Spatial microhabitat selection by *Biomphalaria pfeifferi* in a small perennial river in Tanzania

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Abstract

A study was carried out in the Mlali river in south-central Tanzania with two aims. First, to determine microhabitat availability in two sites (A and B) with respect to water depth, water velocity and dominant substratum type. Second, to assess microhabitat use by *Biomphalaria pfeifferi*, the intermediate host snail of intestinal schistosomiasis and to investigate whether these snails show preferences for certain microhabitats. The two sites differed significantly with respect to width, water depth, water velocity and substratum composition. It is suggested that the absence of *B. pfeifferi* from site B is mainly associated with the high water velocities at that site, where 62% of the measurements exceeded 30 cm s⁻¹. In site A, the microhabitat use by 327 *B. pfeifferi* snails was assessed by means of direct observation. No significant relationships were found between snail size and the habitat variables investigated, indicating that snail size appeared to be of no importance in spatial microhabitat selection. *B. pfeifferi* snails showed statistically significant preferences for shallow water (depth: 2–7 cm) and the preferred water velocities ranged between 12 and 21 cm s⁻¹ with an estimated optimum at 13.3 cm s⁻¹. No statistically significant preferences for shallow water (depth: 2–7 cm) and the preferences for substratum preferences for substratum type were found.

Introduction

Without adequate knowledge of the population ecology of *Biomphalaria pfeifferi* (Krauss), an intermediate host snail of intestinal schistosomiasis, a proper understanding of the epidemiology of the disease and its transmission is impossible (Sturrock, 1993). Understanding the microhabitat preferences of *B. pfeifferi* is a key component of this knowledge and may be relevant to the design of appropriate schistosomiasis control programmes (Woolhouse & Chandiwana, 1989; Woolhouse, 1992).

Water current velocity has been identified as a key factor influencing the distribution of snails in lotic environments, i.e. river systems. Several studies have shown that *Biomphalaria* sp. are usually not found where the current has a velocity greater than 30 cm s⁻¹ (Scorza et al., 1961; Appleton, 1978). However, it needs to be emphasised that in these studies the water

velocities were measured in the main stream and not in the microhabitats where snails occur (Thomas & Tait, 1984). Vegetation in stream habitats, for example, reduces the water velocity considerably, as shown by Marti & Tanner (1988).

Descriptions of habitat characteristics are often general and ignore a wide variety of environmental factors which may vary at a microhabitat level and affect the spatial distribution of snails. It is supposed that within these habitats, particular species will select only certain sections of the habitat out of the wide range of sections available, pointing to a preference for individual microhabitats (Odum, 1973). Microhabitat selection by *B. pfeifferi* may be affected not only by environmental characteristics, but also by the presence of other species, and may vary with the age or size of the snail.

Many studies have dealt with aquatic microhabitat selection, for example by fish (Moyle & Baltz,

1985). DeGraaf & Bain (1986) and Morantz et al. (1987) established three microhabitat variables as 'universal': (i) water depth, (ii) water velocity and (iii) substratum. In the perennial river of the present study, investigations revealed that the water composition was favourable for habitation of B. pfeifferi, however, the distribution of this snail species was found to be very focal (Utzinger et al., 1997). Previous malacological surveys carried out over a period of 16 months in a potential transmission site of human schistosomiasis (site B) demonstrated that no B. pfeifferi were found. During the last survey, an additional site (site A) some 2 km upstream was investigated and schistosome infected B. pfeifferi were found. Site A was followed over one year and B. pfeifferi were recorded abundantly, however only towards the end of the dry season.

Therefore, the study had two main aims. The first was to assess and compare the microhabitat availability at study sites A and B with respect to water depth, water velocity and dominant substratum. The two sites were selected because site A was known to be inhabited by *B. pfeifferi*, but in site B no snails were found despite intensive scooping. The second aim was to examine the utilization of different microhabitats by *B. pfeifferi* in site A, and whether a preference was shown for particular microhabitats.

