Hydrological modelling of snail dispersal patterns in Msambweni, Kenya and potential resurgence of *Schistosoma haematobium* transmission

J. A. CLENNON[1]*, C. H. KING[2], E. M. MUCHIRI[3] *and* U. KITRON[1]

[1] *Department of Pathobiology, University of Illinois, 2001 South Lincoln Avenue, Urbana, Illinois 61801, USA*
[2] *Center for Global Health and Diseases, Case Western Reserve University, 10900 Euclid Avenue, Cleveland, Ohio 44106, USA*
[3] *Division of Vector Borne Diseases, Ministry of Health, Nairobi, Kenya*

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SUMMARY

Urinary schistosomiasis is an important source of human morbidity in Msambweni, Kenya, where the intermediate host snail, *Bulinus nasutus* is found in ponds and water pools. In the past, aquatic habitats in the area have been studied separately; however, recent collections of *B. nasutus* snails and shells indicated that many of these ponds are in fact connected during and following sufficient rains. Satellite imagery and a geographical information system (GIS) were used to survey the main water courses and potential drainage routes, to locate potential source populations of snails and to determine probable snail dispersal routes. The 2 water bodies implicated as being the most important *Schistosoma haematobium* transmission foci in the area were found to differ in their degree of connectivity to other *B. nasutus* source habitats. One pond becomes connected even after normal rains, while the other pond requires prolonged rains or flooding to become connected with source habitats. Consequently, the transmission foci differ in their susceptibility to snail population control measures. Spatially explicit dispersal models that consider the spatial and temporal patterns of connectivity between aquatic habitats will contribute to improved snail surveillance and more focused control for urinary schistosomiasis at a local level.

Key words: *Bulinus nasutus*, dispersal, eco-epidemiology, GIS, hydrology, remote sensing, *Schistosoma haematobium*, schistosomiasis, snail, Kenya.

INTRODUCTION

Urinary schistosomiasis, is endemic in much of subSaharan Africa where suitable habitats for snails of the genus *Bulinus*, the intermediate hosts of *Schistosoma haematobium* are abundant (Jordon and Webbe, 1993; Brown, 1994). Along coastal Kenya, *Bulinus globosus* and *Bulinus nasutus* species are the predominant intermediate hosts of *S. haematobium*. In Msambweni, where *B. nasutus* is the only intermediate host, 52% of school-aged children are infected with *S. haematobium* (Clennon *et al.* unpublished obsevations), despite chemotherapy programmes targeting school children during the 1980s and 1990s (King *et al.* 1991; Muchiri *et al.* 1996; Satayathum *et al.* 2006). Concurrent control measures directed at the intermediate host in the region may be necessary for sustained suppression of human infection.

Bulinids are aquatic snails found in streams, ponds and temporary water pools (O'Keefe, 1985; Kariuki *et al.* 2004). Control of these snail populations is difficult because they can auto-reproduce and aestivate (McCullough *et al.* 1968). Aestivation, when snails may be found under vegetation or burrowed into the soil in a condition of reduced metabolic activity, is triggered by the drying of water pools, (Brown, 1994). When rainwater fills the pond beds and creates water pools, the snails emerge from aestivation and repopulate the water bodies (Webbe and Msangi, 1958; Donnelly *et al.* 1983; Sturrock *et al.* 1990). Live snails are limited to locations with standing water or with enough moisture for survival of aestivating snails, while shells can also be found along dry sections of the drainage corridors that connect such locations.

Infected *B. globosus* snails are considered more efficient shedders of cercariae than *B. nasutus* (Hamburger *et al.* 2004): however, these findings do not consider differential snail survival under adverse weather conditions, such as dry periods. This is an important consideration since *B. globosus* inhabits stable aquatic habitats while *B. nasutus* is found in less stable habitats (Stothard *et al.* 2000, 2002*a*).

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* Corresponding author and current address: Department of Molecular Microbiology and Immunology, Johns Hopkins Bloomberg School of Public Health, 615 North Wolfe Street, Baltimore, MD 21205, USA. Tel: +410 955 3708. Fax: +410 955 0105. E-mail: jclennon@jhsph.edu

