FINE-SCALE HABITAT ASSOCIATIONS OF SOFT-SEDIMENT GASTROPODS AT CAPE MACLEAR, LAKE MALAWI

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ABSTRACT

Lake Malawi harbours a high diversity of gastropod species, yet little is known of their distributions or habitat affiliations. We conducted a study of the gastropods present on soft sediments at five sites around Cape Maclear, in the south of the lake. The two most common taxa were *Bulinus nyassanus*, a known vector for *Schistosoma haematobium* and *Melanoides*. Both were found to be in much higher abundance than ever previously recorded. Densities of these gastropods were highly dependent upon habitat characteristics including depth, sediment particle size and sediment organic content. Together these factors explained 49 and 70% of variance in *B. nyassanus* and *Melanoides* abundance, respectively. There were no significant differences between the five sites after accounting for habitat variables. These data indicate that habitat characteristics are substantially important in determining the geographic differences in gastropod abundance, thus we propose that nearshore habitat variables may be strongly linked to schistosomiasis prevalence among lakeshore human populations.

INTRODUCTION

The Lake Malawi basin harbours a high species richness and abundance of molluscs (Crowley, Pain & Woodward, 1964; Brown, 1994). Among the most frequently encountered are representatives of the basommatophoran genus *Bulinus* and the thiarid caenogastropod genus *Melanoides*. Several species of *Bulinus* are present in Malawi including *B. globosus* (Morelet) and *B. truncatus* (Audouin), that are generally restricted to inflowing streams, dams and peripheral backwaters of the lake (Brown, Hughes, Kaukas, Kumwenda, Rollinson & Sullivan, 1996; Madsen, Bloch, Phiri, Kristensen & Furu, 2001). Additionally *B. nyassanus* (Smith) and *B. succinoides* (Smith) are found exclusively within the lake itself (Crowley *et al.*, 1964; Brown, 1994). Nine species of *Melanoides* are recorded from Malawi, all of which occupy the main lake body (Crowley *et al.*, 1964; Brown, 1994) and, with the exception of *M. tuberculata* (Müller), all are listed as endemic (Brown, 1994).

B. nyassanus is an intermediate host for the trematode *Schistosoma haematobium* (Bilharz), a highly infectious gonochoric blood fluke that parasitizes primarily humans (Madsen *et al.*, 2001). In Malawi high proportions of the lakeshore communities, many tourists and resident expatriates contract schistosomiasis each year (Cetron, Chitsula, Kaukas, Kumwenda, Rollinson & Sullivan, 1996; Stauffer, Arnegard, Cetron, Sullivan, Chitsulo, Turner, Chiotha & McKaye, 1997; Madsen *et al.*, 2001). It is likely that infection, at least for visitors to the lakeshore, is largely a consequence of exposure to cercariae harboured by *B. nyassanus* in the lake itself, rather than other *Bulinus* species in peripheral swamps and pools (Madsen *et al.*, 2001). Infection risks vary between sites around the lake (Cetron *et al.*, 1996), but one of the locations of highest risk is Chembe the main village at Cape Maclear on the tip of the Nankumba Peninsula. Here, risk of infection after 1 day of exposure to the lake water has been estimated to be as high as 52–74% and, after 10 days of exposure, the risk escalates to between 79 and 90% (Cetron *et al.*, 1996). Rates of infection have risen considerably over the last twenty years (Stauffer *et al.*, 1997; Madsen *et al.*, 2001).

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To understand the distribution of molluscs, their associated parasites and risk of infection, it is useful to have a comprehensive knowledge of the abundance and habitat associations over both macro- (Brooker, 2002) and micro-scales (Utzinger, Mayombana, Smith & Tanner, 1997). However, the most comprehensive quantitative sampling of mollusc community composition within Lake Malawi is, to our knowledge, a study of the abundance of *Bellamya, Bulinus, Lanistes* and *Melanoides* along one 24-m deep soft sediment transect at Cape Maclear in 1981 (Louda, Gray, McKaye & Mhone, 1983). In that study, all genera were in their highest densities at depths between 3.0 and 4.5 m. It was unclear why such a depth effect was present, but it is indicative of strong habitat affinity, in which case gastropod abundance may differ considerably between sites on the basis of fine-scale differences in habitat alone. Given that the nearshore waters of Lake Malawi are a spatially heterogeneous continuum of rock, sand and reed dominated habitats (McKaye & Gray, 1984), identifying fine-scale associations of *Bulinus* and other gastropods with environmental variables could explain broader-scale biogeographic patterns, and enable us to better understand spatial variation in schistosome exposure risk.

