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The burrowing behaviour of *Bulinus nyassanus*, intermediate host of *Schistosoma haematobium*, in Lake Malaŵi

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There is evidence that transmission of *Schistosoma haematobium* has increased in some areas in the southern part of Lake Malaŵi, where transmission occurs both along open shorelines and at inland sites. Transmission along open shores in the lake is via *Bulinus nyassanus* as intermediate host. Although the snail is rarely seen on top of the sediment, it seems to be an efficient path for transmission. *Bulinus nyassanus* does descend into the sediment, but it is restricted to the top 2 cm of the sediment.

Keywords: anti-predator behaviour, diurnal behaviour, fish predation, sediment

Introduction

Urinary schistosomiasis due to *Schistosoma haematobium* is highly prevalent in people living in lake-shore communities around Lake Malaŵi (Madsen et al. 2011). Furthermore, in some areas in the southern part of the lake, transmission has increased along open shorelines in addition to the more traditional transmission sites in inland habitats and along protected shorelines (Madsen et al. 2011). We postulated (Stauffer et al. 2006, Madsen et al. 2011) that transmission along open shores is caused by an increased density of *Bulinus nyassanus*, the intermediate host along open, sandy shores in the lake. Moreover, this increased density is a result of overfishing (Stauffer et al. 1997), which is suppressing the density of molluscivore fishes, primarily *Trematocranus placodon*.

We initially interpreted the behaviour of *Bulinus nyassanus* descending into the sediment (Wright et al. 1967) as an anti-predator response. When placed on top of the sediment *in situ*, the snails descend rapidly (ranging from a few minutes to 60 minutes) into the sediment. However, *Trematocranus placodon,* one of the most abundant molluscivorous fishes, with large lateral-line pores on the lower jaw (Konings 2007), can detect snails within the sediment. *Trematocranus placodon* preferentially feeds on *B. nyassanus* (Evers et al. 2006), especially during the period when this snail species is at highest density (Madsen et al. 2010). The distribution of *B. nyassanus* is also affected by sediment composition (Genner and Michel 2003).

Their burrowing behaviour is also relevant to transmission, as miracidia probably cannot infect snails within the sediment, and *B. nyassanus* might display a diurnal activity pattern, as has been demonstrated for other species in the lake. We hypothesised the selection pressure of the schistosome would favour release of cercariae when snails are at or near the top of the substratum. The prevalence of *S. haematobium* infections in snails is quite low (Madsen et al. 2011), yet this maintains a high level of infection in people (Stauffer et al. 2006). Therefore, it was important to know to what depth snails descend and whether this pattern would change on a diel cycle.

Materials and methods

Snail sampling

Since the sediment was rather loose we decided to sample the sediment column from the sediment surface (0 cm) to various depths, i.e. 0–2, 0–6 or 0–10 cm and compare densities among the three samples, instead of using a corer to sample different depths. The action of forcing a corer into the sediment could easily force snails deeper into the sediment. Also, sampling successively to different depths in the same spot could make snails descend deeper. Sampling sites were chosen such that the bottom did not slope steeply (<40 cm over 9 m) at a water depth of 3–4 m at a distance of 20–25 m from the shore. At this depth and distance offshore, infected snails are rarely encountered (Madsen and Stauffer 2011). Sampling, however, was done from August to October when density of *B. nyassanus* is generally high (Madsen et al. 2011). Water temperatures are relatively low in July, i.e. 22–23 °C, and then increase to 28–29 °C during the rainy season (Eccles 1974, Halfman 1993, Chavula et al. 2009). The snail fauna is dominated by *Melanoides* spp., but *Bellamya*, *Lanistes* and *Gabbiella* species were found at low densities. In this habitat the only pulmonate snail found is *B. nyassanus*, which is easily recognised by its strong shell and depressed spire (Mandahl-Barth 1972). Other *Bulinus* species also found in Lake Malaŵi are *B. globosus*, *B. forskalii* and *B. succinoides*; the first two being found only in shallow water along protected shorelines, while *B. succinoides* occurs in

deeper water where it is usually associated with *Valisneria* beds (Brown 1994, Evers et al. 2006).

At each sample site near Chembe Village six 8 m-long strings were positioned on the lake bottom, perpendicular to the shoreline, at intervals of 8 m. Along each string, there were three marks (3 m apart) showing the depth into the sediment to which sampling should be done, such that at each site each depth was sampled twice to avoid bias. An adjacent area was selected for sampling during the night-time (20:00–22:00) following the same method. This sampling procedure was repeated at four different positions along the Chembe shoreline. Snails were collected using a specially-designed 30 cm-wide dredge supplied with adjustable runners such that sediment could be sampled to different depths (Figure 1). The dredge, operated by two divers, was inserted into the sediment next to the marking on the line and pulled for a distance of 90 cm; one of the divers pulled the dredge and the other ensured that the dredge runners maintained contact with the sediment surface. The dredge's content was deposited into a plastic bag under water and brought into a boat and sieved. All specimens of *B. nyassanus* were collected and counted; other species were not sampled.

