Journal of Helminthology (2002) **76,** 283–293 DOI: 10.1079/JOH2002132

Larval trematode infections in freshwater snails from the highveld and lowveld areas of Zimbabwe

G. Chingwena[1]*, S. Mukaratirwa[1], T.K. Kristensen[2] and M. Chimbari[3]

[1]University of Zimbabwe, Department of Paraclinical Veterinary Studies, Box MP 167, Harare, Zimbabwe: [2]Danish Bilharziasis Laboratory, Jaegersborg Alle 1D, 2920 Charlottenlund, Denmark: [3]University of Zimbabwe Lake Kariba Research Station, PO Box 48, Kariba, Zimbabwe

Abstract

Between November 1998 and October 2000, freshwater snails were collected monthly from the highveld and lowveld areas of Zimbabwe to determine the occurrence of larval trematodes. A total of 13,789 snails, representing ten species, were collected from 21 sites and 916 (6.6%) harboured patent trematode infections. Eight morphologically distinguishable types of cercariae were identified. *Bulinus tropicus* had the highest overall prevalence of infection (13.1%). The echinostome was the most common type of cercaria recovered, contributing 38.2% of all infections. *Schistosoma* cercariae were recovered mainly from the highveld and comprised 8.0% of all infections. Amphistome cercariae contributed 37.6% of all infections and were recorded from both the highveld and lowveld areas with a peak prevalence occurring during the post-rainy period (March–May). The main intermediate host for amphistomes was *B. tropicus*. Infections in *B. globosus*, *B. forskalii* and *Biomphalaria pfeifferi* with amphistome cercariae are new records for Zimbabwe.

Introduction

Studies on larval trematode infections in freshwater snails in Africa are modest in number (Loker *et al.*, 1981; Appleton & Brock, 1985; Okafor, 1990) in spite of the fact that the documentation of snail species and their larval trematode fauna help in our understanding of snail-borne diseases present as well as the location of potential transmission sites.

Larval trematodes may act as regulators of snail populations if prevalences of infection in natural populations are high (May, 1983; Brown *et al.*, 1988). It is known that certain trematodes may in some cases be responsible for the elimination of snail populations (Loker *et al.*, 1981). In order to assess the regulatory effect of larval trematodes on snail populations, the natural prevalence of trematode infections must be determined. Studies on larval trematodes can also reveal the possible existence of certain trematode species that could be manipulated to achieve biological control of snail-transmitted diseases (Combes, 1982; Davis, 1998). Larval trematode infections can also be used as bio-indicators of environmental quality (Kuris & Lafferty, 1994; Keas & Blankespoor, 1997) in that a change in species richness and prevalence of infection over time may reflect environmental change.

In Zimbabwe, extensive research has been done on the epidemiology and distribution of *Schistosoma haematobium* and *S. mansoni* (Shiff *et al.*, 1975; Clarke, 1977; Taylor & Makura, 1985; Chandiwana *et al.*, 1987, 1988; Woolhouse & Chandiwana, 1989) and *S. mattheei* (Lawrence & Condy, 1970; Chandiwana *et al.*, 1987). Little or no information is available, however, on the abundance, diversity and intermediate host relationship of other trematode species and the present study addresses this by investigating larval trematodes in freshwater snails in the highveld and lowveld areas of Zimbabwe.

*Fax: 263 4 333 683
E-mail:gchingwena@yahoo.com

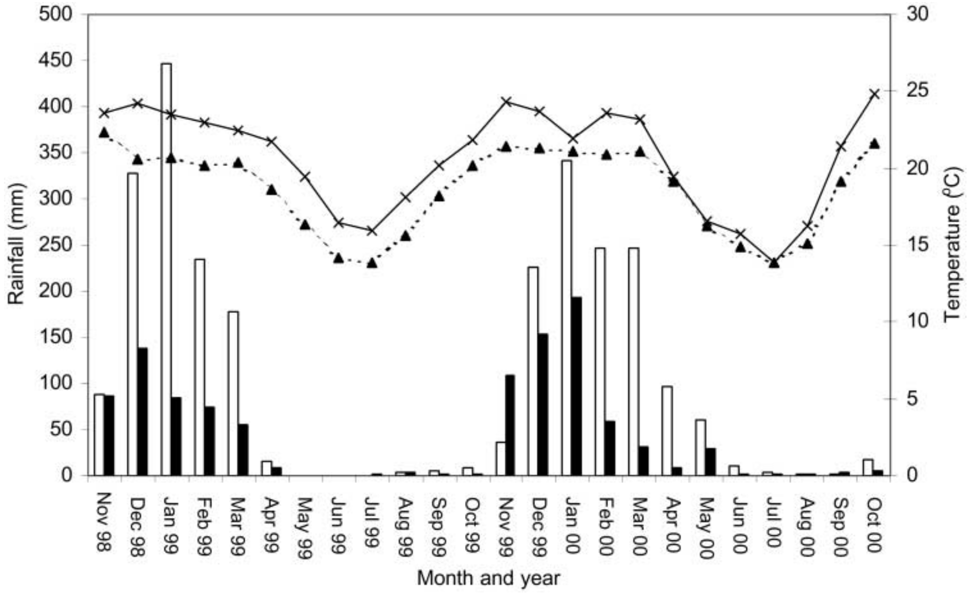

Fig. 1. Mean temperature and rainfall for the highveld (▲, □) and lowveld (× , ■) areas of Zimbabwe between November 1998 and October 2000.

Materials and methods

Study area

The study was carried out in the highveld and lowveld areas of Zimbabwe. The highveld extends from 1000 to 1500 m above sea level and covers most of the northern half of the country. The climate is characterized by temperatures ranging from 25 to 30°C during the rainy season and 15 to 20°C during the dry season. The area receives a mean annual rainfall of 800 to 1200 mm (fig. 1) and is characterized by many swampy areas. The potential snail habitats are generally wide-

Table 1. The overall prevalence (%) of trematode infections in snails collected from 21 habitats in the highveld and lowveld areas of Zimbabwe.

