Lemna* and shallow water may serve as food or space refugia for *Biomphalaria* when in competition with *Marisa* (Oliver-Gonzalez *et al.* 1956; Léon 1975). As a result the two species might be able to coexist. (iii) *Marisa* and *Helisoma* may not be well adapted to survive in African or South American water bodies. This possibility is indicated by the difficulties encountered in the attempts to establish *Helisoma* in semi-artificial bodies in South Africa (Brown 1980). (iv) There might be technical difficulties in evaluating their impact on the snail hosts. For example, Prentice *et al.* (1977) found that there were considerable problems in distinguishing *Helisoma* from *Biomphalaria* under field conditions. (v) These exotic species might serve as hosts for parasites of man or domestic animals. However, this is considered not to be a serious problem (Brown 1980).

### 8.4.3. *Control by introduction of predators, parasites and pathogens*

There is strong circumstantial evidence that species of aquatic birds may be vital in controlling populations of snails in draw-down areas of African lakes (Thomas 1966; Thomas & Ratcliffe 1973). The various species of waders and other birds that feed actively in these areas are listed by Thomas (1966). Further research is needed to quantify their impact on the snail hosts and to ascertain which measures could be taken to increase their effectiveness.

Various fish species, including several predominantly piscivorous cichlid species, have been advocated as agents for biological control (Greenwood 1974), and there is empirical evidence that *Haplochromis mellandi* Blgr and *Astatoreochromis alluandi* have caused significant reductions in the populations of the snail hosts (De Bont 1956; Mvogo & Bard 1964). Other West African fish species with molluscivorous habits are also worthy of consideration. They include *Hemichromis fasciatus* Peters, *Hemichromis bimaculatus* Gill, *Chana obscura* Günther, *Calamichthis calabaricus* J. A. Smith, and members of the family Claridae.

A large number of aquatic invertebrates are known to prey on pulmonate snails. They include ostracods, crustacea and insects such as sciomyzid flies and the hemipteran *Limnogeton* spp. (Michelson 1957; Malek 1962; Chernin *et al.* 1960; Michelson 1961 *a*, 1963; Berg 1964; Jordan & Webbe 1969; Brown 1980). However, as yet, none of these has been shown to be effective in regulating snails under natural conditions.

Larval stages of trematode parasites are known to sterilize and kill snails (Berrie 1970). Theoretically, control of snail populations could be achieved by introducing a long-living definitive host–parasite combination into the aquatic ecosystem, provided the larval parasite could castrate or kill the snails. Larval trematodes have many of the attributes of successful biological control agents, because in addition to causing mortality and decreased fecundity in snail populations, they have high reproductive and host searching capabilities. The results of experiments aimed at controlling a schistosome species with echinostome larvae, suggest that any success achieved may have been mainly owing to parasite induced snail mortality (Lie *et al.* 1971; Lim & Heynemann 1972). A very interesting model is also provided by the work of Nassi *et al.* (1979) on *Ribeiroia marini guadeloupensis* Nassi, a parasite that castrates *B. glabrata*, the snail host of *S. masoni* in Guadeloupe. They found that the introduction of eight million eggs of this parasite into a pond, during the course of a field trial, was followed by the virtual disappearance of *B. glabrata*. A search among the helminth fauna of fish, amphibia, reptiles or birds in Africa may yield suitable candidates for this approach. Bacteria, microsporidia and other pathogens are also potential agents for snail control (Hairston *et al.* 1975; Canning 1975). The possibility of using non-host competitor snail species as carriers for organisms such as microsporidia requires consideration.

As with lotic habitats, successful control in lentic systems is more likely to be achieved by adopting a holistic approach, and manipulating certain of the key factors described above at the same time. Perhaps the simplest model to aim for is a lentic habitat in which the phytoplankton are the sole primary producers in the water column. In the diagrammatic representation of such a system (figure 11 *a*) the plankton could be used by species of *Tilapia*, which could serve as a valuable food source for the human population. In such relatively simple ecosystems the organic material tends to break down with release of nutrient ions in the upper zone of the water column, and as a result only relatively small amounts enter the sediment as detritus (Thomas 1966; Thomas & Ratcliffe 1973). The pulmonate snail hosts could be denied access to even this meagre resource by the introduction of efficient detritivores, such as prosobranch species (for example, *M. tuberculata*, *Cleopatra bulimoides* and *Bellamya unicolor*), bivalves (for example, *Aspatharia* (*S.*) *adansoni*, see Brown (1980), or fish species (for example, *Labeo coubie* or *Tilapia galilea*). The two latter species are efficient bottom-deposit feeders (Imevbore & Okpo 1975). Alternatively more generalized feeders such as *Citharinus citharus* G. St Hilaire, or species of *Clarias* could be used. According to Bakare (1970) and Imevbore & Bakare (1970) *Citharinus citharus* is an efficient bottom-deposit feeder, although it can also switch to feeding on plankton. It might be particularly advantageous to introduce species of *Clarias*

