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The biology of *Biomphalaria choanomphala* and *B. sudanica* in relation to their role in the transmission of *Schistosoma mansoni* in Lake Victoria at Mwanza, Tanzania

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A study of the intermediate snail hosts of Schistosoma mansoni *in Lake Victoria at Mwanza, Tanzania, was begun in October 1969, the main aims being to investigate the distribution and seasonal variations in population densities of* Biomphalaria choanomphala *and* B. sudanica *in relation to the nature of the lake bottom and the biological features of the lake shore, the factors influencing variations in the intensity of* S. mansoni *transmission along the Mwanza shoreline, and the age structure of populations of* B. choanomphala. *Field surveys were made at 70 sites near Mwanza and in nearby bays,* B. choanomphala *being collected from the lake bottom by means of a wire-mesh dredge. Variations in the distribution and population density of* B. choanomphala *were correlated with the nature of the bottom and its depth profiles at depths of 0.5–6.0 m. Approximately 1–20 snails/m² were found on mixed sand and mud but only about 1 snail/m² on the predominantly muddy bottom farther out from the shore. Seasonal variations in the age structure and fluctuations in the population densities of* B. choanomphala *of as much as 10–13-fold were observed. A large and a small form of* B. choanomphala, *possibly ecophenotypes, were found.* S. mansoni *infection rates in* B. choanomphala *ranged from 0.2% to 3.3%, suggesting a tendency to higher infection rates in mature snails.*

For the past 12 years the East African Institute for Medical Research at Mwanza, Tanzania, has conducted intensive research on schistosomiasis. In addition, the WHO/Tanzania Schistosomiasis Pilot Control and Training Project (Tanzania 2101) has, among its other activities, recently examined the factors influencing the transmission of intestinal schistosomiasis in Mwanza (McCullough et al., 1972; McCullough & Eyakuze, unpublished data; McCullough & Magendantz, unpublished data). These studies, together with those of Wijers & Munanga (1971), indicate that transmission of *Schistosoma mansoni* in Lake Victoria and its tributaries is an increasing public health problem, especially as towns and villages along the shores of the lake are growing rapidly.

Lake Victoria contains an endemic species of *Biomphalaria* of the *Choanomphala* group, which lives on the bottom at distances up to 150 m offshore and is highly susceptible to infection with *S. mansoni*. In addition, *B. pfeifferi* is found in streams draining into the lake, and *B. sudanica* in habitats near the shores of the lake. These three species were first shown to be susceptible to *S. mansoni* infections by Cridland (1955), while Webbe (1962) and McClelland & Jordan (1962) first described the role of *B. choanomphala* in the transmission of *S. mansoni* at Mwanza and Bukoba, respectively. An apparatus was designed by Prentice (1966) to collect *B. choanomphala* and to study the transmission of *S. mansoni* at Entebbe, Uganda (Prentice et al., 1970); more recently, Prentice (1970) has experimented with the application of molluscicides to the lake, Baalawy (1971) reported high densities of *B. choanomphala* at Mwanza, low densities at Musoma and Bukoba,

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and no snails at Kisumu. These studies have provided considerable information about the distribution of *B. choanomphala*, but little on its population dynamics and natural rate of infection with *S. mansoni*.

Webbe (1962) found infected specimens of *B. sudanica* in backwaters behind the lake shore, and regarded them as an important source of *S. mansoni* transmission. In Uganda, Berrie (1964) related the growth and reproductive rate of this snail to seasonal changes. However, little is known about the growth of *B. sudanica* and the rates of infection with *S. mansoni* in different types of habitat.

The main aims of the present study, carried out from October 1969 to August 1971, were to investigate the distribution and seasonal variations in density of *B. choanomphala* and *B. sudanica* in relation to bottom substrata and physical and biological features of the lake shore, the factors influencing variations in intensity of *S. mansoni* transmission along the Mwanza shorelines, and the age structure of populations of *B. choanomphala*. It is hoped that these studies, together with those already mentioned, will contribute to the planning of more satisfactory control measures against *S. mansoni* in Mwanza.

MATERIALS AND METHODS

Field methods

Field surveys for *B. sudanica* and *B. choanomphala* were made at 70 sites in Mwanza North and South bays, at one site in Nyegezi Bay, and at two in Pasiansi Bay. *B. choanomphala* was collected with a 2-mm wire mesh dredge measuring 75 cm deep and 55 cm wide at the opening, supported on a triangular frame. The net was dropped from a boat at distances of 20, 40, and 60 m from the shore, pulled for a measured distance, and then lifted out of the water. This simple method of dredging yielded hundreds of snails in a relatively short time (about 1 hour). The samples were washed through a 1–2-mm mesh sieve to remove snails and egg masses, which were then spread out in shallow basins and covered with water so that the smaller snails could be more easily seen. The average number of *B. choanomphala* per haul was calculated by dividing the total number collected by the number of hauls. In order to assess the sensitivity of the dredge in collecting snails, this method was compared with an exhaustive stationary sampling method, in which 1-m² plots on the lake bottom were marked off with a circular frame. The bottom material inside the frame was dug out to a depth of 4 cm and sieved as described above. Altogether, 10 such samples and 2 30-m dredge hauls (starting 30 m from the shore and passing as close as possible to the stationary sampling stations) yielded the following data for *B. choanomphala*.

