Spatial distribution and habitat characterization of schistosomiasis host snails in lake and land habitats of western Kenya

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Abstract

Intermediate host snails of schistosomiasis were surveyed in this study to determine their abundance and distribution in the lake and land aquatic habitats of Lake Victoria basin of Kenya. Several sites were sampled at eight locations, both in the lake and on the land. The habitat and/or vegetation type (i.e. open water, hippo grass, hyacinth, ambatch trees, other vegetation, stream, swamp, pond, dam) of the sampled aquatic sites within the locations were also differentiated, water physicochemical parameters were determined, and the abundance of different species or taxa of phytoplankton and zooplankton were enumerated and correlated with the abundance of schistosomiasis snails in the sites. The results indicated significantly more *Biomphalaria sudanica* snails than *Bulinus africanus* snails in different physical habitats on land (Student's *t*-test, $P < 0.05$), as well as in different locations on land (Student's *t*-test, $P = 0.026$). Regression analyses revealed that several physicochemical parameters, including dissolved oxygen ($R^2 = -0.659$; $n = 8$; $P = 0.014$), pH ($R^2 = 0.728$; $n = 8$; $P = 0.007$) and turbulence ($R^2 = -0.616$; $n = 8$; $P = 0.02$), were predictive of *Biomphalaria* spp. abundance, while pH ($R^2 = 0.610$; $n = 8$; $P = 0.02$) and turbulence ($R^2 = -0.578$; $n = 8$; $P = 0.028$) were predictive of *Bulinus* spp. abundance in different locations in the lake. Cyanobacteria ($R^2 = 0.638$; $n = 8$; $P = 0.02$) and chlorophyceae ($R^2 = -0.50$; $n = 8$; $P = 0.05$) were shown to be predictive of both *Biomphalaria* spp. and *Bulinus* spp. abundance in different locations in the lake. Zooplankton abundance varied significantly between different locations in the lake (One-way ANOVA, $P < 0.001$). *Bosmina* spp. were found to be predictive of both *Biomphalaria* spp. ($R^2 = -0.627$; $n = 8$; $P = 0.01$) and *Bulinus* spp. ($R^2 = -0.50$; $n = 8$; $P = 0.05$) in different locations in the lake. The results from this study will help inform policy regarding control measures for schistosomias and intermediate snail hosts in Lake Victoria waters, as well as in adjacent terrestrial aquatic habitats and even beyond.

Key words

aquatic habitats, *Biomphalaria* and *Bulinus* snails, Lake Victoria basin, physicochemical parameters, phytoplankton, zooplankton.

INTRODUCTION

Schistosomiasis, a disease caused by parasites of the genus *Schistosoma*, is currently estimated to have infected at least 200 million people, among an estimated at-risk population of 779 million (Steinmann *et al.* 2006). Further estimates suggest sub-Saharan Africa exhibits a disproportionately high burden of the disease, with 85% of all schistosomiasis cases occurring in the region (Chitsulo *et al.* 2000). In fact, two forms, urinary schistosomiasis caused by *S. haematobium* and intestinal schistosomiasis caused by *S. mansoni,* are endemic in sub-Saharan Africa.

There are several principal intermediate host snails belonging to two genera. *Bulinus* transmits *Schistosoma haematobium* and *Biomphalaria* transmits *S. mansoni* (Brown 1994). It follows that the transmission of schistosomiasis is spatially and temporally restricted to water

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Accepted for publication 12 May 2013.

Doi: 10.1111/lre.12032

bodies inhabited by intermediate host snails, whereby humans come in contact during occupational or recreational activities with water infested with cercariae. Accordingly, schistosomiasis has been classified as an environmental disease (Malone 2005; Liang *et al.* 2007). Thus, a better understanding of the ecological factors that enhance the development of the parasite-intermediate host snail system is important to facilitate control interventions (Simoonga *et al.* 2008, 2009).