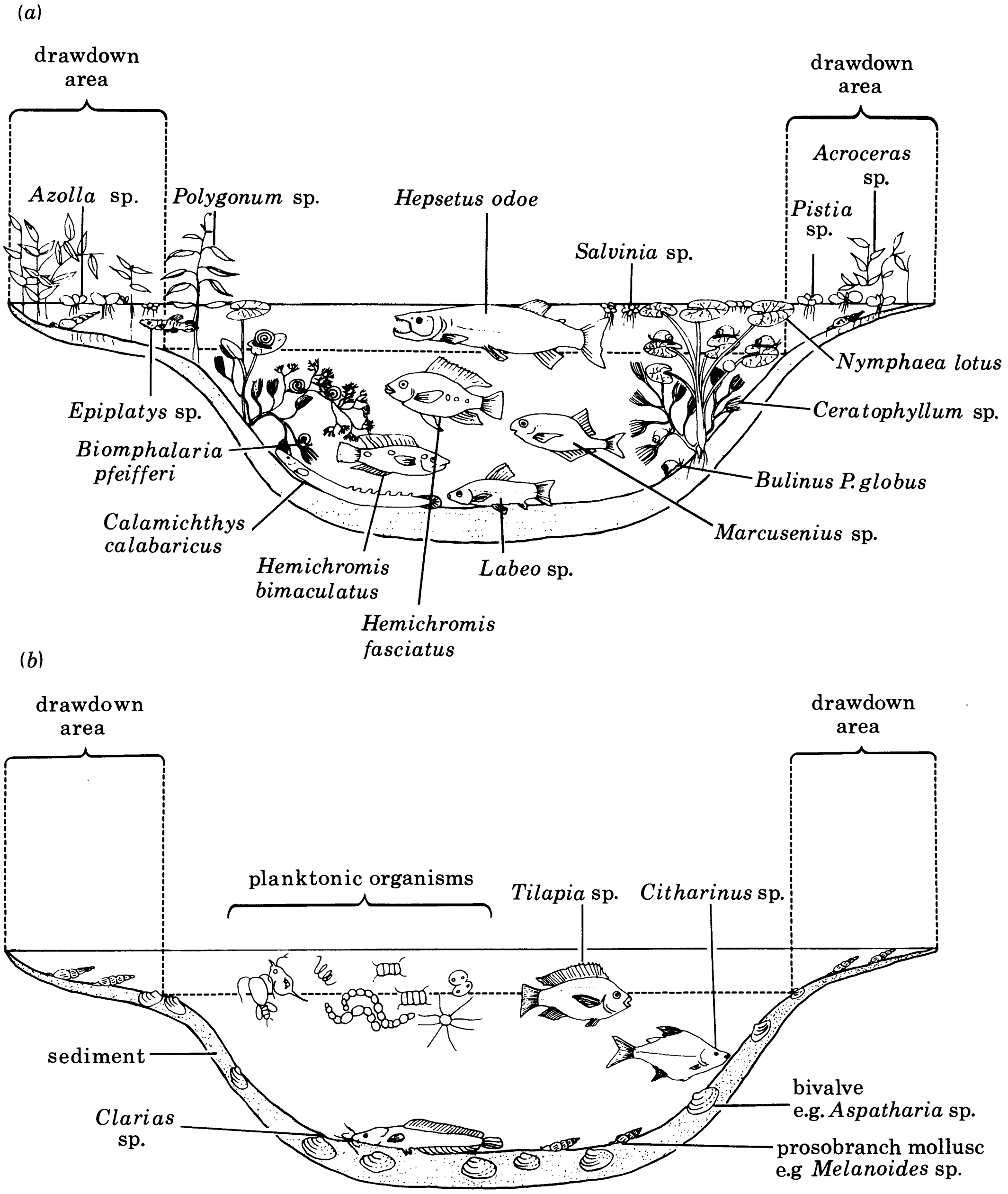

FIGURE 11. (*a*) Diagrammatic representation of lentic ecosystems in which solar energy is fixed by phytoplankton and epiphitic algae in Africa with dense growth of macrophytes. (*b*) The type of lentic habitat normally encountered.

as they are capable of playing a predatory as well as competitive role by feeding on bottom-deposits (Thomas 1966). In the more complex natural ecosystems, diagrammatically represented in figure 11*b*, the conditions are clearly more favourable to the host snails and also to mosquito vectors of water-related disease organisms. This model (figure 11*a*) and related ones would require testing under field conditions. Some encouragement for this idea is provided by the observation that the plankton–*Tilapia*–*Clarias* system in the fishpond (station P) was devoid of snail hosts. This was also the case in a similar, though more ion poor, lentic system in Ghana described by Thomas & Ratcliffe (1973).

It is encouraging that the kind of integrated approaches advocated here have resulted in the control of water related diseases, such as malaria and schistosomiasis in other parts of the world. Successful examples of integrated schistosomiasis control are described by Hairston *et al.* (1975) and Hairston & Santos (1961) and include projects in East Transvaal, Crocodile Valley, St Lucia, Puerto Rico, China and Leyte in the Philippines. According to Pesigan & Hairston (1961), Hairston & Santos (1961) and Hairston *et al.* (1975) it is only in the latter case that non-chemical methods of snail control have been assessed in a suitably scientific manner.

To increase the probability of successful control of schistosomiasis, the measures directed against the snails should be combined with chemotherapy, aimed at reducing the longevity of the adult parasites, as well as other preventive measures, to reduce contact with infested water and contamination of water resources. In the more developed countries, integrated bioengineering approaches were applied as preventive measures against water-related diseases as soon as the basic biological principles were understood, and long before the advent of modern chemicals. According to Hackett (1937) the eradication of malaria in many European countries can be attributed largely to habitat alteration and the use of chemicals merely supplied the *coup de grâce*.

There are many other additional benefits to this type of approach. The measures advocated could, first, be followed by reductions in other water-related diseases, such as malaria, filariasis, fascioliasis, dracontiasis, bacillary dysentry and cholera, and secondly, in increased yields of much-needed edible protein.

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## REFERENCES

Abdallah, A. & Nasr, T. 1973 *Helisoma duryi* as a means of biological control of schistosomiasis vector snails. *J. Egyptian med. Ass.* **56**, 514–520.

Alston, A. H. G. 1959 *The ferns and fern-allies of West Tropical Africa.* Millbank, London: Crown Agents.

Appleton, C. C. 1975 The influence of stream geology on the distribution of the bilharzia host snails, *Biomphalaria pfeifferi* and *Bulinus* (*Physopsis*) sp. *Annls trop. Med. Parasit.* **69**, 241–255.

Appleton, C. C. 1976 The influence of abiotic factors on the distribution of *B. pfeifferi* (Krauss, 1848) (Planorbidae: Mollusca) and its life in south-eastern Africa. M.Sc. thesis, Rhodes University.

Appleton, C. C. 1978 Review of literature on abiotic factors influencing the distribution and life cycle of bilharziasis intermediate host snails. *Malacol. Rev.* **11**, 1–25.

Appleton, C. C. & Stiles, G. 1976 Geology and geomorphology in relation to the distribution of the snail intermediate hosts of bilharzia in South Africa. *Annls trop. Med. Parasit.* **70**, 189–198.

Arfaa, F. 1975 Studies on schistosomiasis in Somalia. *Am. J. trop. Med. Hyg.* **24**, 280–283.