1-m² samples

Distance from shore and substratum	*No. of snails/m²*
10 m; sand	0
10 m; sand	0
15 m; sand	0
15 m; sand	0
20 m; sand & mud	4
20 m; sand & mud	3
25 m; sand & mud	10
25 m; sand & mud	16
30 m; sand & mud	18
30 m; sand & mud	11

Dredge hauls

96 snails/haul = 12.8 snails/m² [a]
176 snails/haul = 23.4 snails/m² [a]

These data suggest that a single dredge haul for a short distance on a sandy–muddy bottom collects at least 70% of the snails in a transect. Each site of roughly 1 500 m² was transected by an average of 3–4 dredge hauls on each collecting day. It was found that the dredging method was particularly suited to shallow bays with sandy–muddy bottoms and no submerged vegetation, whereas an Eckman grab was ineffective at shallow depths on hard sandy bottoms.

Variations in population structure and infection rates of *B. choanomphala* over a period of 1.5–2 years were followed monthly at 5 sites in Mwanza North and South bays and on 5–12 occasions at 6 sites in these bays and in Nyegezi and Pasiansi bays. All the other sites were surveyed on 1–4 occasions. Sites for repeated collections were selected on the basis of their similarities and contrasts with respect to substrata, depth profiles, human activities, and proximity to housing. Some examples of the different substrata and depth profiles are given in Table 1. Various types of human activity and housing condition were represented. Six of the sites were probably used to a greater degree than any of the others by 30–50 or more different individuals in a single day, for bathing, washing, and fishing.

[a] The calculations were made as follows: between the distances of 30 m and 15 m from the shore each dredge haul traversed an area of 7.5 m². Dividing the number of snails in each of the 2 hauls by 7.5 yields the average number of snails per m².

Table 1. Substrata, depth profiles, and densities of *B. choanomphala* in Mwanza South, Mwanza North, and Pasiansi bays [a]

Distance from shore (m)	M-S (38)			M-S (49)			M-N (6)			M-N (13)			M-N (15)			Pas (2)			Pas (1)		
	Sub-stratum	Depth (m)	dn [b]	Sub-stratum	Depth (m)	dn [b]	Sub-stratum	Depth (m)	dn [b]	Sub-stratum	Depth (m)	dn [b]	Sub-stratum	Depth (m)	dn [b]	Sub-stratum	Depth (m)	dn [b]	Sub-stratum	Depth (m)	dn [b]
20	sand/mud	0.6	123	sand	0.9	65	sand	2.1	1	sand	1.8	30	sand	0.9	5	sand	0.6	0	sand	1.5	50
40	sand/mud	1.2	67	sand	1.5	43	sand	2.7	1	mud	2.7	2	sand/mud	1.8	15	sand	0.9	2	sand/mud	1.5	100
60	mud/sand	1.5	40	mud/sand	2.7	6	sand	3.4	5	mud	3.4	0	sand/mud	2.7	15	sand	1.2	6	sand/mud	1.8	20
80	mud	2.4	1	mud	3.6	0	sand	4.6	20	mud	4.3	0	mud	3.4	1	sand	1.5	15	sand/mud	3.4	0
100	mud	2.7	0	mud	4.6	0	sand	6.4	—	mud	4.6	0	mud	4.6	0	sand	1.5	55	sand/mud	4.6	—

[a] M-S, Mwanza South Bay; M-N, Mwanza North Bay; Pas, Pasiansi Bay.
[b] dn, Average number of snails found in 20-m hauls (from 20 m–shore; 40–20 m; 60–40 m; 80–60 m; 100–80 m).

In the Mwanza bays there are virtually no sites with access to the lake that are not frequented, except those near the Capri Point water supply inlet for Mwanza where it is forbidden to bathe and settle.

B. sudanica was collected with a scoop net in emergent vegetation, irrigation furrows, and grassy seepages along the Mwanza North Bay and South Bay shores. Seasonal variations in the population structure of *B. sudanica* were followed monthly at two sites. When these sites began to dry out, snails could only be collected with forceps.

Laboratory methods

B. sudanica and *B. choanomphala* collected in both Mwanza bays were screened for mammalian schistosome infections by placing snails in glass vials containing 15 ml of filtered lake water under a lamp for 12 hours at a temperature of 25–26°C. Albino mice were exposed to mammalian-type schistosome cercariae pooled from 3 or more *B. sudanica* or *B. choanomphala* by partially submerging them in 50 ml of filtered lake water containing 150–200 cercariae. The identification of human schistosome cercariae was confirmed by the recovery of *S. mansoni* ova from the livers of mice autopsied 2–3 months after exposure to the cercariae.