Previous studies indicate that most transmission of the intestinal form of bilharzia in the Lake Victoria basin tends to be closely confined to narrow zones along the shores of large bodies of water, such as Lake Victoria itself, where it is endemic, and the intermediate hosts are found (Kabaterine *et al.* 2001; Handzel *et al.* 2003; Mwanga *et al.* 2004). One study, however, reported that *Biomphalaria pfeifferi* exhibited no preference for locations close to the shoreline, possibly because the habitat had a uniform depth (Utzinger & Tanner 2000). A number of studies have been carried out in Kenya to assess the risk of schistosomiasis at a micro-scale (Handzel *et al.* 2003; Booth *et al.* 2004; Clennon *et al.* 2004). High *S. haematobium* infection intensities along the southern coast of Kenya, for example, were clustered around water bodies containing high numbers of infected intermediate host snails (Clennon *et al.* 2004). The prevalence of intestinal schistosomiasis among children attending schools near Lake Victoria was positively associated with their proximity to the lake shore and with specific water-related activities such as swimming, fishing and collecting water (Handzel *et al.* 2003; Stothard *et al.* 2005). In contrast, there is no transmission of *Schistosoma mansoni* in Msambweni, coastal Kenya, which is attributed to the absence of the *Biomphalaria* species intermediate host snail from most of this coastal province region, except for Taita-Taveta (Brown *et al.* 1981). In most coastal regions, higher temperatures are among the factors that might explain the lack of *Biomphalaria* species, as they are not as temperature tolerant as *Bulinus* species (Sturrock 1993).

Schistosomiasis is widespread in the Lake Victoria region, with the intermediate hosts being snails that are closely linked to the lake. There are two types of schistosomiasis along the Kenyan Lake Victoria region, namely *Schistosoma mansoni* and *Schistosoma haematobium.* Both species are focal in their distribution around the lake, with their intermediate hosts being *Biomphalaria sudanica, Biomphalaria pfeifferi* and *Bulinus africanus.* Seasonal fluctuation in the population density of *B. sudanica* elsewhere has been reported to be highly associated with rainfall, lake water levels, vegetation availability and abundance (Handzel *et al.* 2003). Although 37 species of *Bulinus* have been recognized (Brown 1994), only a few are involved in transmission. The *Bulinus africanus* group in Kenya is represented by *Bulinus* (*africanus*) *globosus*, *Bul* (*a*) *africanus*, *Bul* (*a*) *nasutus* and *Bul* (*a*) *ugandae*. Except for *Bul* (*a*) *ugandae*, all are important hosts of *Schistosoma haematobium* (Kariuki *et al.* 2004). Other studies indicate that the prevalence and severity of schistosomiasis are inversely related to the distance from the lake (Handzel *et al.* 2003). Karanja *et al.* (1997) reported, for example, that persons employed as vehicle washers in the town of Kisumu, Kenya, are exposed for several hours each day to water in Lake Victoria that contains *Schistosoma mansoni*–infected *Biomphalaria pfeifferi* snails, resulting in a focus of intense endemicity for schistosomiasis in the Lake Victoria region.

Bulinus species occupy a wide range of habitats in coastal Kenya, including quarry pits, streams, drainage canals, dams and seasonal pools (O'Keefe 1985). Another factor significantly associated with snail density is the presence of horizontal vegetation, namely water lilies (*Nymphaea* spp.). Most snails were observed resting on the underside of the lilies in areas probably rich in oxygen because of photosynthesis. The water lilies also provide egg-laying surfaces, shelter from the sun and food for many snail species. The snails feed on the microflora and decaying plant matter of the water lily leaves (O'Keefe 1985).

A previous study by Ofulla *et al.* (2010) indicated a considerable presence of the schistosomiasis host snails, which were associated with aquatic weeds in the Nyanza Gulf of Lake Victoria. Studies by Chlyeh *et al.* (2006) also showed that *B. truncatus* was positively associated with macrophytes. The link between snails and aquatic plant species occurs because the plants serve as sources of shelter, protection and surfaces for oviposition, as well as sources of snail food after decomposing for weeks and months in water (Alves & Blair 1953). Studies by Arora and Mehra (2003) indicated that *Eichhornia* supported more diverse rotifer fauna, some of which can be foods for snails, than did *Salvinia.* This association was so intense that some species of sessile rotifers were recorded exclusively in association with *Eichhornia* roots. It is possible the thick bushy rhizoids of *Eichhornia* provide abundant food, as well as protection from predators (Arora & Mehra 2003). Habitats without higher plant life, but which are rich in algae and diatoms might also support thriving snail populations (Alves 1957). Dense populations of certain species are found in sewage-contaminated water, leading to the conclusion that the snails are attracted by the increased food supply from

organic waste material (Alves 1957). The snails can be dispersed by a number of human activities, particularly fishing. Nets often become entangled and fouled with weeds, and cleaning the nets near villages can bring in the snails (Odei 1979). Furthermore, the aquatic macrophytes have been shown to play vital roles in the distribution of snails in different parts of Africa (Ofoezie 1999).

