Density of Trematocranus placodon *(Pisces: Cichlidae): A Predictor of Density of the Schistosome Intermediate Host,* Bulinus nyassanus *(Gastropoda: Planorbidae), in Lake Malawi*

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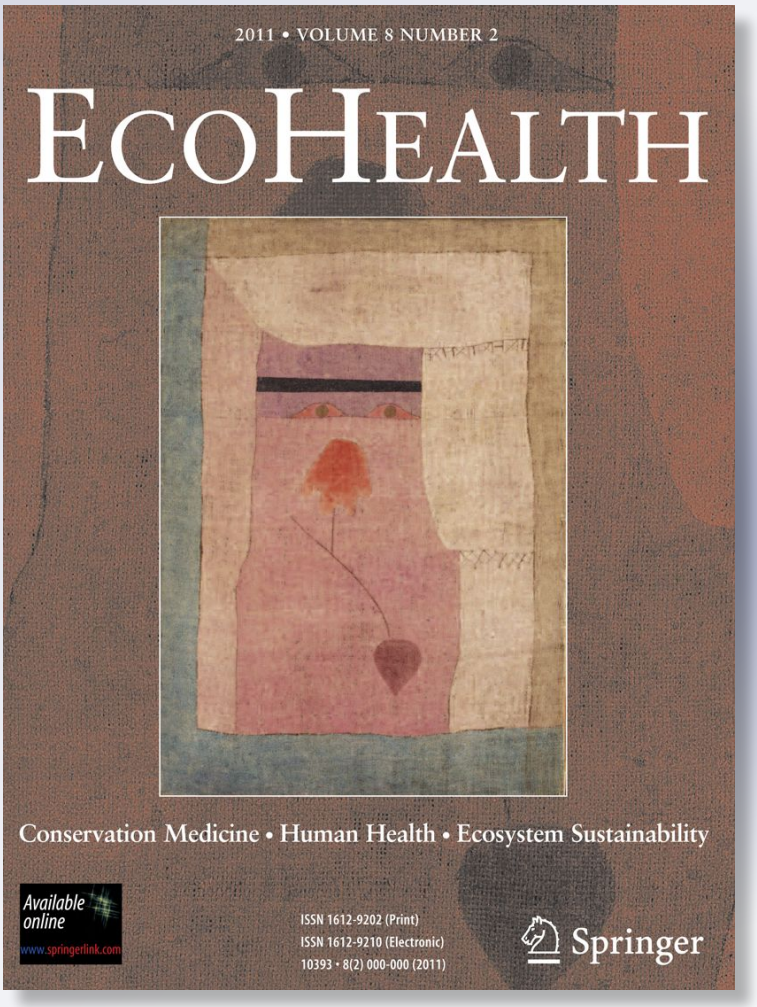

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Original Contribution

Density of *Trematocranus placodon* (Pisces: Cichlidae): A Predictor of Density of the Schistosome Intermediate Host, *Bulinus nyassanus* (Gastropoda: Planorbidae), in Lake Malaŵi

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Abstract: From the mid-1980s, we recorded a significant increase in urinary schistosomiasis infection rate and transmission among inhabitants of lakeshore communities in the southern part of Lake Malaŵi, particularly on Nankumba peninsula in Mangochi District. We suggested that the increase was due to over-fishing, which reduced the density of snail-eating fishes, thereby allowing schistosome intermediate host snails to increase to higher densities. In this article, we collected data to test this hypothesis. The density of both *Bulinus nyassanus*, the intermediate host of *Schistosoma haematobium*, and *Melanoides* spp. was negatively related to density of *Trematocranus placodon*, the most common of the snail-eating fishes in the shallow water of Lake Malaŵi. Both these snails are consumed by *T. placodon*. Transmission of *S. haematobium* through *B. nyassanus* only occurs in the southern part of the lake and only at villages where high density of the intermediate host is found relatively close to the shore. Thus, we believe that implementation of an effective fish ban up to 100-m offshore along these specific shorelines in front of villages would allow populations of *T. placodon* to increase in density and this would lead to reduced density of *B. nyassanus* and possibly schistosome transmission. To reduce dependence on natural fish populations in the lake and still maintain a source of high quality food, culture of indigenous fishes may be a viable alternative.

Keywords: schistosomiasis, over-fishing, *S. haematobium*, Lake Malaŵi

Introduction

Human urinary schistosomiasis caused by *Schistosoma haematobium* is a major public health problem in Lake Malaŵi lakeshore communities, increasing in certain areas within the last 20 years (Stauffer et al. 1997, 2006b; Madsen et al. 2011). Previously, the lake's open shores were considered free from schistosome transmission (Teesdale and Chitsulo 1983); however, in the mid-1980s, transmission was documented in the southern part of the lake (Nankumba Peninsula, Fig. 1) where transmission is possible in both vegetated areas of the lake, and along open shorelines with a sandy bottom (Madsen et al. 2001, 2004, 2011). Historically (pre-1991; Stauffer et al. 1997), transmission was effected by *Bulinus globosus* only in protected areas of the lake and in inland habitats. The observed change in the transmission pattern was due in part to *Bulinus nyassanus* also serving as an intermediate host (Madsen et al. 2001). *B. nyassanus* (Smith 1877)