In this study, we tested the hypothesis that densities of gastropods in Lake Malawi are dependent upon the physical characteristics of their environment. We found that spatial differences in the two most abundant taxa, *B. nyassanus* and *Melanoides* were strongly linked to substrate composition and depth. These data indicate that fine-scale habitat affiliations are important in determining spatial variation in the abundance of molluscs within Lake Malawi.

MATERIAL AND METHODS

The molluscan fauna at five sites around Cape Maclear was surveyed (Fig. 1) between 15 and 18 September 2002. Using SCUBA, three samples of the gastropod fauna and the sediment were collected at depths of 5 and 10 m at each site. To collect molluscs a hand net (stretched mesh 2.25 mm, square gape 20 cm) was dredged through the top 3–5 cm of sediment for 50 cm, thus capturing a surface area of $0.1 \times 1\ m^2$. The sediment collected inside the net was shaken through the mesh and

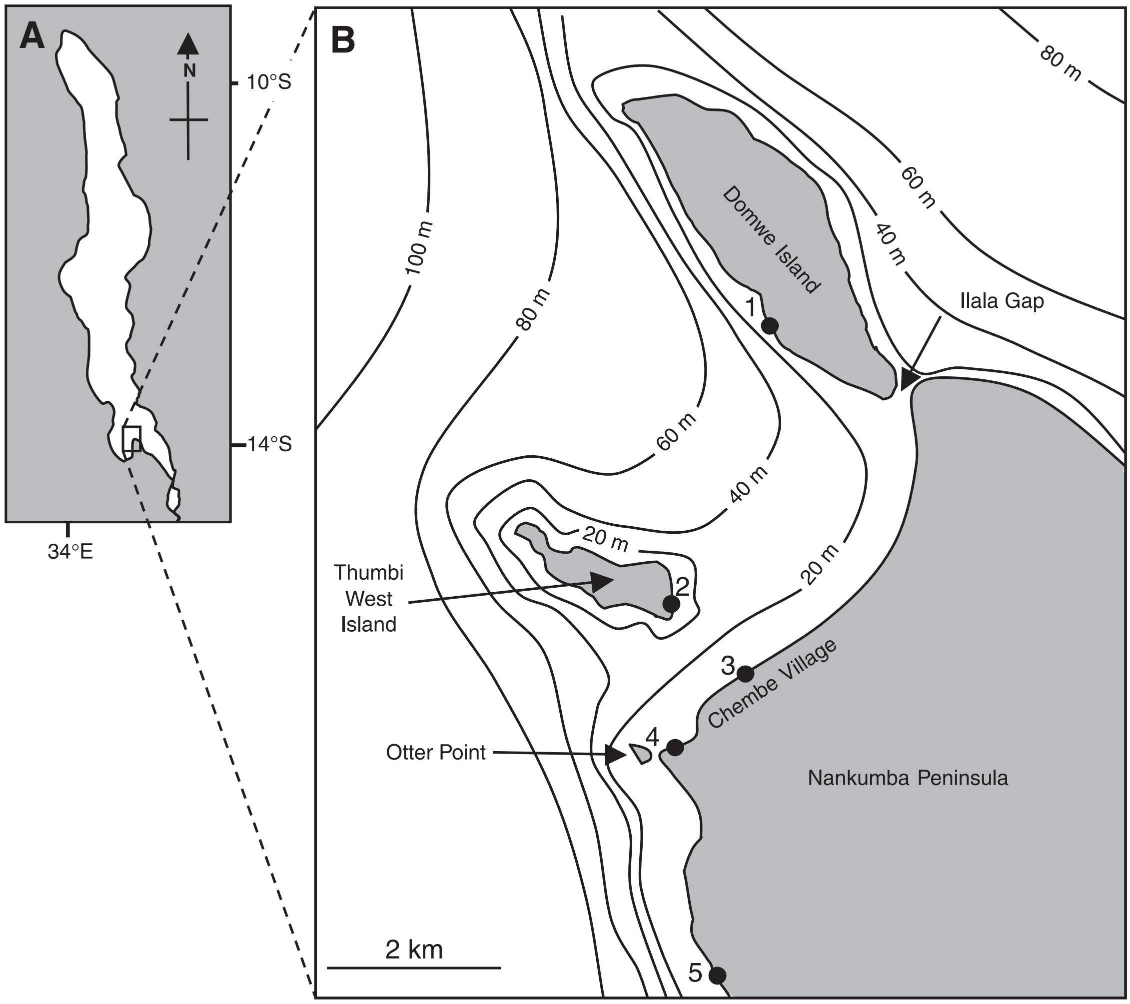

Figure 1. Cape Maclear on the tip of the Nankumba Peninsula in the south of Lake Malawi. Study sites are labelled 1–5. Depth contours are in 20-m intervals.