Materials and methods

Study area

The investigation was carried out at two sites along the Mlali River, a small perennial river in the Morogoro Region, south-central Tanzania (Figure 1). The river originates in the Uluguru mountains and reaches Mlali village some 10 km NW of its source. In the village it passes through agricultural land, with maize, cassava and aubergine being the dominant crops. Another 3 km downstream its water is used in the Mlali irrigation scheme. Finally, after a further 5 km NE, the river drains into a large swamp. In Mlali village, both intestinal and urinary schistosomiasis are prevalent, with 73% and 26% of the school children, respectively, being infected in 1993 (Charles Mayombana, unpublished data). Further details of the study area are provided elsewhere (Utzinger et al., 1997).

Two study sites were investigated. Site A is a wide, shallow river section 8.4 m wide, with slow flowing water. The dominant substrate fraction consists of sand and fine gravel. Dense emergent vegetation grows on the banks of both shorelines and reaches frequently into the stream, at some locations to an extent of up to 1.5 m. In contrast, site B is a narrower river section with faster flowing and less shallow water and a coarser substrate composition to site A. Emergent vegetation is present, but not dense.

Data collection

Microhabitat availability

Data on microhabitat availability in sites A and B were collected in December 1994, during a period of low water discharge. Microhabitat availability was quantified as Bovee (1982) proposed in his transect method. The river sections in the two study sites were divided into segments by marking transects every 3 m, located at right angles to the main current. The transects were marked by stretching a rope from the right to the left river shore. Across each transect, physical characteristics of the habitat were measured systematically every 50 cm for site A and every 25 cm for site B. Stream width was measured to the nearest 10 cm, and at each point the following measurements were recorded: (i) total depth of the water column, (ii) water velocity 4-5 cm above the riverbed and (iii) main substratum composition (Bain et al., 1985). The total depths were read directly from a top setting wading rod to the nearest cm. Velocity measurements were made with an Ott current meter, fitted with a 3-cm diameter propeller (Ott AG, Kempten, Germany) to the nearest cm s^{-1} at locations where the water depth was at least 4 cm. Due to the physical resistance of the Ott current meter only velocities above 2 cm s⁻¹ could be measured. The dominant substratum type in an area of 5×5 cm beneath each point was classified according to a system presented by Heggenes & Saltveit (1990) and modified by the authors as follows: class 1 = plants; class 2 = clay/silt (0.004-0.06 mm); class 3 = sand (0.07-2.0 mm); class 4 = fine gravel(2.1-8 mm); class 5 = gravel (8.1-16 mm); class 6 = small pebbles (16.1–32 mm); class 7 = pebbles (32.1– 64 mm); class 8 = small cobbles (64.1–128 mm); class 9 = cobbles (128.1 - 256 mm); class 10 = large cobbles,boulders and bedrock (> 256.1 mm).

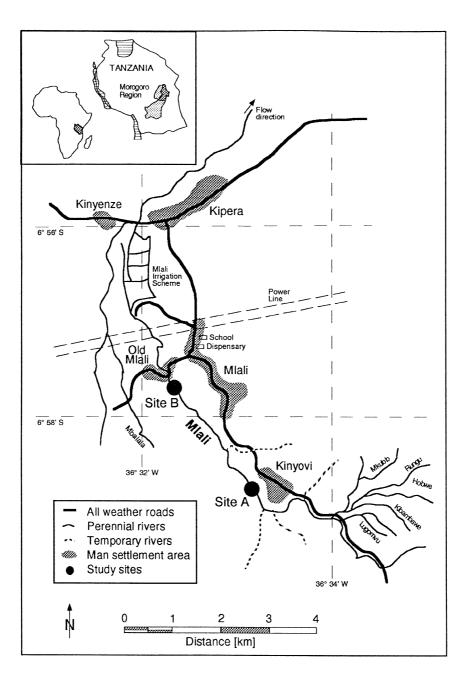


Figure 1. Map of the study area with the Mlali river in the Morogoro Region, south-central Tanzania. Locations of study site A (snails present) and site B (snails absent) are indicated.

Microhabitat use

In site A, along the same transects, microhabitat use by *B. pfeifferi* was assessed by searching for all the visible snails on the riverbed in a segment of 10 cm width. For each snail seen, the following microhabitat characteristics were recorded: (i) total depth of the water column, (ii) water velocity 4–5 cm above the snail's shell and (iii) main substratum composition. These measurements were taken as described above.