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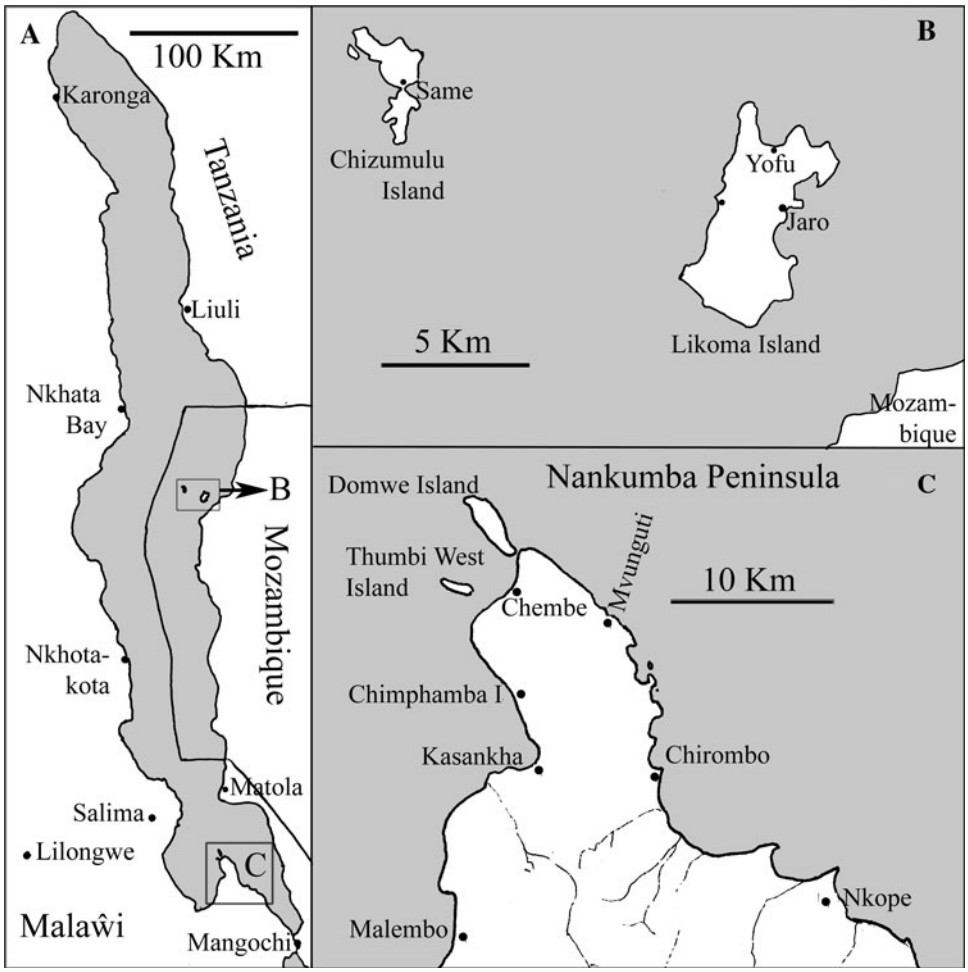

Figure 1. Lake Malawi and some of our sampling sites.

is a member of the *B. truncatus/tropicus* group and is endemic to Lake Malawi; it can be found along open sandy shorelines at water depths from about 0.7 m to more than 15 m and has a preference for habitats devoid of vegetation and with coarse and, to a smaller extent, fine sand substrate, where it is normally found in the upper 2–3 cm (Wright et al. 1967; Madsen et al. 2004, 2011). It has been suggested (Stauffer et al. 1997) that the reason behind transmission along some open shore stretches in the southern part of the lake (Nankumba Peninsula; Fig. 1) is that predation pressure on *B. nyassanus* had been reduced by over-fishing (Cetron et al. 1996; Stauffer et al. 1997). Several fish species, including those that primarily feed on freshwater snails, have declined in abundance (Stauffer et al. 2006b). Lake Malawi harbors the most diverse ichthyofauna of any freshwater lake in the world, with as many as 850 species (Konings 2001; Stauffer et al. 2006a). There are signs of over exploitation and an increased fishing effort has resulted in decreased catch rates, and depletion of larger species, especially in southern Lake Malawi where the concentration of fishing effort is greatest (Weyl et al. 2010). The shallow-water sand-dwelling fishes, including the molluscivores are particularly vulnerable to the artesian fishing gear during spawning. We attribute the observed decrease in density of *Trematocranus placodon* (observed at Chembe village), which is the most widespread snail-eating cichlid species, from 1978 to 2003 (Stauffer et al. 1997) to overfishing and the increased use of fine-meshed beach seines that collect juvenile fishes. There are several other molluscivore fish species in the lake (Darwall et al. 2010) but *T. placodon* is the dominant species in potential habitats of *B. nyassanus* in shallow water. Although *T. placodon* prefers to prey upon *B. nyassanus*, it is not the only species consumed (Evers et al. 2006) and increased density of other suitable snails, particularly *Melanoides tuberculata*, could result in reduced predation on *B. nyassanus*. Further, distribution of *B. nyassanus* is affected by sediment composition (Genner and Michel 2003).

Here, we summarize data collected on density of *B. nyassanus* and *T. placodon* over a 4-year period in various parts of Lake Malawi to test whether density of *B. nyassanus* is related to density of *T. placodon*.

Description of Study Sites

Lake Malaŵi (Fig. 1), the most southerly lake in the East African Rift valley system, is over 600-km long (Beadle 1974), 75-km wide at its widest point, and 760-m deep with a total surface area of ~29,600 km^2. It is bordered by Malaŵi, Mozambique, and Tanzania.

The climate is tropical, with a rainy season from Nov to April. There is little to no rainfall throughout much of the country from May to Oct. It is hot and humid from Sep to April, with average daytime maxima between 27 and 29°C. From June to Aug, the daytime maxima are around 23°C, and night-time lows between 10 and 14°C (Eccles 1974; Halfman 1993; Chavula et al. 2009). During the cold months the prevailing wind is southerly.

Bulinus globosus is common in inland habitats and occurs in the lake, especially in swampy areas or along sheltered shorelines, while *B. nyassanus* is common in lake sites (Madsen et al. 2004, 2011). Populations of *B. globosus* in inland sites are rather erratic, mainly found during and a few months after the rainy season (Madsen et al. 2011). At such sites, transmission of *S. haematobium* through *B. globosus* can take place from at least April (after the rainy season) until the site dries out in July/Aug or, if sites persist in close proximity of the lake, until about Nov (Madsen et al. 2011). In the lake, *B. nyassanus* numbers increase from about May, reaching a peak between Aug and Nov and infected snails were found between July and Nov (Madsen et al. 2011).

Inhabitants of villages close to the lake shore have higher prevalence of *S. haematobium* infection than those living in inland villages, with the highest prevalence (>87%) in school-aged children (Madsen et al. 2011).

Methods

Sampling Schedule

For repeated sampling, we chose Matola (Makanjila), Same Bay (on Chizumulu Island), and Yofu (on Likoma Island), while on Nankumba Peninsula we selected four villages, Chembe, Chimphamba, Mvunguti, and Chirombo Bay (Fig. 1). Sites on the two islands and Matola were visited 2–3 times per year (in Jan/Feb, June/July, and Sep/Oct) for estimation of snail and fish densities, while snail sampling in the four sites on Nankumba Peninsula was conducted monthly and fish populations were estimated quarterly (Jan, April, July, and Sep). Sample points are summarized in Table 1.