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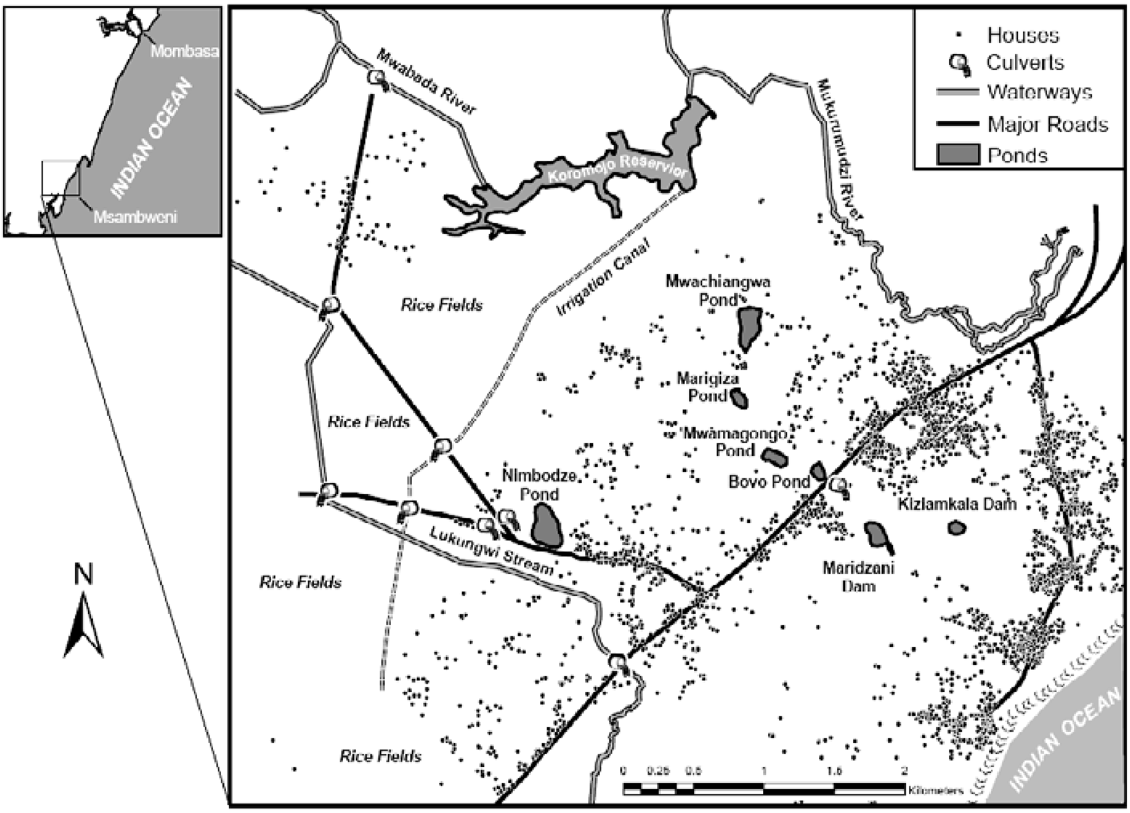

Fig. 1. Aquatic habitats located in Msambweni Division, Kwale District, Kenya.

As environmental factors (e.g. rainfall, water drainage and vegetation cover) fluctuate temporally, they influence transmission patterns by changing the distribution and density of competent snail hosts (Kariuki *et al.* 2004). How population dynamics of *B. nasutus* are affected by fine-scale spatial heterogeneity remains largely undetermined in dynamic environments such as coastal Kenya. The patterns of snail dispersion and dispersal within and between aquatic habitats are determined by habitat suitability and connectivity (Utzinger *et al.* 1997). Since dispersal is important for maintaining local and meta-populations following droughts and floods (Marti *et al.* 1985; Mavarez *et al.* 2002), the connectivity of suitable breeding and transitory aquatic habitats needs to be considered for implementation of effective control measures targeting snail populations.

The predominant method for determining snail habitat connectivity has long been capture-mark-recapture (Thomas and Tait, 1984; Woolhouse, 1992) and, more recently, molecular-based studies (e.g. polymerase chain reaction (PCR)) to examine the genetic relatedness of aquatic snail populations (Stothard *et al.* 2001; Chlyeh *et al.* 2002; Mavarez *et al.* 2002). In this study, we used fine-resolution satellite imagery and field data from aquatic habitats to detect potential dispersal pathways and probable locations of snail aestivation and develop a hydrologically based dispersal model. We applied indicators used commonly by palaeontologists to study processes leading to fossilization of organisms (taphonomy) in order to reconstruct prior habitat conditions and to validate the dispersal model. Our objectives were to evaluate landscape corridors that connect fragmented patches of habitats suitable for breeding of *B. nasutus* and enable its dispersal, and to determine habitat suitability for snail aestivation throughout our study area in Msambweni Division in coastal Kenya.

MATERIALS AND METHODS

Research setting

The study area is Msambweni Division, Kwale District, Coast Province, Kenya (Fig. 1), where prevalence of *S. haematobium* remains high despite long-term intensive chemotherapy campaigns. The climate is tropical with low temperatures of 23·5 °C in July to 26·9 °C in March–April and highs of 26·7 °C in August to 36·3 °C in February. Annual precipitation fluctuates widely, averaging 1200 mm, with 2 rainy seasons, the long rains (usually March–July) and the short rains (October–November). However, since 2001 and through 2005, the normal

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precipitation pattern in the area has been interrupted by a severe drought. Located on the coastal plains, the land cover is a mosaic of grasslands, rice and maize plots, and mango, palm and cashews trees, some in plantations. The soil composition ranging from clay loam to extremely sandy soils over crystalline and coralline limestone that generally provide good drainage heading southeast through the area towards the Indian Ocean (Mzuga *et al*. 1998).

Water bodies include several rain-filled ponds (Marigiza, Kiziamkala, Maridzani, Bovo, Nimbodze, Mwachiangwa, Mwamagongo), and the Koromojo Reservoir (Fig. 1). Spring-fed waterways include the perennial Mukurumudzi River, and the seasonal Mwabanda River and Lukungwi Stream. The water levels in the rain-filled ponds and seasonal waterways fluctuate with rainfall and dry out during periods of prolonged drought. Fortnightly and monthly snail scooping was conducted at these water sources during March 1984–July 1987 (Sturrock *et al*. 1990) at 40 human water contact sites and February 2001–August 2004 (during the drought period) at 24 human water contact water sites (Kariuki *et al*. 2004). When the ponds and various locations along the waterways contain water, various snail species can be collected, including *B. nasutus* (Stothard *et al*. 2002*b*), the only intermediate host of *S. haematobium* in the study area. Of all open water sources in the area, Nimbodze Pond, Maridzani Dam and Kiziamkala Dam (Fig. 1) have been the most important transmission foci with the highest numbers and proportion of *B. nasutus* shedding human cercariae (Sturrock *et al*. 1990; Clennon *et al*. 2004; Kariuki *et al*. 2004; Clennon *et al*. unpublished observations).