Asumu, D. I. 1975 Studies on the biology of snails and their larval trematodes in Ibadan freshwater systems. Ph.D. thesis, University of Ibadan.

Ayad, N. 1956 Bilharziasis survey in British Somaliland, Eritrea, Ethiopia, Somalia, the Sudan and Yemen. *Bull Wld Hlth Org.* **14**, 1–117.

Ayad, N., Mousa, A. H. & Ishak, M. M. 1973 A preliminary study on biological control of the snail intermedate hosts of schistosomiasis in U.A.R. by *Helisoma duryi* snails. *Hydrobiologia* **35**, 196–202.

Bailey, N. T. J. 1980 *Statistical methods in biology.* London: Hodder & Stoughton.

Bakare, O. 1970 Bottom deposits as food of inland freshwater fish. In *Kainji, a Nigerian man-made lake. Kainji Lake studies*, vol. 1 (ed. S. A. Visser), pp. 65–85. Ibadan University Press.

Ball, I. R. 1967 The relative susceptibilities of some species of freshwater fish to poisons. 1. Ammonia. *Wat. Res.* **1**, 767–775.

Beauchamp, R. S. A. 1953 Sulphates in African inland waters. *Nature, Lond.* **171**, 769–771.

Beeston, D. & Morgan, E. 1979 A crepuscular rhythm of locomotor activity in the freshwater prosobranch, *Melanoides tuberculata* (Müller). *Anim. Behav.* **27**, 284–291.

Bennett, F. D. 1974 Biological control. In *Aquatic vegetation and its use and control*, pp. 99–106. Paris: U.N.E.S.C.O.

Bennett, G. W. 1971 *Management of lakes and ponds.* New York, London: V.N.R.

Berg, C. O. 1964 Snail control of trematode diseases: the possible value of scyomyzid larvae, snail killing diptera. In *Advances in parasitology*, vol. 2 (ed. Ben Dawes), pp. 259–309. London: Academic Press.

Berrie, A. D. 1964 Observations on the life cycle of *Bulinus* (*Physopsis*) *ugandae* Mandahl-Barth, its ecological relation to *Biomphalaria sudanica tanganyiensis* Smith and its role as an intermediate host of *Schistosoma. Annls trop. Med. Parasit.* **58**, 457–466.

Berrie, A. D. 1970 Snail problems in African schistosomiasis. In *Advances in parasitology*, vol. 8 (ed. Ben Dawes), pp. 43–91. London and New York: Academic Press.

Blacklock, D. B. & Thompson, M. G. 1924 Human schistosomiasis due to *Schistosoma haematobium* in Sierra Leone. *Annls trop. Med. Parasit.* **18**, 211–233.

Boettger, C. R. 1944 Basommatophora. In *Die Tierwelt der Nord und Ostsee*, vol. 35 (ed. G. Grimpe & G. Wagler), pp. 241–478. Leipzig: Akademische Verlagsgesellschaft.

Borght, O. Van der & Van Puymbroeck, S. 1966 Calcium metabolism in freshwater molluscs: quantitative importance of water and food supply for calcium during growth. *Nature, Lond.* **210**, 791–793.

Bousfield, J. D. 1978 Rheotaxis and chemoreception in the freshwater snail *Biomphalaria glabrata* (Say): Estimation of the molecular weights of active factors. *Biol. Bull.* **154**, 361–373.

Boycott, A. E. 1936 The habitats of freshwater molluscs in Britain. *J. Anim. Ecol.* **5**, 116–186.

Brown, D. S. 1974 A survey of the Mollusca of Lake Chad, Central Africa. Appendix A. *Rev. Zool. afr.* **88**, 331–343.

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

Calow, P. 1973 Field observations and laboratory experiments on the general food requirements of two species of freshwater snail, *Planorbis contortus* (Linn.) and *Ancylus fluviatilis* Müll. *Proc. malac. Soc. Lond.* **40**, 483–489.

Calow, P. 1974 Evidence for bacterial feeding in *Planorbis contortus* Linn. (Gastropoda: Pulmonata). *Proc. malac. Soc. Lond.* **41**, 145–156.

Canning, E. V. 1975 The microsporidian parasites of platyhelminthes; their morphology, development, transmission and pathogenicity. Commonwealth Institute of Helminthology miscellaneous publications, no. 2.

Chernin, E. 1967 Behaviour of *Biomphalaria glabrata* and of other snails in a thermal gradient. *J. Parasit.* **53**, 1233–1240.

Chernin, E., Michelson, E. H. & Augustine, D. L. 1960 Studies on the biological control of schistosome bearing snails. *Am. J. trop. Med. Hyg.* **64**, 297–314.

Choudhry, A. W. 1974 Seven year control of Mwea irrigation settlement, Kenya: results and costs. *E. Afr. med. J.* **51**, 600–609.

Chu, K. Y., Massoud, J. & Arfaa, F. 1968 Distribution and ecology of *Bulinus truncatus* in Khuzestan, Iran. *Bull. Wrld Hlth Org.* **39**, 609–639.

Chu, K. Y. & Vanderberg, J. A. 1976 Techniques for estimating densities of *Bulinus truncatus rohlfsi* and its horizontal distribution in Volta Lake, Ghana. *Bull. Wrld Hlth Org.* **54**, 411–416.

Combrinck, C. & van Eeden, J. A. 1969 The influence of substratum on population increase and habitat selection by *Lymnaea natalensis* Krs and *Bulinus* (*B.*) *tropicus* (Mollusca, Basommatophora) *Malacologia* **9**, 39.

Cowper, S. G. 1959 Notes on the snail vectors of *Schistosoma haemotobium* in the Ibadan Area of Nigeria: with some observations on the pathology of the liver and spleen of mice experimentally infected with *S. haematobium* and *S. mansoni. W. Afr. med. J.* **8**, 191–196.

Cowper, S. G. 1963 Schistosomiasis in Nigeria. *Annls trop. Med. Parasit.* **57**, 307–322.

Dazo, B. C., Hairston, N. G. & Dawood, I. K. 1966 The ecology of *Bulinus truncatus* and *Biomphalaria alexandrina* and its implication for the control of bilharziasis in the Egypt 49 project area. *Bull. Wrld Hlth Org.* **35**, 339–356.

