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Food selection by freshwater snails in the Gezira irrigation canals, Sudan

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Abstract

Stomach content analysis was carried out on samples of the freshwater snail species *Biomphalaria pfeifferi*, *Bulinus truncatus*, *Bulinus forskalii* (Pulmonata, Planorbidae), *Lymnaea natalensis* (Pulmonata, Lymnaeidae), *Melanoides tuberculata*, *Cleopatra bulimoides* (Prosobranchia, Thiaridae) and *Lanistes carinatus* (Prosobranchia, Ampullariidae) from different irrigation canals in Sudan. In order to evaluate overlap in diet selection among these species, sites with two or more of the above-mentioned species present were selected. For some species food choice was examined in relation to size groupings. In addition, samples of *Marisa cornuarietis* (Prosobranchia, Ampullariidae) from small ponds in Sudan, samples of *Biomphalaria pfeifferi* and *Helisoma duryi* (Pulmonata, Planorbidae) from drainage canals in an irrigation scheme in northern Tanzania, and samples of *H. duryi* from fish ponds in the coastal area of Kenya were also analysed.

The results indicate a great similarity in the food choice of these species, especially among the pulmonate species. All species feed on fine detritus, epiphytic algae and decaying macrophytes. No fresh fragments of aquatic macrophytes were found and animal remains were found only on a few occasions. However, the stomach contents of the ampullarid species were characterized by large fragments of dead macrophyte tissue, while the composition of the finer particles showed a great resemblance to that of the pulmonate species. The diet of the thiarid species is essentially the same as that of the pulmonate species, although in one site *Cleopatra bulimoides* showed a greater preference for green algae. Apart from the avoidance of blue-green algae, there was little evidence of selection of certain algal components of the Aufwuchs for the pulmonate species. Detritus constitutes the major component of the stomach content of all these snail species.

Introduction

Earlier snail surveys in the Gezira-Managil irrigation canals in Sudan revealed strong positive association between several pairs of snail species (Madsen *et al.*, 1988). The most important of these associations were between *Biomphalaria pfeifferi* (Krauss), *Bulinus truncatus* (Audouin), *Cleopatra bulimoides* (Olivier) and *Lanistes carinatus* (Olivier) (Madsen *et al.*, 1988). The distribution of these snail species in relation to habitat (i.e. canal type or section of canal) and various plant species indicated a great similarity in their habitat preferences (Madsen *et al.*, 1988). Therefore, interspecific competition between them might be expected, unless some unidentified niche differences exist or if character displacement occurs in sympatric populations as has been demonstrated for some species of the Hydrobiidae (Fenchel, 1975; Fenchel & Kofoed, 1976).

One of the factors that might form the basis of niche separation between the freshwater snails could be the food. The present study was therefore designed to compare the food choice of a number of sympatric populations of the freshwater snails present in the Gezira irrigation canals. It was considered that such information would be highly relevant to research on biological control of the intermediate hosts by other snail species which are non-susceptible to schistosome infection and which may act as competitors. At present, this is the most promising approach to biological control of the intermediate hosts (World Health Organization, 1984b). Therefore, the food choice of two species of such potential competitors was also examined. These were *Helisoma duryi* (Wetherby) (World Health Organization, 1984a) and *Marisa cornuarietis* (L.) (World Health Organization, 1982). Madsen (1983) found virtually no overlap in the distribution of *Biomphalaria pfeifferi* and *Helisoma duryi* in drainage canals in an irrigation scheme in northern Tanzania, although *H. duryi* had existed in the area for several years and *B. pfeifferi* was wide spread. Laboratory trials have shown that competition for food resources is involved in the competition between *H. duryi* and various species of intermediate hosts (see World Health Organization, 1984a for references).

Methods

Sites and species studied and field sampling

The primary part of this study was carried out in the Gezira Agricultural Scheme and this area and its canal system have been described by Madsen *et al.* (1988). In this area the following snail species are abundant: *Biomphalaria pfeifferi*, *Bulinus truncatus*, *Bulinus forskalii* (Ehrenberg) (Pulmonata, Planorbidae), *Lymnaea natalensis* Krauss (Pulmonata, Lymnaeidae), *Melanoides tuberculata* (Müller), *Cleopatra bulimoides* (Prosobranchia, Thiaridae) and *Lanistes carinatus* (Prosobranchia, Ampullariidae) (Madsen *et al.*, 1988). Study sites were located in minor canals or 'Abu Eshreens', i.e. field canals fed from minor canals (Madsen *et al.*, 1988). Study sites where relatively dense populations of two or more species occurred were selected. Snails were sampled within a homogenous part of the canal (in terms of aquatic weeds) and preserved directly in 70% ethanol. The shells of larger specimens of pulmonate snails and shells of all prosobranch snails were pierced to facilitate penetration of the fixative. Upon return to the laboratory the fixative was renewed.

For some sites, samples of the Aufwuchs (McMahon *et al.*, 1974) including the associated detritus particles on the submerged aquatic plants were taken for comparison with the composition of the snail stomach content. Samples of the submerged plants were shaken to remove excess water and then squeezed over a wide-mouthed container (West & Fritsch, 1927). These samples were preserved in 10% formalin. A few samples of the uppermost part (2–3 mm) of the sediment were also taken for analysis of algal components as described below for the samples of stomach content.

For some populations, snails were divided into various size classes depending on the species (see results).

Samples of *Marisa cornuarietis* (L.) (Prosobranchia, Ampullariidae) were taken as described above from small earth-lined ponds established for breeding of this species in the Gezira Scheme, Sudan. These ponds were free from aquatic macrophytes apart from a few reeds.

Three samples of *Biomphalaria pfeifferi* and two samples of *Helisoma duryi* (Pulmonata, Planorbidae) from drainage canals in an irrigation scheme in northern Tanzania (Madsen, 1983) were treated as above. The selected drainage canals were rich in aquatic macrophytes, both submerged and emergent. Furthermore, four samples of *H. duryi* from fish ponds (Haller, 1974) in the coastal area of Kenya were included. The ponds selected contained dense growth of *Myriophyllum* sp. and/or *Nymphaea* sp..

Isolation and characterization of stomach content

For all pulmonate snail species (see above), the stomach (i.e. part of the oesophagus, the crop, the gizzard and pylorus) was dissected out and transferred to 10% formalin for later analysis. Only the crop content was utilized for the analysis of food choice. The crop was opened by using two sharp needles and the content gently shaken out. The crop contents of a number of snails (depending on the collection) were pooled for the analysis.

For the ampullarid snails, *Lanistes carinatus* and *Marisa cornuarietis*, the stomachs were dissected out and part of the content of the cardiac section (Demian, 1964; Berthold, 1988) was taken out. The stomach contents from several specimens were pooled.

For the thiarid snails, *Cleopatra bulimoides* and *Melanoides tuberculata*, the content of the posterior part of the stomach, i.e. opposite the pouch containing the crystalline style, was used (Berry, 1974). Some stomachs were found to be empty in these species, and the crystalline style was not observed in all specimens.

For a sample of 10 specimens of *Biomphalaria pfeifferi* and *Helisoma duryi* the content of the pylorus was taken out for comparison with their crop content, and for 10 specimens of *Lanistes carinatus* and *Cleopatra bulimoides*, the composition of faecal samples was compared with that of the stomach content.