Estimation of Fish Density

Fish density was estimated along transects extending up to 200 m from shore at the following depths, if present: 1.5, 3.0, 4.5, 6.0, 7.5, and 9.0 m from 2003 to 2006. A 50-m measuring tape was laid down at each depth parallel to the shoreline and all molluscivorous fishes seen within a 2-m zone on either side of the tape were videoed by a diver swimming along the tape in one direction, and the same procedure was immediately followed swimming in the opposite direction. The video was reviewed later in the laboratory and the number of the molluscivorous fish, *T. placodon*, was counted for each pass along the tape and the average was used as number of fish per 200 m^2 (50 × 4 m).

Snail Sampling in Transects

Samples were taken at the following depths, if present within 200 m from the shoreline: 1.5, 3.0, 4.6, 6.0, 7.5, and 9.0 m monthly from Feb 2003 to Dec 2006 at transects at Nankumba Peninsula, while other sites were sampled 2–3 times per year. Three 1 × 1-m quadrats were carefully sampled by SCUBA divers using plastic buckets to remove the top 2–3 cm of sediment, which was transferred to one plastic bag for each quadrat. Samples were brought to the shore and sorted for snails. The sediment was sieved through a wire mesh of 1.5 mm and the retained material searched for live snails. The *Bulinus* snails were checked for cercarial shedding, while other snails were counted and preserved in 80% ethanol. *B. nyassanus*, *B. globosus*, and *Bulinus succinoides* collected during the morning were checked for cercarial shedding on the same day, while if snails could not be checked before 14:00 h, they were transferred to aquaria and checked the following morning. Snails were transferred individually to small plastic beakers (12.5 ml) with 6 ml of water and exposed to light outside (not in direct sunlight) for 2–3 h before containers were inspected for the presence of cercariae using a dissecting microscope. Fork-tailed cercariae were preserved for later verification.

Snail Sampling (Scooping)

A number of 50-m stretches of shoreline outside the transect areas was searched for snails by two people for 60 min, using the standard snail scoops. The ''snail scoopers'' used waders to minimize their risk of becoming

Table 1. Sampling stations

Village	Description	Latitude (S°, min, s)	Longitude (E°, min, s)
Nankumba			
Chembe			
GSSOP	Golden sands/otter point	S14°2′20.3″	E34°49′28.8″
GSS	Golden sands	S14°2′9.2″	E34°49′35.3″
FRS	Fisheries station	S14°1′55.5″	E34°49′39.3″
FM	Fat monkey	S14°1′27.0″	E34°50′26.9″
SWP	Chembe swamp	S14°1′1.6″	E34°50′51.4″
Chimphamba			
MSK1	Msaka, transect 1	S14°4′20.9″	E34°50′47.2″
MSK2	Msaka, transect 2	S14°4′10.7″	E34°50′37″
MSK3	Msaka, transect 3	S14°4′2.9″	E34°50′27.5″
Mvunguti			
MVUN1	Mvunguti, transect 1	S14°2′8.8″	E34°54′8.3″
MVUN2	Mvunguti, transect 2	S14°28.2″	E34°54′6.2″
Chirombo Bay			
CBSWP	Chirombo Bay, swamp	S14°6′45.8″	E34°55′33.0″
CBNUN	Nunes Cottage	S14°6′35.5″	E34°55′34.2″
CBPENN		S14°6′18.9″	E34°55′38.8″
Makanjila			
Matola	Matola	S13°39′26.8″	E34°51′11.9″
Northern sites			
Same Bay	Same Bay (Chizumulu Island)	S12°1′34.5″	E34°37′30.6″
Yofu	Yofu (Likoma Island)	S12°02′36.3″	E34°44′22.4″

infected. The scoop was made from a kitchen sieve supported by an iron frame mounted on 3- to 4-m-long bamboo rod. The scoop was passed through the top sediment for some distance (2–5 m). During this passage, the net was held perpendicular to the sediment surface and at the end of the passage the net was turned 90° and immediately lifted to the surface. Care was taken not to lose the retained material while retrieving the scoop. Carefully repeated washing of the scoop brought the snails to the surface and all *Bulinus* species were transferred to a plastic container. Other snail species were ignored.

Sediment Composition

At each transect point, two sediment samples were taken while SCUBA diving using Kajak sampler tubes. 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 to those of the first sample. One sample was preserved by adding 25 ml of 96% ethanol. This procedure was repeated, such that samples were taken at 0–2-, 2–4-, and 4–6-cm sediment depth. 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 other sample using wet oxidation ($K_2Cr_2O_7$) method (Wakley and Black 1934).

Statistical Analysis

For graphical presentation of density of *T. placodon* and snail species, counts were transformed by $\log_e(x + 1)$ and averaged across periods or sites. These mean values and their 95% confidence limits were back transformed to the original scale and presented as ''geometric mean'' number per 200 m^{-2} and m^{-2} for fish and snails, respectively. Count models (Hilbe 2008) were used to compare fish and snail counts across various factors such as water depth, village, or others either using the GLM procedure adjusting for clustering within transects or as panel data if a time factor (year or month) was to be adjusted. In these analyses, we first used Poisson regression (Hilbe 2008),

which involves estimation of one parameter, the mean (μ); we checked for overdispersion, and if present, modeled using negative binomial regression where the variance was modeled as $V = \mu + \alpha * \mu^2$. The ancillary parameter (α) was estimated using full maximum likelihood estimation (Hilbe 2008). The ancillary parameter was then entered into a Generalized Linear Model and model fit was assessed using dispersion statistics to check for overdispersion and Anscombe residuals were used to check for outliers (see Hilbe 2008). Comparison of competing models was done using AIC and BIC statistics (Hilbe 2008). All analyses were completed in Stata 11 and differences with probability value of $P < 0.05$ were considered significant. Predictors that were not significant ($P > 0.05$) were eliminated from the final model.

Sediment composition was analyzed 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) after adjusting for differences among transect points. Thereafter, a pooled composition was computed for each point and a new PCA was calculated and PCA scores saved as variables; then these variables were used as predictors in negative binomial models with density of *B. nyassanus* during that year as the dependent variable.