Site	Habitat type*	District	Region	Nature of use of site by people and cattle	Number of snails collected	Number infected with trematodes (%)
Rosa	Stream	Chiweshe	Highveld	D, S, F	1476	52 (3.5)
Nzvimbo	Stream	Chiweshe	Highveld	D, B	461	11 (2.4)
Jaji	Stream	Chiweshe	Highveld	D, W, B	338	41 (12.1)
Manyimo	Dam	Hwedza	Highveld	D, F, L	630	60 (9.5)
Chisasike	Dam	Hwedza	Highveld	D, B, L, F	1011	62 (6.1)
Madzimbahwe	Dam	Hwedza	Highveld	D, B, L, F	649	17 (2.6)
Murewa	Stream	Murewa	Highveld	D, B, F	738	79 (10.7)
Murewa	Dam	Murewa	Highveld	D, B, F	144	9 (6.3)
Chiwake	Dam	Murewa	Highveld	D, F, L	369	37 (10.0)
Madzima	Dam	Zvimba	Highveld	D, F	643	20 (3.1)
Mucheri	Stream	Zvimba	Highveld	D, L	125	2 (1.6)
Murombedzi	Stream	Zvimba	Highveld	D, W	575	11 (1.9)
Vaka	Dam	Zvishavane	Lowveld	D, F	698	170 (24.4)
Zvishavane	Dam	Zvishavane	Lowveld	D, F, L	678	94 (13.8)
Majoni	Dam	Zvishavane	Lowveld	D, F, W, S	1687	25 (1.5)
Skova	Dam	Mberengwa	Lowveld	D, F, W, S	1008	3 (0.3)
Danga	Dam	Mberengwa	Lowveld	D, F, B	601	26 (4.3)
Langeni	Dam	Mberengwa	Lowveld	D, F, W	441	15 (3.4)
Matole	Dam	Plumtree	Lowveld	D, F, W	411	41 (10.0)
Tekwani	Dam	Plumtree	Lowveld	D, B, L	687	95 (13.8)
Madlambuzi	Dam	Plumtree	Lowveld	D, F, L	419	46 (11.0)

D, drinking site for cattle; F, fishing; S, swiming; B, bathing; L, laundry, W, watering vegetables.
* Habitat types are those defined by Makura & Kristensen (1991).

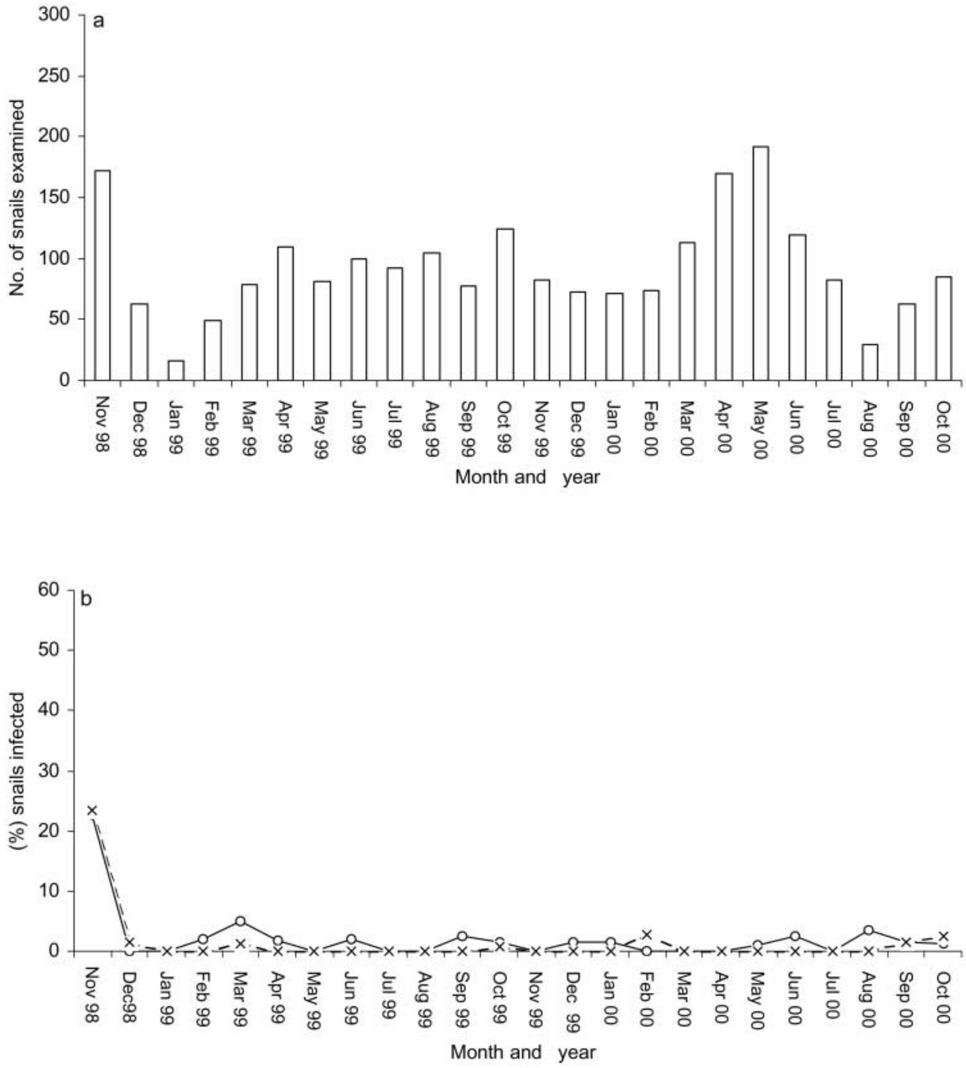

Fig. 2. Variation in (a) the number of *Bulinus globosus* sampled in the highveld from November 1998 to October 2000 and (b) the proportion of *B. globosus* infected with *Schistosoma* (○) and echinostome (×) cercariae.

spread, comprising mainly streams and man-made dams.

The lowveld extends from 500 to 1000 m above sea level and lies mostly in the southeastern part of the country. It is hot throughout the year with temperatures ranging from 29 to 34°C during the rainy season and 23 to 28°C during the dry season. The area receives a mean annual rainfall of 400 to 650 mm (fig. 1) and droughts are common. Potential snail habitats are restricted to small man-made dams and temporary streams that provide drinking water for humans and livestock.

The year in Zimbabwe is divided into four seasons according to temperature and rainfall; rainy (December to February), post-rainy (March to May), cold-dry (June to August) and hot-dry (September to November) (Chandiwana *et al.*, 1987).

Snail collection and identification of cercariae

Snail sampling was conducted at monthly intervals from November 1998 to October 2000, from six streams and six dams in the highveld and from nine dams in the lowveld areas (table 1). Snails were sampled using a scoop made from a kitchen sieve supported on an iron frame mounted on a 1.5 m long wooden handle as described by Coulibaly & Madsen (1990). Scooping at each site was done by one person for 15 min. The snails were identified according to Brown & Kristensen (1989).

Shedding of cercariae was induced by exposing snails to artificial illumination for 2 h as described by Frandsen & Christensen (1984). Cercariae were identified to their morphological types on the basis of gross morphological characteristics, swimming behaviour,

https://doi.org/10.1079/JOH2002132 Published online by Cambridge University Press

Table 2. The prevalence (%) of infection with various types of cercariae in snails from the highveld and lowveld areas of Zimbabwe.