Stomach content samples were transferred to 25 ml of 10% formalin and broken up using a magnetic stirrer for 20 minutes. The relative proportions of the various food items were estimated from a subsample using a haemocytometer. A drop of the suspension was placed in the haemocytometer and the numbers of each of the different items were assessed by systematically scanning through each subsample. Twenty replicate aliquots were taken for each sample.

Food items were categorized in the following way: detrital particles $< 10\ \mu m$; detrital particles 10–25 μm; detrital particles 25–50 μm; detrital particles $> 50\ \mu m$; colony-forming blue-green algae; filamentous blue-green algae; diatoms; desmids; filamentous green algae (recorded as the number of cells); other green algae; plant epidermis.

The stomach content of the two ampullarid species was dominated by large fragments of decaying aquatic macrophytes and these could not be quantified by the above method since they could not enter the pipette and sedimented rapidly. Therefore a one ml sample (i.e. macrosample) was taken out after thorough mixing and examined under a dissecting microscope at 40 × magnification. The numbers of plant tissue and of animal tissue remains were counted, while their sizes were not determined. This analysis was also done for samples from pulmonates. The number of plant parts per mg of organic material (see below) or per snail stomach was calculated. These figures, however, are difficult to compare between the pulmonate and the large prosobranch snails as the size of plant parts varied between the two groups.

After estimating the food components, samples were filtered through a Whatman GF/C filter that had been heated to 500 °C for 40 min, cooled in a desiccator and weighed to the nearest 0.1 mg. Filters were dried at 70 °C for 18 hours and the total dry weight was determined, and then samples were heated to 500 °C for 40 min and after cooling the filters were weighed. Percentage weight loss (organic content) was calculated only for samples with a dry weight of more than 0.5 mg.

Food choice experiment in laboratory

Freshly collected *Ceratophyllum demersum* L., *Potamogeton crispus* L. and *P. perfoliatus* L. were put into an aquarium with 25 litres of water and then 30 snails each of, *Helisoma duryi*, *Biomphalaria pfeifferi* and *Bulinus truncatus*, were allowed to feed for 48 hours. Snails were removed and treated as described for field collected snails.

Analysis of findings

Comparisons of the abundance of the various food items among species or size groups were done by G-test (Sokal & Rohlfs, 1969).

Niche overlap in diet use was calculated according to the formula given by Pianka (1973), where overlaps among species (O_{xy}) are given by

$$O_{xy} = \frac{\sum_{i}^{n} p_{xi} p_{yi}}{\sqrt{\sum_{i}^{n} p_{xi}^2 p_{yi}^2}},$$

where p_{xi} and p_{yi} represent the percentage use by species x and y of the same resource category. Values > 0.75 are generally considered indicative of high overlap between species (Pianka & Pianka, 1976). The formula was also employed to compare the similarity of the abundance of food items in the Aufwuchs and in the stomach content of snails.

Results

A total of 1281 snails were collected from 7 sites in the Gezira Agricultural Scheme. In addition, 224 snails from 5 sites in drainage canals in the Tanganyika Planting Company (Madsen, 1983) and 93 snails from 4 fish ponds at the Bamburi Cement Factory, Kenya (Haller, 1974) were included.

Comparison of the crop and pylorus content in one sample of 10 specimens of *Biomphalaria pfeifferi* and a similar sample of *Helisoma duryi* (Fig. 1) did not show statistical significant differences in relative composition, while the stomach content and faecal pellets varied significantly in composition in *Lanistes carinatus* ($P < 0.001$) and in *Cleopatra bulimoides* ($P < 0.001$).

Results from all samples are summarized in Table 1 and 2. The total dry weight of the content per stomach varied considerably among samples of the same snail species; part of this variation

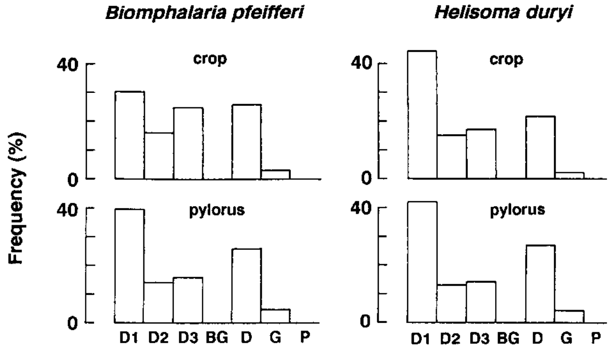

Fig. 1. Percentage composition of crop and pylorus content of a sample of 10 specimens of *Biomphalaria pfeifferi* and *Helisoma duryi.* D1: detritus particles <25 μm; D2: detritus particles 25–50 μm; D3: detritus particles >50 μm; BG: bluegreen algae; D: diatoms; G: green algae and P: plant parts.

could be attributed to variations in the sizes of snails (see below), and in some samples of *Bulinus truncatus* the crop was empty wherefore samples were then taken from the pylorus. The amount of organic material in the crop content also varied considerably among samples, the minimum recorded was 7% in a sample from *Lymnaea natalensis* Krauss and the maximum (93%) in *B. pfeifferi* from Tanzania. Also the Aufwuchs and sediment samples varied considerably in the content of organic material. The inorganic material in the crop of pulmonates was mainly small sand grains, while these were not common in any of the prosobranch species. The number of plant parts (in the 1 ml macro sample) per mg organic material or per snail stomach are not comparable among the pulmonate species and the large prosobranch snails, i.e. *Lanistes carinatus* and *Marisa cornuarietis*. The content of these two species was dominated by large parts of dead plant material. In the pulmonate species and the two thiarid species the occurrence of plants as estimated from the microsample is more useful.

It is evident that the food choice of all the snail species was quite similar with detritus forming the major component followed by diatoms and green algae (Table 2). Blue-green algae were consumed only to a limited extent except for one sample of *M. cornuarietis* (Table 2). However, there was a

Table 1. Total dry weight, organic content (%), no. of plant fragments mg^{-1} and no. of plant fragments $snail^{-1}$ of stomach content samples of various snail species and Aufwuchs or sediment samples. Numbers in brackets indicate minimum and maximum values observed.

Species	No	Dry weight $snail^{-1}$ (mg)	No	Organic content (%)	No	Plants mg^{-1}	No	Plants $snail^{-1}$
Sudan								
B. pfeifferi	9	0.07 (0.005–0.17)	8	34 (18–67)	8	87 (0–302)	9	30 (0–65)
B. truncatus	8	0.21 (0.03–0.48)	8	29 (22–43)	7	28 (6–45)	8	58 (4–194)
B. forskalii	1	0.05	1	20	0	–	1	8
L. natalensis	6	0.18 (0.03–0.33)	6	29 (7–64)	4	8 (0–11)	6	18 (0–34)
L. carinatus	6	1.62 (0.44–4.14)	6	46 (19–71)	6	77 (15–311)	6	838 (106–2525)
M. cornuarietis	3	1.63 (0.43–3.23)	3	47 (37–62)	3	202 (49–476)	3	2188 (557–3175)
C. bulimoides	2	0.08 (0.03–0.12)	1	58	1	6	2	20 (10–30)
M. tuberculata	1	0.22	1	38	1	17	1	35
Aufwuchs samples	–	–	2	20 (7–32)	2	2 (2–2)	–	–
Sediment samples	–	–	3	19 (10–32)	3	10 (1–10)	–	–
Tanzania (TPC)								
B. pfeifferi	3	0.16 (0.08–0.30)	3	58 (21–93)	3	146 (1–340)	3	106 (4–193)
H. durvi	2	0.09 (0.02–0.17)	2	49 (23–75)	2	200 (47–353)	2	77 (47–106)
Kenya (Bamburi)								
H. durvi	4	0.33 (0.15–0.55)	4	37 (31–41)	4	35 (8–107)	4	71 (15–160)

Table 2. Relative abundance (% of all particles) of various food categories in stomach content samples of various snail species and Aufwuchs or sediment samples. Numbers in brackets indicate minimum and maximum values observed.