Results

Density of *T. placodon*

The distribution of fish showed an aggregated pattern. The maximum number of fish counted in one transect point was 69 on Nankumba (observed at Chimphamba), 28 at Matola, and 64 in the Northern sampling stations (observed at Same Bay). Density of *T. placodon* varied considerably between visits at Matola and on one occasion we observed intense seine-net fishing at this location. Sampling points with zero counts comprised 32–38% in the three areas, but the proportion of sites with low counts (2 fish/200 m^2 or less) was higher in Nankumba and Matola than in the northern sampling stations. Density of *T. placodon* increased with depth in all areas (Fig. 2). The highest density was found at the Northern sites. We were able to achieve the best fit with the negative binomial regression. Since, some transects were sampled only to 4.5 m, we pooled all depths from 4.5 to 9.0 m. Distribution by depth differed between Matola and the other two areas combined ($P < 0.001$). Adjusting for clustering within transects, density of *T. placodon* at 1.5 and 3.0 m at the northern sites was 4.5 and 25.9%, respectively, of that at depths from 4.5 to 9.0 m combined; similar values from Nankumba sites were 1.6 and 9.2% and 6.0 and 34.9% at Matola (maximum depth sampled was 4.5 m). The same model showed that density of *T. placodon* at Nankumba was 35.5% of that found in the northern sites. The Pearson dispersion statistic was close to unity indicating that data were not overdispersed. Year to year variation was not as pronounced at Chembe and Chirombo Bay, while at Chimphamba more fish were counted in 2004 than during the other years and at Mvunguti the counts were highest in 2003.

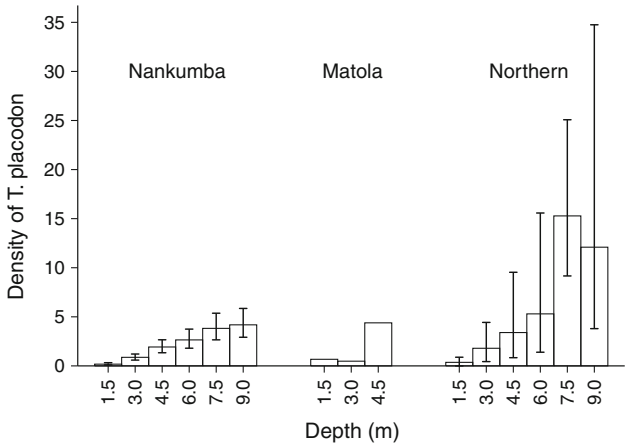

Figure 2. Fish density (geometric mean fish count 200 m^{-2}) by depth and area. *Error bars* 95% CL.

Distribution of Snails

Qualitative searches at various lake sites, revealed species rarely found in our routine sampling, i.e., *Ferrisia* spp., *Lymnaea natalensis*, *Gyraulus costulatus*, *Bulinus forskalii*, *B. globosus*, and *Ceratophallus natalensis*. *B. globosus* was found in many locations around the lake but not in transect samples. Many inland sites close to the shore that are water-filled, primarily by wave action, harbored dense populations of *B. globosus* and occasionally *Biomphalaria pfeifferi* (intermediate host for *S. mansoni*). Of 324 *B. globosus* collected at Chimphamba, 22 were positive for schistosome infection, and of 200 collected at Mvunguti, 12 were positive. At Chembe and Chirombo Bay, no *B. globosus* were found in the routine collections but more thorough qualitative surveys have revealed *B. globosus* also from inland habitats around these villages. *B. globosus* can also be found in parts of the lake sheltered from wave action. The areas

include bays or areas sheltered by islands or sand barriers and occasionally comprising dense vegetation.

Snail Density (Transect Sampling)

Melanoides spp. was by far the most abundant snail species in all areas (Table 2). Distribution of snails varied greatly from quadrate to quadrate showing a clumped distribution, with many zero counts and a few samples with very high counts. Among the transect samples on Nankumba, 67.5% had zero counts of *B. nyassanus*, and at Matola and the northern sites this percentage was 59.1 and 90.0%, respectively. Zero counts of *Melanoides* spp. were 7.1, 19.7, and 13.0% at Nankumba, Matola, and northern sites, respectively. The mean density of *Melanoides* spp. was somewhat higher at sites on Nankumba Peninsula than those at Matola and more northern sites and density of *Melanoides* was locally very high (3,080 m^{-2}).

Bulinus nyassanus was distributed widely within the lake but its density was lower at the northern sites than at Nankumba and Matola (Fig. 3). Snail counts from Matola were not directly comparable to those at Nankumba, because average values from Nankumba were collected monthly while at Matola and the northern sites, sampling was done primarily when densities were high. These overall patterns mask a lot of variation among villages and among individual transects. Density of *B. nyassanus* was highest at 1.5-m depth at Chembe, while at Chimphamba maximum density was found at 6.0 m (Fig. 4). These patterns, however, varied among transects. Density of *B. nyassanus* at Chirombo Bay and Mvunguti was generally low. Density of *B. nyassanus* was lower in 2003 than during the 3 following years ($P < 0.01$). Adjusting for clustering within transects and effects owing to year, density varied by depth and differed among the three areas ($P < 0.001$).The ancillary parameter was estimated to 1.80 and the Pearson dispersion statistic was 0.94.

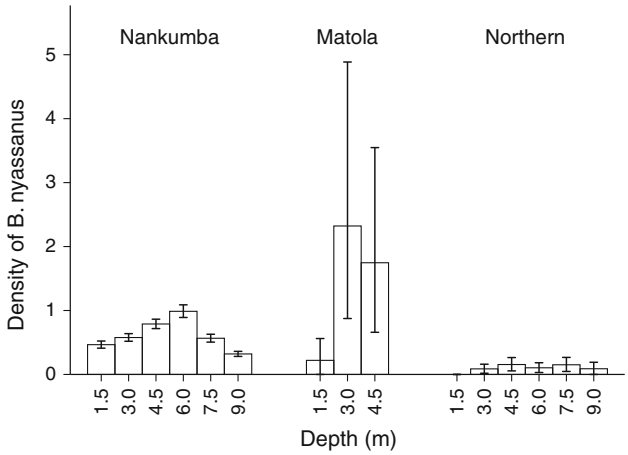

Figure 3. *Bulinus nyassanus* average density (geometric mean no. of snails m^{-2}) by depth in different areas. *Error bars* 95% CL.