De Bont, A. F. 1956 Biological control of freshwater molluscs and of the diseases transmitted by them. *Annls Soc. belge Med. trop.* **34**, 667–670.

Demian, E. S. & Kamel, E. G. 1973 Effects of *Marisa cornuarietis* on *Bulinus truncatus* populations under semi-field conditions in Egypt. *Malacologia* **14**, 439.

Demian, E. S. & Lufty, R. G. 1965 Predatory activity of *Marisa cornuarietis* against *Bulinus* (*Bulinus*) *truncatus*, the transmitter of urinary schistosomiasis. *Annls trop. Med. Parasit.* **59**, 331–336.

Demian, E. S. & Lufty, R. G. 1966 Factors affecting the predation of *Marisa cornuarietis* on *Bulinus* (*B.*) *truncatus*, *Biomphalaria alexandrina* and *Lymnaea caillaudi*. *Oikos* **17**, 212–230.

Dowdeswell, R. M. 1938 Schistosomiasis in the Kavirondo district of Kenya. *Trans. R. Soc. trop. Med. Hyg.* **31**, 673–688.

Duke, B. O. & Moore, P. J. 1976*a–c* The use of molluscicide in conjunction with chemotherapy to control *Schistosoma haematobium* at the Barombi Lake foci in Cameroon, parts 1–3. *Z. tropenmed. Parasit.* **27**, 297–313; 489–508.

Eisenberg, R. M. 1966 The regulation of density in a natural population of the pond snail, *Lymnaea elodes*. *Ecology* **47**, 889–906.

Eisenberg, R. M. 1970 The role of food in the regulation of the pond snail *Lymnaea elodes*. *Ecology*, **51**, 680–684.

El-Hassan, A. A. A. 1974 *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. Congress Parasit. München*, **3**, 1597–1598.

Ferguson, F. F. 1977 The role of biological agents in the control of schistosome bearing snails. Atlanta, Georgia: U.S. Department of Health, Education and Welfare.

Ferguson, F. F., Palmer, J. R. & Jobin, W. R. 1968 Control of schiotosomiasis on Vieques Island, Puerto Rico. *Am. J. trop. Med. Hyg.* **17**, 858–863.

Frandsen, F. & Madsen, H. 1979 A review of *Helisoma duryi* in biological control. *Acta Trop.* **36**, 67–84.

Frank, G. H. 1964 The ecology of the intermediate hosts of bilharzia. In *Ecological studies in southern Africa* (ed. D. H. S. Davis), pp. 353–362. The Hague: W. Junk.

Freitas de, J. R. 1976 Ecologia de vetores de doensas, o habitat primitivo da *Biomphalaria glabrata*. *Cienc. Cult.* **28**, 212–217.

Gazzinelli, G., Ramalho-Pinto, F. J. Pellegrino, J. & Gilbert, B. 1970 Uptake of $Fe^{59}$ as a tool for study of the crowding effect in *Biomphalaria glabrata*. *Am. J. trop. Med. Hyg.* **19**, 1034–1037.

Gerber, J. H. 1952 Bilharzia in Boojibu, part 1. *J. trop. Med. Hyg.* **55**, 52–58.

Gillet, J., Bruaux, P. & Wolfs, J. 1960 Results of malacological explorations in the depths of Lake Kivu and investigations on the survival of *Biomphalaria* in deep water. *Annls Soc. belge Med. trop.* **40**, 643–649.

Gordon, R. M., Davey, T. N. & Peaston, H. 1934 Transmission of human schistosomiasis in Sierra Leone with an account of the schistosomes concerned, *Schistosoma mansoni* and *Schistosoma haematobium*. *Annls trop. Med. Hyg.* **28**, 323–419.

Greenwood, P. H. 1974 *Cichlid fishes of Lake Victoria, East Africa: the biology and evolution of a species flock*. London: British Museum (Natural History).

Hackett, L. N. 1937 *Malaria in Europe*. Oxford University Press.

Hairston, N. G. & Santos, B. C. 1961 Ecological control of the snail host of *Schistosoma japonicum* in the Philippines. *Bull. Wrld Hlth Org.* **25**, 603–610.

Hairston, N. G., Wurzinger, K. H. & Burch, J. B. 1975 Non-chemical methods of snail control. World Health Organization.

Harrison, A. D., Nduku, W. & Hooper, A. S. C. 1966 The effects of a higher magnesium to calcium ratio on the egg-laying rate of the aquatic planorbid snail, *Biomphalaria pfeifferi*. *Annls trop. Med. Parasit.* **60**, 212–214.

Harrison, A. D. & Shiff, C. J. 1966 Factors influencing the distribution of some species of aquatic snails. *S. Afr. J. Sci.* **62**, 253–258.

Harrison, A. D., Williams, N. V. & Greig, G. 1970 Studies on the effects of calcium bicarbonate concentrations on the biology of *Biomphalaria pfeifferi* (Krauss) (Gastropoda: Pulmonata). *Hydrobiologia* **36**, 317–327.

Hira, P. R. 1966 Studies on the ecology of intermediate snail hosts of *Schistosoma haematobium* in Ibadan, Western Nigeria and some aspects of the biology of the parasite. Ph.D. Thesis, University of Ibadan.

Hira, P. R. 1968 Larval trematodes from *Bulinus* (*Bulinus*) *forskalii*, Ehrenberg in Ibadan, Nigeria. *Niger. J. Sci.* **2**, 121–130.

Hira, P. R. 1969 The temperature, pH and oxygen content of water harbouring the intermediate snail host of *Schistosoma haematobium*. *Niger. J. Sci.* **3**, 131–138.

Hira, P. R. 1970 Aspects of the spread and control of schistomiasis in Ibadan, Nigeria. *W. Afr. med. J.* **19**, 180–183.

Hira, P. R. & Müller, R. 1966 Studies on the ecology of snails transmitting urinary schistosomiasis in Western Nigeria. *Annls trop. Med. Parasit.* **60**, 198–211.

Hoffman, D. B. 1979 *Schistosomiasis research: The strategic plan*. New York: Edna McConnell Clark Foundation.