B. pfeifferi snails were collected by hand, put into numbered plastic tubes and brought to the laboratory,

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where their shell diameter was measured on the same day to the nearest 0.1 mm using calipers. Other snail species were recorded but not collected.

Data analysis

The microhabitat availability was compared between the two study sites, by computing the mean and the standard deviation for the river width, the water depth and the water velocity, as well as the median for substrate composition. Frequency distributions for the microhabitat availability variables were analysed and compared between the two study sites, using Kolmogorov-Smirnov (K-Sm) tests for continuous variables (water depth and water velocity) and chi square (χ^2) tests for substratum (Sokal & Rohlf, 1981).

Linear regression was used to analyse the relationships between snail size and the microhabitat variables investigated, such as water depth, water velocity and substratum composition. Logistic regression was used to test the statistical significance of differences in water velocity, depth, and substrate between places where snails were found (cases) and the representative sample of points (controls).

Values of microhabitat preference (D) were calculated from the formula of Jacobs (1974):

$$D = \frac{r-p}{(r+p) - 2rp},$$

where r is the proportion of snails using a specific microhabitat (e.g. gravel, or a water depth of 2 cm, or a water velocity of 3-7 cm s⁻¹), and p the proportion of the environment consisting of that microhabitat feature. Thus, D is a value ranging between -1 and +1. Negative values indicate that the microhabitat is used less than would be expected from its availability (microhabitat avoidance), a zero value would indicate that the microhabitat is used in proportion to its availability (neither avoidance nor preference) and positive values indicate that it is used more than expected (microhabitat preference).

Results

Microhabitat availability

In both study sites, the occurrence of particular physical characteristics of the microhabitat was assessed along 10 transects. In study site A, the water depth and substratum composition were measured for 161 points, while water velocity measurements were taken for 114 of those points. In study site B, 115 water depth and substrate fraction measurements were taken, while water velocity was measured 101 times (Table 1).

Study site B is a narrower stream section than site A, the mean widths being 3.4 ± 1.0 m and 8.4 ± 0.3 m, respectively. Water velocities showed the largest differences between the two sites (Figure 2). Site B is a section with a faster flowing current than site A (mean velocity 39.8 ± 20.9 cm s⁻¹, n = 101, compared with 20.1 ± 6.5 cm s⁻¹, n = 114, K-Sm test, P < 0.001) with 62% of the velocity measurements taken being greater than 30 cm s⁻¹, compared with 4% in site A. The water depth in the two sites also differs significantly and site B consists of deeper water (mean depth 7.7 ± 3.3 cm, n = 115, compared with 6.5 ± 2.5 cm, n = 161, K-Sm test, P < 0.001). In sites A and B, the two dominant substrate classes were recorded as fine gravel and sand, together forming 60% and 68% of the total substrate at site A and site B, respectively. Site B consisted of significantly larger substratum fractions than site A (Likelihood Ratio $\chi^2 = 21.8, 8 \text{ d.f.},$ P = 0.007).

Microhabitat use and preference

In study site A, three different snail species were identified. *B. pfeifferi* was the most abundant and represented 93% (327/350) of the snails found (for size distribution see Figure 3). *Bulinus globosus* (Morelet) accounted for 5% (19/350) and *Lymnaea natalensis* (Krauss) was found sporadically in small numbers (4/350). For 327 *B. pfeifferi* snails, the microhabitat utilization was assessed and its pattern was compared with that of microhabitat availability (Figure 4). The linear regression analysis showed no significant correlation between snail size and either water depth, water velocity or substratum composition, indicating that snail size appeared to be of no importance in spatial microhabitat selection.

The water depths associated with the snails were significantly lower than those systematically measured along the transects (P < 0.001, K-Sm test) and B. *pfeifferi* preferred shallow waters with a depth ranging between 2 and 7 cm. Deeper water habitats were avoided, especially those deeper than 11 cm (Figure 5).

Only velocities above 2 cm s^{-1} were included in the analysis because smaller values could not be measured due to the physical resistance of the Ott current meter. Therefore no conclusions can be drawn

Table 1. Physical characteristics of the two river sections in the Mlali river, where microhabitat availability was assessed along transects. Asterisks indicate number of measurements.