residual material was sealed in a labelled ziplock bag. Undisturbed surface sediment was collected in sealable 500-cm^3 capacity labelled containers.

Live gastropods in samples were preserved in 99% ethanol and later identified to species where possible. The current systematics of *Melanoides* present within the lake renders it impossible to reliably delimit species, thus these taxa were grouped. Sediment size profiles were obtained for each undisturbed sediment sample by wet sieving the material through a rack of five sieves of mesh sizes 1.4 mm, and 500, 250, 125 and 63 μm. Material collected on each sieve was weighed and using established techniques the median particle diameter (Mdϕ, the central tendency of particle size distribution), quartile deviation (QDϕ, the evenness of particle size distribution) and quartile skewness (Skqϕ, the asymmetry of particle size distribution) were calculated (see Holme & McIntyre, 1971). We used the loss-on-ignition method to obtain a measure of the organic content within sediment. Results from this method typically correlate strongly with those from dry combustion methods used to measure total organic carbon (Sutherland, 1998). On average 4.2 g (±2.8 SD) of dried sediment was used, combustion was at 375°C for 16 h. Statistical analyses focussed on the most abundant taxa and were conducted in Statistica (Statsoft, Tucson, USA). Taxon abundance data were $\log_{10}(x + 1)$ transformed.

RESULTS

Melanoides and *B. nyassanus* were the most abundant taxa at Cape Maclear, comprising 95.7 and 4.1% of the total 1456 gastropods in the samples, respectively. The balance was made up of *Bellamya capillata* (Frauenfeld) (three specimens) and *Gabbiella stanleyi* (Smith) (three specimens). *Lanistes nyassanus* Dohrn and *L. ellipticus* Martens were present at sampling sites, but not in samples.

Multiple forward stepwise regression revealed that significantly greater densities of both *B. nyassanus* and *Melanoides* were present on shallower sediments with smaller median sediment particle size and lower organic content (*B. nyassanus*, $F_{3,26} = 8.45$, $r^2 = 0.49$, $P < 0.001$; *Melanoides*, $F_{3,26} = 19.68$, $r^2 = 0.69$, $P < 0.001$). QDϕ and Skqϕ did not significantly explain additional variance in the abundance of either taxon. Survey locations 2, 3 and 4 possessed both the finest sediments and the highest densities of both these taxa in shallow waters (Fig. 2A–C). Abundance of *Melanoides* and *B. nyassanus* were highly positively correlated (Pearson's product moment; $n = 30$, $r = 0.77$, $P < 0.001$). The highest densities of *B. nyassanus* were found at 5 m depth at site 3, Chembe (mean 90 individuals/m^2 ± 70 SD; Fig. 2A), while the highest densities of *Melanoides* were at 5 m depth at site 4 (mean 1370 individuals/m^2 ± 244 SD; Fig. 2B). Site had no significant effect on either *B. nyassanus*