B. choanomphala snails collected from the lake bottom did not readily lay egg masses in aquaria. However, during the first few days after being brought into the laboratory they deposited egg masses in glass vials. These egg masses were carefully removed to initiate a laboratory colony of *B. choanomphala* in the following way. The egg masses were placed in linen cloths suspended in aerated lake water in basins or aquaria. Aeration was necessary to prevent the egg masses from quickly becoming covered with bacterial and fungal slime. For a few weeks before use the cloths were allowed to become coated with green and blue-green algae on which the hatchling snails could feed. After the snails emerged they were fed a mixture containing boiled lettuce, calcium carbonate, ground-up mouse pellets, and sand. Once a week the cloths were rinsed to remove faecal matter and bacteria. The young snails grew to maturity and laid eggs abundantly on the cloths.

RESULTS

Biomphalaria choanomphala: distribution and variation in population density in relation to bottom substrata

From the distribution of *B. choanomphala* and *B. sudanica*, and the variations in population density of the former species, in Mwanza South and North bays, it appears that *B. choanomphala* is mainly a bottom-dwelling species, although Webbe (1962) reported finding it on submerged vegetation as well as on the lake bottom. In the present study, *B. choanomphala* was found on the bottom, but never on emergent vegetation or on the shoreline, except when living snails were washed up after a storm. At some sites there were many empty shells of *B. choanomphala*, but at other sites with more steeply sloping shores there were few or no shells, even though high densities of snails were found on the adjacent lake bottom. The lack of shells on the shore could therefore not be used to indicate the absence of snails at any particular site. On the lake bottom, variations in snail density were closely correlated with various types of substratum. No snails, or very few (1–5 snails per 40-m dredge haul), were found on mud bottom situated offshore from extensive areas of emergent grasses, sedges, and papyrus and containing much silt and decaying vegetation. Extensive emergent vegetation bordered approximately 5 km in a stretch of 10 km of the South Bay and 1 km in a stretch of 5 km of the North Bay, but there was none bordering the 10 km of Pasiansi Bay. Moderately high to high densities of *B. choanomphala* (>15 snails per 40-m haul) were found on sand and mud bottom offshore from a small zone of emergent vegetation or from an exposed shore. Roughly one-half of both the North Bay and South Bay sites had this type of bottom and these snail densities. At both sites in Pasiansi Bay, which had the same type of bottom, there were high densities of B. *choanomphala*.

In order to obtain a rough idea of the number of *B. choanomphala* on the lake bottom in certain areas, population densities can be roughly estimated from the following equation:

$$\frac{\text{total no. of snails collected within a certain distance from the shore}^{a}}{\text{area of lake bottom dredged}} = \frac{\text{total no. of snails collected within a certain distance from the shore}^{a}}{0.55\ \text{m}^{b} \times \text{distance dredged} \times \text{no. of dredge hauls}}$$

For example, the density of *B. choanomphala* at site 46 in Mwanza South Bay on 23 March 1970, based on data in Table 2, is calculated from the above equation as follows:

$$\frac{205\ (\text{total no. of snails collected in one 40-m haul})}{0.55 \times 40 \times 1} = 9.3\ \text{snails/m}^2.$$

At this site at the time of dredging maximum snail densities were found within a distance of 10–40 m from the shore. Thus, taking a section of lake bottom 100 m long and 30 m wide within a distance of 10–40 m from the shore, the total area would be 3 000 m². For a population density of 9.3/m², a rough estimate of the total number of snails along a 100-m stretch of beach within 40 m from the shoreline is $3\,000 \times 9.3 = 27\,000$ snails per 3 000 m². Such calculations of the total number of snails at a particular site indicates the high densities of *B. choanomphala* in some areas.

There was such marked variation in the substrata, depth profiles, and snail densities in Mwanza North and South bays and Pasiansi Bay that the bays could not readily be characterized. Table 1 shows these variations for several sites in each bay. Densities of *B. choanomphala* declined to low levels (1–5 snails per 40-m haul) at various distances from the shore where the bottom was predominantly mud. In Mwanza South Bay the highest snail densities (15–300 snails per 40-m haul) occurred within 60 m from shore on mixed sand/mud bottom at depths of 0.75–3.0 m, whereas beyond a distance of 60 m densities declined to 1–5 snails/40-m haul on predominantly muddy bottom. In contrast, at some Mwanza North Bay sites and in Pasiansi Bay, where mixed sand/mud bottom extended beyond 100 m from the shore in some places, high densities of *B. choanomphala* continued out to distances of 80–150 m from the shore at depths of 1–6 m. Thus, the type of bottom rather than depth (at least up to a depth of 7 m) appears to be the main factor determining the maximum distance from the shore at which high densities of *B. choanomphala* are found.

Since the shoreline is undergoing rapid alteration as a result of drifting papyrus islands, shifting agriculture, and various fishing and housing practices, and since this is leading to changes in the bottom, the distribution of *B. choanomphala* is likely to change considerably in the future. It would be of interest to repeat the dredging operations in Mwanza at intervals in order to monitor the changing patterns influencing the bionomics of *B. choanomphala*.

[a] 20, 40, and 60 m. [b] Width of the dredge.