Dispersal modelling: landscape characterization

LandSat 5 Thematic Mapper (TM) imagery (courtesy of the U.S. Geological Survey) (28·5 m multispectral) taken in June 1986 (a non-drought period) during the long rains was used to identify the most likely corridors for *B. nasutus* to transverse during dispersal by applying a normalized difference moisture stress index (NDMSI) using bands 4 (near-infrared, 0·7–1·3 microns) and 5 (middle-infrared, 1·3–2·5 microns) (Rock *et al*. 1986). Pan-sharpened, LandSat 7 Enhanced Thematic Mapper (ETM+) imagery (courtesy of the U.S. Geological Survey) (14 m panchromatic, 28·5 m multispectral) taken during the drought (January 20, 2003) were used to detect suitable locations for aestivation (in soil or under vegetation) by applying the NDMSI and performing unsupervised classification. Multispectral Ikonos imagery (acquired on 4 March 2001) was obtained, and then pan-sharpened (1 m resolution) for detailed mapping of the Msambweni landscape and for verifying that no major landscape changes influencing the water drainage had occurred since 1986. All imagery was processed in Imagine 8.7 software (ERDAS, Atlanta, GA), and georectified to Universal Transverse Mercator (UTM) zone 37S projection, 1984 datum.

LandSat 5 TM satellite imagery (which preceded LandSat 7 ETM+) from 1986 was used because obtaining relatively cloud-free imagery for the Msambweni study area during the long rainy season is very difficult and few images are available. Thus, the 1986 imagery allowed us to determine where flooding occurs, while the 2003 drought imagery taken in the dry season during the drought allowed us to assess the soils for suitability for aestivation.

Dispersal modelling: delineation of drainage pathways

To determine the major pathways of water drainage through the study area, Shuttle Radar Topography Mission (SRTM) level 1 Digital Terrain Elevation Data (DTED) (courtesy of the U.S. Geological Survey) of 3-arc seconds (~90 m) horizontal resolution and 1 m vertical resolution for the study area (path 165, row 63, World Geographic System 2) were obtained (Fig. 2A). The relative vertical accuracy is ±6 m (90% vertical error), but approaches 3 m in flat areas with little vegetation; relative horizontal accuracy is ±15 m (90% circular error). Elevation values represent the reflective surface, be it vegetation (e.g. trees), soil or manmade structures (e.g. houses). The advantage of using multi-frequency, multi-polarization radar system is the ability to collect terrain data through clouds, that often obscure the south coast of Kenya.

The DTED was initially processed in Imagine 8.7 and imported into ESRI ArcGIS 9.0 (Redlands, CA), using the Terrain Analysis Using Digital Elevation Models extension (TauDem; Tarboton, Utah State University, 2005) to characterize the landscape's terrain and model water flow. Smoothed elevation data were used to calculate slope per pixel, that subsequently allowed the determination of flow direction and flow accumulation, the variables needed to identify major drainage lines (Fig. 2B and C). Flow direction was estimated based on steepest slope on a triangular facet (Tarboton, 1997) and the flat area flow direction method (Garbrecht and Martz, 1997). Flow accumulation was calculated as the number of upslope cells flowing into a cell. The initial drainage network model did not account for the irrigation system that transverses the area, as the irrigation canal is merely 2 m wide, so it was added to the network. In addition, a topographical wetness index was estimated as the ratio between slope and the area for a specific catchment to predict areas of water concentration. A visual accuracy assessment comparing *a priori* knowledge (known stream and river routes), the 1986 LandSat imagery and the unclassified 2001 Ikonos imagery with the predicted