	No	Detritus total	Blue-green algae	Diatoms	Green algae	Plants
Sudan						
B. pfeifferi	9	73 (45–86)	0.2 (0.0–0.8)	17 (7–49)	9 (0–17)	1 (0–3)
B. truncatus	8	75 (49–92)	0.1 (0.0–0.5)	16 (5–45)	8 (1–13)	1 (0–1)
B. forskalii	1	93	0.0	1	3	3
L. natalensis	6	63 (50–79)	0.5 (0.0–2.9)	31 (9–45)	4 (2–6)	2 (0–5)
L. carinatus	6	75 (54–87)	0.0	23 (13–37)	2 (0–9)	1 (0–3)
M. cornuarietis	3	89 (78–96)	3.3 (0.0–9.9)	6 (4–7)	1 (0–2)	1 (0–2)
C. bulimoides	2	52 (33–72)	0.0	9 (2–16)	37 (10–64)	1 (1–2)
M. tuberculata	1	71	0.0	27	1	1
Aufwuchs samples	2	55 (30–79)	24.1 (0.0–48.2)	13 (8–18)	7 (3–12)	1 (0–1)
Sediment samples	3	80 (51–98)	0.4 (0.0–1.1)	19 (1–47)	1 (1–1)	0
Tanzania (TPC)						
B. pfeifferi	3	76 (69–81)	3.1 (1.3–6.1)	17 (9–23)	1 (0–3)	3 (3–4)
H. durvi	2	85 (79–92)	0.3 (0.0–0.7)	10 (4–17)	0	4 (3–5)
Kenya (Bamburi)						
H. durvi	4	67 (42–83)	0.7 (0.0–1.3)	30 (14–57)	0	2 (1–4)

great variation among samples in the relative composition of the various food items, and this variation probably depended on the composition of the available food in the site. Some of the samples will be discussed in greater detail below.

Site 1

The site was a 2 m stretch in the proximal part of an 'Abu Eshreen' i.e. field canal approximately 0.7–1.0 m wide and 0.6 m deep (see Madsen *et al.*, 1988), and contained a dense growth of *Potamogeton crispus* (degree of cover > 75%) and dense populations of *Biomphalaria pfeifferi* and *Bulinus truncatus* and some *Cleopatra bulimoides*. Details about the samples analysed are given in Table 3.

The dry weight of the stomach content per snail increased with size category. The percentage weight loss is slightly greater in the largest size groups of both *B. pfeifferi* and *B. truncatus*, and the number of plants per snail seems to be somewhat greater in the two larger size groups of *B. truncatus* (Table 3). The organic content of the Aufwuchs sample is rather low i.e. 7% and this is due to silt particles that have settled on the plants. The weight loss of the stomach contents was considerably greater than that of the Aufwuchs.

The composition of the stomach content of the various size groups is shown in Fig. 2. Differences among size groups in percentage composition of the various food items were significant ($P < 0.001$) in *B. truncatus* while this was not the case in *B. pfeifferi*. However, niche overlaps between size classes are very high in both species, with the lowest values recorded for comparisons between the smallest and largest snails (Table 4).

The pooled results for all size groups of each species are shown in Fig. 3. There is a great similarity between *B. pfeifferi* and *B. truncatus*, and the differences were not statistically significant. The stomach content composition also showed a great similarity to the composition of the Aufwuchs, though there were significant differences ($P < 0.001$) for both species. The great similarity among these samples was also reflected in the great niche overlaps (Table 5). *C. bulimoides* on the other hand showed a great preference for green algae (Fig. 3).

Table 3. Details, i.e. no. of snails, dry weight, organic content, and plant fragments (in macro-sample) of stomach content samples of *Biomphalaria pfeifferi* and *Bulinus truncatus* of various sizes, *Cleopatra bulimoides* and a sample of the Aufwuchs in site 1.

	Size (mm)	No. of snails	Dry weight (mg)	Dry weight snail^{-1}	Organic content (%)	Plant parts mg^{-1}	Plant parts snail^{-1}
B. pfeifferi	<3	43	0.2	0.005	–	–	8
	3.1–5.0	74	2.4	0.032	25	302	61
	5.1–8.0	103	5.7	0.055	18	148	36
	8.1–10.0	67	5.5	0.082	25	125	65
	10.1–13.0	13	1.7	0.131	35	53	62
B. truncatus	<3	30	0.8	0.027	25	–	5
	3.1–5.0	71	6.0	0.085	28	45	27
	5.1–8.0	83	8.7	0.105	23	26	15
	8.1–10.0	44	14.1	0.321	24	38	74
	10.1–13.0	21	10.0	0.476	32	36	136
	> 13.1	8	3.7	0.463	43	39	194
C. bulimoides	–	10	0.3	0.030	–	–	30
Aufwuchs	–	–	59.9	–	7	2	–

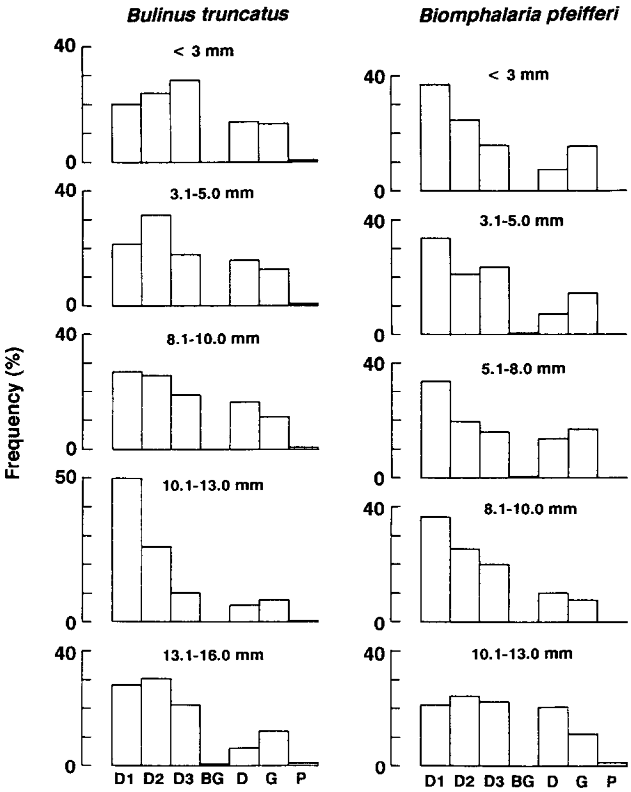

Fig. 2. Percentage composition of the crop content of *Bulinus truncatus* and *Biomphalaria pfeifferi* of various sizes from site 1. Symbols as in Fig. 1. The size class 5.1–8.0 mm of *B. truncatus* was omitted as detritus particles were wrongly classified.