Holm, L. G., Weldon, L. W. & Blackburn, R. D. 1968 Aquatic weeds. *Science, N.Y.* **166**, 699–709.

Hunter, W. R. 1961 Annual variations in growth and density in natural populations of freshwater snails in the west of Scotland. *Proc. Zool. Soc. Lond.* **136**, 219–259.

Hutchinson, J. & Dalziel, J. M. 1954–72 *Flora of West Tropical Africa*, vols 1–3. Millbank, London: Crown Agents.

Iloeje, N. P. 1976 *A new geography of Nigeria*. Ikeja: Longmans Nigera Ltd.

Imevbore, A. M. A. & Bakare, O. 1970 The food and feeding habits of non-cichlid fishes of the river Niger in the Kainji reservoir area. In *Kainji, a Nigerian man-made lake*, vol. 1, *Ecology* (ed. S. A. Visser). Ibadan University Press.

Imevbore, A. M. A. & Okpo, W. S. 1975 Aspects of the biology of Kainji Lake fishes. In *The ecology of Lake Kainji* (ed. A. M. A. Imevbore & O. S. Adegoke), pp. 163–178. Ife, Nigeria: University of Ife Press.

Jenkins, S. H. 1979 Engineering, science and medicine in the prevention of tropical water-related diseases. In *Progress in water technology*. **11** vii + 490 pp. Oxford: Pergamon Press.

Jobin, W. R. 1970*a* Control of *Biomphalaria* in a small reservoir by fluctuation of the water level. *Am. J. trop. Med. Hyg.* **19**, 1049–1054.

Jobin, W. R. 1970*b* Population dynamics of aquatic snails in three farm ponds of Puerto Rico. *Am. J. trop. Med. Hyg.* **19**, 1038–1040.

Jobin, W. R. & Berrios-Duran, L. A. 1970 Cost of harvesting and spreading *Marisa cornuarietis* for biological control of *Biomphalaria glabrata* in Aibonito, Puerto Rico. *Bull. Wrld Hlth Org.* **42**, 177–179.

Jobin, W. R., Ferguson, F. F. & Berrios-Duran, L. A. 1973 Effect of *Marisa cornuarietis* on populations of *Biomphalaria glabrata* in farm ponds in Puerto Rico. *Am. J. trop. Med. Hyg.* **22**, 278–284.

Jobin, W. R., Ferguson, F. & Palmer, J. R. 1970 Control of schistosomiasis in Guayama and Arroyo, Puerto Rico. *Bull. Wrld Hlth Org.* **42**, 151–156.

Jobin, W. R. & Michelson, E. H. 1969 Operation of irrigation reservoirs for snail control. *Am. J. trop. Med. Hyg.* **18**, 297–304.

Jordan, P. 1972 Epidemiology and the control of schistosomiasis. *Br. med. Bull.* **28**, 55–59.

Jordan, P. & Webbe, G. 1969 *Human schistosomiasis*. London: Heinemann Medical Books.

Joy, J. E. 1971 The influence of day length upon egg laying of *Biomphalaria glabrata*. *Annls trop. Med. Parasit.* **65**, 573–578.

Kloos, H. & Lemma, A. 1974 Bilharziasis in the Awash valley 2. Molluscan fauna in irrigation farms and agricultural development. *Ethiopian med. J.* **12**, 157–173.

Klumpp, R. K. & Chu, K. Y. 1977 Ecological studies of *Bulinus rohlfsi*, the intermediate host of *Schistosoma haematobium* in the Volta Lake. *Bull. Wrld Hlth Org.* **55**, 715–730.

Krebs, C. J. 1972 *Ecology: the experimental analysis of distribution and abundance*. New York: Harper and Row.

Lanoix, J. N. 1958 Relation between irrigation engineering and bilharziasis. *Bull. Wrld Hlth Org.* **18**, 1101–1135.

Lantz, K. E., Davies, J. T., Hughes, J. S. & Schafer, H. E. Jr. 1967 Water level fluctuations: Its effects on vegetation control and fish population management. *Proceedings of the 18th Annual Conference, South East Association of Game and Fish.*

Léger, N. & Léger, P. 1974 L'extension de *Potamopyrgus jenkins* (Smith, 1889) *Annsl Parasit. hum. comp.* **49**, 343–347.

Leon, A. C. 1975 Interactions between *Biomphalaria glabrata* and *Marisa cornuarietis*. Ph.D. thesis, University of Sussex.

Lévêque, C. 1967 Mollusques aquatiques de la zone est du lac Tchad. *Bull. Inst. Français Afr. noire* **29**, 1494–1533.

Lie, K. J., Kwo, E. H. & Owyang, C. K. 1971 Further field trials to control *Schistosoma spindale* by trematode antagonism. *S. E. Asian J. trop. Med. Pub. Hlth* **2**, 237–243.

Lim, H. K. & Heynemann, D. 1972 Intramolluscan intertrematode antagonism. A review of factors influencing the host parasite system and its possible role in biological control. In *Advances in parasitology*, vol. 10 (ed. Ben Dawes), pp. 191–268. London, New York: Academic Press.

Little, E. C. S. 1975 Aquatic plants. In *Man-made lakes and human health* (ed. N. F. Stanley and M. P. Alpers), pp. 293–300. London: Academic Press.

Macan, T. T. 1950 Ecology of freshwater mollusca in the English Lake District. *J. Anim. Ecol.* **19**, 124–146.

Madsen, H. 1982 Development of egg masses and growth of newly hatched snails of some species of intermediate hosts of schistosomiasis in water conditioned by *Helisoma duryi* (Wetherby) (Pulmonata: Planorbidae) *Malacologia* **22**, 427–434.

Madsen, H. & Frandsen, F. 1979 Studies on the interspecies competition between *Helisoma duryi* (Wetherby) and *Biomphalaria camerunensis* (Boettger): size and weight relationships and laboratory competition experiments. *Hydrobiologia* **66**, 17–23.

Malek, E. A. 1958 Factors conditioning the habitats of bilharziasis intermediate hosts of the family Planorbidae. *Bull. Wrld Hlth Org.* **18**, 785–818.

Malek, E. A. 1962 *Laboratory guide and notes for medical malacology*. Minneapolis: Burgess.