Habitat variable	Study site A (snails +)		Study site B (snails -)	
	(mean \pm st. dev.)	n^*	(mean \pm st. dev.)	n^*
River width (m)	8.4 ± 0.3	10	$3.4\pm~1.0$	10
Water depth (cm)	6.5 ± 2.5	161	$7.7\pm~3.3$	115
Water velocity (cm s ⁻¹)	20.1 ± 6.5	114	39.8 ± 20.9	101
Median substrate (class)	Sand (3)	161	Fine gravel (4)	115

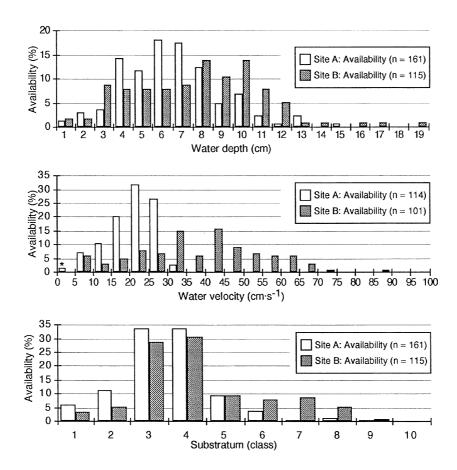


Figure 2. Comparison between the availability of microhabitats in site A (snails present) and site B (snails absent) in the Mlali river. For classification of the dominant substratum refer to Materials and methods. (*: omitting 0 values).

whether *B. pfeifferi* prefer or avoid stagnant or very slow flowing waters. Waters with velocities between 3 and 11 cm s⁻¹ were avoided and intermediate velocities (12–21 cm s⁻¹) were preferred slightly, whereas few snails were found at faster water velocities (Figure 5). This may be because they are flushed away. Water velocities associated with *B. pfeifferi* were sig-

nificantly lower than those measured systematically along the transects (P = 0.007, K-Sm test).

The preference histograms for substrate particle sizes suggested that *B. pfeifferi* snails may prefer gravel (class 6), small pebbles (class 7) and clay/silt (class 3). Pebbles and larger substratum fractions (class \geq 8) seemed to be avoided. However, there was no statis-

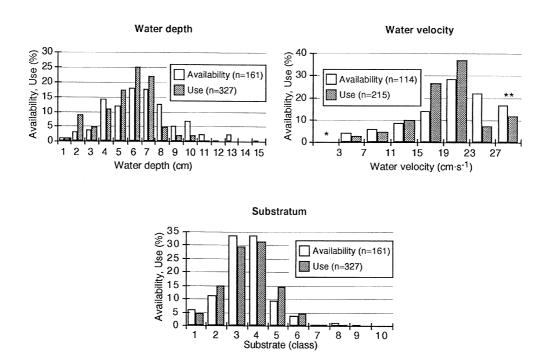


Figure 4. Microhabitat availability (open bars) and microhabitat use by *Biomphalaria pfeifferi* (grey bars) in study site A. For classification of the dominant substratum refer to Materials and methods. (*: omitting 0 values; **: $27-33 \text{ cm s}^{-1}$).

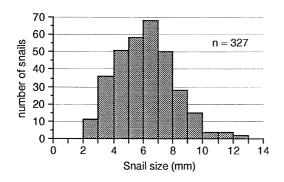


Figure 3. Frequency distribution of *Biomphalaria pfeifferi* snail size, as assessed in study site A.

tically significant difference between usage of dominant substrates by *B. pfeifferi* and substrate availability (Likelihood Ratio $\chi^2 = 9.1, 8 \text{ d.f.}, P = 0.3$).

The logistic regression indicated that the effect of water depth was highly statistically significant even allowing for the water velocity effects ($\chi^2 = 16.9$, 1 d.f., P < 0.001). Allowing for water depth, there was a significant quadratic effect of water velocity ($\chi^2 = 6.1$, 1 d.f., P = 0.046), with an optimal velocity estimated from the regression at 13.3 cm s⁻¹.