In areas containing snail populations, the seasonal rainfall is followed by a period of intense breeding. In contrast, rainfall also might sharply reduce population densities because of flushing out of streams and a temporary suppression of breeding. High snail population densities in a given volume of impounded water might result in reduced snail reproduction. Light is a factor that particularly influences snail motility. Water salinity, electrical conductivity, calcium and magnesium ion concentrations, and oxygen tension also appear to be of significance (Wright 1956). Freshwater snails generally tolerate wide limits of chemical and physical environmental conditions (Agi & Okwuosa 2001). A preference for different environmental conditions, such as abundant microflora, water depth, oxygen content and other physicochemical factors, as well as natural behavioural modes of adaptation, might explain why the snail species can exhibit marked differences in each locality (Opisa *et al.* 2011). *Bithynia funiculata,* the intermediate host of *Opisthorchis viverrini,* prefers habitats with clear water, which typically exists at depths <30 cm, temperatures between 24.48 and 31.78 °C, dissolved oxygen concentrations between 2.03 and 7.66 mg L^{-1}, dissolved oxygen saturation of 26.70–95.00%, electrical conductivity of 0.000–0.2642 mS cm^{-1}, turbidity of 16.00–288.00 NTU and pH of 6.58–7.56 (Radchadawan *et al.* 2006).

Snails can tolerate a wide range of water temperatures, with optimum temperatures being between 20 and 27 °C (de Kock & Van Eeden 1981). Low temperatures tend to reduce activity and breeding (Wright 1956). Of the planorbid snails, *B. pfeifferì* are less tolerant of higher temperatures, being absent where temperatures exceed 27 °C for more than 120 hours per week. In contrast, bulinid snails appear to be better adapted to higher temperatures. Hussein *et al.* (2011) reported a positive correlation between water temperature and *L. carinatus* and *B. unicolor* abundance. Appleton's review (1978) suggested water temperature is the most important abiotic snail-related factor in lentic environments, whereas velocity is the key factor in lotic environments. Cañete *et al.* (2004) reported that temperature plays an important role in *Lymnaea* spp. abundance. Kazibwe *et al.* (2006) also observed a positive correlation between *Biomphalaria sudanica* abundance and water temperature.

The water pH was positively correlated with *C. bulimoides*, *M. tuberculata* and *T. niloticus*, while negatively correlated with *L. carinatus* and *B. unicolor* (Hussein *et al.* 2011). This finding agrees with the results of Owojori *et al.* (2006) who reported that *Potadoma freethi* was correlated positively with pH (pH range 6.9–7.5), while Kazibwe *et al.* (2006) reported that *Biomphalaria sudanica* abundance was negatively correlated with pH. In contrast, Ofoezie (1999) and Cañete *et al.* (2004) concluded that pH is rarely a factor limiting the distribution of the snails.

Lymnea carinatus and *B. unicolor* were negatively correlated with the dissolved oxygen concentration, while *C. bulimoides* and *B. alexandrina* were positively correlated with it (Hussein *et al.* 2011). These results support those of Ofoezie (1999), who stated that pulmonate snail species increased with increasing dissolved oxygen concentration, while the density of prosobranch snails decreased. Abdel Malek (1958) reported that the oxygen content of the water is very important in conditioning the habitat of bilharzia vector snails. Maqbool *et al.* (2003) also observed that *Lymnaea* species were seen floating in the surface because they exhibited a high rate of oxygen consumption.