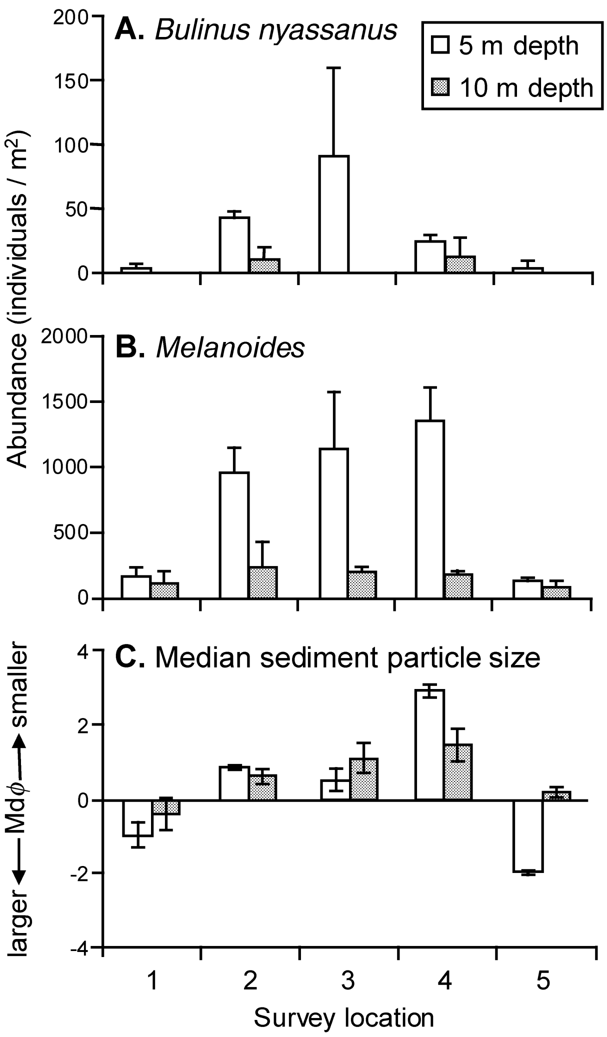

Figure 2. A, B. Mean abundance of *Bulinus nyassanus* and *Melanoides* at study locations. **C.** Median particle size at study locations. Error bars represent the standard deviation.

or *Melanoides* abundance when depth and the four sediment characters were used as covariates (one-way ANCOVA; *B. nyassanus*, $F_{4,20} = 1.88$; $P = 0.15$; *Melanoides*, $F_{4,20} = 2.22$, $P = 0.10$).

DISCUSSION

In the previous quantitative study of the abundance of Lake Malawi gastropods, Louda *et al.* (1983) found maximum densities of *Bulinus* and *Melanoides* of 1.6 and 123 individuals/m^2, respectively. In contrast, we found average densities over 56 times greater for *B. nyassanus* and over 11 times greater for *Melanoides* (Fig. 2A, B). We can only speculate on the reasons for the disparity, but the scale of the contrasts may be because of differences in surveyed habitat or sampling protocol. Alternatively, *Melanoides* and *B. nyassanus* may have dramatically increased in abundance. It is known that abundance of gastropods can change substantially, even over short time-scales (Brown, 1994). Louda *et al.* (1983) also found moderately high densities of *Lanistes* in samples, whereas they were absent from ours. Again, this may be because considerable abundance changes have taken place, but it is also possible that Louda *et al.* misidentified *Bulinus nyassanus* as juvenile *Lanistes nyassanus* for they are similar in external appearance (Crowley *et al.*, 1964) and that specimens identified as *Bulinus* were exclusively *B. succinoides*. In any case, it does not change our result that densities of *Melanoides* and *Bulinus* are much higher than previously observed in Lake Malawi.

Our results revealed no significant differences in the abundance of *Melanoides* or *B. nyassanus* among sites after accounting for habitat variation. This indicates that geographic differences in abundance of these gastropods may not be exclusively governed by factors such predation by molluscivorous cichlids that have been suggested to be important control agents (Stauffer *et al.*, 1997). The data do, however, indicate that gastropod densities are strongly dependent on habitat characteristics. Both *B. nyassanus* and *Melanoides* were most abundant in shallower waters with smaller sediment particle sizes. This may be a consequence of lower levels of predation or greater mobility that leads to more effective food acquisition. However, it also likely to be associated with a greater food abundance in the environment. Benthic algae contribute substantially to Lake Malawi gastropod diets (M. J. Genner, personal observation), and lighter, warmer and shallower sediments promote high benthic algal productivity (Cyr, 1998). Fine sediments might also have high productivity due to large surface areas, providing compaction does not reduce available space between particles and lead to unfavourable chemical conditions for benthic production (Buat, Ramlal & Guildford, 2002). Our observations of high abundance of *B. nyassanus* on finer sediments also correspond well with observed morphological and behavioural traits of the species that have been described as adaptations for a soft-sediment lifestyle. These include the heavy globular shell that would be resistant to damage during burrowing in the sediment, and having a predominantly nocturnal activity pattern that would be useful for the avoidance of visual predators (Wright, Klein & Eccles, 1967).