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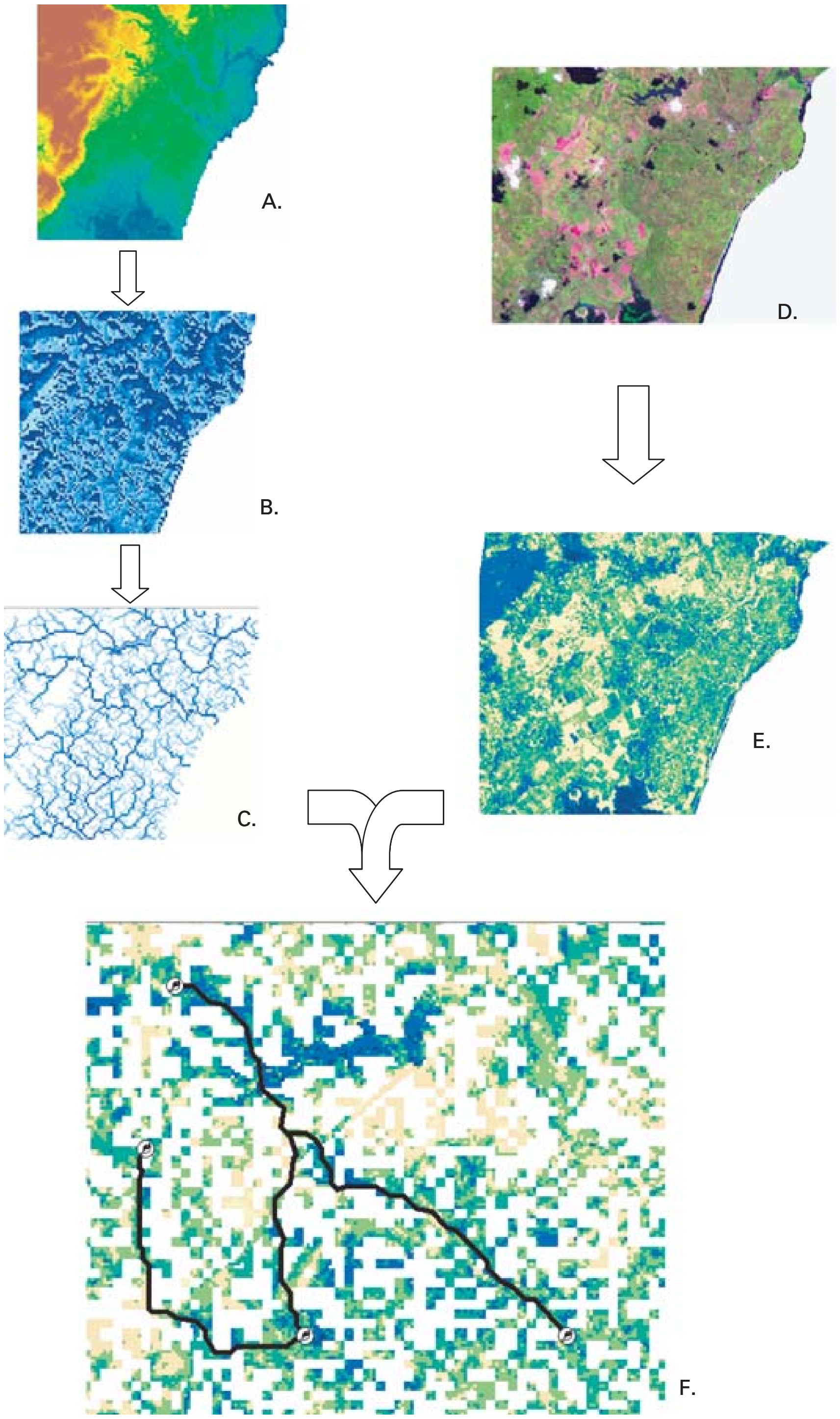

Fig. 2. Hydrological model processing steps. (A) Digital elevation model; (B) flow direction; (C) drainage network; (D) 1986 LandSat in false true colour; (E) moisture stress; (F) least cost dispersal routes between 2 source habitats to 2 sink habitats: ——.

major drainage pathways to ensure the correctness of the calculations.

Dispersal modelling: dispersal least-cost analysis

Populations of snails are needed upstream along a drainage corridor for dispersal, but they do not need to be permanent. Permanent/semi-permanent populations were chosen for our model starting points, because they allowed us to use transient population locations to validate our model. Additionally, dispersal may at times require individual snails as well as their progeny to cross the Msambweni drainage system to other permanent/semi-permanent aquatic habitats.

To determine the least cost surface for *B. nasutus* snails to disperse across the Msambweni landscape, a weighted NDMSI map for habitat suitability

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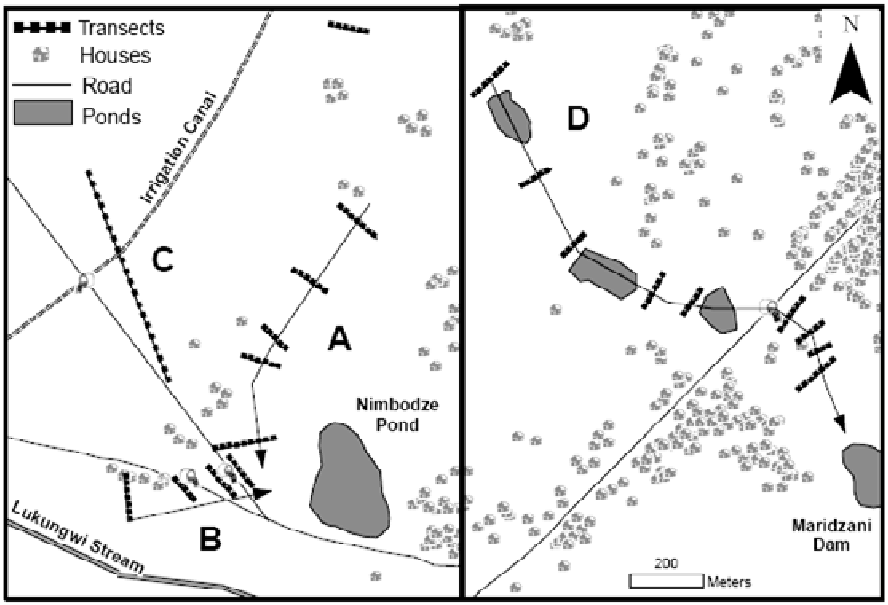

Species	A	B	C	D*
B. nasutus	23.2% (57)	59.9% (375)	1.6% (10)	4.4% (10)
Lanistes	17.1% (42)	26.8% (168)	57.4% (35)	94.7% (216)
B. forskalii	23.2% (57)	0.8% (5)	13.1% (8)	0.4% (1)
Lymnaea	6.5% (16)	0.0% (0)	6.6% (4)	0.0% (0)
Cleopatra	0.4% (1)	0.3% (2)	0.0% (0)	0.0% (0)
Neritina	0.0% (0)	0.5% (3)	0.0% (0)	0.0% (0)
Pila	0.0% (0)	1.0% (6)	1.6% (1)	0.4% (1)
Melanoides	29.7% (73)	10.7% (67)	19.7% (12)	0.0% (0)

* *Bulinus nasutus* maybe slightly under represented along the Maridzani Dam drainage line because of the initial exploratory snail collections conducted in 2003.