Melanoides spp. were most dense at 1.5 m at Nankumba peninsula density declined at depths of 7.5 and 9.0 m (Fig. 5). Interestingly, density of *Melanoides* spp. was similar in the three regions at 4.5 m and deeper and the most conspicuous difference was the high density in shallow waters in Chembe. Since, density of *Melanoides* spp. varied among 4.5–9.0 m depth, the analysis of snail counts was done only at depths covered by all transects (i.e., to 4.5 m). Density of *T. placodon* was a negative predictor ($P < 0.01$) of density of *Melanoides* spp. when adjusting for depth ($P < 0.001$), year to year variation ($P < 0.001$), area ($P < 0.05$), and the interaction between area and depth ($P < 0.001$). The highest densities of *Melanoides* spp. were recorded from Chembe, especially transects CHFM and CHSWP. *Melanoides* was most dense in shallow water at all villages on Nankumba Peninsula (Fig. 6).

Table 2. The snail fauna

	Nankumba	Matola	Northern
No. of quadrates	9,122	66	369
Total snails	582,577	2,884	14,236
Average density (no./m^2)			
Melanoides spp.	61.9	41.1	38.6
Gabbiella humerosa	0.0	0.0	0.3
Bellamya spp.	0.3	0.0	0.0
Lanistes spp.	0.1	0.0	0.0
B. nyassanus	1.5	2.6	0.2
B. succinoides	0.0	0.0	0.1
Percentage composition			
Melanoides spp.	96.9	94	98.5
Gabbiella humerosa	0.1	0	0.7
Bellamya spp.	0.5	0	0.1
Lanistes spp.	0.2	0	0.1
B. nyassanus	2.4	6	0.4
B. succinoides	0	0	0.3
Maximum number in one quadrate			
Melanoides spp.	3,080	237	775
Gabbiella humerosa	6	1	33
Bellamya spp.	28	0	2
Lanistes spp.	6	1	3
B. nyassanus	46	29	4
B. succinoides	1	0	12

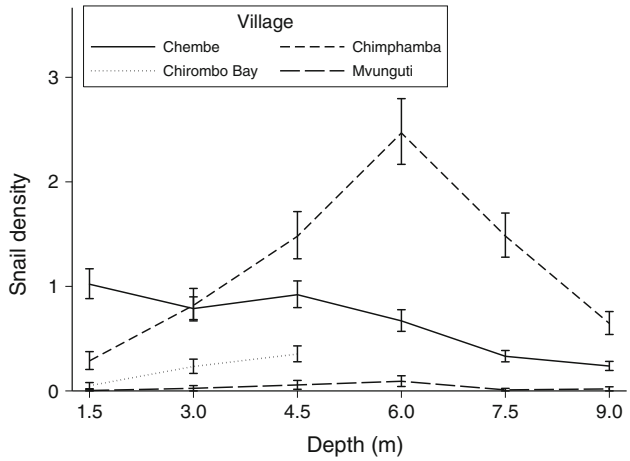

Figure 4. Density of *B. nyassanus* (geometric mean no. of snails m^{-2}) by depth at the four villages on Nankumba Peninsula. *Error bars* 95% CL.

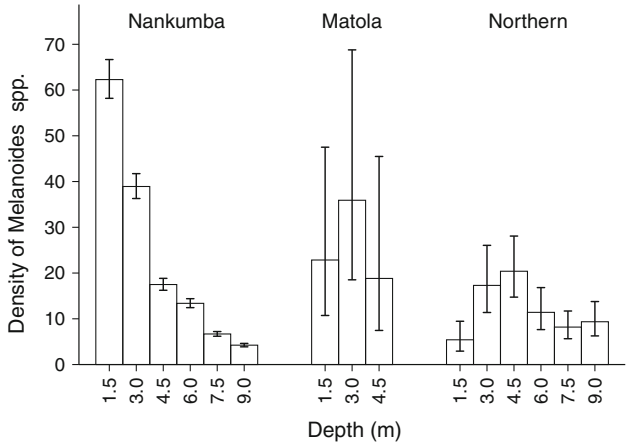

Figure 5. Average density (geometric mean no. of snails m^{-2}) *Melanoides* spp. by depth in different areas. *Error bars* 95% CL.

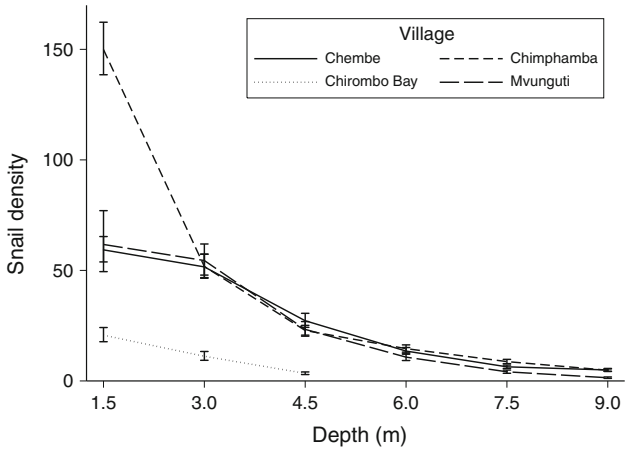

Figure 6. Average density (geometric mean no. of snails m^{-2}) *Melanoides* spp. by depth at the four villages on Nankumba Peninsula. *Error bars* 95% CL.

B. nyassanus (Scooping)

The number of *B. nyassanus* collected from scooping sites along the Chembe shoreline declined from the southern part (sites 1 and 2) to the northern sites (Table 3). This pattern was consistent over the 4-year period. Very few *B. nyassanus* were collected at Chimphamba and Mvunguti and none at Chirombo Bay. *S. haematobium* infections in *B. nyassanus* were reported only from among snails collected by scooping (Table 4). The overall prevalence of infection was 0.36% (118/32675), but varied from zero to 2.05% among the ten scooping sites at Chembe (Table 3). In the deeper water, *B. nyassanus* was found occasionally infected with other fork-tailed cercariae (i.e., clinostomes), in which fish is the second intermediate host and fish eating birds the definitive host. *B. succinoides* was checked whenever collected and at Matola and other sites about 400 specimens were checked for infections. Summarizing all findings it seems that a precondition for transmission through *B. nyassanus* was its existence at high density relatively close to the shore (Table 5). At Matola, density of *B. nyassanus* was high at water depths of 1.5–3.0 m but this was relatively far from the shore (>30 m). In the lake, infected *B. nyassanus* were found only at Chembe except for sporadic sampling at Malembo, Kasankha, and Nkope (Madsen et al. 2011).