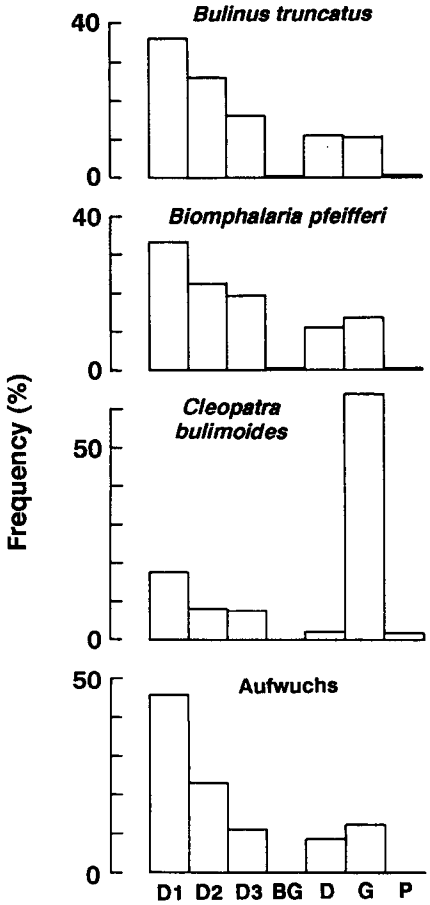

Fig. 3. Percentage composition of the crop content of *Bulinus truncatus*, *Biomphalaria pfeifferi*, *Cleopatra bulimoides* and the percentage composition of organic particles in the Aufwuchs sample from site 1. Symbols as in Fig. 1.

Table 4. Niche overlap (Oxy-values) between various size categories of *Biomphalaria pfeifferi* and *Bulinus truncatus* from site 1.

Size (mm)	Size (mm)				
	<3.0	3.1–5.0	5.1–8.0	8.1–10.0	10.1–13.0
Bulinus truncatus					
3.1–5.0	0.96	–	–	–	–
5.1–8.0	*	*	–	–	–
8.1–10.0	0.96	0.98	*	–	–
10.1–13.0	0.75	0.80	*	0.87	–
13.1–16.0	0.75	0.80	*	0.87	1.00
Biomphalaria pfeifferi					
3.1–5.0	0.98	–	–	–	–
5.1–8.0	0.98	0.97	–	–	–
8.1–10.0	0.98	0.98	0.97	–	–
10.1–13.0	0.90	0.92	0.93	0.92	–

* Omitted as detrital particles were wrongly classified.

Table 5. Oxy-values between *Biomphalaria pfeifferi* (pooled data for all size groups), *Bulinus truncatus* (pooled data of all size groups), *Cleopatra bulimoides* and the Aufwuchs sample from site 1.

	Biomphalaria pfeifferi	*Bulinus truncatus*	*Cleopatra bulimoides*
Bulinus truncatus	0.95	–	–
Cleopatra bulimoides	0.54	0.43	–
Aufwuchs	0.96	0.99	0.50

Site 2

The site was a 2 m stretch in the proximal part of a field canal (i.e. 'Abu Eshreen'; Madsen *et al.*, 1988) with dense growth of submerged plants composed primarily of *Potamogeton crispus* and *P. perfoliatus* (degree of cover: 25–50%). In addition, a dense growth of filamentous blue-green algae (*Anabaena* sp.) was observed. Snail and Aufwuchs samples were taken from the submerged plants.

Results are summarised in Table 6 and Fig. 4. The Aufwuchs sample was dominated by blue-green algae and diatoms, while detrital and silt particles were less abundant than in the Aufwuchs sample from site 1. This may be due to a more swift flow of water. The variation could also be due to variations in the turbidity between the minor canals from where they receive water. The three species showed a great similarity in their feeding niches (Table 7), but there were significant differences among the species in the relative abundance of the various components ($P < 0.01$). The algal content was dominated by diatoms in both *Biomphalaria pfeifferi* and *Bulinus truncatus*, while

Table 6. Details, i.e. no. of snails, dry weight, organic content and plant fragments (in macro-sample) of stomach content samples of snails from site 2-4.

	Size (mm)	No. of snails	Dry weight (mg)	Dry weight snail^{-1}	Organic content (%)	Plant parts mg^{-1}	Plant parts snail^{-1}
Site 2							
B. pfeifferi	6.0–9.0	36	1.2	0.033	67	0	0
B. truncatus	7.0–10.0	71	7.4	0.104	35	7	6
L. natalensis	11.0–15.0	18	2.8	0.156	7	–	10
Aufwuchs	–	–	42.7	–	32	2	–
Site 3							
B. pfeifferi	8.0–15.0	63	10.4	0.165	19	23	18
B. truncatus	8.0–10.0	47	5.1	0.109	22	6	4
L. natalensis	< 10.0	43	1.4	0.033	64	0	0
	10.1–13.0	56	4.6	0.082	20	11	4
	13.1–18.0	45	14.5	0.322	28	11	26
	> 18.0	7	2.3	0.329	48	8	32
Site 4							
B. pfeifferi	5.0–10.0	72	3.2	0.044	31	10	3
B. forskalii	12.0–15.0	10	0.5	0.050	20	–	8
L. natalensis	10.0–11.0	26	4.1	0.158	10	–	34
L. carinatus	9.0–14.0	50	22.1	0.442	48	20	106
	14.1–20.0	37	21.8	0.589	57	29	243
	20.1–27.0	14	17.6	1.257	71	30	659
	27.1–33.0	19	34.0	1.789	59	15	405
M. tuberculata	15.0–30.0	17	3.7	1.789	38	17	35

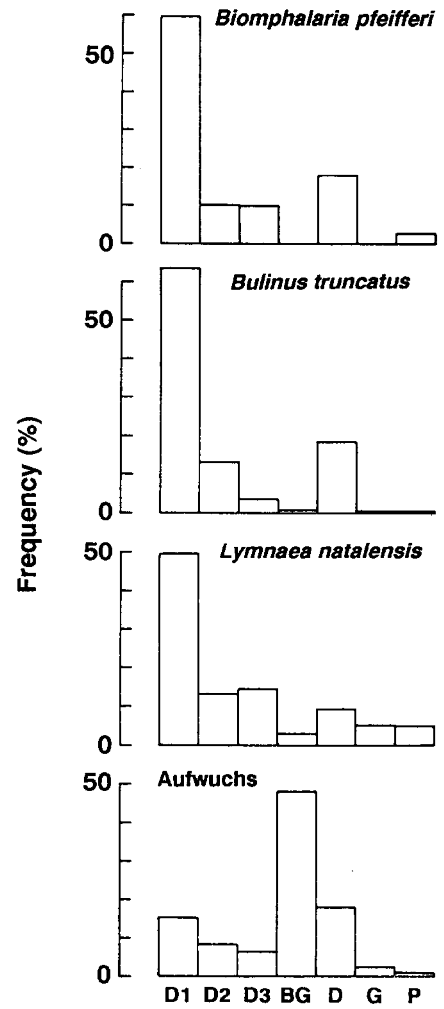

Fig. 4. Percentage composition of the crop content of *Biomphalaria pfeifferi*, *Bulinus truncatus* natalensis and the percentage composition of organic particles in the Aufwuchs sample from site 2. Symbols as in Fig. 1.