	Highveld			Lowveld		
Snail species	No. of snails collected	Cercarial type	No. of snails infected with cercarial type (%)	No. of snails collected	Cercarial type	No. of snails infected with cercarial type (%)
Pulmonates						
Bulinus globosus	2220	Mammalian schistosome*	62 (2.8)	714	Mammalian schistosome	11 (1.5)
		Amphistome (pigmentata)	3 (0.1)		Amphistome (pigmentata)	1 (0.1)
		Echinostome	48 (2.2)		Echinostome	2 (0.3)
		BAM	3 (0.1)		BAM	2 (0.3)
Bulinus tropicus	1285	Amphistome (pigmentata)	58 (4.5)	2795	Amphistome (pigmentata)	274 (9.8)
		Echinostome	15 (1.2)		Echinostome	109 (3.9)
		Strigea (LPD)	29 (2.3)		Strigea (LPD)	43 (1.5)
		Vivax (LPM)	1 (0.1)		Vivax (LPM)	2 (0.1)
		BAM	2 (0.2)		BAM	3 (0.1)
Biomphalaria pfeifferi	1054	*Schistosoma mansoni*	0 (0)	1481	*Schistosoma mansoni*	1 (0.1)
		Amphistome (pigmentata)	3 (0.3)		Amphistome (pigmentata)	4 (0.3)
		Echinostome	7 (0.7)		Echinostome	3 (0.2)
		Xiphidiocercaria	4 (0.4)		Xiphidiocercaria	2 (0.1)
		Strigea	0 (0)		Strigea	2 (0.1)
Lymnea natalensis	2475	Echinostome	132 (5.3)	842	Echinostome	34 (4.0)
		Strigea	18 (0.7)		Strigea	11 (1.3)
		Vivax	0 (0)		Vivax	3 (0.4)
		BAM	5 (0.2)		BAM	3 (0.4)
		Xiphidiocercaria	9 (0.4)		Xiphidiocercaria	3 (0.4)
Bulinus forskalii	62	Amphistome (pigmentata)	1 (1.6)	8	Amphistome (pigmentata)	0 (0)
Ceratophallus natalensis	14	Strigea	1 (7.1)	10	Strigea	0 (0)
Gyraulus costulatus	35	–	–	–	–	–
Prosobranchs						
Bellamya capillata	13	–	–	–	–	–
Melanoides tuberculata	–	Ophthalmo-xiphidiocercaria	0 (0)	740	Ophthalmo-xiphidiocercaria	2 (0.3)
Lanistes ovum	1	–	–	40	–	
Total	7159		401	6630		515

* *Schistosoma haematobium* or *S. mattheei*.
BAM, brevifurcate apharyngeate monostome cercaria; LPD, longifurcate pharyngeate distome cercaria (strigea); LPM, longifurcate pharyngeate monostome cercaria (vivax).

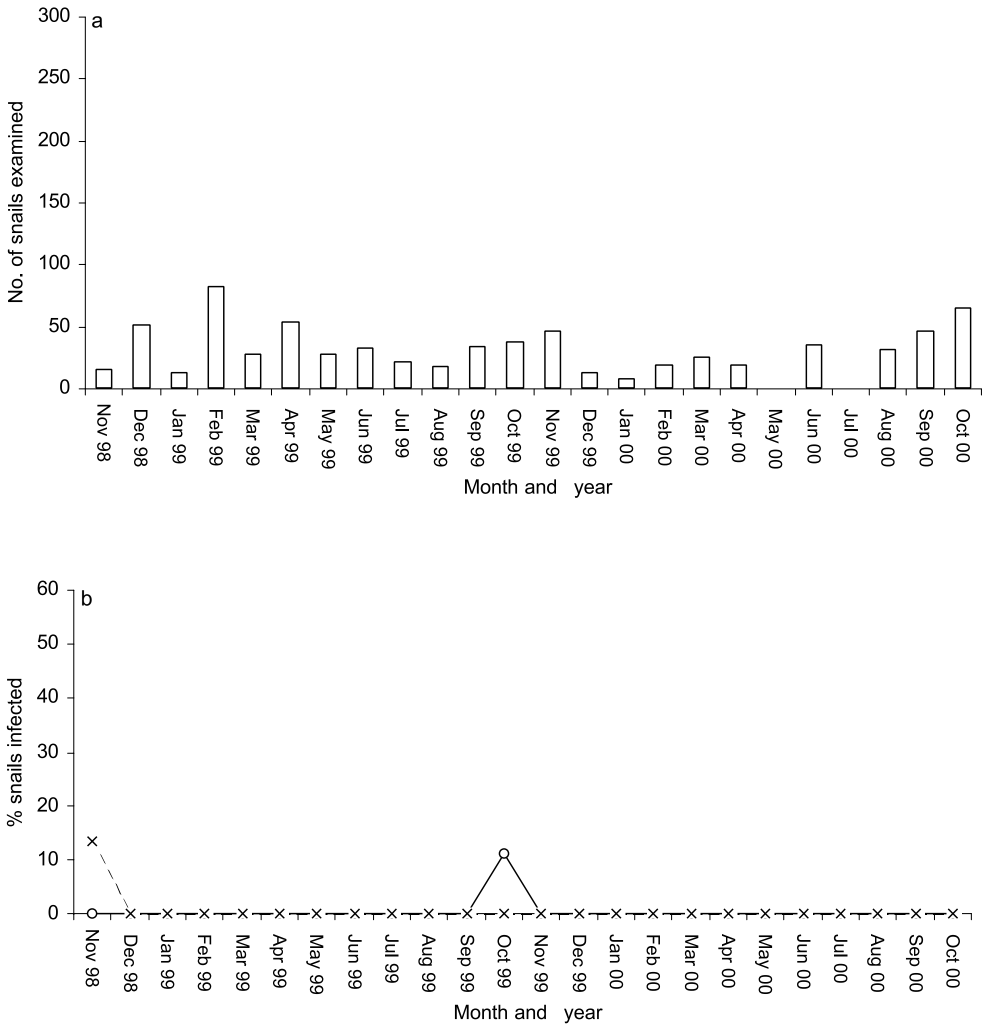

Fig. 3. Variation in (a) the number of *Bulinus globosus* sampled in the lowveld from November 1998 to October 2000 and (b) the proportion of *B. globosus* infected with *Schistosoma* (○) and echinostome (×) cercariae.

resting position and further cercarial development as described by Frandsen & Christensen (1984) and Schell (1985). Cercariae belonging to the *Schistosoma* genus were identified to species level based on adult worm and egg morphology following hamster infections as described by Ozumba *et al.* (1989), combined with knowledge of their snail hosts.

Results

From 21 habitats sampled, a total of 13,789 snails were collected of which 916 (6.6%) harboured patent larval trematode infections. A total of ten snail species harbouring eight different morphological types of cercariae were recorded from the study sites (table 2). No patent double infections were observed.