At Chembe, maximum snail numbers were found from Aug to about Nov/Dec, while numbers were low from Jan to May/June (Fig. 7, 8). Infected *B. nyassanus* were generally found from about June to Oct, but were found occasionally during other months as well. Lake level rose quickly during the rainy season and was highest in April/May and then declined during the dry season. The initial drawdown phase coincided with low temperatures and the

Table 3. Total number of *B. nyassanus* collected by scooping in the various sites over a 4-year period

Village/site no.	Local landmarks	Latitude (S°, min, s)	Longitude (E°, min, s)	No. collected	No. positive	% infected
Chembe						
1	Near otter point	S14°2′16.6″	E34°49′31.1″	11,875	6	0.1
2		S14°2′2.1″	E34°49′37.1″	12,875	41	0.3
3	Fisheries	S14°1′49.5″	E34°49′51.6″	5,033	32	0.6
4	Kajak Africa	S14°1′42.9″	E34°50′4.2″	1,847	24	1.3
5		S14°1′33.1″	E34°50′19.1″	684	14	2.0
6		S14°1′21.0″	E34°50′33.6″	257	1	0.4
7	Fat monkey	S14°1′13.4″	E34°50′42.1″	56	0	0
8		S14°1′6.5″	E34°50′48.3″	35	0	0
9		S14°0′50.6″	E34°50′57.1″	1	0	0
10	Chembe lodge	S14°0′46.6″	E34°51′1.1″	12	0	0
Chimphamba	Four sites			3	0	0
Mvunguti	Two sites			1	0	0
Chirombo Bay	Four sites			0	0	

Table 4. Infections in *B. nyassanus*

Location/area	No. collected	Additional sampling[a]	No. infected	Prevalence (%)
Area (transect sampling)				
Nankumba	13,890		0	0.00
Matola	172	500	0	0.00
Northern	59	600[b]	0	0.00
Nankumba (scooping only)				
Chembe	32,675		118	0.36
Chimphamba	3		0	0
Chirombo Bay	1		0	0
Mwunguti	0		0	0
Kasanka		322	1	0.31
Malembo		278	3	2.00
Nkopola lodge		10	0	

[a]Includes additional sampling primarily by dredging (figures are approximate).
[b]Including sites on the Tanzanian shoreline.

period when *B. nyassanus* numbers increased. In transects at Chembe and Chimphamba, density of *B. nyassanus* varied more in the shallower water than in deeper water (Fig. 9). Otherwise, the pattern coincided with that observed in scooping.

Sediment Composition

Sediment composition did not differ significantly among the three depth layers sampled. Composition differed among transects ($P < 0.001$) but there was little variation with water depth within transects. Principal component analysis showed that the first two eigenvectors explained 68% of the variation and the four eigenvectors 91%. The first two components had eigenvalues above 1. The factor loading for clay in the first component was negative while those for the sand fractions were positive, while on the second component the silt and organic fractions had the highest loadings (Table 6). Negative binomial regression showed that the first component was negatively associated with density of *B. nyassanus* which means that clay, which had the highest absolute value of the negative loadings, was positively associated with density of *B. nyassanus* The clay fraction ranged from <1 to 59% while the sand fractions combined ranged from 3 to 87%. Some of the extreme sediment types were not included in the analysis because they could not be sampled. Sampling very fine sediments, such as found at Chembe swamp, was not possible because the corer could not be forced into the sediment. Also some locations with very coarse sediment could not be sampled because samples could not be retrieved.

Relationship Between *B. nyassanus* and *T. placodon*

This analysis was complicated by the repeated estimation of fish and snail density and the unbalanced design. We averaged fish density for each transect for each year and used the $\log_e$-transformed value as a predictor of density of *B. nyassanus* (density at each transect and depth and each year). Fish could easily move across different depths and hence snail counts at different depths could be dependent

Table 5. Comparisons between sites where *B. nyassanus* is involved in transmission (Nankumba) and sites where it is not?

Village[a]	No. of transect visits	Maximum depth sampled (m)	Minimum depth sampled (m)	Mean density (snails m^{-2})[b]	Maximum density (snails m^{-2})	Mean density at 1.5 m (snails m^{-2})[a]	Mean density in shallows (1.5–3.0 m) (snails m^{-2})[a]
Nankumba							
Chembe	246	9.0	1.5	1.57	6.58	2.54	2.12
Chimphamba	147	9.0	1.5	2.48	8.07	1.14	1.36
Chirombo Bay	106	4.5	1.5	0.36	1.94	0.07	0.26
Mvunguti	61	9.0	1.5	0.07	0.89	0.01	0.03
Kasankha	2	6.0	1.5	2.78	2.08	1.50	4.08
Matola	6	4.5	1.5	2.61	8.42	0.44	2.89
Northern sites							
Nkhata Bay	2	9.0	7.5	1.33	0.13	0.00	0.00
Nkhuyu	2	6.0		–	0.00	0.00	0.00
Yofu	8	9.0	3.0	0.30	1.11	0.00	0.39
Same Bay	8	9.0	6.0	0.16	0.36	0.00	0.00
Usisuya	2	6.0	4.5	1.33	0.76	0.00	0.00
Chilumba	2	6.0	4.5	0.67	0.38	0.00	0.00

[a]Only the first four villages sampled regularly.
[b]All depths where snails found.

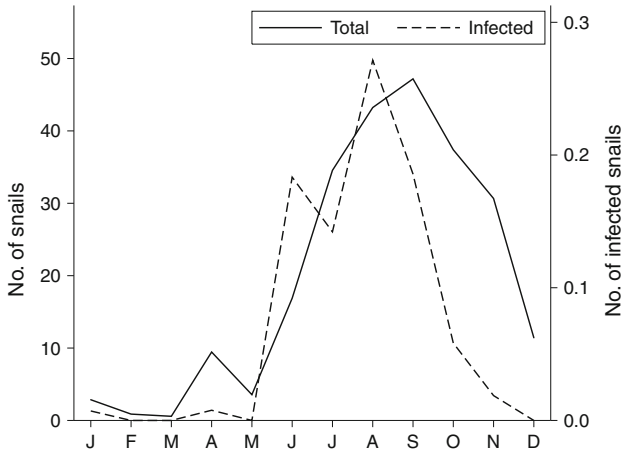

Figure 7. Variation over time in number of *B. nyassanus* collected man-hour search^{-1} at sites at Chembe village (average over years 2003–2006).

on fish recorded at other depths as well. Using data from all villages included in longitudinal sampling and selecting, only the months sampled in all areas, showed that density of *B. nyassanus* was negatively associated with fish density ($P < 0.05$) and positively with density of *Melanoides* spp. ($P < 0.001$); a one-unit increase in fish density on a $\log_e$-scale was associated with 25% lower density of *B. nyassanus* while a similar increase in density of *Melanoides* corresponded to 60% higher density of *B. nyassanus*. Adjusting for the effect of area would change the significance of fish density since fish density varies by area.