Table 7. Oxy-values between *Lymnaea natalensis*, *Biomphalaria pfeifferi*, *Bulinus truncatus* and the Aufwuchs sample from site 2.

	Biomphalaria pfeifferi	*Bulinus truncatus*	*Lymnaea natalensis*
Bulinus truncatus	0.99	–	–
Lymnaea natalensis	0.98	0.96	–
Aufwuchs	0.39	0.39	0.42

in *Lymnaea natalensis* blue-green and green algae were relatively more abundant (Fig. 4).

Site 3

The site was a 2 m stretch in a minor canal (Madsen *et al.*, 1988) with growth of *Vossia cuspidata* (Roxburgh) along the bank and outside this, some growth of *Potamogeton perfoliatus*. Snails were only collected from the *V. cuspidata*. Results are summarised in Table 6 and Figs. 5 and 6. The various size classes of *Lymnaea natalensis* showed very similar food choice with O_{xy}-values ranging from 0.90 to 1.00. Diatoms were the dominating algal component. However, there was a significant difference in the percentage com-

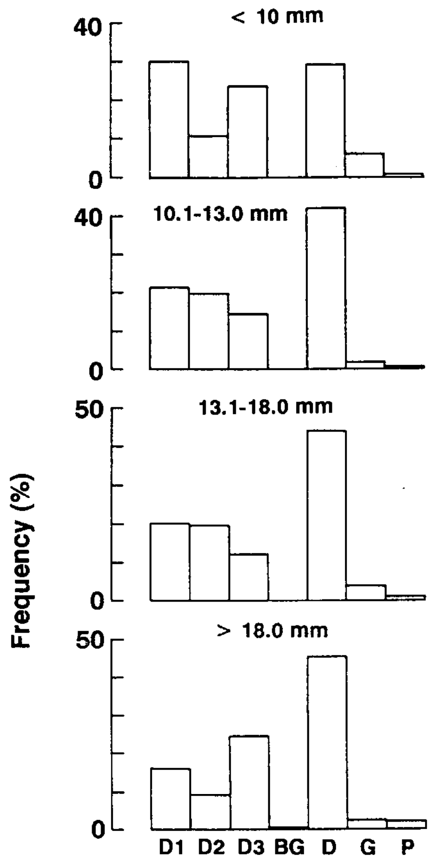

Fig. 5. Percentage composition of the crop content of *Lymnaea natalensis* of various sizes from site 3. Symbols as in Fig. 1.

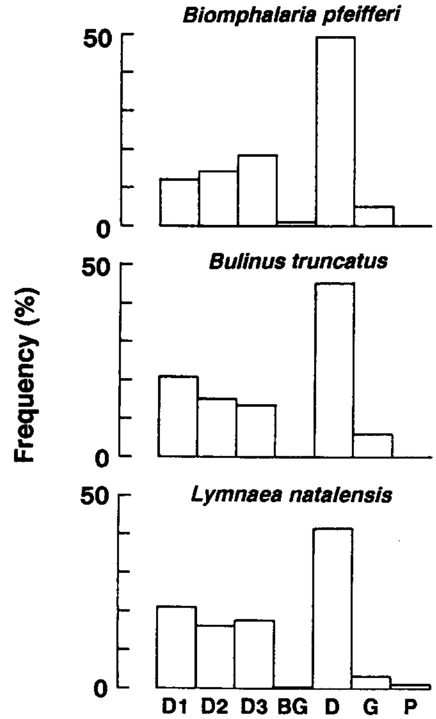

Fig. 6. Percentage composition of the crop content of *Biomphalaria pfeifferi*, *Bulinus truncatus*, and *Lymnaea natalensis* from site 3. Symbols as in Fig. 1.

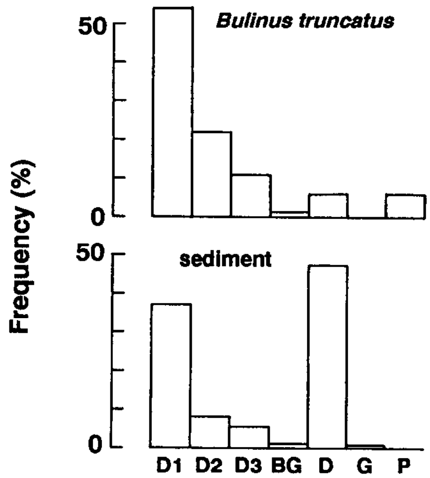

Fig. 7. Percentage composition of the crop content of *Bulinus truncatus* and the percentage composition of organic particles in a sediment sample from site 5. Symbols as in Fig. 1.

position of the various items among size groups ($P < 0.01$). This difference perhaps could be attributed mainly to the variation in the abundance of various size classes of detrital particles. The three species showed very similar food choice with almost identical feeding niches (i.e. O_{xy}-values: 0.98–0.99).

Site 4

The site was a 5 m stretch of a small canal (slightly larger than an Abu Eshreen) with dense growth of *Potamogeton nodosus* Poiret and in patches some grasses and *P. crispus*. Results are summarised in Table 6. The composition of the small particles in the 4 size classes of *Lanistes carinatus* was very similar, with O_{xy} values 0.97–0.99. Likewise, the number of larger plant parts per mg organic material was quite similar in the 4 size classes (Table 6). The overlap values between species were generally high particularly between *Biomphalaria pfeifferi*, *Lymnaea natalensis* and *Lanistes carinatus* (Table 8).

Table 8. Niche overlap (Oxy-values) between *Biomphalaria pfeifferi, Bulinus forskalii, Lymnaea natalensis, Lanistes carinatus* and *Melanoides tuberculata* from site 4.

	Biomphalaria pfeifferi	*Bulinus forskalii*	*Lymnaea natalensis*	*Lanistes carinatus*
Bulinus forskalii	0.88	–	–	–
Lymnaea natalensis	0.99	0.86	–	–
Lanistes carinatus	0.98	0.92	0.99	–
Melanoides tuberculata	0.94	0.76	0.98	0.95

Site 5

The site was located in the terminal part of an 'Abu Eshreen' with no aquatic macrophytes, but with some decaying plants. The sediment was very rich in organic matter, i.e. weight loss 32%, and contained a dense growth of diatoms (Fig. 7). The relative abundance of diatoms in the crop content of *Bulinus truncatus* was much less than in the sediment.

Food choice experiment in laboratory

Results showed a great similarity between species, i.e. O_{xy}-values was 0.84 for *B. pfeifferi*--*B. truncatus*; 0.95 and 0.96 for *H. duryi* compared to *B. pfeifferi* and *B. truncatus*, respectively.

Discussion

The present results confirm that freshwater pulmonate snails are generalist feeders grazing on epiphytic algae, decaying macrophytes and fine detritus as has been demonstrated for several species belonging to the Lymnaeidae, Physidae and Planorbidae (Pimental & White, 1959; Gohar & El-Gindy, 1961; Hunter, 1961; Malek, 1958; Clampitt, 1970a, b; Storey, 1971; Reavell, 1980; Hunter, 1980). No fresh fragments of aquatic macrophytes were found in the present studies and animal remains were found only on a few occasions. Animal remains have also been found in the stomach content of other snail species (Bovbjerg, 1965; Hunter, 1961; Reavell, 1980 and others).