Bulinus tropicus, *Biomphalaria pfeifferi* and *Lymnaea natalensis* harboured five types of cercariae each (table 2). No trematodes were recovered form *Bellamya capillata*, *Lanistes ovum* or *Gyraulus costulatus*. An ophthalmo-xiphidiocercaria was recovered from *Melanoides tuberculata* with prevalence of infection of 0.3%. The snail species with the highest prevalence of infection was *Bulinus tropicus* (13.1%). Of all the trematode infections recorded in this study, 58.5% were from *B. tropicus* and 23.8% were from *Lymnaea natalensis*.

The most common type of cercaria recovered was the echinostome type, which contributed 38.2% of all larval trematode infections recorded. This was followed by the amphistome of the pigmentata sub-type, which accounted for 37.6% of infections while *Schistosoma* cercariae only contributed 8.0% of all larval trematode infections recorded.

The overall prevalence of larval trematode infections in the habitats ranged between 0.3 and 24.4% (table 1). The

https://doi.org/10.1079/JOH2002132 Published online by Cambridge University Press

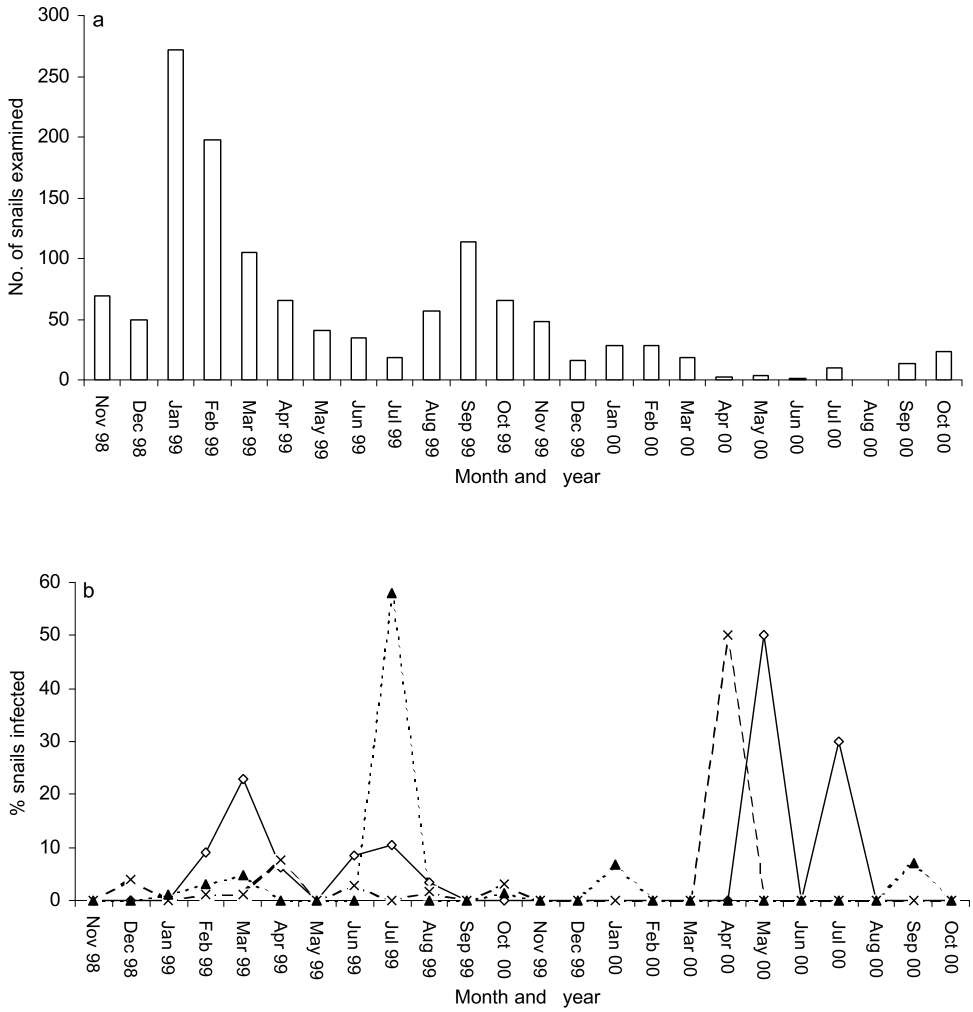

Fig. 4. Variation in (a) the number of *Bulinus tropicus* sampled in the highveld from November 1998 to October 2000 and (b) the proportion of *B. tropicus* infected with amphistome (◇), echinostome (×) and strigea cercariae (▲).

prevalence was particularly high in Vaka (24.4%) due to a large proportion of infected *B. tropicus* and particularly low in Skova (0.3%) which supported a large population of *M. tuberculata* with few infections.

The overall prevalence of larval trematode infections in the highveld was 5.6% compared with 7.8% in the lowveld. Mammalian schistosome cercariae (*S. haematobium* or *S. mattheei*), amphistome, echinostome, strigeid and vivax cercariae, brevifurcate apharyngeate monostome cercariae and xiphidiocercariae were all recorded from the highveld and lowveld areas (table 2). Ophthalmo-xiphidiocercariae and *S. mansoni* cercariae were only recorded from the lowveld area (table 2).

Mammalian schistosome cercariae (*S. haematobium* or *S. mattheei*) were recovered from *B. globosus* from both the highveld and lowveld whereas *S. mansoni* cercariae were only recorded from a single specimen of *Biomphalaria pfeifferi* from the lowveld. Amphistome cercariae of the pigmentata type were recorded from *Bulinus tropicus*, *B. globosus*, *B. forskalii* and *Biomphalaria pfeifferi* (table 2). *Bulinus tropicus* contributed the majority of amphistome infections (96.5%), followed by *Biomphalaria pfeifferi* (2%), *Bulinus globosus* (1.2%) and *B. forskalii* (0.3%).

The prevalence of mammalian schistosome cercariae in *B. globosus* was 2.8% in the highveld and 1.5% in the lowveld, while the prevalence of amphistome cercariae in *B. tropicus* was 4.5% in the highveld and 9.8% in the lowveld.