Fig. 3. Maps of drainage corridors and species compositions (by percentages and numbers) of aquatic snail shells per drainage corridor collected using transect sampling.

along drainage corridors was created using 1986 LandSat imagery (Fig. 2D and F). Then, least-cost dispersal route corridors between known locations of *B. nasutus* breeding habitats were determined. The path of least cost maximizes the amount of soil/vegetation moisture (a measure of dispersal suitability) encountered along the water drainage network between source and destination, while also minimizing the distance travelled. This is done by using a weighted-distance function where the cost per cell is equal to the moisture stress index multiplied by the cell resolution (e.g. 28·5 m). The final accumulative cost is the sum of all movements between the source and sink habitat.

Model validation

To validate the spatial dispersal model and to better understand the underlying dispersal process of *B. nasutus* distribution in Msambweni, we investigated aquatic snail shell distributions and taphonomy prior to model creation and, then, examined fortnightly and monthly temporal sequences of *B. nasutus* collection data from water sites previously not considered to be connected.

Snail and shell characteristics and distribution. Two methods, exploratory surveying and transect sampling, were used to determine potential water drainage corridors and presence/absence of snails prior to model creation. Exploratory surveying (August 2003 and June–July 2004) consisted of walking along probable water drainage pathways, collecting aquatic snail shells and live *B. nasutus*, and taking global positioning system (GPS) readings (Trimble, GeoExplorer II GPS). While the distribution of *B. nasutus* shells was our focus, shells of other aquatic snails were also collected, as they also indicate previous water flow through an area. Transect sampling for aquatic snail shells was conducted along 4 drainage corridors during June–July 2004 (Fig. 3). Printed maps of the Ikonos imagery (1 m resolution) were used for precise mapping of sampling locations. All shells from 4 m^2 plots were collected along these transects. Different sections

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along the drainage valleys vary in width, so sampling plots were selected every 2–10 m starting from the lowest point of the valley depression and outward on each side for at least 50 m or until a defined slope was reached. Rice fields were sampled across the rice field grids, or with verbal consent of the owner. Locations where exploratory collections were conducted prior to plot sampling were noted. Each sampling plot was described in terms of distance to the valley centre, soil type and percentage of vegetation cover (ranked by quantiles as <25%, 26–50%, 51–75%, >75%).

Distribution patterns and taphonomic characteristics of shells (operculum presence or articulation, dissolution, rounding, breakage and concentration, size) were considered in order to assess the environmental conditions (e.g. water energy levels and possible post-mortem transportation) of each drainage corridor.

RESULTS

Survey sampling

Aquatic snails (or shells) of 8 species (*B. nasutus*, *Lanistes purpureus*, *Melanoides tuberculata* (2 morphotypes), *Cleopatra* spp., *Bulinus forskalii*, *Pila ovata*, *Lymnaea natalensis* and *Neritina* [*pulligera*] *knorri*) were collected (Fig. 3). We also found snails and shells of an amphibious snail, *Lymnaea columella*.

Exploratory survey. During the initial exploratory survey (August 2003), *B. nasutus* were found consistently nearly every 10 m between Mwamagongo and Maridzani dams, with the exception of the 100 m leading to Maridzani Pond, where the drainage corridor widened and was covered by dense vegetation. In 2004, live *B. nasutus* snails were found along the Mwabanda River and at the culverts northwest of Koromojo Reservoir, and *B. nasutus* shells (and occasionally live snails) were found repeatedly along an abandoned irrigation channel connecting Koromojo Reservoir in the north to Lukungwi Stream in the south. *Bulinus nasutus* shells were also found east of Koromojo Reservoir by the Mukurumudzi River. Along the Lukungwi Stream flood plain, shells of *L. natalensis*, *M. tuberculata* and *B. nasutus* were collected (Fig. 3).

Transect sampling. Concentrations of shells (including *B. nasutus*) were found across the rice fields north Nimbodze and Lukungwi Stream drainage lines and not only on the sides of the valleys as would be expected following deposition by flowing waters (Fig. 3). Shell concentrations (including shells of *B. nasutus*) were scattered across the northern portion of the valley leading to Mwamagongo and Maridzani ponds, and were found more evenly distributed in the extreme south. Shells were generally most abundant in sandy loam or heavily silted soil, regardless of percentage of vegetation cover.

The transects along the Maridzani Dam drainage line had more shell breakage and generally uniform shells in terms of size and shape, whereas shells found along transects leading to Nimbodze Pond exhibited low levels of shell breakage and a greater diversity in size, indicative of relatively calmer environments (Fig. 3).

Lymnaea natalensis shells were collected just outside a sampling plot at a culvert near Nimbodze Pond and in the Maridzani Dam corridor (Fig. 3). They were also found along the northern portion of the irrigation scheme, some 300 m south of Koromojo Reservoir. The presence of *L. natalensis* suggests that permanent water sources, flowing or stagnant, are connected to these areas (Brown, 1994; Utzinger and Tanner, 2000). Notably, several shells of *N. knorri*, a snail that inhabits rivers and streams were collected (with intact operculums) in the drainage corridor just past the culverts south of Nimbodze Pond.