Other studies of the stomach content of pulmonate snails also indicate that live macrophyte tissue is rarely consumed (Boycott, 1936; Calow, 1970; Clampitt, 1970a; Stiglingh & van Eeden, 1970; Reavell, 1980) but there is some controversy about the role of live macrophyte tissue in snail nutrition. Various authors have shown that certain snails will consume live macrophytes (Gaevskaya, 1969 and references therein). Reavell (1980) found fragments of macrophytes more commonly in the larger pulmonates than in the smaller species and the prosobranchs. *Biomphalaria glabrata* (Say) will eat both decaying and fresh macrophytes, but decaying plant material is more important (Pimental & White, 1959; Thomas *et al.*, 1985). Scheerboom & van Elk (1978) found that aquatic macrophytes were not consumed by *Lymnaea stagnalis* (L.) in early summer, but only in the period from August to October and mainly in decomposed condition. Aquatic vascular macrophytes probably have a low nutritional value as judged from their high C : N ratios (McMahon *et al.*, 1974). Thus assimilation and growth of *Biomphalaria glabrata* fed on macrophytes was less than of snails fed on lettuce (Thomas *et al.*, 1983a).

Parts of decaying macrophytes are common in the stomachs of both the pulmonates and the large prosobranchs. Bacteria involved in the decay of both plant and animal remains release appreciable amounts of C-2 to C-5 acids (Patience *et al.*, 1983; Sterry *et al.*, 1985) and there is evidence that these acids may be utilized directly as an energy resource by *Biomphalaria glabrata* (Thomas *et al.*, 1984) and snails are attracted to such compounds (Thomas, 1987). For a detailed discussion of these interactions refer to Thomas (1987).

The composition of the diet depends on the epiphytic community and the stomach contents of snails from different sites reflect differences in the Aufwuchs. However, the present study showed that snails are capable of selecting against blue-green algae. Blue-green algae are rarely preferred by freshwater animals (Calow, 1973b). Thus *Ancylus fluviatilis* (Müller) digests blue-green algae least efficiently and this may explain their reduced appeal to this species (Calow, 1973b). Also *Oncomelania quadrasi* Möllendorff rarely ingested blue-green algae (Dazo & Moreno, 1962). However, certain species of blue-green algae can be used for laboratory maintenance of planorbid snails (Xavier *et al.*, 1968; Thompson, 1984). Blue-green algae gave a good growth in adult *Lymnaea peregra* (Müller), but these algae were inferior for the production of eggs (Skoog, 1978).

Apart from the selection against blue-green algae there was little evidence of selection of certain algae types in the present study. Also Hunter (1980) found that three pulmonate snails appeared to be essentially non-selective within their 'normal' range of food dimensions. Below this range, mechanical selection is likely to occur involving escape of cells which are too small and/or adherent to the substrata (Hunter, 1980). Thus it has been shown that *Coconeis* sp. will not be consumed by grazing snails (Patrick, 1970; Higashi *et al.*, 1981). *Helisoma trivolvis* (Say) showed no evidence of feeding selectivity (Smith, 1989). Baluku *et al.* (1987) found that *Biomphalaria pfeifferi* consumed all the algal forms present, but certain forms were slightly preferred and others slightly neglected. Also *Ancylus fluviatilis* ingests the total range of algal material available to it in nature, but certain types of diatoms are selectively ingested (Calow, 1973b), while *Lymnaea pereger obtusa* (Kobelt) prefers and is able to digest green algae (Calow, 1970, 1973a). Lodge (1986) also found that *L. peregra* selected filamentous green algae, while *Planorbis vortex* (L.) selected diatoms.

There is only slight differences in the food choice of different size groups of both *Biomphalaria pfeifferi*, *Bulinus truncatus* and *Lymnaea natalensis*. The amount of food in the stomach is dependent on snail size. Similarly, Baluku *et al.* (1987) found that the amount of algae in the stomach is proportional to snail size and the amount of algae present on the substrate. Also Baluku *et al.* (1987) found that small snails did not seem to have a more marked food preference than large snails. However, juvenile *Biomphalaria glabrata* has been shown to have a broader chemoreception niche (Thomas & Assefa, 1979; Thomas *et al.*, 1980, 1983b) and a broader feeding niche (Cedeño-León & Thomas, 1982) than adult conspecifics. Thomas *et al.* (1985) found that juvenile *B. glabrata* eat less living macrophytes and fewer large diatoms, but much greater quantities of decaying plants than adults. Ontogenetic differences in diet were also indicated for *Lymnaea peregra* (Skoog, 1978).

Detritus seems to constitute a major component of the food of these freshwater pulmonate snail species. Reavell (1980) also found that detritus formed the bulk of the stomach contents of a number of British freshwater snails and found a tendency for an increase in relative intake of detritus from the larger lymnaeids, through the planorbids to the prosobranchs. Pinel-Alloul & Magnin (1979) found that detritus constituted 50–61% of the gut content of *Lymnaea catascopium catascopium* (Say).

The stomach content of the large prosobranch *Lanistes carinatus* is dominated by big parts of dead macrophytes. There is also a great content of fine detrital particles and an abundance of diatoms. Live macrophytes seem to play no role in the diet of *L. carinatus*. Also *Marisa cornuarietis* in the present investigation seems to feed primarily on decaying macrophytes and fine detrital particles and diatoms. In one pond it also fed on blue-green algae (*Microcystis* sp.) which were abundant. However, the sites from where the snails were collected were free from macrophytes apart for a few reeds. Various authors have demonstrated that *M. cornuarietis* is a voracious consumer of aquatic macrophytes (Demian & Ibrahim, 1969; World Health Organization, 1982 and references in these), and *M. cornuarietis* has been suggested as a biological control agent of aquatic macrophytes (Seaman & Porterfield, 1964). In a small pond in Tanzania, *M. cornuarietis* consumed *Cyperus* spp. (Nguma *et al.*, 1982). Recently, Karoum & Madsen (1989) showed that the establishment of *M. cornuarietis* in irrigation canals in the Sudan led to the almost complete elimination of submerged macrophytes.

Other species belonging to the Ampullariidae have been reported to feed on aquatic macrophytes (Graham, 1955; Andrews, 1965; Paulinyi & Paulini, 1972; Thomas, 1975; Pointier *et al.*, 1988).

The food choice of the smaller prosobranch species, *Cleopatra bulimoides* and *Melanoides tuberculata* resembles that of the pulmonate snails. Pointier & McCullough (1989) also noted that the diet of *M. tuberculata* was essentially the same as that of *Biomphalaria glabrata*. *M. tuberculata* seems to be primarily a bottom dweller in the irrigation canals and the sediments contain a considerable but variable amount of organic matter as well as a dense growth of particularly diatoms. Karim & Ali (1985) also noted a dense growth of diatoms in the sediments of these canals.