Discussion

It is widely acknowledged that for the full understanding of schistosomiasis transmission, temporal and spatial heterogeneities of the snail, which is the intermediate host, is of importance and in particular for the estblishment of any schistosomiasis control programme (Woolhouse & Chandiwana, 1989). Habitat features required by the snails are described in rather general terms in the literature (e.g. Webbe & Jordan, 1982; Madsen et al., 1987; Ndifon & Ukoli, 1989; Sturrock, 1993; Brown, 1994; Odermatt, 1994) and the description do not detail the microhabitats (Thomas & Tait, 1984; Madsen et al., 1988; Woolhouse & Chandiwana, 1989).

Temporal heterogeneity in the present study revealed that *B. pfeifferi* only occurred towards the end of the dry season and the highest infection rates with schistosomes were recorded in December and January. Therefore the present study was focused on spatial microhabitat selection during such a period. As the water composition was previously found to be favourable for *B. pfeifferi* inhabitation (Utzinger et al., 1997), the three 'universal' microhabitat variables – water column depth, water velocity and substratum composition (DeGraaf & Bain, 1986; Morantz et al.,

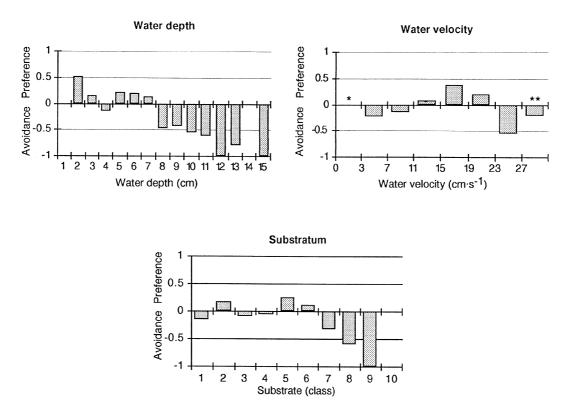


Figure 5. Microhabitat preference by *Biomphalaria pfeifferi* in study site A. For classification of the dominant substratum refer to Materials and methods. (*: omitting 0 values; **: 27–33 cm s⁻¹).

1987) – were investigated in two study sites and it was found that all of them varied significantly. Water velocity varied the most and, in agreement with Scorza et al. (1961) and Appleton (1978), this feature is likely to be the principle one that makes study site B unfavourable for the habitation of *B. pfeifferi*. In fact, 62% of the water velocities measured exceeded the value of 30 cm s⁻¹ described as critical by Scorza et al. (1961), despite the fact that the present investigation was carried out in the dry season during low water discharge.

For the investigation of the use of different microhabitats, *B. pfeifferi* snails were actively searched for on the riverbed in site A and collected by hand. This methodology is simple, and is probably reasonably reliable since snails are positively rheotactic in currents, provided the observers approach against the current to avoid snails being flushed away. The disadvantage of the method is that it only can be applied in clear and shallow water during periods of low discharge and that walking in the habitat may destroy certain microhabitats. In addition, it is well established that the smallest snails will be under-represented because they are difficult to see (Dazo et al., 1966). When the present study was undertaken, the different prerequisites for the applied methodology were met.

In study site A, microhabitat preference by *B. pfeif-feri* snails was assessed, using the formula of Jacobs (1974). He recommended its use to quantify food selection. However, in previous studies it has been applied to habitat selection, i.e. to the selection of features such as water depth, water velocity and substratum composition (e.g. Heggenes & Saltveit, 1990). The same approach was used in the present study and it was found that *B. pfeifferi* show a distinct spatial microhabitat selection.

It can be summarized that in this river *B. pfeif-feri* snails show a statistically significant preference for shallow waters and that they avoid microhabitats with a depth of more than 8 cm, confirming previous findings by Thomas & Tait (1984). Furthermore, *B. pfeifferi* prefer intermediate water velocities ranging between 12 and 21 cm s⁻¹, with an estimated optimum at 13.3 cm s⁻¹. However, no statistically signifi-

icant preference for substrate usage could be found, although there seemed to be a tendency for large particles to be avoided which would be in agreement with findings by Thomas & Tait (1984). In conclusion, it is most likely to find *B. pfeifferi* snails towards the end of the dry season during a period of low water discharge in microhabitats where the water is shallow and slow-flowing.

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