Sediment sampling and analysis

Subsequent to sampling with the dredge during the day, while SCUBA diving using Kajak sampler tubes, two sediment samples were taken close to the midpoint of each string length. The top 2 cm of the sediment was split into two approximately equal parts and transferred to separate containers. The same was done to the second sample and the two parts pooled with those of the first sample. One sample was preserved by adding 25 ml of 96% ethanol. This procedure was repeated twice more for samples taken at sediment depths of 2–4 and 4–6 cm. In the laboratory, particle size composition was determined using wet filtration through a series of brass sieves with decreasing mesh size after digestion of the organic material using hydrogen peroxide (Schumacher 2002). Organic content was determined for the sample preserved in ethanol using wet oxidation ($K_2Cr_2O_7$) method (Wakley and Black 1934).

Analysis

Snail counts were analysed using negative binomial regression (Hilbe 2008). This was done in generalised linear models using a log-link function and the ancillary parameter was estimated using full maximum likelihood estimation. Model fit was assessed using dispersion statistics to check for overdispersion and Anscombe residuals were used to check for outliers (Hilbe 2008). Comparison of competing models was done with Akaike and Bayesian information criterion statistics (Hilbe 2008). For graphical presentation, snail counts were log-transformed (base 10) after adding 1, averaged across sites and/or sampling times, and the mean and confidence limits back-transformed to the original scale.

Sediment composition was analysed using principal component analysis (PCA) and the PCA scores were then used in multivariate analysis of variance to first compare composition among the three layers of sediment (i.e. 0–2, 2–4 and 4–6 cm from the surface).

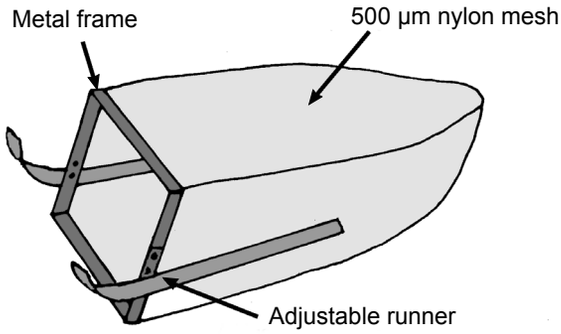

Figure 1: Dredge design

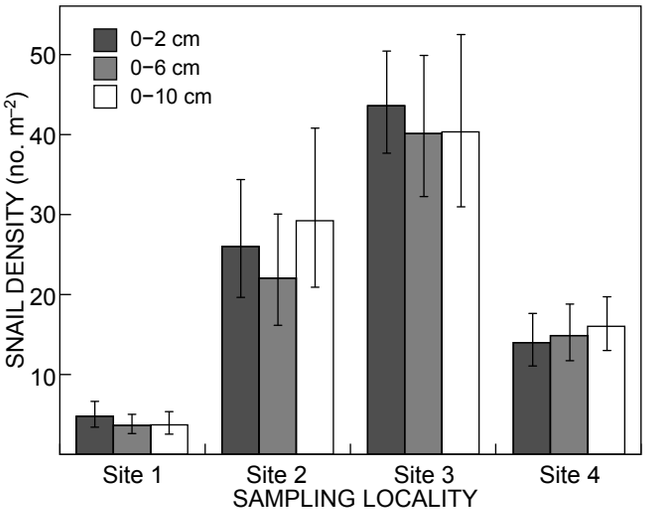

Figure 2: Snail density estimated by sampling at different depths (day and night samples combined) into the sediment at four sites along the shore at Chembe village, Lake Malaŵi during August–October 2006. Error bars show 95% confidence limits (n = 12 for each bar)

Results

Snail counts varied considerably among the four sites. Totals for *B. nyassanus* collected at sites 1, 2, 3 and 4, respectively, were 129, 999, 1 526 and 533, but there was no clear trend across the depths sampled (Figure 2). Statistical analysis showed that snail counts varied significantly among the four sites ($p < 0.001$) but did not differ significantly among depths sampled (Table 1). However, counts were about 20% higher during night-time than during the day sampling (Table 1). The interaction between site and period of sampling (Figure 3) was not significant.

We did not collect more snails when sampling the top 10 cm or top 6 cm than when sampling the top 2 cm. Therefore, *B. nyassanus* was primarily found in the top 2 cm of the sediment. At Site 1, we recorded sediment composition (Table 2). Multivariate analysis of variance did not detect differences in composition with depth and among positions within this site and we did not see any correlation between the principal component scores and density of *B. nyassanus*.