The present results show that the pulmonate snails have a great similarity in their food choice with very high niche overlaps. Furthermore, the species included in this study showed very great positive association and thus a great habitat sharing (Madsen *et al.*, 1988) which makes interspecific competition between these species a possibility, particularly between *B. pfeifferi* and *B. truncatus*. In light of the great similarity in feeding niches this competition could be for food. Consumptive competition is by far the most common in freshwater systems and the only other common type is encounter competition (Schoener, 1983). There is evidence that food quantity and/or quality may limit snail populations (Eisenberg, 1966, 1970; Skoog, 1978).

In laboratory choice experiments the stomach contents of *Helisoma duryi*, *Biomphalaria pfeifferi* and *Bulinus truncatus* showed only minor differences. Together with samples from other areas it can be concluded that *H. duryi* essentially feeds on the same diet as the intermediate hosts. *H. duryi* has been suggested as an agent for biological control of the intermediate host snails of schistosomes and the interactions with the intermediate hosts involve consumptive competition as well as encounter competition (World Health Organization, 1984a and references therein). Manipulative field experiments would be required to demonstrate interspecific competition between these species.

There is evidence that competitors may eliminate populations of the intermediate hosts. Thus *Melanoides tuberculata* and *Thiara granifera* occurred in the Caribbean area about 35 years ago and as they have spread they have apparently reduced *Biomphalaria glabrata* populations in certain habitats (Pointer & McCullough, 1989). Experimental introduction of this species into water cress beds resulted in the disappearance of *Biomphalaria glabrata* and *B. straminea* (Pointier *et al.*, 1989). The mechanisms of competition may be based on interference due to the high densities of *M. tuberculata* in these habitats and food competition. *M. tuberculata* feeds on essentially the same diet as *B. glabrata* (Pointier *et al.*, 1989). However, in irrigation canals in the Sudan there was no indication of a negative association between *M. tuberculata* and the intermediate host species (Madsen *et al.*, 1988).

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References

Andrews, E. B., 1965. The functional anatomy of the gut of the prosobranch gastropod *Pomacea canaliculata* (D'Orb.) and some other pilids. Proc. Zool. Soc. Lond. 145: 19–36.

Baluku, B., G. Josens & M. Loreau, 1987. Le régime alimentaire de *Biomphalaria pfeifferi* (Gastropoda: Planorbidae) au Zaïre oriental. Revue Zool. afr. 101: 279–282.

Berry, A. J., 1974. The anatomy of West Malaysian snails of parasitological significance. Malay. Nat. J. 27: 131–165.

Berthold, T., 1988. Anatomy of *Afropomus balanoideus* (Mollusca, Gastropoda, Ampullariidae) and its implications for phylogeny and ecology. Zoomorphology 108: 149–159.

Bovbjerg, R. V., 1965. Feeding and dispersal in the snail *Stagnicola reflexa* (Basommathophora: Lymnaeidae). Malacologia 2: 199–207.

Boycott, A. E., 1936. The habitats of fresh-water Mollusca in Britain. J. anim. Ecol. 5: 116–186.

Calow, P., 1970. Studies on the natural diet of *Lymnaea pereger obtusa* (Kobelt) and its possible implications. Proc. malac. Soc. Lond. 39: 203–215.

Calow, P., 1973a. 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., 1973b. The food of *Ancylus fluviatilis* (Müll.), a littoral stone-dwelling, herbivore. Oecologia 13: 113–133.

Cedeño-León, A. & J. D. Thomas, 1982. Competition between *Biomphalaria glabrata* (Say) and *Marisa cornuarietis* (L.): feeding niches. J. appl. Ecol. 19: 707–721.

Clampitt, P. T., 1970a. Comparative ecology of the snails *Physa gyrina* and *Physa integra* (Basommatophora: Physidae). Malacologia 10: 113–151.

Clampitt, P. T., 1970b. The role of substratum and food in the distribution of the pulmonate snails of Douglas Lake, Cheboygan County, Michigan. Am. Zool. 10: 325.

Dazo, B. C. & R. G. Moreno, 1962. Studies on the food and feeding habits of *Oncomelania quadrasi*, the snail intermediate host of *Schistosoma japonicum* in the Philippines. Trans. am. Microsc. Soc. 81: 341–347.

Demian, E. S., 1964. The anatomy of the alimentary system of *Marisa cornuarietis* (L.). Medd. Göteborgs Mus. Zool. Avd., 138 (Göteborgs K. Vetensk. Vitterh. Samh. Handl., Ser. B. 9 (7): 1–75).

Demian, E. S. & A. M. Ibrahim, 1969. Feeding activities of the snail *Marisa cornuarietis* (L.) under laboratory conditions. Proc. 6th. Arab. Sci. Congr., Damascus 1969 1: 145–165.

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.

Fenchel, T., 1975. Character displacement and coexistence in mud snails (Hydrobiidae). Oecologia 20: 19–32.

Fenchel, T. & L. H. Kofoed, 1976. Evidence for exploitative interspecific competition in mud snails (Hydrobiidae). Oikos 27: 367–376.

Gaevskaya, N. S., 1969. The role of higher aquatic plants in the nutrition of the animals of fresh-water basins. Trans. DG Maitland Müller (ed. KH Mann), vol 1, Ch. 1 & 2. National Lending Library for Science and Technology, Boston Spa, Yorkshire, England.

Gohar, H. A. F. & H. I. El-Gindy, 1961. Food of snail vectors of bilharziasis and fascioliasis. J. Egypt. Med. Ass. 44: 976–982.

Graham, A., 1955. Molluscan diets. Proc. malac. Soc. Lond. 31: 144–159.

Haller, R. D., 1974. Rehabilitation of a limestone quarry. Report of an environmental experiment. Bamburi Portland Cement Co., Ltd., Mombasa, Kenya.

Higashi, M., T. Miura, K. Tanimizu & Y. Iwasa, 1981. Effect of the feeding activity of snails on the biomass and productivity of an algal community attached to a reed stem. Verh. int. Ver. Limnol. 21: 590–595.

Hunter, R. D., 1980. Effects of grazing on the quantity and quality of freshwater Aufwuchs. Hydrobiologia 69: 251–259.

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: 219–253.

Karim, A. G. A. & O. M. M. Ali, 1985. Studies on the freshwater algae of the Sudan. Sudan. J. Sci. 1: 1–12.

Karoum, K. O. & H. Madsen, 1989. Field trials to control the intermediate hosts of schistosomes in Gezira irrigation canals by competitor snails. Abstr. 10th. Int. Malacol. Congr. Tübingen p. 125.

Lodge, D. M., 1986. Selective grazing on periphyton: a determinant of freshwater gastropod microdistributions. Freshw. Biol. 16: 831–841.

McMahon, R. F., R. D. Hunter & W. D. Russell-Hunter, 1974. Variation in Aufwuchs at six freshwater habitats in terms of carbon biomass and of carbon : nitrogen ratio. Hydrobiologia 45: 391–404.

Madsen, H., 1983. Distribution of *Helisoma duryi*, an introduced competitor of intermediate hosts of schistosomiasis, in an irrigation scheme in northern Tanzania. Acta Trop. 40: 297–306.

Madsen, H., A. A. Daffalla, K. O. Karoum & F. Frandsen, 1988. Distribution of freshwater snails in irrigation schemes in the Sudan. J. appl. Ecol. 25: 853–866.

Malek, E. A., 1958. Factors conditioning the habitat of bilharziasis intermediate hosts of the family Planorbidae. Bull. WHO 18: 785–818.