Dispersal least-cost analysis. A drainage network model was developed from digital elevation model (DEM) (Fig. 2C). The results of the least-cost analysis for dispersal from potential reservoir *B. nasutus* populations upstream of known transmission sites are shown in Fig. 2F. The drainage line calculations revealed 3 defined dispersal pathways connecting different *B. nasutus* breeding habitats. One path connects the Mwabanda River in the northwest to Marigiza Pond and then all the way to Maridzani Dam. Two other paths lead to Nimbodze pond, one begins along the irrigation system just west of Nimbodze Pond, and one along Lukungwi Stream.

Landscape characterization. The 1986 flood imagery revealed considerable amounts of pooled water in the Lukungwi and Nimbodze drainage corridors where we found shells in high abundance. Of particular importance, it shows a series of temporary habitats from Lukungwi Stream through a drainage corridor south of Nimbodze pond that are probably suitable not only for survival but also for reproduction of *B. nasutus*. Indeed, live snails or shells of *B. nasutus* were found in locations where pooling of water was predicted based on topographic wetness values and where soil moisture was moderate or high (Fig. 4).

Temporal malacological data. During 1984–1987 the spatial distribution of *B. nasutus* followed a temporal trend starting with snails collected along Lukungwi Stream (Site A) followed by increasing numbers of snails collected downstream at a road culvert (Site B) leading to Nimbodze Pond and, finally, at Nimbodze Pond (Site C) (Fig. 5).

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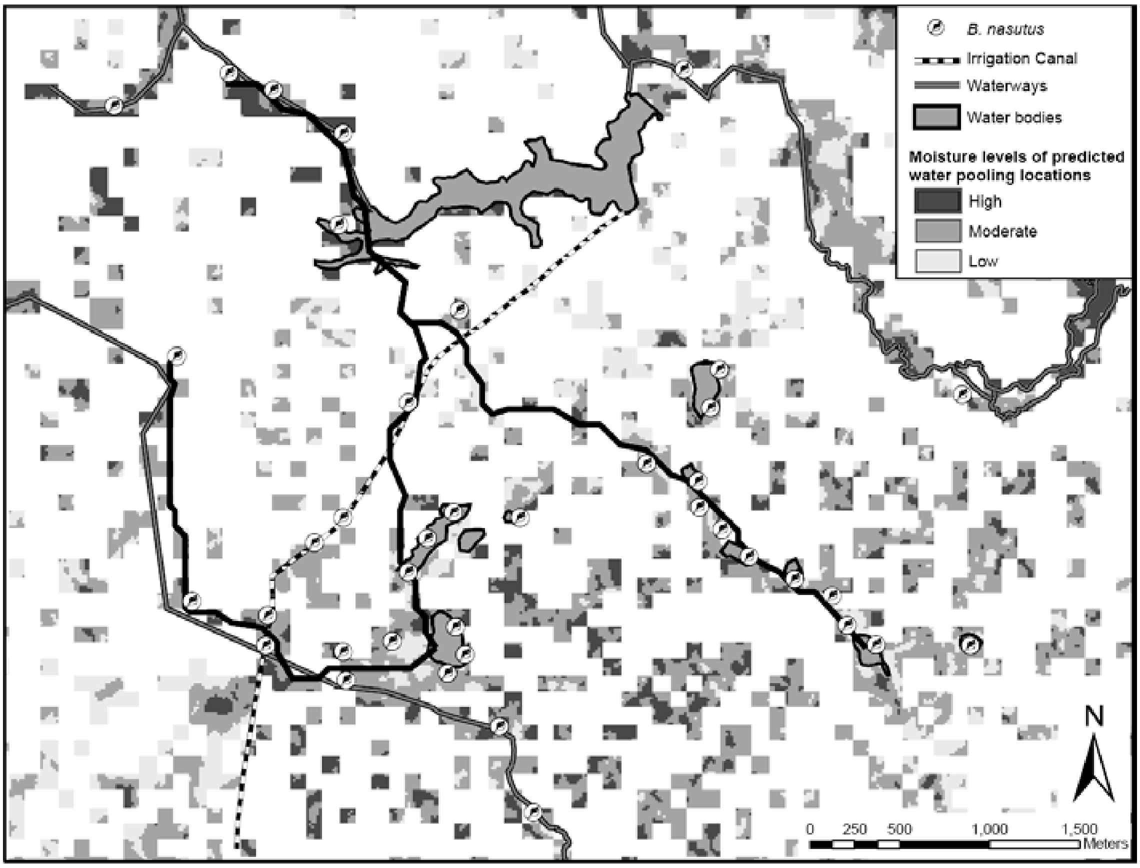

Fig. 4. Moisture levels at predicted locations for water pooling and at sites where *Bulinus nasutus* have been collected.

Time lags of differing lengths between water presence at habitats and *B. nasutus* presence were also observed during the drought period of 2001–2004. In 2001, the *B. nasutus* snail population fluctuations at Bovo Pond were similar to those upstream at Mwamagongo Pond, but snail activity was higher at Bovo during 2002 and 2003. In fact, a population peak in September 2003 associated with flooding coincided with flooding and subsequent appearance of *B. nasutus* after an 8·5 month absence at Maridzani Dam, just south of Bovo. Since January 2002, there have been no sightings of *B. nasutus* at Kiziamkala Dam which is connected to the Maridzani Dam water drainage pathway, although water was present during 8 collection periods.

In the southwest portion of the area, the Lukungwi Stream connects the rice field site with Nimbodze Pond and 2 stream sites (Fig. 5). There were only 2 occasions when water was present in the rice field site and no *B. nasutus* were collected. Nimbodze Pond, a known epicentre for *S. haematobium* transmission, was found to have *B. nasutus* snails from February 2001 to 2002. Although water returned to the pond in May 2003, a lag of 4 months occurred before any *B. nasutus* were found again.