Table 2. Representative data on the distribution and population densities of *B. choanomphala* and *B. sudanica* and their rates of infection with *S. mansoni* at several sites Lake Victoria at Mwanza [a]

Date	*B. choanomphala*		
	No. per haul [b]	Total no. collected [c]	Percentage infected
	site 5		
7 Nov. 1969	20	59	0.0
2 Dec. 1969	33	100	0.0
23 Jan. 1970	27	80	—[d]
21 Feb. 1970	36	118	0.0
17 April 1970	42	83	0.0
30 June 1970	14	41	0.0
1 Oct. 1970	17	52	0.0
18 Nov. 1970	15	149	2.7
17 Dec. 1970	5	37	0.0
	site 49		
18 June 1970	269	269	0.7
15 Aug. 1970	156	780	0.0
26 Sept. 1970	50	99	0.0
13 Dec. 1970	23	206	0.0
13 Jan. 1971	85	170	1.1
9 Feb. 1971	38	130	0.8
13 March 1971	27	162	0.0
20 April 1971	89	267	0.4
	site 46		
22 Dec. 1969	39	116	—[d]
5 Feb. 1970	80	326	—[d]
23 March 1970	205	387	0.0
30 April 1970	276	612	0.0
12 May 1970	169	339	0.0
6 June 1970	173	520	0.0
7 July 1970	24	48	0.0
4 Aug. 1970	34	135	0.0
12 Sept. 1970	49	98	0.0
16 Oct. 1970	15	74	1.4
25 Nov. 1970	21	148	0.0
4 Jan. 1971	19	132	0.0

Date	*B. choanomphala*		
	No. per haul [b]	Total no. collected [c]	Percentage infected
	site 38		
18 Nov. 1969	31	134	0.0
24 Nov. 1969	51	207	—[d]
14 Jan. 1970	32	162	—[d]
19 Feb. 1970	123	422	—[d]
14 April 1970	279	627	0.0
16 May 1970	217	425	0.0
8 June 1970	141	842	0.0
13 July 1970	162	325	0.0
17 Aug. 1970	151	453	0.0
4 Sept. 1970	52	155	0.0
26 Oct. 1970	110	438	0.0
3 Nov. 1970	70	139	0.7
1 Dec. 1970	30	301	0.0
2 Jan. 1971	35	248	0.0
8 Feb. 1971	45	268	0.5
14 March 1971	124	371	0.3
22 April 1971	60	300	0.0
26 April 1971	57	170	0.6
29 July 1971	89	444	0.0
	Nyegezi site		
16 Oct. 1969	24	95	0.0
22 April 1970	96	289	0.0
16 June 1970	106	351	0.3
22 July 1970	187	374	0.5
24 Aug. 1970	263	1 049	0.2
14 Oct. 1970	111	277	0.0
8 Nov. 1970	96	383	0.5
2 Dec. 1970	21	170	1.1
31 Dec. 1970	18	126	0.0
30 Jan. 1971	12	108	0.9
1 July 1971	133	530	0.2
6 Aug. 1971	96	382	0.5

[a] Complete data for all 70 sites are available at the East African Institute of Medical Research, Mwanza.
[b] Dredge dropped at a distance of 40 m from the shore. The number of snails collected per 40-m haul is the average number per haul
[c] Total number of snails collected at 20, 40, and 60 m from the shore.
[d] Not recorded.

Table 2 (*continued*)

Date	*B. choanomphala* No. per haul [a]	*B. choanomphala* Total no. collected [b]	*B. choanomphala* Percentage infected	Date	*B. choanomphala* No. per haul [a]	*B. choanomphala* Total no. collected [b]	*B. choanomphala* Percentage infected
	site 46				Nyegezi site		
9 Feb. 1971	13	54	0.0	5 Sept. 1971	436	486	0.2
22 March 1971	17	149	0.7				
14 April 1971	60	240	0.4				
30 July 1971	77	540	0.2				

Date	*B. sudanica* Total no. collected [b]	*B. sudanica* Percentage infected	Date	*B. sudanica* Total no. collected [b]	*B. sudanica* Percentage infected
	site 9			site 38	
28 April 1970	88	0.0	17 Dec. 1969	53	—[c]
10 May 1970	100	0.0	19 Feb. 1970	407	0.0
24 June 1970	312	0.0	25 April 1970	164	1.8
2 Sept. 1970	47	2.1	25 May 1970	139	0.7
12 Oct. 1970	160	0.0	3 July 1970	65	0.0
3 Nov. 1970	253	0.0	13 Aug. 1970	33	0.0
4 Dec. 1970	151	0.0	3 Sept. 1970	86	0.0
7 Jan. 1971	201	0.0	17 Oct. 1970	57	1.8
2 April 1971	193	1.0	26 Nov. 1970	67	0.0
12 Sept. 1971	51	0.0	2 Dec. 1970	66	0.0
			2 Jan. 1971	89	0.0
			3 Feb. 1971	37	0.0

[a] Dredge dropped at a distance of 40 m from the shore. The number of snails collected per 40-m haul is the average number per haul.
[b] Total number of snails collected at 20, 40, and 60 m from the shore.
[c] Not recorded.