Although variation existed between sites, prevalence data were pooled to describe the general pattern of transmission in the highveld and lowveld areas. The monthly variation of *B. globosus* and the infection rate by *Schistosoma* and echinostome cercariae in the highveld is shown in figs 2a–b and 3a–b and that of *B. tropicus* and the infection rate by amphistome, echinostome and strigea sampled in the highveld and lowveld is shown in figs 4a–b and 5a–b respectively. Variation in the number of *L. natalensis* and the infection rate by

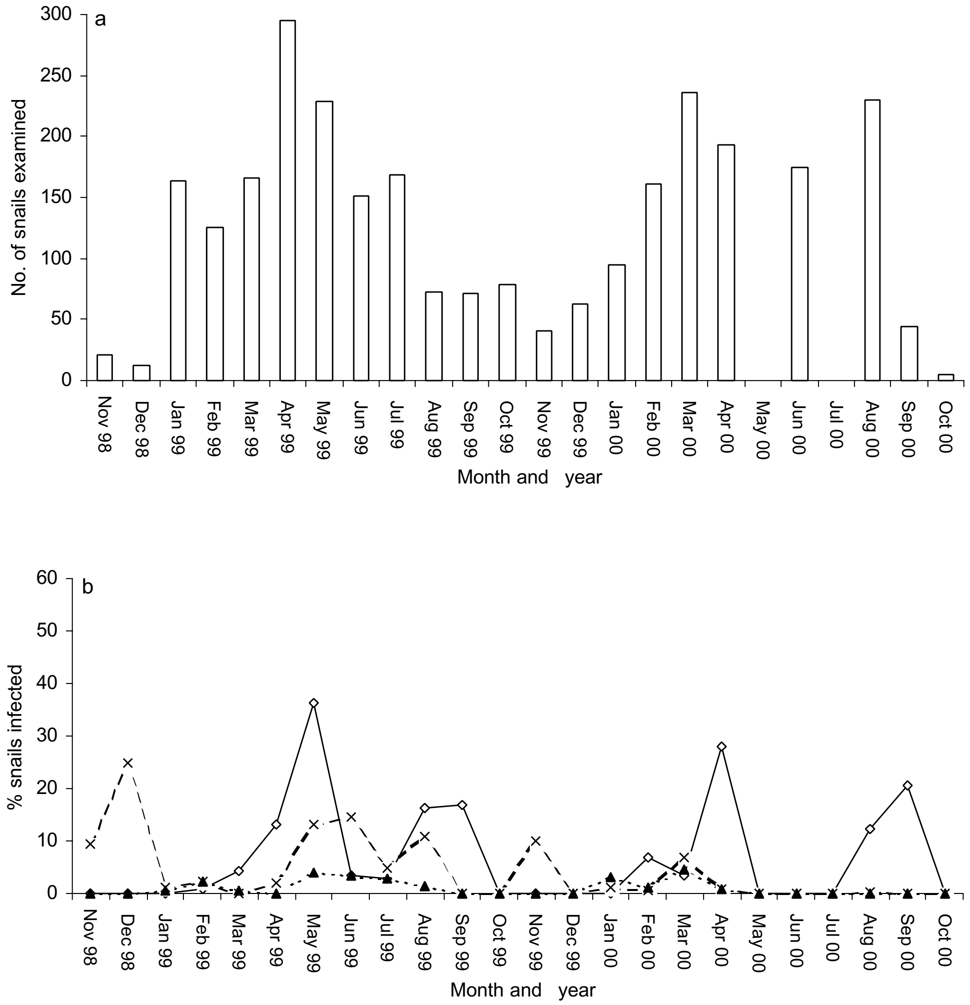

Fig. 5. Variation in (a) the number of *Bulinus tropicus* sampled in the lowveld from November 1998 to October 2000 and (b) the proportion of *B. tropicus* infected with amphistome (◇), echinostome (×) and strigea cercariae (▲).

echinostome and strigeid cercariae are shown in figs 6a–b and 7a–b for the highveld and lowveld respectively.

Discussion

Eight morphologically different types of larval trematodes infecting freshwater snails were recorded in the present study. This emphasizes the fact that trematodes of medical and veterinary importance, like the mammalian schistosomes and the amphistomes, do not occur in isolation and should be considered in the context of other concurrent trematode infections. Results indicate a low overall infection rate of snails with larval trematodes. This is in line with findings from other studies (Anderson & May, 1979; Loker *et al.*, 1981; Mattison *et al.*, 1995; Kigadye, 1998; Toledo *et al.*, 1998). Wright (1966) and Sousa (1992) attributed such low infection rates in natural snail populations to a direct consequence of high rates of parasite-induced mortality. On the other hand, Begon *et al.* (1990) argued that as a result of host–parasite co-evolution, hosts usually develop acquired resistance to infection and thus the observed low levels of prevalence. The low prevalences of infection could also be due to low parasite pressure, simply making contact between miracidia and snails a rare event.

No double infections were recorded in the present study and this is in agreement with Brown *et al.* (1988), Williams & Esch (1991), Chao *et al.* (1993) and Schmidt & Fried (1997). Sousa (1993) and Lafferty *et al.* (1994) assumed that inter-species antagonism was the explanation for the scarcity of the double infections. Sousa (1992) also speculated that double infections could be more pathogenic as compared to single species infections and as a result, snails with multiple infections suffer higher mortality as compared to those with single infections and may therefore be under-represented in snail collections. However, temporal and spatial variation in the abundance of eggs and miracidia of different