DISCUSSION

Environmental and meteorological data derived from coarse satellite imagery (spatial resolution of 1 km or more) have been used to develop risk maps for schistosomiasis at country, regional and continental scales for human schistosomes (Malone *et al.* 1994; Bavia *et al.* 1999, 2001; Bergquist *et al.* 2000; Abdel-Rahman *et al.* 2001; Zhou *et al.* 2001). Such risk models allow for general predictions of presence of snail intermediate hosts over wide areas, but do not take into account local heterogeneity (Kitron, 2000). Fine spatial resolution imagery (30 m or less: LandSat, SAR, Ikonos) can be used to study ecological processes operating on a local level (Kitron *et al.* 2006). While such modelling efforts have been initiated for the amphibious intermediate host of *S. japonicum* in China (Zhou *et al.* 2001, 2002; Guo *et al.* 2005; Zhang *et al.* 2005), they have not been applied to bulinid snails whose distribution is restricted to aquatic habitats.

In a study of *S. japonicum* in China, the spatial distribution of the miracidia and cercariae was associated with a survey-based hydrological model of a water drainage network (Maszle *et al.* 1998). More recently, Shaman and colleagues (2002, 2005)

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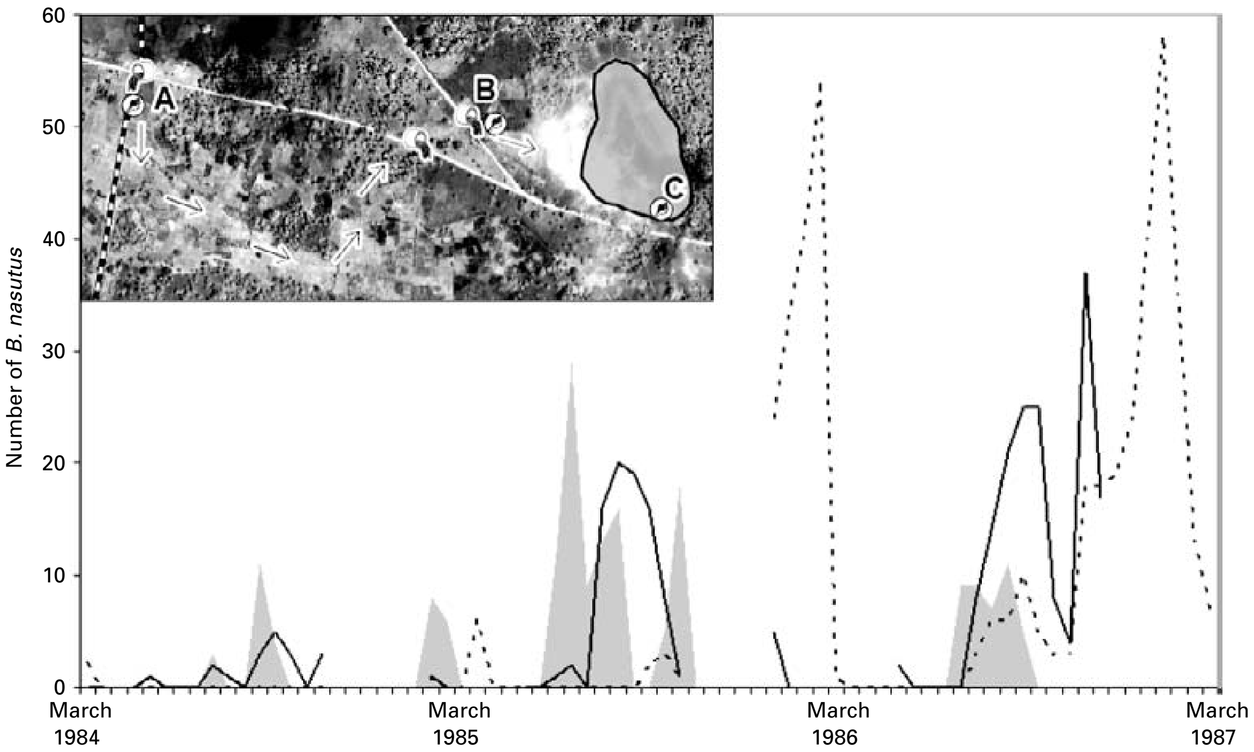

Fig. 5. Biweekly number of *Bulinus nasutus* collected at three sites in the Msambweni, Kenya study area. March 1984–March 1987. Sites: ▨ A, ——— B, - - - - C

applied a hydrological model based on topography and soil moisture to predict mosquito abundance within watersheds. Hydrological modelling is highly suitable for understanding the connectivity of spatially distributed breeding and aestivation habitats of bulinid snails, and for determining the repopulation potential of habitats following mollusciciding.

Bulinus nasutus populations can tolerate the dynamic drought-flood process occurring in Msambweni. Coupled with low *S. haematobium* patent infection rates, this may sustain *B. nasutus* metapopulations while facilitating *S. haematobium* transmission. The patches where *B. nasutus* live snails and shells were found included dispersal pathways (which are only very transiently occupied), temporary habitats and breeding habitats. Dispersal pathways in Msambweni are generally characterized as having little vegetation, with predominantly light, sandy soil along water drainage routes where water often moves relatively swiftly. Temporary habitats with dark, sandy soil and a certain degree of shade (suitable for aestivation) are present along these pathways.