Malek, E. A. 1972 Snail ecology and man-made habitats. In *Schistosomiasis. Proceedings of a symposium on the future of schistosomiasis control*, pp. 57–60. Department of Tropical Medicine and Parasitology. Tulane University, Feb. 1–6, U.S.A.

McCullough, F. S. 1956 Transmission of *Schistosoma haematobium* by *Bulinus* species in the Ke District of the Gold Coast. *Trans. R. Soc. trop. Med. Hyg* **50**, 449–457.

McCullough, F. S. 1957 The seasonal density of populations of *Bulinus* (*P.*) *globosus* and *B. forskali* in natural habitats in Ghana. *Annls trop. Med. Parasit.* **51**, 235–248.

McCullough, F. S. 1964 Observations on bilharziasis and the potential snail hosts in the Republic of the Congo (Brazzaville). *Bull. Wrld Hlth Org.* **30**, 375–388.

McCullough, F. S. 1981 Biological control of the snail intermediate hosts of human schistosoma spp. a review of its present status and future prospects. *Acta Trop.* **38**, 5–13.

McCullough, F. S. & Duke, B. O. L. 1954 Schistosomiasis in the Gambia. 1. Observations on the potential snail vectors of *Schistosoma haematobium* and *Schistosoma mansoni*. *Annls trop. Med. Parasit.* **48**, 277–286.

McJunkin, F. E. 1975 *Water, engineers, development and disease in the tropics*. Washington D.C.: Agency for International Development.

McKillop, W. B. & Harrison, A. D. 1980 Hydrobiological studies of Eastern Lesser Antillean Islands. V. St Lucia: Freshwater habitats, water chemistry and distribution of freshwater molluscs. *Arch. Hydrobiol.* **57** (3), 25–290.

McMullen, D. B. 1962 The modification of habitats in the control of bilharziasis, with special reference to water resource development. In *Bilharziasis* (ed. G. E. W. Wolstenholme & M. O'Connor), pp. 382–396. Boston: Little Brown.

McMullen, D. B. 1963 Schistosomiasis control in theory and practice. *Am. J. trop. Med. Hyg.* **12**, 208–295.

McMullen, D. B. 1973 Biological and environmental control of snails. In *Epidemiology and control of schistosomiasis* (ed. N. Ansari), pp. 533–591. Basel: Karger & Baltimore: University Park Press.

Michelson, E. H. 1957 Studies on biological control of schistosome-bearing snails. Predators and parasites of freshwater mollusca: a review of the literature. *Parasitology* **47**, 413–426.

Michelson, E. H. 1961*a* An acid fast pathogen of freshwater snails. *Am. J. trop. Med. Hyg.* **10**, 423–433.

Michelson, E. H. 1961*b* The effects of temperature on growth and reproduction of *Australorbis glabratus* in the laboratory. *Am. J. Hyg.* **73**, 66–74.

Michelson, E. H. 1963 *Plistophora hussayi* sp.nov., a microsporidian parasite of aquatic pulmonate snails. *J. Insect Path.* **5**, 28–38.

Milward de Andrade, R. 1962 Ecology of *Australorbis glabratus* in Belo Horizonte, Brazil. 1. Annual fluctuations in population density and in the infection indices by *Schistosoma mansoni* (Pulmonata, Planorbidae). *Revta bras. Malar. Doenç. trop.* **14**, 261–289.

Mvogo, L. & Bard, J. 1964 Seconde note d'information sur *l'Astatoreochromis allaudi* poisson malacophage. *Bull Soc. Path. Exot.* **57**, 21–23.

Nassi, H., Pointer, J. P. & Golvan, Y. J. 1979 Bilan d'un essai de contrôle de *Biomphalaria glabrata* en Guadeloupe à l'aide d'un trématodes stérilisant. *Annls Prasit.* **54**, 185–192.

Ndifon, G. T. 1979 Studies on the feeding biology, anatomical variations and ecology of vectors of schistosomiasis and other freshwater snails in South-Western Nigeria. Ph.D. thesis. University of Ibadan.

Nicholson, A. J. 1958 The self-adjustment of populations to change. *Cold Spring Harb. Symp. quant. Biol.* **22**, 153–172.

Obeng, L. A. 1969 The invertebrate fauna of aquatic plants of the Volta Lake in relation to the spread of helminth parasites. In *Man-made lakes: The Accra symposium* (ed. L. A. Obeng), pp. 320–325. Accra: Ghana Universities Press.

Odei, M. A. 1961 A review of the distribution and ecology of the snail hosts of bilharziasis in West Africa. Part 1. Gambia, Ghana, Sierra Leone, Nigeria and the British Camerouns. *J. trop. Med. Hyg.* **64**, 27–41.

Odei, M. A. 1964 Some observations on the water situation and the problem of bilharziasis in North-Western Ghana. *W. Afr. med. J.*, **19**, 60–70.

Odei, M. A. 1972 Some preliminary observations on the distribution of bilharzia host snails in the Volta Lake. *Bull. Inst. français Afr. noire* **34** (A), 534–543.

Odei, M. A. 1973 Observations on some weeds of malacological importance in the Volta Lake. *Bull Inst. français Afr. noire* **35** (A), 57–66.

Ökland, J. 1969 The distribution and ecology of freshwater snails (Gastropoda) in Norway. *Malacologia* **9**, 143–151.

Okwuoso, V. N. 1979 The ecological studies of freshwater snails with particular reference to schistosome vectors in Lagos, Oyo and Ogun States of Nigeria. Ph.D. thesis, University of Ibadan.

Oliver-Gonzales, J. Baumann, P. M. & Benenson, A. S. 1956 Effect of the snail, *Marisa cornuarietis* on *Australorbis glabratus* in natural water bodies in Puerto Rico, *Am. J. trop. Med. Hyg.* **5**, 290–296.

Paperna, I. 1969*a* Study of an outbreak of schistosomiasis in the newly formed Volta Lake in Ghana. *Z. Tropenmed. Parasit.* **21**, 411–424.

Paperna, I. 1969*b* Aquatic weeds, snails and transmission of bilharzia in the new man-made Volta Lake in Ghana. *Bull. Inst. français Afr. noire* **31** (A), 487–499.