Here, we addressed microhabitat affiliations of Lake Malawi gastropods, but similar work on other African freshwater molluscan faunas suggests that fine-scale habitat preferences are widespread. Variations in abundance have been linked to many chemical and physical variables, including pH, dissolved salt concentrations, turbidity, oxygen, temperature, substrate type and depth (Appleton, 1978; Brown, 1994; Michel, 1994; Stothard, Loxton & Rollinson, 2002). For example, *Biomphalaria pfeifferi* (Krauss) is most abundant in extreme shallows close to shorelines and on substrates of plant detritus and bedrock (Utzinger & Tanner, 2000). This previous work, taken together with this study, demonstrates that an array of environment variables may need to be measured to adequately explain spatial differences in gastropod densities.

From a human health perspective, it has long been a desired goal to manage the abundance of molluscan intermediate hosts of schistosomes in African freshwaters (Stauffer *et al.*, 1997; Engels, Chitsulo, Montresor & Savioli, 2002). Potential mechanisms of control include habitat destruction, use of chemical pesticides and the employment of natural and introduced predators and competitors (Brown, 1994). Given the exceptional biodiversity within Lake Malawi, it would be unethical to undertake physical habitat modification, use chemicals or introduce alien fish (Kristensen & Brown, 1999). However, one possible mechanism of control may be to reduce fishing for demersal cichlids, for it has been suggested that the high levels of schistosomiasis in the region are symptomatic of declines in the sizes of molluscivorous cichlid populations (Stauffer *et al.*, 1997). Such a strategy, though, should only be undertaken with caution, for whether fish can successfully control molluscan schistosome vectors in large water bodies is as yet unknown. Indeed, it has recently been shown that in Lake Kariba effective biological control of pulmonate snails by the molluscivorous cichlid fish *Sargochromis codringtonii* (Boulenger) is unfeasible, simply because consumption rates are too low (Moyo, 2002).

Lake Malawi has been subject to increased levels of sediment input from inflowing rivers over recent years. This change has been attributed to higher rates of erosion in the lake's catchment due largely to alterations in agricultural land use practices (Mkanda, 2002). Our results revealed that gastropod abundance was higher in finer substrates and, as such, increased rates of sediment input may be potentially enlarging the favourable habitat of soft-sediment molluscs. Thus, spatial and temporal variation in schistosome-bearing snail abundance within Lake Malawi may also be a consequence of an increased presence of fine-particulate matter or enhanced benthic algal productivity, that has come about through human agricultural intensification.

In conclusion, significant associations were found between habitat characteristics, and the abundance of both *Melanoides* and *B. nyassanus.* Such fine-scale habitat affiliations are likely to result in geographic differences in abundance at locations around the lake. Thus, observed spatial and temporal variance in risk of schistosomiasis infection (Cetron *et al.*, 1996) may not be as dependent upon gastropod predator abundance as has been previously implied (e.g. Stauffer *et al.*, 1997). In our view, the escalating incidence of schistosomiasis in lakeshore human populations at Cape Maclear over the last twenty years is likely to be intrinsically linked to increasing human population density in the region (Smith, 1993), with transmission being facilitated by a large population of *B. nyassanus* present in favourable nearshore benthic habitat.

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REFERENCES

APPLETON, C.C. 1978. Review of the literature on abiotic factors influencing the distribution and life cycles of bilharziasis intermediate host snails. *Malacological Review,* **11**: 1–25.

BROOKER, S. 2002. Schistosomes, snails and satellites. *Acta Tropica,* **82**: 207–214.

BROWN, D.S. 1994. *Freshwater snails of Africa and their medical importance,* 2nd edn. Taylor & Francis, London.

BROWN, D.S., HUGHES, S., KAUKAS, A., KUMWENDA, N., ROLLINSON, D. & SULLIVAN, J.J. 1996. Further record of *Bulinus truncatus* (Mollusca: Planorbidae) for Malawi, with evidence of compatibility with *Schistosoma haematobium. Journal of African Zoology,* **110**: 333–339.

BUAT, P., RAMLAL, P.S. & GUILDFORD, S.J. 2002. The relationship between organic matter, invertebrates, and bacteria in the sediments of Lake Malawi. *Aquatic Ecosystem Health and Management,* **5**: 307–314.

CETRON, M.S., CHITSULA, L., KAUKAS, A., KUMWENDA, N., ROLLINSON, D. & SULLIVAN, J.J. 1996. Schistosomiasis in Lake Malawi. *Lancet,* **348**: 1274–1278.