Following sufficient rains, *B. nasutus* snails have been found in pools along the drainage corridors not only persisting but, in habitats with relatively stagnant waters over less sandy, dark soil, at times also breeding. Koromojo Reservoir has not been found to maintain *B. nasutus* populations, but rather appears to be part of the aquatic route along which snails disperse. Indeed, culverts in the area have been found to provide very suitable habitats for *B. nasutus*.

Two main routes, the drainage systems from the Lukungwi stream and from the rice fields northwest of the pond, have now been identified as leading to Nimbodze Pond, and both routes include breeding sites for *B. nasutus*. The rice field site is particularly important in that it is not only linked with the irrigation scheme, but is also connected to Lukungwi Stream that, in turn, links it to other breeding habitats. An old irrigation system west of the human population centres continues to impact the study area not only through water drainage but also by acting as a well-defined dispersal corridor for *B. nasutus* snails.

These recent findings suggest that within Msambweni, snails, specifically *B. nasutus*, are not merely travelling through flood plains from sources to transmission sites (e.g. Nimbodze Pond). Rather, they are using well-defined dispersal corridors along the irrigation scheme and streams/rivers. The primary route of snail dispersal is not necessarily the shortest route linking source to destination, but rather the route with the better defined corridor and lower levels of moisture stress. This is in agreement with recognized routes of spread for snails elsewhere (Marti *et al*. 1985), and highlights the role of anthropogenic changes to the landscape (construction of irrigation canals and road culverts) that increase the availability and connectedness of aquatic habitats suitable for intermediate host snails (Steinmann

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et al. 2006). In Msambweni, the likely result is a more continuous input of host snails into areas of *S. haematobium* transmission and less dependence on floods and heavy rains.

Nimbodze Pond, where transmission of *S. haematobium* has been most intense in our study area, exemplifies the importance of connectivity. Given that Nimbodze Pond was dry for a prolonged period (19 months in 2002–2003) and repeated burnings of vegetation, it is unlikely that *B. nasutus* have survived there continuously through aestivation. Rather, Nimbodze Pond receives water from a northern hilly area and from rice fields and a stream, where *B. nasutus* have been found, and that following a heavy rain, remain connected with Nimbodze for several days.

The primary landscape change that occurred between 1986 and 2000 was a shift from sugar to rice agriculture in the western portion of Msambweni. In our study, we used 1986 LandSat imagery to determine wetness levels along potential dispersal routes, because of the difficultly of getting imagery with low levels of cloud cover during the long rains. A comparison between the 1986 LandSat and 2001 Ikonos revealed a high level of similarity between the boundaries of areas where water has often flowed or accumulated. If anything, the conversion to rice agriculture may have increased the potential for snail dispersal, through additional water pooling in those fields and increased connectivity to Nimbodze Pond.

Aquatic sites that have now been demonstrated to be linked with Nimbodze Pond, have been found to contain not only uninfected *B. nasutus*, but also *B. nasutus* shedding *S. haematobium* cercariae (Sturrock *et al.* 1990). One implication is that measuring *S. haematobium* water contamination by humans using snail-based methods (Hamburger *et al.* 2004) at a particular pond, may be confounded by infected snails entering the habitat from elsewhere.

It has been documented that *B. nasutus* due to its superior aestivation strategy is more tolerant than *B. globosus* of the dynamic drought-flood patterns that are found in Msambweni (Rollinson *et al.* 2001). While *B. globosus* snails may be dispersed in the same manner (Marti *et al.* 1985), their ability to survive long distances using very temporary habitats is questionable. Snails with patent schistosome infections are less likely to survive into aestivation than those with pre-patent infections (Sturrock, 1993), and their reproductive output is curtailed as infection nears patency, at which point they stop laying eggs entirely (Gracio, 1988). Of *B. nasutus* collected in Msambweni, the vast majority of those infected with *S. haematobium* have pre-patent rather than patent infections (Hamburger *et al.* 2004). While *B. nasutus* snails may not shed cercariae as profusely as *B. globosus*, they are more than adequate *S. haematobium* intermediate hosts, as is manifested in more than half of school-aged children in Msambweni being infected (Clennon *et al.* unpublished observations). Thus, although *B. globosus* may be a superior intermediate host in sustained aquatic habitats, *B. nasutus* is an efficient intermediate host under dynamic conditions with transient aquatic habitats, as are found in Msambweni.

High concordance between the distribution of live snails and of snail shells in relatively unperturbed freshwater systems allows for reconstruction of past environmental conditions (Cummins, 1994). Understanding the processes affecting snail distribution and shell condition, is a less expensive alternative to molecular profiling, and one that can be pursued during dry periods to study snail dispersal in an area. Phylogenetic analyses can confirm whether the snails in the sinks/destinations are more closely related to snails in various source habitats.

After flooding or sufficient rains, individual snails and potentially snail populations can traverse environmental boundaries between different aquatic habitats within the study area. Dispersal routes throughout the study area (some better defined than others) connect many of these habitats. When considering dispersal routes, the directionality of dispersal along a route needs to be taken into account (e.g. knowing the source of dispersal to optimize mollusciciding or to construct mechanical barriers).

Our findings have applications for *S. haematobium* transmission control programmes targeting *B. nasutus* snail populations along the southern coast of Kenya. Highly connected dispersal routes allow for reintroduction of bulinid snails and re-emergence of *S. haematobium* transmission within the area following human chemotherapy campaigns and mollusciciding. Determining the spatial and temporal patterns of connectivity between aquatic habitats allows for identification of potential dispersal pathways of *B. nasutus* snails, and needs to be considered in *S. haematobium* transmission control programmes targeting snail populations.

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