Seasonal variations in population density and age structure

Seasonal fluctuations in the population densities of *B. choanomphala* were recorded during the period October 1969 to September 1971 at four sites in Mwanza North and South bays and in Nyegezi Bay. In Mwanza South and Nyegezi bays from March to August 1970, snail densities were 3–6 times those found from November 1969 to January 1970 and from September 1970 to February 1971 (Table 2). In 1971 the population densities began increasing at one site in January, while at two other sites and at Nyegezi the population increase took place in March and April.

An upsurge in population density took place at one site in the North Bay in April 1970, and a decline occurred in late October and November (Table 2). In Nyegezi, on the other hand, *B. choanomphala* densities were highest from August to October, had fallen 14-fold by December, and by March 1971 had again increased to one-third of the density recorded in August 1970 (Table 2).

Repeated collections at four sites showed that the age structure of *B. choanomphala* populations changed during the year. The most marked changes are seen when the September–November and the January–July collections from Mwanza South are compared: in the former, 50–80% of the snails were 6–8 mm in diameter, but in the latter, 50–70% were immature or young mature snails less than 5.5 mm in diameter. Marked changes in age structure also occurred in the Nyegezi population, but they did not coincide in time with those in the Mwanza Bay population. During October 1970, over 50% of the snails in the Nyegezi population were juveniles, whereas only 20% in the Mwanza populations were immature.

Variations in shell growth in populations of B. choanomphala

In Mwanza Bay and nearby bays large and small forms of *B. choanomphala*, which are possibly ecophenotypes, have been found. The larger form has been collected in Mwanza North Bay and the smaller form in Nyegezi, Mwanza South, and Butimba bays. In Mwanza North Bay, particularly at sites near the outflow of the Mirongo stream, 10–15% of the snails in dredge hauls are 8.0–9.5 mm in diameter, whereas in Pasiansi, Mwanza South, and Nyegezi bays the number of snails exceeding 8.0 mm in diameter collected at any time of the year seldom exceeds 5%. Both the larger and smaller forms are found in fairly shallow water (0.5–3.0 m), but the larger Mwanza North Bay form is found on sand/mud bottoms inshore from silt-laden substrata. The greater shell growth of the Mwanza North Bay form possibly reflects a richer supply of organic and mineral nutrients in the North Bay. The Mwanza North Bay form corresponds to that described by Mandahl-Barth (1957) as the " Mwanza form ".

Egg production

The egg masses of *B. choanomphala*, like those of all planorbid snails, are oval in shape, and are commonly found on mollusc shells and decaying vegetation. They can be distinguished from the egg masses of *Bulinus truncatus trigonus*, which is also abundant at some sites on the lake bottom, because the latter have thicker egg capsules and a more pronounced terminal tail. The egg masses of these two species can also be readily identified by examining the hatchling snails.

Fluctuations in *B. choanomphala* densities during the year may be the result of variations in egg production (natality) and/or variations in survival rates (mortality) of snail embryos or snails in various size classes. It was observed that the number of egg masses in dredge hauls varied considerably during the year. At Mwanza South Bay large numbers (100–300 egg masses per 5 40-m dredge hauls) were collected between February and July 1970, while between October and December 1970 egg masses were found only with difficulty (50 egg masses in 5 40-m hauls).

The mortality rates of embryos collected throughout the year ranged from 22% to 59%, but higher rates did not coincide with lower snail densities. Predation by ciliate protozoa and annelid worms was an important cause of mortality.

S. mansoni infection rates in B. choanomphala in the lake

Infected *B. choanomphala* were found in Mwanza South Bay at 10 sites, in Mwanza North Bay at 4 sites (including the Karumo ferry landing), and at 1 site in Nyegezi Bay. Pollution of the water with human faeces was evident at all these sites, particularly at a site where there is only one public water tap on a 3-km stretch of Mwanza South Bay shore, and where some 2 350 people are dependent on the lake for their entire water needs.

S. mansoni infection rates in *B. choanomphala* ranged from 0.2% to 3.3%. These data on seasonal infection rates, though insufficient, suggest a tendency towards higher infection rates when seasonal densities are at their lowest and when snail populations consist mainly of mature individuals. For example, infection rates in Mwanza South Bay between October 1970 and January 1971 were generally 1.5–3 times those during March and April 1971. Further studies over a period of several years should be made, uniformly large samples of snails from several sites being screened to determine whether seasonal variations in infection rates occur.

All infected snails were collected from depths of 0.5–3.0 m in the various bays. In Pasiansi Bay infected snails were found on one occasion only, but they occurred in most of the monthly collections from Nyegezi Bay.

Biomphalaria sudanica : distribution along the lake shore

B. sudanica snails were found in numerous habitats above the lake level, particularly in grassy seepages and irrigation furrows.