Nguma, J. F. M., F. S. McCullough & E. Masha, 1982. Elimination of *Biomphalaria pfeifferi*, *Bulinus tropicus* and *Lymnaea natalensis* by the ampullarid snail, *Marisa cornuarietis*, in a man-made dam in northern Tanzania. Acta Trop. 39: 85–90.

Patience, R. L., P. R. Sterry & J. D. Thomas, 1983. Changes in the chemical composition of a decomposing aquatic macrophyte, *Lemna paucicostata*. J. Chem. Ecol. 9: 889–911.

Patrick, R., 1970. Benthic stream communities. A discussion of the factors that affect their structure and how they function. Am. Sci. 58: 546–549.

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

Pianka, E. R., 1973. The structure of lizard communities. Ann. Rev. Ecol. Syst. 4: 53–74.

Pianka, E. R. & H. D. Pianka, 1976. Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australian desert. Copeia 1976: 125–142.

Pimentel, D. & P. C. White Jr., 1959. Biological environment and habits of *Australorbis glabratus*. Ecology 40: 541–550.

Pinel-Alloul, B. & É. Magnin, 1979. Étude de la nourriture de *Lymnaea catascopium catascopium* (Gastropoda, Lymnaeidae) dans le lac Saint-Louis, fleuve Saint-Laurent, Québec. Naturaliste Can. 106: 277–287.

Pointier, J. P., A. Théron & D. Imbert-Establet, 1988. Decline of a sylvatic focus of *Schistosoma mansoni* in Guadeloupe (French West Indies) following the competitive displacement of the snail host *Biomphalaria glabrata* by *Ampullaria glauca*. Oecologia 75: 38–43.

Pointier, J. P., A. Guyard & A. Mosser, 1989. Biological control of *Biomphalaria glabrata* and *B. straminea* by the competitor snail *Thiara granifera* in a transmission site of schistosomiasis in Martinique, French West Indies. Ann. Trop. Med. Parasit. 83: 263–269.

Pointier, J. P. & F. McCullough, 1989. Biological control of the snail hosts of *Schistosoma mansoni* in the Caribbean area using *Thiara* spp. Acta Trop. 46: 147–155.

Reavell, P. E., 1980. A study of the diets of some British freshwater gastropods. J. Conch. 30: 253–271.

Scheerboom, J. E. M. & R. van Elk, 1978. Field observations on the seasonal variations in the natural diet and the haemolymph-glucose concentration of the pond snail *Lymnaea stagnalis* (L.). Proc. Kon. Ned. Akad. Wet., Ser. C., 81: 365–376.

Schoener, T. W., 1983. Field experiments on interspecific competition. Am. Nat. 122: 240–285.

Seaman, D. E. & W. A. Porterfield, 1964. Control of aquatic weeds by the snail *Marisa cornuarietis*. Weeds 12: 87–92.

Skoog, G., 1978. Influence of natural food items on growth and egg production in brackish water populations of *Lymnaea peregra* and *Theodoxus fluviatilis* (Mollusca). Oikos 31: 340–348.

Smith, D. A., 1989. Tests of feeding selectivity in *Helisoma trivolvis* (Gastropoda: Pulmonata). Trans. am. Microsc. Soc. 108: 394–402.

Sokal, R. R. & F. J. Rohlf, 1969. Biometry. The principles and practice of statistics in biological research. WH Freeman and Company; San Francisco.

Sterry, P. R., J. D. Thomas & R. L. Patience, 1985. Changes in the concentrations of short-chain carboxylic acids and gases during decomposition of the aquatic macrophytes *Lemna paucicostata* and *Ceratophyllum demersum*. Freshw. Biol. 15: 139–153.

Stiglingh, I. & J. A. van Eeden, 1970. Notes on the feeding behaviour of *Bulinus* (*Bulinus*) *tropicus* (Krauss) Basommatophora: Planorbidae. Wet. Bydr. P.U.C.H.O. Reeks B Naturwet. 22: 1–14.

Storey, R., 1971. Some observations on the feeding habits of *Lymnaea peregra* (Müller). Proc. malac. Soc. Lond. 39: 327–331.

Thomas, J. D., 1987. An evaluation of the interactions between freshwater pulmonate snail hosts of human schistosomes and macrophytes. Phil. Trans. R. Soc., Lond. B315: 75–125.

Thomas, J. D. & B. Assefa, 1979. Behavioural responses to amino acids by juvenile *Biomphalaria glabrata*, a snail host of *Schistosoma mansoni*. Comp. Biochem. Physiol. 63C: 99–108.

Thomas, J. D., B. Assefa, C. Cowley & J. Ofosu-Barko, 1980. Behavioural responses to amino acids and related compounds, including propionic acid by adult *Biomphalaria glabrata* (Say) a snail host of *Schistosoma mansoni*. Comp. Biochem. Physiol. 66C: 17–27.

Thomas, J. D., B. Grealy & C. F. Fennell, 1983a. The effects of varying the quantity and quality of various plants on feeding and growth of *Biomphalaria glabrata* (Gastropoda). Oikos 41: 77–90.

Thomas, J. D., D. I. Nwanko & P. R. Sterry, 1985. The feeding strategies of juvenile and adult *Biomphalaria glabrata* (Say) under simulated natural conditions and their relevance to ecological theory and snail control. Proc. R. Soc. Lond. B226: 177–209.

Thomas, J. D., J. Ofosu-Barko & R. L. Patience, 1983b. Behavioural responses to carboxylic and amino acids by *Biomphalaria glabrata* (Say), the snail hosts of *Schistosoma mansoni* (Sambon) and other freshwater molluscs. Comp. Biochem. Physiol. 75C: 57–76.

Thomas, J. D., P. R. Sterry & R. L. Patience, 1984. Uptake and assimilation of short chain carboxylic acids by *Biomphalaria glabrata* (Say), the freshwater pulmonate snail host of *Schistosoma mansoni* (Sambon). Proc. R. Soc. Lond. B222: 447–476.

Thomas, K. J., 1975. Biological control of *Salvinia* by the snail *Pila globosa* Swainson. Biol. J. Linn. Soc. 7: 243–247.

Thompson, S. N., 1984. *Spirulina* as a nutrient source in experimental media for maintaining the schistosome vector, *Biomphalaria glabrata*. Ann. Trop. Med. Hyg. 78: 547–548.

West, G. S. & F. E. Fritsch, 1927. A Treatise on the British Freshwater Algae. Cambridge, University Press.

World Health Organization, 1982. Data sheet on the biological control agent, *Marisa cornuarietis* (Linn.). WHO/VBC/82.837, VBC/BCDS/82.18.

World Health Organization, 1984a. Data sheet on *Helisoma* spp. as biological control agents. WHO/VBC/84.894, VBC/BCDS/84.19.

World Health Organization, 1984b. Report of an informal consultation on research on the biological control of snail intermediate hosts. TDR/BCV-SCH/SIH/84.3.

Xavier, M. de L. S., J. F. de A. Azevedo & I. Avelino, 1968. Importance d'*Oscillatoria formosa* Bory dans la culture au laboratoire des mollusques vecteurs du *Schistosoma haematobium*. Bull. Soc. Path. Exot. 61: 52–66.