Since, villages on Nankumba Peninsula were surveyed much more intensely than the Matola and northern areas; the analysis was also completed on these villages separately. Using only $\log_e$-transformed fish density and $\log_e$-transformed density of *Melanoides* as predictors yielded the same results. Density of *T. placodon* in shallow water (depth 1.5–3.0 m) was very low at the four villages on Nankumba peninsula (Fig. 2), while in deeper waters (7.5–9.0 m), fish density was higher. Considering depths above 3.0 m only showed that a one-unit (on a $\log_e$-scale) increase in *T. placodon* density was associated with a density ratio for *B. nyassanus* of 0.76 ($P < 0.05$), while the ratio was 2.52 ($P < 0.001$) if density of *Melanoides* increased by one unit (on a $\log_e$-scale).

Discussion

Our data suggest a negative effect of *T. placodon* on densities of *B. nyassanus* and *Melanoides* spp., and a positive relationship between densities of the two snail species. Both

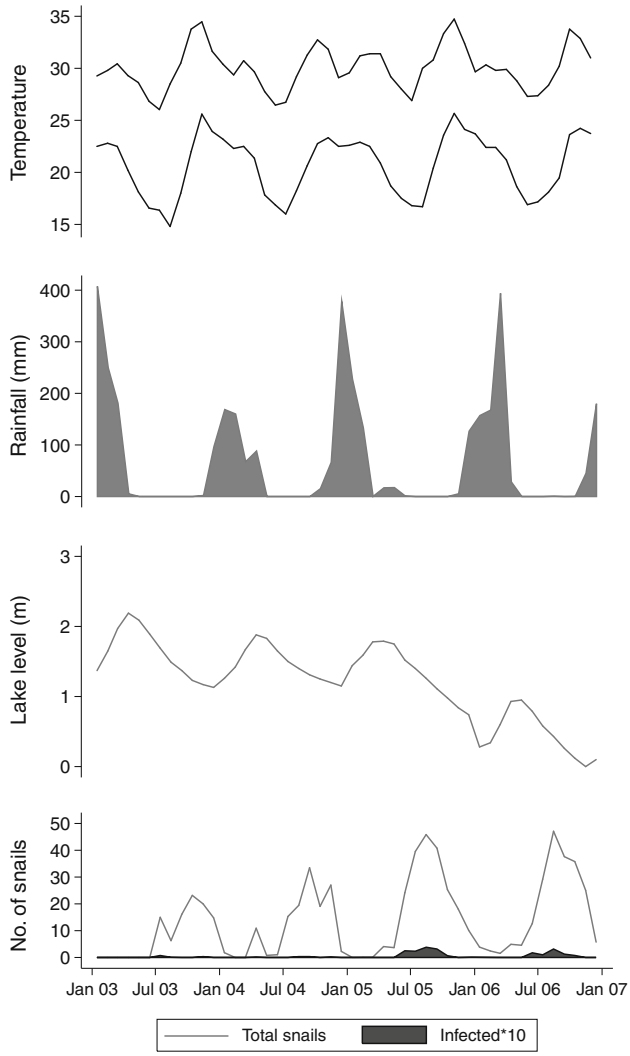

Figure 8. Variation over time in number of *B. nyassanus* and number of snails infected by *S. haematobium* (×10) man-hour search^{-1} at ten sampling stations at Chembe village together with temperature (monthly mean minimum and maximum), rainfall and lake level (as deviation from the minimum level recorded from 2003 to 2007).

snail species are major elements in the diet of *T. placodon* and *B. nyassanus* appears to be the preferred species (Evers et al. 2006), especially during times of its highest abundance (Madsen et al. 2010). These relationships are clearer in deeper waters, where density of *T. placodon* is higher.

Whether the changed distribution pattern of *T. placodon* (Stauffer et al. 2006b) is, however, entirely the result of overfishing and the cause of high density of *B. nyassanus* in shallow water should be evaluated by following changes in fish density and snail distribution after implementation of a fish ban. Our data show that changes in fish populations may occur rapidly and therefore, we are optimistic that a fishing ban in village areas would lead to increases in

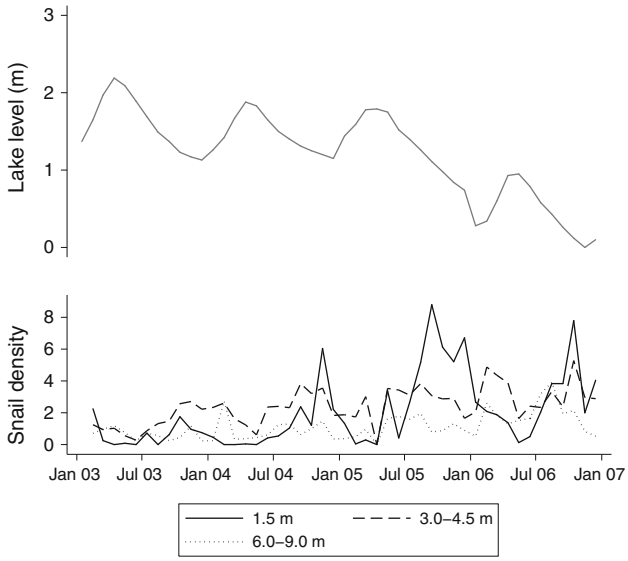

Figure 9. Variation over time in density of *B. nyassanus* (snails m^{-2}) in transects at Chembe and Chimphamba village at various depths together with lake level.

T. placodon density. Whether this would be sufficient to reduce both density of *B. nyassanus* and schistosome transmission remains to be seen, although previous data have shown a negative relationship between snail density and level of infection (Stauffer et al. 2006b). Only experimental studies can substantiate our hypothesis. Alternatively, explanations for the reduced density of *T. placodon* could be related to increased human water contact repelling fishes from foraging in shallow water or an increased organic loading with organic waste from human water contact activities could benefit *B. nyassanus* (increased food availability). An important finding is that relatively few *B. nyassanus* are infected and they are found primarily in shallow water and this level of infection in the intermediate host can result in intense transmission to people. This means that very significant reductions in density of *B. nyassanus* would be required to influence transmission to people.