Patience, R. L., Sterry, P. R. & Thomas, J. D. 1983 Changes in chemical composition of a decomposing macrophyte *Lemna paucicostata J. chem. Ecol.* **9**, 889–991.

Paulini, E. 1963 Field observations on the upstream migration of *Australorbis glabratus*. *Bull. Wrld Hlth Org.* **29**, 838–841.

Paulinyi, H. M. & Paulini, E. 1972 Laboratory observations on the biological control of *Biomphalaria glabrata* by a species of *Pomacea* (Ampullariidae). *Bull. Wrld Hlth Org.* **46**, 243–247.

Pesigan, T. P., Farooq, M., Hairston, N. G., Jauregni, J. J., Garcia, E. G., Santos, A. T., Santos, B. C. & Besa, A. A. 1958*a* Studies on *Schistosoma japonicum* infection in the Philippines. 1. General considerations and epidemiology. *Bull. Wrld Hlth Org.* **18**, 345–455.

Pesigan, T. P., Farooq, M., Harston, N. G., Jauregni, J. J., Garcia, E. G., Santos, A. T., Santos, B. C. & Besa, A. A. 1958*b* Studies on *Schistosoma japonicum* in the Philippines 2. The Molluscan host. *Bull. Wrld Hlth Org.* **18**, 481–578.

Pesigan, T. P. & Hairston, N. G. 1961 The effects of snail control on the prevalence of *Schistosoma japonicum* infection in the Philippines. *Bull. Wrld Hlth Org.* **25**, 479–482.

Petr, T. 1968 Population changes in aquatic invertebrates living in two water plants in a tropical man-made lake. *Hydrobiologia* **32**, 449–485.

Pettet, A. & Pettet, S. J. 1970 Biological control of *Pistia stratiotes* L. in Western Nigeria, *Nature, Lond.* **226**, 282.

Prentice, M. A., Barnish, G. & Christie, T. D. 1977 An ecophenotype of *Helisoma duryi* closely resembling *Biomphalaria glabrata*. *Annls trop. Med. Parasit.* **71**, 237–238.

Radke, M. G. & Ritchie, L. S. 1961 Field observations on the migration of marked *Australorbis glabratus* snails. *J. Parasit.* **47**, 712.

Rankin, J. J. & Harrison, A. D. 1979 Hydrobiological studies of Eastern Lesser Antillean Islands. IV. St Vincent: Comparison of field and laboratory populations of *Physa marmorata* Guilding (Gastropoda: Pulmonata). *Arch. Hydrobiol.* Supplement **57**, (1) 89–116.

Rasmussen, O. 1974 Biological control of *Biomphalaria pfeifferi* by *Helisoma duryi*. *Proceedings of the Third International Congress of Parasitology. Munchen* **3**, 1598–9.

Reid, K. G. 1961 *Ecology of inland waters and estuaries*. New York: Reinhold.

Richard, M. J. & Frank, R. 1966 *Life in the soil*. Institute of Biology, Studies in Biology, no. 2. London: Edward Arnold.

Ritchie, L. S. 1973 Chemical control of snails. In *Epidemiology and control of schistosomiasis* (ed. N. Ansari), pp. 458–532. Basel: Karger and Baltimore: University Park Press.

Rowan, W. B. 1959 Seasonal effects of heavy rains on the population density of *Australorbis glabratus* in a Puerto Rican watershed. *Am. J. trop. Med. Hyg.* **8**, 570–574.

Saliternik, Z. & Witenberg, G. 1959 Investigation on the control of bilharziasis vectors in Israel. *Bull. Wrld Hlth Org.* **21**, 161–177.

Van der Schalie, H. & Berry, E. G. 1973 The effects of temperature on growth and reproduction of aquatic snails. *Sterkiana* **50**, 1–92.

Scheerboom, J. E. M. & Geldof, A. A. 1978 A quantitative study of assimilation of different diets in the pond snail, *Lymnaea stagnalis* (L), introducing a method to prevent coprophagy. *Proc Koninklijke Nederl. Akad. Wetenschappen, Amsterdam*, series C. **81**, 184–197.

Scorza, J. V., Bilva, J., Gonzales, L. & Machado, R. 1961 Stream velocity as a gradient in *Australorbis glabrata* (Say, 1818). *Z. Tropenmed. Parasit.* **12**, 191–196.

Sevilla, J. Z. 1965 The effects of temperature on the intrinsic rate of increase of three species of pulmonate snails. Ph.D. thesis, University of Michigan.

Shiff, C. J. 1964 Studies on *Bulinus* (*Physopsis*) *globosus* in Rhodesia. 1. The influence of temperature on the intrinsic rate of natural increase. *Annls trop. Med. Parasit.* **58**, 94–105.

Shiff, C. J. & Garnett, B. 1967 The influence of temperature on the intrinsic rate of natural increase of the freshwater snail *Biomphalaria pfeifferi* (Krauss) (Pulmonata: Planorbidae). *Arch. Hydrobiol.* **62**, 429–438.

Smithers, S. R. 1956 On the ecology of schistosome vectors in the Gambia, with evidence of their role in transmission. *Trans. R. Soc. trop. Med. Hyg.* **50**, 354–365.

Southwood, T. R. E. 1978 *Ecological methods*. London: English Language Book Society and Chapman.

Speeg, K. V. Jr & Campbell, J. W. 1969 Arginine and urea metabolism in terrestrial snails. *Am. J. Physiol.* **216**, 1003–1012.

Stott, B. 1974 Biological control of weeds. In *Biology in pest and disease control* (ed. D. Price-Jones & M. E. Solomon), pp. 233–238. Oxford, London: Blackwells.

Sturrock, R. F. 1966 The influence of temperature on the biology of *Biomphalaria pfeifferi*, an intermediate host of *Schistosoma mansoni*. *Annls trop. Med. Parasit.* **60**, 100–105.

Sturrock, R. F. 1970 An investigation of some factors influencing the survival of St Lucian *Biomphalaria glabrata* deprived of water. *Annls trop. Med. Parasit.* **64**, 365–371.