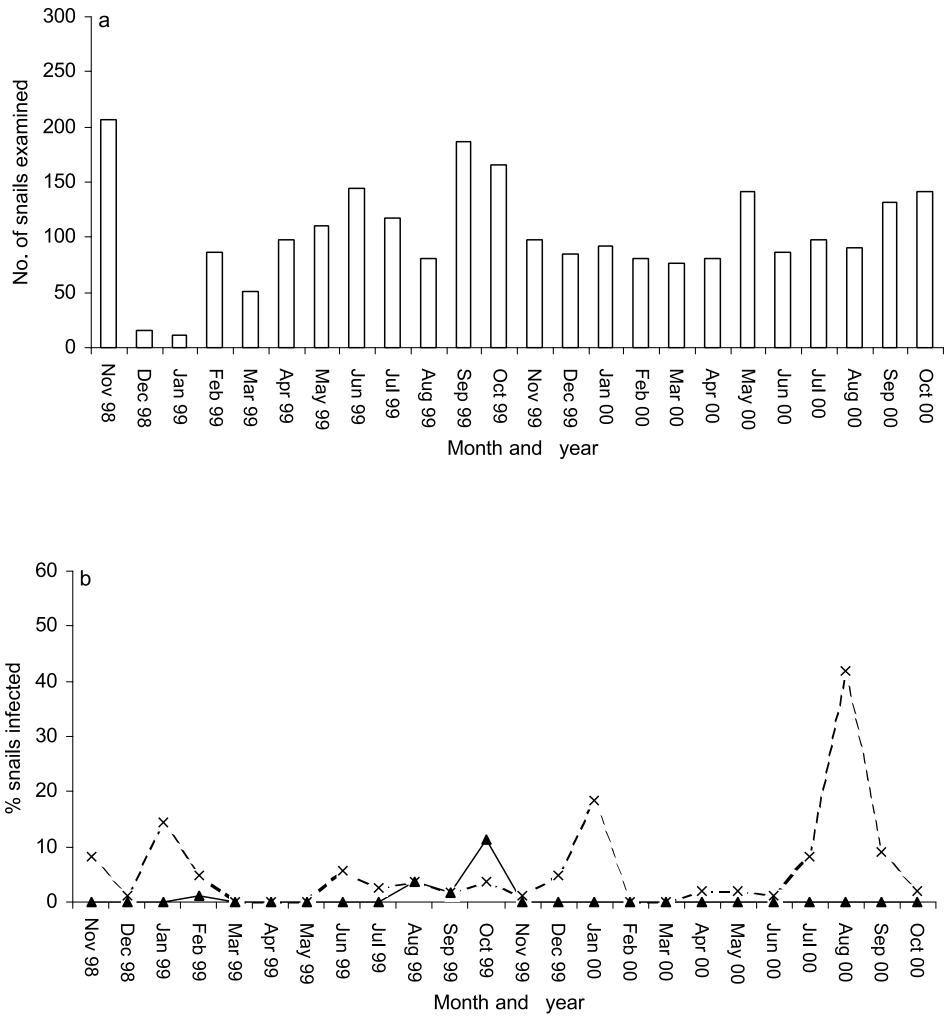

Fig. 6. Variation in (a) the number of *Lymnaea natalensis* sampled in the highveld from November 1998 to October 2000 and (b) the proportion of *L. natalensis* infected with echinostome (×) and strigea (▲) cercariae.

trematode species have been considered to be more important in determining how often a snail is simultaneously infected by two or more species or how often established infections are challenged (Sousa, 1990, 1993; Fernandez & Esch, 1991a,b; Williams & Esch, 1991).

With the exception of opthalmo-xiphidiocercariae and vivax cercariae, the cercarial types recovered were similar to those recorded by Loker *et al.* (1981) from the Mwanza region of Tanzania. Results from the present study suggest that *B. tropicus* may play a major role as a host for a variety of larval trematodes. Loker *et al.* (1981) recorded *L. natalensis* as the most important intermediate snail host for transmitting a wide variety of trematode species.

Snails in which no larval trematodes were recorded could have been resistant to infection. Resistance of snails to trematode infection has been reported to play a role in determining infection rates (Bayne & Yoshino, 1989). However, snails with no larval trematodes in the present study were recorded in low numbers and prevalences of larval trematode infections have been reported to be dependent on snail numbers (Ewers, 1964; Anderson & May, 1979).

Amphistome cercariae were recorded in *B. tropicus*, *B. globosus*, *B. forskalii* and *Biomphalaria pfeifferi* with infections in *Bulinus globosus*, *B. forskalii* and *Biomphalaria pfeifferi* being new records for Zimbabwe. Natural infections of *Bulinus tropicus* with amphistomes have been reported in Zimbabwe (Mukaratirwa *et al.*, 1998), South Africa (Dinnik, 1965) and Kenya (Dinnik & Dinnik, 1954; Southgate *et al.*, 1989). Natural infections with amphistomes in *Biomphalaria pfeifferi* have been reported in Zambia and Kenya by Dinnik (1965) and in Ethiopia by Graber & Daynes (1974) whereas records of infection in *Bulinus forskalii* have been made in Zambia and Mauritius by Dinnik (1961) and in Zambia by Wright *et al.* (1979). *Bulinus globosus*, *B. forskalii* and *Biomphalaria pfeifferi* seem to play a minor role in the transmission of amphistomes in Zimbabwe as compared to *Bulinus tropicus*, which contributed the majority of amphistome infections.

https://doi.org/10.1079/JOH2002132 Published online by Cambridge University Press

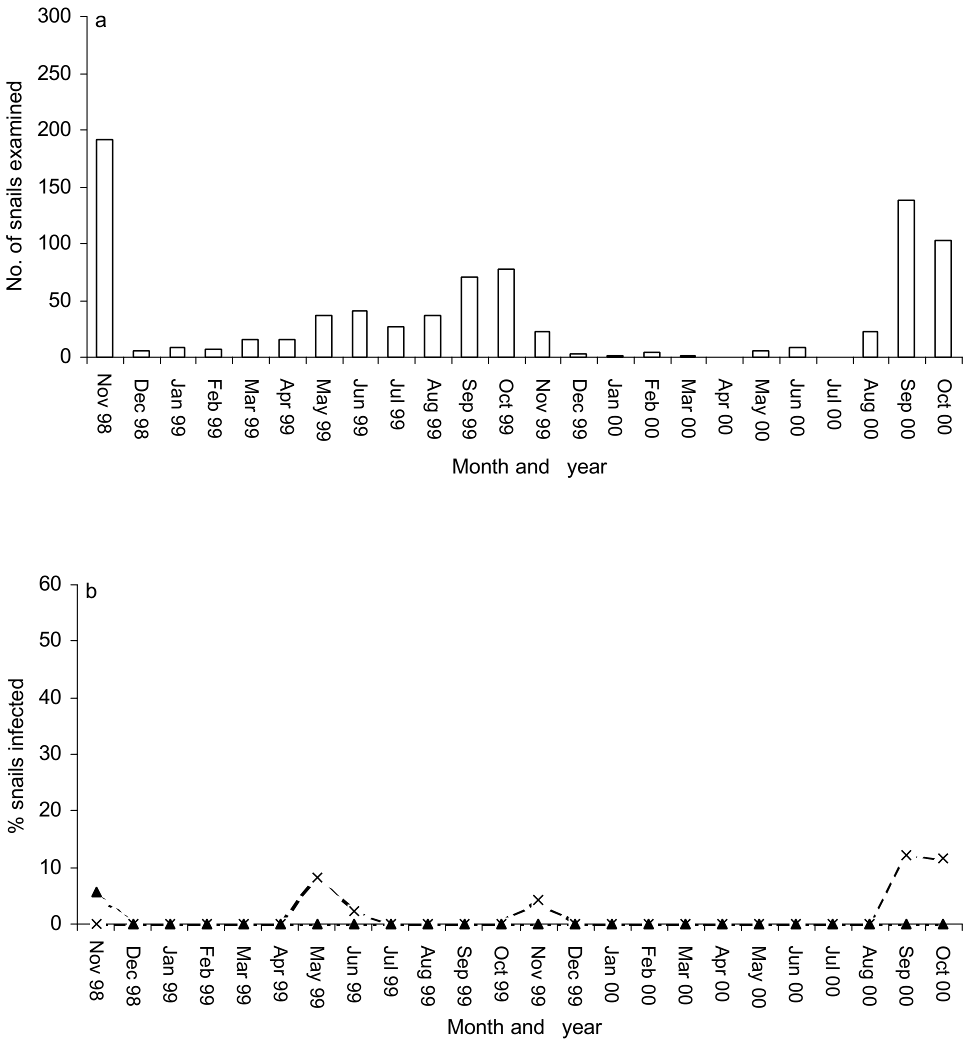

Fig. 7. Variation in (a) the number of *Lymnaea natalensis* sampled in the lowveld from November 1998 to October 2000 and the proportion of *L. natalensis* infected with echinostome (×) and strigea (▲) cercariae.