The intermediate host, *B. nyassanus*, undergoes marked seasonal variation in density in the very shallow water (i.e., water depth less than about 1.5 m) close to the shore. Each year in Dec–Jan, *B. nyassanus* is virtually absent from these depths at Chembe Village, likely owing to wave action (Madsen et al. 2011). Other factors associated with rainfall, however, could also be involved, for example increased turbidity. Although we do not have detailed data on storms and wave action, it seems that populations can persist during this period in sheltered sites. During this period, *B. nyassanus* populations persist in deeper water, where the density fluctuations are much less pronounced. The major build-up of *B. nyassanus* population density occurs from about May when water level drops and water temperatures are low (Madsen et al. 2011). Since, we have done quantitative data of snail density at different depths, these changes are real and not a result of concentration of snails due to declining water level. Laboratory studies (Kubiriza et al. 2010, unpublished observations) show that *B. nyassanus* has optimal reproduction and growth at around 25°C as most other *Bulinus* species and the snail can reach maturity during 4–6 weeks at a shell height of 5–6 mm. That means that the population build-up could start during the last part of the rainy season; our sampling is just not efficient in detecting the juvenile snails. Reproduction, however, is intense during the cold dry season as egg masses are frequently found during sampling (Madsen et al. 2011).

Schistosome transmission is very intense in some lake shore communities including Chembe and Chimphamba (Madsen et al. 2011) and it is imperative that transmission control, including control of the intermediate host snails, is implemented. Otherwise, medical treatment will have to be administered frequently over a long time to prevent morbidity.

Table 6. Principal components (eigenvectors) from principal component analysis of sediment samples

Sediment fraction	Comp1	Comp2	Comp3	Comp4	Comp5
Clay	−0.5103	−0.3842	0.2514	0.2718	0.1567
Silt	−0.2804	0.6263	−0.4261	−0.2915	−0.1865
Coarse sand	0.4247	−0.1721	−0.6728	0.3647	0.3794
Medium sand	0.4948	−0.1837	0.1150	0.0668	−0.7459
Fine sand	0.4719	0.1565	0.4233	−0.4490	0.4879
Organic material	0.1142	0.6102	0.3320	0.7085	0.0474

Preventing schistosome eggs from reaching the lake water or reducing water contact seem unlikely in the setting at Lake Malaŵi. Hence, the most realistic approach to transmission control, apart from sustained chemotherapy, would be snail control. The only acceptable option for snail control in Lake Malaŵi would be protection of native molluscivorous fishes. Chemical snail control can be eliminated as an option because of the effects the chemical might have on the fish fauna, the cost of chemicals, and logistic problems in ensuring exposure of snails to the chemical, i.e., because of wave action, the water depth at which snails are found and the burrowing behavior of *B. nyassanus*. Introduction of non-indigenous species as competitors (other snails) or predators (mainly fish species) is unacceptable because of the unforeseen effects this would have on the local fauna.

It seems that transmission in the lake through *B. nyassanus* is restricted to the southern part of the lake. Thus, infected *B. nyassanus* was found only on Nankumba Peninsula. Further, *S. haematobium* transmission through *B. nyassanus* is limited to sites where it occurs in shallow water close to shore. In the northern part of the lake, density of *B. nyassanus* is low, even at sheltered shorelines such as Same Bay, Nkhata Bay and Liuli (Tanzania), and *T. placodon* density is high. The main reason for *B. nyassanus* not being infected in northern sites is probably its low density and absence close to the shore. Based on these findings potential sites with transmission within the lake could be mapped from satellite or aerial photographs using the following criteria, i.e., sandy shoreline with the presence of village facing in a northern to western direction, with fairly steep slopes (a proxy for slope could be the presence of *Valisneria* beds, visible during periods of clear water, within 5–10 m from the shore). It might well be that sites with transmission along sandy shorelines in front of villages are few; rocky shorelines are not transmission sites. A fish ban should only be implemented along these specific shorelines and the ban should cover up to 100-m off-shore.

Although the use of fish for biological control of freshwater snails often has failed elsewhere in Africa (Slootweg et al. 1994; Slootweg 1995), this should not happen in the case of *T. placodon* in Lake Malawi, because food availability for the fishes or interactions with other species are likely to remain constant. Attempts should be made therefore through government extension workers to introduce a community enforced shallow water fishing ban.

Even if *T. placodon* can control *B. nyassanus* and transmission along open shorelines, *S. haematobium* transmission will persist in inland habitats and other measures will have to be implemented there. Many villages have several inland sites where *B. globosus* can exist; often streams that during the dry season turn into a series of ponds. Several of the inland sites may contain water through the dry season almost until the following rainy season, while many others just contain water for a few months into the dry season. Beach seining may constitute an important source of protein for local people and, if banned, many people may not be able to afford to purchase fish from fishermen. We, therefore, think that possibilities of utilizing these inland sites for aquaculture should be explored. Although aquaculture has well-documented positive effects, i.e., improved nutrition, better food security, better job opportunities, and financial benefits, and has been demonstrated as sustainable in Africa (Brummett et al. 2008), there are also concerns that such activities may lead to increased transmission of various water-related diseases because installations (canals and ponds) often function as excellent habitats for intermediate hosts of trematodes including schistosomes (Slootweg et al. 1993). Furthermore, cultured species should be from the local watershed because of the high risk of escape to the lake. Fish ponds would probably be organically loaded and this might favor proliferation of the intermediate host snails, i.e., *B. globosus* and possibly *Biomphalaria pfeifferi*. Aquaculture using polyculture including molluscivore species might not control the intermediate host snails although Chiotha et al. (1991a, b) have demonstrated that a mix culture that included *T. placodon* significantly reduced density of intermediate hosts. Experience from Cameroon and elsewhere was not promising because soft food items might be abundant in inland waters and molluscivores might shift to such food items and this can lead to reduction in the crushing mill reducing their ability to crush snails (Slootweg et al. 1994). It may be necessary to control access to the fish ponds such that they do not become transmission sites even if they sustain dense populations of intermediate host snails.

In conclusion, our data provide support for the hypothesis that local over-fishing explains establishment of schistosomiasis transmission along open shorelines in the southern part of the lake. Whether, the situation can be reversed must be determined after implementation of an effective fish ban up to 100-m offshore along these specific shorelines in front of villages.

Acknowledgments

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