Seasonal variations in population density and structure

Thousands of young snails migrated from shallow grassy seepages to shallower upshore seepages at the time of heavy flooding in April and May 1970. In June, those seepages farthest (about 60 m) from the shoreline, where grass was sparse, quickly dried out and the numerous exposed snails died within a month. On the other hand, about 20 m from the shore, where there were taller clumps of grass providing shade, 30% of the snails survived for 3 months until September, after which time no live snails were recovered. Still closer to the shoreline (about 5–10 m), behind a zone of *Typha* sp. in small pockets of water that periodically filled and dried up, a few surviving *B. sudanica* snails were found until March 1971. No snails were found during the rains of April and May 1971; in the previous year there was a migration of thousands of snails, and infected snails were collected on several occasions.

At a site in Mwanza South Bay young snails ($\leqslant$6.0 mm in diameter) constituted about half the *B. sudanica* population during the long rainy season from February to May 1970; from July to September 30–40% were juveniles, and between October and December 1970, when the rainfall was half the average figure, less than 20% were young snails.

In a markedly different site, a group of irrigation furrows in Mwanza North Bay, young snails were rare during the heavy flooding in April. In this habitat, the main period of reproductive activity appeared to be delayed until the early part of the dry season. Moreover, high population densities were maintained throughout the dry season, as the water level only slowly receded and the irrigation furrows never completely dried out. Such high densities during the dry season were also described by Berrie (1964) for a *B. sudanica* population in a roadside ditch or a papyrus swamp near Kampala.

Rates of S. mansoni infection in B. sudanica

B. sudanica snails infected with *S. mansoni* were collected at 4 sites in the North Bay and at 6 in the South Bay. Much pollution with human faeces was observed at these sites, which were all close to open beaches. Infection rates in the two bays ranged from 0.5% to 7.7%, averaging 1.6%. Lateral-spined *S. mansoni* ova were recovered from mice exposed to mammalian schistosome cercariae pooled from naturally infected *B. sudanica.* No *S. rodhaini* ova, as described by Schwetz (1951), were recovered from the mice.

No infected *B. sudanica* were found along the South Bay in irrigation furrows in an area where there is neither access to the lake nor signs of obvious faecal pollution in the dense growth of papyrus and sedges.

DISCUSSION

The marked variations in population density of *B. choanomphala* snails in different sites in Lake Victoria at Mwanza are probably influenced by a number of environmental factors, the main one being, perhaps, the nature of the lake bottom. The highest snail densities occurred on mixed sand/mud substrata that had a rich algal growth and contained a moderate amount of organic matter. On the other hand, the reduction of *B. choanomphala* observed on predominantly muddy substrata may be related to the presence of large amounts of organic matter and organic acids. Analyses of bottom mud from Lake Victoria have shown that its organic content shows little tendency to decompose (Fish, 1955). Generally, in the temperate zone, molluscs are abundant in eutrophic lakes with hard water and a high calcium content, but they tend to be scarce in acid dystrophic lakes. Similarly, some tropical lakes (including Lake Victoria) that are rather alkaline support relatively large populations of molluscs, at least locally. Lakes that are surrounded by sphagnum bogs or papyrus swamps (e.g., Lake Nabugabo near the north-western shore of Lake Victoria) have low pH, oxygen, and salinity levels, and contain very few molluscs (Beadle & Lind, 1960). Similar conditions probably prevail in the muddy substrata of Lake Victoria, particularly offshore from extensive areas of emergent grasses and papyrus. Although the actual factors that determine the population density of molluscs in such conditions have not been carefully examined, laboratory studies have shown that *B. sudanica* fails to develop under conditions of low salinity and oxygen levels (Beadle & Beadle, 1969). Probably, very muddy substrata are hazardous mainly to the embryos and hatchlings. The decline of *B. choanomphala* in increasingly muddy substrata is not due to the depth of water since these substrata often occur even in shallow water up to 1.0 m deep, compared with the 3–12 m depth at which *B. choanomphala* was found by Webbe (1962). However, the maximum depth of water in which *B. choanomphala* can survive may be determined by oxygen depletion in the bottom layers resulting from thermal stratification in bays (Talling, 1957), since this species has not been observed to rise to the surface for air. Other lake-dwelling pulmonates, including two species of *Bulinus*, have been collected from even greater depths (up to 104 m) in Lake Malawi (Wright et al., 1967).

Although *B. choanomphala* is associated with particular substrata, no association with emergent vegetation was observed. The absence of these snails from such vegetation contrasts with the marked attractiveness of certain aquatic plants for some other lake-dwelling snail hosts of schistosomes, such as *Bulinus truncatus rohlfsi* in the new Volta Lake in Ghana (Paperna, 1969) and *Bulinus (Physopsis)* *africanus* and *Biomphalaria pfeifferi* in Lake Kariba in Zambia (Hira, 1969).