The seasonal pattern observed in the infection of *B. tropicus* with amphistome cercariae is consistent with that observed in Tanzania (Loker *et al.*, 1981), Nigeria (Schillorn, 1980) and India (Gupta *et al.*, 1987) where the prevalence of infection of snails with larval trematodes increased during the dry season and decreased during the rainy season. The increase in the prevalence of amphistome infections during the dry season could be attributed to reduced water volumes in the habitats during the dry season, accompanied by increased contact with livestock due to the scarcity of pasture, and increased grazing around water bodies, thereby favouring the accumulation of amphistome eggs in close proximity to potential snail habitats. These factors could lead to increased frequency of contact between miracidia and snail intermediate hosts hence increasing the prevalence of infection in snails.

There were temporal variations in larval trematode infections in snails, which have previously been related to temperature (Crews & Esch, 1986; Abdul-Salaam *et al.*, 1994, 1997; Esch & Fernandez, 1994; Mattison *et al.*, 1995; Toledo *et al.*, 1998, Yonder & Coggins, 1998; Al-Kandari *et al.*, 2000) and host behaviour (Esch & Fernandez, 1994). Temperature influences the population biology of trematodes by inducing seasonal changes in the behaviour and abundance of hosts, longevity and infectivity of larval trematode stages and the rate of development of larval and adult stages (Al-Kandari *et al.*, 2000).

The present study reveals the diversity of larval trematode parasites in snails in the highveld and lowveld areas of Zimbabwe and the need to examine interactions between larval trematodes in snail hosts and abiotic and biotic factors. Further work should include laboratory experiments where snails are exposed to more than one trematode species to verify the field observations, which in the present case showed no double infections in snails.

Acknowledgements

We are grateful to Professor Niels Ø. Christensen for his comments on the manuscript. We would like to thank Regis Muchabaiwa, Morgan Makuremwe, Tendai Zimunya and the late Patrick Sibanda for technical assistance, and Elaine Svenningsen for linguistic comments. This work was supported financially by Danish International Development Assistance and the Danish Bilharziasis Laboratory.

References

Abdul-Salam, J., Sreelatha, B.S. & Al-Kandari, W. (1997) Temporal variation in infection of a population of *Clypeomorus bifasciata* (Gastropoda: Prosobranchia) by a digenean microphallid larva in Kuwait Bay. *Journal of Helminthology* **71**, 1–7.

Abdul-Salam, J., Sreelatha, B.S. & Ashkanani, H. (1994) Seasonal prevalence of trematode cercaria in *Clypeomorus bifasciata* (Gastropoda: Prosobranchia) in Kuwait Bay. *Folia Parasitologica* **41**, 247–252.

Al-Kandari, W.Y., Abdul-Salam, J. & Meakins, R. (2000) Temporal variation in the infection of a population of *Cerithidea cingulata* by larval trematodes in Kuwait Bay. *Journal of Helminthology* **74**, 17–22.

Anderson, R.M. & May, R.M. (1979) Prevalence of schistosome infection within molluscan populations: observed and theoretical predictions. *Parasitology* **79**, 63–94.

Appleton, C. & Brock, K. (1985) Trematode cercariae occurring in the snail intermediate hosts of bilharzia in the Durban and Pietermaritzburg areas of Natal. *South African Journal of Laboratory Technology* **31**, 49–52.

Bayne, C.J. & Yoshino, T.P. (1989) Determinants of compatibility in molluscs–trematode parasitism. *American Zoologist* **29**, 399–407.

Begon, M.L., Harper, L. & Townsend, C.R. (1990) *Ecology.* 2nd edn. Oxford, Blackwell Publishers.

Brown, D.S. & Kristensen, T.K. (1989) A field guide to African freshwater snails, southern African species. Danish Bilharziasis Laboratory Publication number 383.

Brown, K.M., Leathers, B.K. & Minchella, D.J. (1988) Trematode prevalence and the population dynamics of freshwater pond snails. *American Midland Naturalist* **120**, 289–301.

Chandiwana, S.K., Christensen, N.Ø. & Frandsen, F. (1987) Seasonal patterns in the transmission of *Schistosoma haematobium*, *S. mattheei* and *S. mansoni* in the highveld region of Zimbabwe. *Acta Tropica* **44**, 433–444.

Chandiwana, S.K., Taylor, P. & Clarke, V. de V. (1988) Prevalence and intensity of schistosomiasis in two rural areas in Zimbabwe and their relationship to village location and snail infection rate. *Annals of Tropical Medicine and Parasitology* **83**, 163–173.

Chao, D., Wang, L. & Huang, T. (1993) Prevalence of larval helminths in freshwater snails of the Kinmen Islands. *Journal of Helminthology* **67**, 259–264.

Clarke, V. de V. (1977) Studies of transmission of bilharziasis in Rhodesia. *Central African Journal of Medicine* **23**, 2–6.

Combes, C. (1982) Trematodes, antagonism between species and sterilizing effects on snails in biological control. *Parasitology* **84**, 151–175.

Coulibaly, G. & Madsen, H. (1990) Seasonal density fluctuations of intermediate hosts of schistosomes in two streams in Bamako, Mali. *Journal of African Zoology* **104**, 201–212.

Crews, A.E. & Esch, G.W. (1986) Seasonal dynamics of *Halipegus occidualis* (Trematoda: Hemiuridae) in *Helisoma anceps* and its impact on the fecundity of the snail host. *Journal of Parasitology* **72**, 646–651.

Davis, N.E. (1998) Population dynamics of and larval trematode interactions with *Lymnaea tomentosa* and the potential for biological control of schistosome dermatitis in Bremner Bay, Lake Wanaka, New Zealand. *Journal of Helminthology* **72**, 319–324.

Dinnik, J.A. (1961) *Paramphistomum phillerouxi* sp. nov. and its development in *Bulinus forskalii*. *Journal of Helminthology* **35**, 69–90.

Dinnik, J.A. (1965) The snail hosts of certain Paramphistomidae and Gastrothylacidae (Trematoda) discovered by the late Dr P.L. Le Roux in Africa. *Journal of Helminthology* **39**, 141–150.

Dinnik, J.A. & Dinnik, N.N. (1954) The life cycle of *Paramphistomum microbothrium* Fischoeder 1901 (Trematoda: Paramphistomidae). *Parasitology* **44**, 285–299.

Esch, G.W. & Fernandez, J.C. (1994) Snail–trematode interactions and parasite community dynamics in aquatic systems: a review. *American Midland Naturalist* **131**, 209–237.

Ewers, W.H. (1964) The influence of the density of snails on the incidence of larval trematodes. *Parasitology* **54**, 579–583.

Fernandez, J.C. & Esch, G.W. (1991a) Guild structure of larval trematodes in the snail *Helisoma anceps*: patterns and processes at the individual host level. *Journal of Parasitology* **77**, 528–539.