CROWLEY, T.E., PAIN, T. & WOODWARD, F.R. 1964. A monographic review of the mollusca of Lake Malawi. *Annales de la Musée royal de l'Afrique Centrale: Sciences Zoologiques,* **131**: 1–58.

CYR, H. 1998. How does the vertical distribution of chlorophyll vary in littoral sediments of small lakes? *Freshwater Biology,* **40**: 25–40.

ENGELS, D., CHITSULO, L., MONTRESOR, A. & SAVIOLI, L. 2002. The global epidemiological situation of schistosomiasis and new approaches to control and research. *Acta Tropica,* **82**: 139–146.

HOLME, N.A. & McINTYRE, A.D. 1971. *Methods for study of the marine benthos.* Blackwell Scientific Publishing, Oxford.

KRISTENSEN, T.K. & BROWN, D.S. 1999. Control of intermediate host snails for parasitic diseases—a threat to biodiversity in African freshwaters? *Malacologia,* **41**:103–112.

LOUDA, S.M., GRAY, W.N., McKAYE, K.R. & MHONE, O.K. 1983. Distribution of gastropod genera over a vertical depth gradient at Cape Maclear, Lake Malawi. *Veliger,* **25**: 387–292.

MADSEN, H., BLOCH, P., PHIRI, H., KRISTENSEN, T.K. & FURU, P. 2001. *Bulinus nyassanus* is an intermediate host for *Schistosoma haematobium* in Lake Malawi. *Annals of Tropical Medicine and Parasitology,* **95**: 353–360.

McKAYE, K.R. & GRAY, W.N. 1984. Extrinsic barriers to gene flow in rock-dwelling cichlids of Lake Malawi: macrohabitat heterogeneity and reef colonisation. In: *Evolution of fish species flocks* (A. A. Echelle & I. Kornfield, eds), 169–181. University of Orono Press, Orono.

MICHEL, A.E. 1994. Why snails radiate: a review of gastropod evolution in long-lived lakes, both recent and fossil. In *Speciation in ancient lakes* (K. Martens, B Gooderis & G. Coulter, eds), *Advances in Limnology/ Archiv für Hydrobiologie, Beiheft,* **44**: 267–283.

MKANDA, F.X. 2002. Contribution by farmers' survival strategies to soil erosion in the Linthipe River catchment: implications for biodiversity conservation in Lake Malawi/Nyasa. *Biodiversity and Conservation,* **11**: 1327–1359.

MOYO, N.A.G. 2002. Aspects of the feeding ecology of *Sargochromis codringtonii* in Lake Kariba, Zimbabwe. *African Journal of Ecology,* **40**: 241–247.

SMITH, L. 1993. A historical perspective on the fishery of Chembe Enclave Village in Lake Malawi National Park. *Nyala,* **17**: 49–60.

STAUFFER, J.R., ARNEGARD, M.E., CETRON, M., SULLIVAN, J.J., CHITSULO, L.A., TURNER, G.F., CHIOTHA, S. & McKAYE, K.R. 1997. Controlling vectors and hosts of parasitic diseases using fishes. A case history of Schistosomiasis in Lake Malawi. *Bioscience,* **47**: 41–49.

STOTHARD, J.R., LOXTON, N.J. & ROLLINSON, D. 2002. Freshwater snails on Mafia Island, Tanzania with special emphasis upon the genus *Bulinus* (Gastropoda: Planorbidae). *Journal of Zoology,* **257**: 353–364.

SUTHERLAND, R.A. 1998. Loss-on-ignition estimates of organic matter and relationships to organic carbon in fluvial bed sediments. *Hydrobiologia,* **389**: 153–167.

UTZINGER, J., MAYOMBANA, C., SMITH, T. & TANNER, M. 1997. Spatial microhabitat selection by *Biomphalaria pfeifferi* in a small perennial river in Tanzania. *Hydrobiologia,* **356**: 53–60.

UTZINGER, J. & TANNER, M. 2000. Microhabitat preferences of *Biomphalaria pfeifferi* and *Lymnaea natalensis* in a natural and a manmade habitat in southeastern Tanzania. *Memorias do Instituto Oswaldo Cruz,* **95**: 287–294.

WRIGHT, C.A., KLEIN, J. & ECCLES, D.H. 1967. Endemic species of *Bulinus* (Mollusca: Planorbidae) in Lake Malawi (=Lake Nyasa). *Journal of Zoology,* **151**: 199–209.