Sturrock, R. F. 1973 Field studies on the transmission of *Schistosoma mansoni* and on the bionomics of its intermediate host, *Biomphalaria glabrata*, on St Lucia, West Indies. *Int. J. Parasit.* **3**, 175–194.

Sturrock, R. F. 1974 Ecological notes on the habitats of the freshwater snail, *Biomphalaria glabrata*, intermediate host of *Schistosoma mansoni* on St Lucia, West Indies. *Caribbean J. Sci.* **14**, 149–162.

Sturrock, R. F. & Sturrock, B. M. 1972 The influence of temperature on the biology of *Biomphalaria glabrata* (Say), intermediate host of *Schistosoma mansoni* on St Lucia, West Indies. *Annls trop. Med. Parasit.* **46**, 385–390.

Tait, A. I. 1982 Field and laboratory studies on the biological control of *Biomphalaria pfeifferi*: a snail intermediate host of schistosomiasis. D.Phil. thesis, University of Sussex.

Talling, J. F. 1957 The longitudinal succession of water characteristics in the White Nile. *Hydrobiologia* **11**, 73–89.

Talling, J. F. & Talling, I. B. 1965 The chemical composition of African lake waters. *Int. Rev. Hydrobiol. Hydrograph.* **50**, 421–463.

Teesdale, C. 1962 Ecological observations on the molluscs of significance in the transmission of bilharziasis in Kenya. *Bull. Wrld Hlth Org.* **27**, 759–782.

Thomas, J. D. 1964 Studies on the growth of trout, *Salmo trutta* from four contrasting habitats. *Proc. Zool. Soc. Lond.* **142**, 459–509.

Thomas, J. D. 1966 Some preliminary observations on the fauna and flora a small manmade lake in the West African Savanna. *Bull. Inst. français Afr. noire* **28** (A), 542–562.

Thomas, J. D. 1973 Schistosomiasis and the control of molluscan hosts of human schistosomiasis with particular reference to possible self-regulatory mechanisms. *Adv. Parasit.* **11** (ed. Ben Dawes), pp. 307–394. London: Academic Press.

Thomas, J. D. 1982 Chemical ecology of the snail hosts of schistosomiasis: snail–snail and snail–plant interactions. *Malacologia* **22**, 81–91.

Thomas, J. D. & Aram, R. H. 1974 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.

Thomas, J. D., Benjamin, M., Lough, A. & Aram, R. H. 1974 The effects of calcium in the external environment on the growth and natality rates of *Biomphalaria glabrata* (Say). *J. Anim. Ecol.* **43**, 839–860.

Thomas, J. D. & Compston, D. 1980 A bioengineering approach to the control of aquatic weeds in a tropical lake. In *Weeds and their control in the humid tropics* (ed. I. O. Akobundu), pp. 182–196. Ibadan, Nigeria: I.I.T.A.

Thomas, J. D., Goldsworthy, G. J. & Aram, R. H. 1975 Studies on the chemical ecology of snails: the effects of chemical conditioning by adult snails on the growth of juvenile snails. *J. Anim. Ecol.* **44**, 1–27.

Thomas, J. D. & Lough, A. 1974 The effects of external calcium concentration on the rate of uptake of this ion by *Biomphalaria glabrata* (Say). *J. Anim. Ecol.* **43**, 861–871.

Thomas, J. D., Powles, M. & Lodge, R. 1976 The chemical ecology of *Biomphalaria glabrata*: the effects of ammonia on the growth rate of juvenile snails. *Biol. Bull.* **151**, 286–297.

Thomas, J. D. & Ratcliffe, P. J. 1973 Observations on the limnology and primary production of a small man-made lake in the West African savanna. *Freshw. Biol.* **3**, 573–612.

Ukoli, F. M. A. & Asumu, D. I. 1979 Freshwater snails of the proposed Federal Capital Territory, Nigeria. *Niger. J. nat. Sci.* **1**, 49–58.

Uvarov, B. 1966 *Grass-hoppers and locusts.* Cambridge University Press.

Van Eeden, J. A. & Combrinck, C. 1966 Distributional trends of four species of freshwater snails in South Africa with special reference to the intermediate hosts of bilharzia. *Zoologica afr.* **2**, 95–109.

Wallwork, J. A. 1970 *Ecology of soil animals.* London: McGraw Hill.

Walton, C. L. 1918 Liver-rot of sheep and bionomics of *Lymnaea truncatula* in the Aberystwyth area. *Parasitology* **10**, 232–266.

Walton, C. L. & Wright, W. R. 1926 Hydrogen ion concentration and the distribution of *Lymnaea truncatula* and L. *peregra* with a note bearing on mosquitoes. *Parasitology* **18**, 363–367.

Watson, J. M. 1950 Studies on bilharziasis in Iraq. Part V. The habitats of the vector snail. *Bulinus truncatus* and its distribution in relation to irrigation. *J. Faculty Med., Iraq.* **14**, 148–182.

Watson, J. M. 1958 The ecology and distribution of *Bulinus truncatus* in the Middle East. *Bull. Wrld Hlth Org.* **18**, 833–894.

Webbe, G. & Msangi, A. S. 1958 Observations on three species of *Bulinus* on the East Coast of Africa. *Annls trop. Med. Parasit.* **52**, 302–314.

W.H.O. 1965 *Snail control in the prevention of bilharziasis.* World Health Organization Monograph Series, no. 50. Geneva, Switzerland.

Williams, N. V. 1970*a* Studies on aquatic pulmonate snails in Central Africa. II. Experimental investigations of field distribution patterns. *Malacologia* **10**, 165–178.

Williams, N. V. 1970*b* Studies on aquatic pulmonate snails in Central Africa. I. Field distribution in relation to water chemistry. *Malacologia* **10**, 153–162.

Wit, C. T. de 1971 On modelling of competitive phenomena. In *Dynamics of populations* (ed. P. J. den Boer & G. R. Gradwell). Advanced Studies Institute.

Worthington, E. B. 1979 Some ecological problems concerning engineering and tropical disease. *Prog. Wat. Tech.* **11**, 5–11.

Zakaria, H. 1955 Further study on the ecology of the intermediate host of *Schistosoma haematobium*, *Bulinus truncatus* Baylis. *Bull. end. Dis.* **1**, 123–155.