Fernandez, J.C. & Esch, G.W. (1991b) The component community structure of trematodes in the pulmonate snail *Helisoma anceps*. *Journal of Parasitology* **77**, 540–550.

Frandsen, F. & Christensen, N. (1984) An introductory guide to the identification of cercariae from African freshwater snails with special reference to cercariae of medical and veterinary importance. *Acta Tropica* **41**, 181–202.

Graber, M. & Daynes, P. (1974) Mollusques vecteurs de trematodoses humaines et animals en Ethiopie. *Revue d'Elevage et de Médecine Vétérinaire des Pays Tropicaux* **27**, 307–322.

Gupta, R.P., Yadav, C.L. & Ruprah, N.S. (1987) Studies on the bionomics of some aquatic snails and their cercarial fauna of Haryana state. *Indian Veterinary Medical Journal* **11**, 77–83.

Keas, B.E. & Blankespoor, H.D. (1997) The prevalence of cercaria from *Stagnicola emarginata* (Lymnaeidae) over 50 years in North Michigan. *Journal of Parasitology* **83**, 536–540.

Kigadye, E.S.P. (1998) *Studies on larval digeneans infecting freshwater snails*. 161 pp. MSc thesis, University of Dar es Salaam, Tanzania.

Kuris, A. & Lafferty, K.D. (1994) Community structure:

larval trematodes in snail hosts. *Annual Review of Ecology and Systematics* **25**, 189–217.

Lafferty, K.D., Sammond, D.T. & Kuris, A.M. (1994) Analysis of larval trematode communities. *Ecology* **75**, 2275–2285.

Lawrence, J.A. & Condy, J.B. (1970) The developing problem of schistosomiasis in domestic stock in Rhodesia. *Central African Journal of Medicine* **16**, 19–22.

Loker, E.S., Moyo, H.G. & Gardner, S.L. (1981) Trematode–gastropod associations in nine non-lacustrine habitats in Mwanza region of Tanzania. *Parasitology* **83**, 381–399.

Makura, O. & Kristensen, T.K. (1991) National freshwater survey of Zimbabwe. *Proceedings of the Tenth International Malacology Congress (Tübingen)*, 227–232.

Mattison, R.G., Dunn, T.S., Hanna, R.E.B., Nizami, W.A. & Ali, Q.M. (1995) Population dynamics of freshwater gastropods and epidemiology of their helminth infections with emphasis on larval paramphistomes in northern India. *Journal of Helminthology* **69**, 125–138.

May, R.M. (1983) Parasitic infections as regulators of animal populations. *American Scientist* **71**, 36–45.

Mukaratirwa, S., Kristensen, T.K., Siegismund, H.R. & Chandiwana, S.K. (1998) Genetic and morphological variation of populations belonging to the *Bulinus tropicus/truncatus* complex (Gastropoda: Planorbidae) in south western Zimbabwe. *Journal of Molluscan Studies* **64**, 435–446.

Okafor, F.C. (1990) Distribution of freshwater gastropods in the lower River Niger and Cross River basins of southeastern Nigeria with reference to their trematode infections. *Beitrage zur Tropischen Landwirtschaft und Veterinärmedizin* **28**, 207–216.

Ozumba, N.A., Christensen, N.O., Nwosu, A.B.C. & Nwaorgu, O.C. (1989) Endemicity, focality and seasonality of transmission of human schistosomiasis in Amagunze village, eastern Nigeria. *Journal of Helminthology* **63**, 206–212.

Schell, S.C. (1985) *Handbook of trematodes of North America, North of Mexico*. 263 pp. Moscow, Idaho, University of Idaho Press.

Schillhorn, V.V.T.W. (1980) Dynamics of *Lymnaea natalensis* populations in the Zaria area (Nigeria) and the relation to *Fasciola gigantica* infections. *Acta Tropica* **37**, 283–294.

Schmidt, K.A. & Fried, B. (1997) Prevalence of larval trematodes in *Helisoma trivolvis* (Gastropoda) from a farm pond in Northampton County, Pennsylvania with special reference to *Echinostoma trivolvis* (Trematoda) cercaria. *Journal of the Helminthological Society of Washington* **64**, 157–159.

Shiff, C.J., Evans, A., Yiannakis, C. & Eardley, M. (1975) Seasonal influence in the production of *Schistosoma haematobium* and *S. mansoni* cercariae in Rhodesia. *International Journal for Parasitology* **5**, 119–123.

Sousa, W.P. (1990) Spatial scale and the processes structuring a guild of larval trematode parasites. pp. 41–67 *in* Esch, G.W., Bush, A.O. & Aho, J.M. (*Eds*) *Parasite communities, patterns and processes*. London, Chapman and Hall.

Sousa, W.P. (1992) Interspecific interaction of larval trematode parasites of freshwater marine snails. *American Zoologist* **32**, 583–592.

Sousa, W.P. (1993) Interspecific antagonism and species coexistence in a diverse guild of larval trematode parasites. *Ecological Monographs* **63**, 103–128.

Southgate, V.R., Brown, D.S., Warlow, A., Knowles, R.J. & Jones, A. (1989) The influence of *Calicophoron microbothrium* on the susceptibility of *Bulinus tropicus* to *Schistosoma bovis*. *Parasitological Research* **75**, 381–391.

Taylor, P. & Makura, O. (1985) Prevalence and distribution of schistosomiasis in Zimbabwe. *Annals of Tropical Medicine and Parasitology* **79**, 287–299.

Toledo, R., Munoz-Antoli, C., Perez, M. & Esteban, J.G. (1998) Larval trematode infections in freshwater gastropods from the Albufera natural park in Spain. *Journal of Helminthology* **72**, 79–82.

Williams, J.A. & Esch, G.W. (1991) Infra- and component community dynamics in the pulmonate snail *Helisoma anceps*, with special emphasis on the hemiurid trematode *Halipegus occidualis*. *Journal of Parasitology* **77**, 246–253.

Woolhouse, M.E.D. & Chandiwana, S.K. (1989) Spatial and temporal heterogeneity in the population dynamics of *Bulinus globosus* and *Biomphalaria pfeifferi* and in the epidemiology of their infection with schistosomes. *Parasitology* **98**, 21–34.

Wright, C.A. (1966) The pathogenesis of helminths in molluscs. *Helminthological Abstracts* **35**, 207–244.

Wright, C.A., Southgate, V.R. & Howard, G.W. (1979) A note on the life cycle of some amphistome flukes in Zambia. *Journal of Helminthology* **53**, 251–252.

Yonder, R.H. & Coggins, J.R. (1998) Larval trematode assemblages in the snail *Lymnaea stagnalis* from southeastern Wisconsin. *Journal of Parasitology* **82**, 259–268.

(Accepted 5 June 2002)