The marked seasonal fluctuations in density and age structure of *B. choanomphala*, and variations between the populations of different bays, could not be accounted for by sampling error of the dredge method alone. Even if the dredge collected only 50% of the snails on the bottom in a transect, differences in snail densities of 10–13-fold at different sites and times of the year could readily be detected. It is suggested that the pronounced seasonal fluctuations in snail densities may depend in part on environmental factors in the lake that may periodically stimulate increased reproductive activity and enhance survival rates. The most obvious cyclic factor is the annual rise and fall in the levels of water averaging 0.5 m (Temple, 1964). In the present study it was seen that peak densities of *B. choanomphala* did not coincide in time in the different populations. Whereas low densities occurred between September 1970 and March 1971 in Mwanza South Bay, high densities were found during the same period in Pasiansi Bay. This suggests that seasonal variations in density are not in fact linked with changes in the level of the lake. On the other hand, fluctuations might be related to more local phenomena, such as the upwellings reported by Fish (1954) and Kitaka (1969), which allow for the mixing of bottom and surface waters and influence the fertility of coastal regions. Thus, it would be of interest to study the annual levels of dissolved nutrients and algal growth in shallow bays in relation to fluctuations in the snail population. Studies on fluctuations in the populations of the ciliates and annelids that are predatory on *B. choanomphala*, might reveal the possibility of biological control. Other more localized phenomena, such as the intermittent inflow of streams carrying nutrient-rich water and predation by fishes, might have more limited effects on particular populations.

The observations on *S. mansoni* infection rates in *B. choanomphala* and *B. sudanica* are preliminary, and further studies over a period of several more years, large samples of snails being screened monthly at several sites, are needed. However, it can at least be said that the relatively high frequency of infection in *B. choanomphala*, despite the large dilution factor in the lake, is no doubt partly a result of the high susceptibility of the species to *S. mansoni*, as shown in laboratory studies. Prentice (1970) reported an infection rate of 38–77% in an Entebbe strain of *B. choanomphala* exposed to 3 miracidia of a local strain of *S. mansoni*. A 57% infection rate has been obtained with a Mwanza strain of *B. choanomphala* exposed to 10 miracidia (Magendantz, unpublished data). Besides variations in the susceptibility of different strains, the following environmental factors might also influence natural infection rates in different populations of *B. choanomphala*: (1) snail densities and age structures on the lake bottom; (2) distance offshore and the depth at which snails occur; (3) the degree of faecal pollution and the nature of the shoreline; and (4) the number of people using particular sites and the proximity of houses and latrines to the lake shore.

Snail densities do not appear to be the decisive factor in determining infection rates since population densities in Pasiansi Bay were as high as those in Mwanza South Bay, but few infected snails were collected from Pasiansi Bay. Second, infected snails were found in Mwanza North Port on several occasions when snail densities were lower than at any time in Mwanza South Bay. In fact, infection rates tended to be directly proportional to the age of the snails and inversely proportional to their density, the highest infection rates occurring when seasonal snail populations contained the largest proportion of adult snails but were at their lowest density. Infection rates also seem to be related to the distance offshore and the depth at which the snails occur. In Pasiansi Bay, where infected snails were collected on only one occasion, the highest densities were found as far as 150 m offshore at depths of 1–3 m, while in many Mwanza North Bay and South Bay sites where infected snails were collected frequently, the highest densities occurred within 30–40 m offshore at depths of 1–3 m. With regard to the nature of the shoreline in relation to infection rates, there is probably a greater chance that faecal matter will be washed into the lake from a sloping shore with continuous seepage, as in Mwanza South Bay, thus allowing for higher infection rates, than from a raised dry shore, as found in much of Pasiansi Bay. Another factor that may contribute to the lower snail infection rates in Pasiansi Bay is the absence of houses and latrines close to the shore, while at Mwanza South there are many houses within 10–50 m from the shore. Nevertheless, despite low snail infection rates, the high prevalence of *S. mansoni* infections in inhabitants using the lake at Pasiansi (McCullough & Eyakuze, unpublished data) suggests that snail infection rates are not necessarily proportional to schistosomiasis prevalence rates. It is possible, however, that if the Pasiansi shore were more heavily inhabited and polluted, snail infection rates and schistosomiasis prevalence would be higher than they are.

It has been suggested that the discharge of sewage from lake steamers contributes to *S. mansoni* transmission in Mwanza North Port. Infected *B. sudanica* and *B. choanomphala* have been found near the Karumo ferry landing, but although the steamers dock nearby, the heavily polluted shore behind the ferry landing is undoubtedly a major source of infection. This landing is considered to be important because of the large numbers of people who pass to and from the ferry and, in the absence of a public latrine and water tap, use the lake.

The present study revealed a relatively high frequency of infected *B. sudanica* in Mwanza in comparison with the results of a recent study on the north shore of Lake Victoria, in which none of 24 500 *B. sudanica* snails from Kampala, Port Bell, and Entebbe were found to be infected (Prentice et al., 1970). Varying infection rates in *B. sudanica*, as in *B. choanomphala*, may be due to both intrinsic and extrinsic (environmental) factors. Different strains of *B. sudanica* seem to vary considerably in susceptibility. McClelland (1962) obtained a 52% infection rate with a Mwanza strain of *B. sudanica* exposed to 8 miracidia. Prentice et al. (1970) reported infection rates of 0–16% in *B. sudanica* from Entebbe and the West Nile exposed to 3 miracidia originating from each of these regions, but an infection rate of 41% with an Entebbe strain of *B. sudanica* exposed to 10 miracidia of a local strain. Local differences in natural infection rates of *B. sudanica* at Mwanza are probably largely the result of external factors; the main factor contributing to high frequencies of infected snails along sections of Mwanza North and South bays appears to be the proximity of snail habitats to open shores where there is much bathing, washing, and fishing, and pollution arising from many houses and latrines. The latter are sometimes so poorly built and badly sited that they drain into the lake. The high frequency of infected *B. choanomphala* and *B. sudanica* suggests that people who are dependent on the lake in any way are likely to be exposed repeatedly to infection. The fact that on average 49% of the children living along the Mwanza South shore are infected with *S. mansoni* (McCullough & Magendantz, 1972) is evidence of intense and regular transmission.