Table 1: Exponentiated regression coefficients from negative binomial regression on number of *Bulinus nyassanus* collected from the surface to three different depths into the sediment, during day and night at four sites along the shore at Chembe village, Lake Malawi, during August–October 2006. CL = confidence limits

Factor	Exp(β)	95% CL
Period		
Night	1.20	1.03–1.41
Day	1	
Site		
Site 1	0.24	0.19–0.31
Site 2	1.85	1.43–2.38
Site 3	2.86	2.46–3.33
Site 4	1	
Depth		
0–2 cm	0.98	0.85–1.13
0–6 cm	0.88	0.73–1.06
0–10 cm	1	

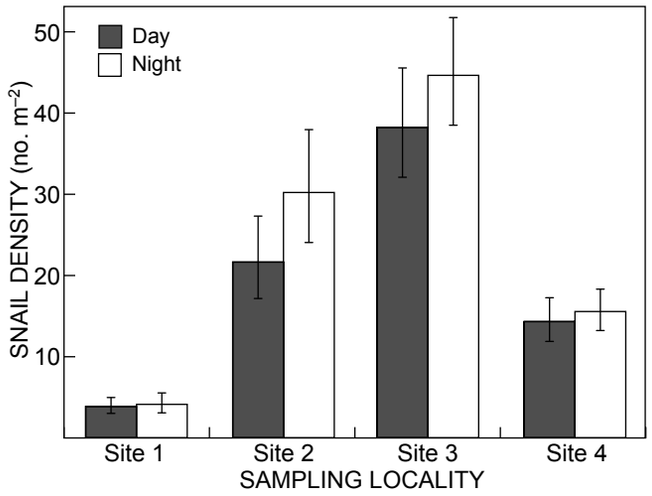

Figure 3: Density of *Bulinus nyassanus* during day and night sampling at four separate sites at Chembe village, Lake Malawi during August–October 2006. Error bars show 95% confidence limits (n = 18 for each bar)

On a larger scale, however, density of *B. nyassanus* was associated with the clay fraction in the sediment (Madsen and Stauffer 2011).

Discussion

Bulinus nyassanus descends into the sediment, where it feeds on detritus (Madsen et al. 2001), but this behaviour could also be an anti-predatory or parasite avoidance behaviour. Our studies have shown that the other known intermediate host of *S. haematobium* in Lake Malawi, *Bulinus globosus*, does not burrow but attaches to aquatic vegetation or rocks along protected shorelines. Prevalence of infection with *S. haematobium* in *B. globosus* in inland sites was 6.5% (range 6.2–6.9 in 3 sites), while that of *B. nyassanus* was 0.4% (range 0–2.0% in 10 sites) (Madsen and Stauffer 2011). Often, however, *B. nyassanus* may just be found under a layer of flocculent organic + silt layer covering the sediment, and may be exposed if this layer is removed. In places where such flocculent material is not present, snails tend to descend quickly into the sandy sediment.

Table 2: Sediment composition at three different depths (n = 6) at Site 1, 20–25 m from the shore at Chembe village, Lake Malawi, in August 2006

Fraction	Median (%)	Range (%)
0–2 cm		
Coarse sand	2.7	0.8–28.4
Medium sand	1.0	0.2–7.6
Fine sand	3.9	1.6–19.5
Silt	7.9	2.4–12.5
Clay	80.7	63.3–89.6
Organic	0.8	0.2–1.5
2–4 cm		
Coarse sand	4.3	1.4–19.4
Medium sand	1.6	0.3–3.6
Fine sand	4.4	1.0–10.7
Silt	3.9	2.6–6.2
Clay	86.6	62.0–93.1
Organic	0.6	0.3–1.4
4–6 cm		
Coarse sand	18.8	0.0–29.9
Medium sand	2.9	0.0–5.0
Fine sand	10.6	4.5–90.7
Silt	2.6	0.0–6.0
Clay	55.7	7.4–92.4
Organic	0.8	0.2–1.3

Bulinus nyassanus is involved in the transmission of *S. haematobium* at relatively few sites in the southern part of lake (Madsen and Stauffer 2011), the most important site being at Chembe village, Cape Maclear, but under those special conditions it seems to be an efficient intermediate host.

The prevalence of infection of *B. nyassanus* by *S. haematobium* ranges from 0% to 2.0% at 10 sites along the Chembe shoreline (Madsen and Stauffer 2011) and it is interesting that miracidia actually manage to infect *B. nyassanus*, and that cercariae manage to be released into the water column despite the hiding/burrowing behaviour of *B. nyassanus*. Schistosome-infected snails, however, are primarily found in the shallow water close to the shoreline (Madsen and Stauffer 2011) where the sediment, at least in some parts, is composed of rather coarse sand. The possibility that miracidia can either actively locate snails inside the sediment, or get washed into the sediment due to the wave action, should be further explored. It is also possible that *B. nyassanus* shows less tendency to descend into the sediment in shallow water, where the density of the molluscivore *Trematocranus placodon* is very low, especially at Chembe village (Madsen and Stauffer 2011).

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