In view of the high prevalence of *S. mansoni* among the inhabitants living near the lake shore, the heavy faecal pollution of the lake in these places, and the high population densities of both *B. choanomphala* and *B. sudanica*, a control programme involving the relocation of housing, improved sanitation, mollusciciding, and chemotherapy will be necessary to reduce *S. mansoni* transmission effectively in Mwanza. Blanket mollusciciding along the entire shoreline (over 13 km), however, would be unwarranted and uneconomic. After the relocation of housing away from the lake shore, land-filling the shoreline, and the provision of more public water taps and latrines, the author would favour selective focal mollusciciding of the lake bottom at selected sites where there is unavoidable human contact with the water, such as at fishing boat landings, and in places where there are high densities of snails. Such focal mollusciciding would not upset the overall balance of aquatic life in the various bays. Clearance of vegetation along the Mwanza shore is to be recommended where it is accompanied by the complete filling-in of the shore and by prohibition of housing, bathing, and defaecation along the shore. By itself, the clearance of emergent vegetation opens up new areas of contact with the lake, removes the source of large amounts of organic matter that are deterrents to the growth of mollusc populations on the lake bottom, and is followed by the formation of grassy seepages and the digging of irrigation furrows in which *B. sudanica* thrive.

In Mwanza, a coordinated " environmental " plan involving the town's medical, water and engineering authorities as well as local leaders and factory managers is urgently needed to safeguard the health of the population. Such a plan should include health education, improved sanitation and water supplies, vector control, and the reduction of industrial pollution.

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RÉSUMÉ

LA BIOLOGIE DE *BIOMPHALARIA CHOANOMPHALA* ET DE *B. SUDANICA* AU REGARD DE LEUR RÔLE DANS LA TRANSMISSION DE *SCHISTOSOMA MANSONI* DANS LE LAC VICTORIA À MWANZA (TANZANIE)

Une étude de la biologie des mollusques hôtes intermédiaires de *Schistosoma mansoni* dans le lac Victoria a été entreprise à Mwanza (Tanzanie) en octobre 1969. On se proposait de déterminer la répartition et les variations saisonnières de *Biomphalaria choanomphala* et de *B. sudanica* en fonction de la nature des sédiments du lac et des caractéristiques de la rive et d'analyser les facteurs agissant sur l'intensité de la transmission de *S. mansoni*.

Les recherches ont été effectuées en 70 endroits, près de Mwanza ou dans les baies voisines, les mollusques étant recueillis à l'aide d'un filet métallique traîné sur le fond du lac. On a relevé une nette corrélation entre d'une part les variations de la répartition et de la densité de *B. choanomphala* et d'autre part les caractéristiques physiques du fond et de la végétation de la rive. Près de la rive, où le fond était formé d'un mélange de sable et de vase, la densité des mollusques atteignait 1–20/m^2; plus au large, où la vase prédominait, elle était inférieure à 1/m^2.

Les populations de *B. choanomphala* présentaient des variations saisonnières de la structure par âge et leur densité fluctuait dans des proportions atteignant 10–13 fois. Des amas d'œufs ont été récoltés en abondance et en nombre variable suivant la saison. Deux formes du vecteur, une grande et une petite, correspondant peut-être à des écophénotypes, ont été identifiées. *B. choanomphala* était infecté par *S. mansoni* dans la proportion de 0,2 à 3,3%; les taux d'infection semblaient plus élevés quand la population était formée en majeure partie de mollusques adultes.

On a découvert *B. sudanica* dans de nombreux habitats situés au-dessus du niveau du lac, principalement dans les zones herbeuses où l'eau s'était infiltrée et dans les rigoles d'irrigation. La période de reproduction maximale de l'espèce s'étendait sur la saison des pluies et le début de la saison sèche. Des populations denses se sont maintenues dans les rigoles d'irrigation pendant la longue saison sèche de 1970–71; dans les zones herbeuses asséchées, les mollusques n'ont pas survécu plus de 3 mois.

On a fréquemment trouvé des *B. choanomphala* et *B. sudanica* émettant des cercaires de *S. mansoni* dans des endroits fortement pollués par des matières fécales et le long des portions de rive les plus fréquentées. Ces facteurs, de même que la fréquence des approvisionnements en eau, la proximité des habitations et la présence d'habitats de mollusques à faible distance de la rive semblent en grande partie responsables des variations des taux d'infection suivant les endroits.

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