A negative correlation was recorded between total hardness and *B. alexandrina* (Hussein *et al.* 2011). Abdel Malek (1958) observed that bilharziasis vectors were tolerant of a wide range of water hardness, with very-low hard waters exhibiting reduced individual numbers and their shells becoming relatively thin. Cañete *et al.* (2004) indicated that total hardness seemed to have some important role in *Lymnaea* abundance. Calcium concentration was negatively correlated with *B. unicolor*, *S. Cleopatra*, *P. acuta* and *B. alexandrina*, which decreased with increasing calcium levels (Hussein *et al.* 2011). A negative correlation was reported between water depth and *C. bulimoides*, *T. niloticus*, *S. cleopatra* and *B. Truncatus* (Hussein *et al.* 2011). El-Kady *et al.* (2000) reported that the most effective ecological factors acting upon snail population density in irrigation channels might be water depth, aquatic weeds and water temperature.

Random sampling was used to determine relationships between environments without snails, environments with snails, the densities of snail populations and the impacts of seasonal environmental change on each environment (Helmy 1953). There are four environmental factors affecting the density and viability of snail populations. Water levels control snail population densities and tend to vary considerably between years and seasons. Optimal snail habitat usually falls into a narrow zone of elevation above the mean low water level for any given region.

Flooding can prove problematic, as annual floods in certain environments have been found to drown adult snails. Large-scale floods have a significant negative impact on snail populations. The water current in riparian environments often determines the density of snail populations and, during times of high water, might serve to re-locate large populations downstream. Flood-driven currents can also devoid areas of snails.

The most abundant phytoplankton genus found in most water bodies is *Microcystis* spp. (Carmichael 1995). *Cylindrospermopsis* is a common cyanobacterium that occurs almost throughout the year. Excessive algal proliferation (algal blooms) might cause death to a number of aquatic animals, however, either from lack of oxygen (at night) or algal toxins (Boney 1975). Previous studies indicate there were 344 species of phytoplankton in 140 genera and 8 phyla in Lake Victoria and surrounding water bodies (Wakwabi *et al.* 2006). The eight identified phyla include Cyanophyta, Chlorophyta, Bacillariophyta, Dinophyta, Euglenophyta, Pyrrophyta, Chrysophyta and Cryptophyta. Bacillariophyta (diatoms) is the most diverse group, with 111 species existing on the Kenyan side of the lake. Cyanophyta (cyanobacteria or blue-green algae) is well represented, often constituting between 60 and 97% of individuals (cells or filaments) in Lake Victoria and surrounding water bodies (Wakwabi *et al.* 2006). Cyanobacteria, especially *Microcystis*, occur in high abundance in Lake Victoria and some of the small water bodies (SWBs) in its basin. In Lake Kyoga, Uganda, however, the phytoplankton varied along a gradient from east to west, being dominated by Cyanobacteria in the east (Green 2009).

Zooplankton are microscopic organisms suspended in water, including various kinds of protozoans, microcrustaceans and other microinvertebrates that are planktonic in water bodies (Moss 1998; Waya & Mwambungu 2004). Benthic microinvertebrates are higher-level invertebrates associated with life at the bottom of streams, ponds, lakes, either crawling, burrowing or attached to different kinds of solid objects such as plants, stones and woods. Zooplankton occupy a strategic trophic level in aquatic ecosystems (Allison *et al.* 1996). Benthic macroinvertebrates, however, are critical in moving energy through food webs. They usually inhabit bottom substrates for at least part of their life cycle (Rosenberg & Resh 1993). More often than not, zooplankton associations play a vital role in the food web of any aquatic ecosystem and can be adversely affected by a number of environmental factors, including low dissolved oxygen concentrations, which have been found to be limiting in maintaining aquatic life in some cases (Allison *et al.* 1996; Moss 1998). A change in the physicochemical aspect of a water body results in a corresponding change in the relative composition and abundance of the organisms in that water, including snails.

Microcystins are hepatotoxic cyclic heptapeptides produced by different freshwater cyanobacterial species (e.g. *Microcystis aeruginosa)*. The occurrence of heavy cyanobacterial blooms is widespread and has resulted in the death of domestic animals and wildlife. They also can cause human illness, an example being dialysis patients in Brazil dying of acute hepatic failure because of cyanobacteria contamination of the dialysis water (Zegura *et al.* 2003). Thus, cyanobacterial contamination also can influence the species composition and population dynamics of other aquatic organisms, including schistosomiasis snails in aquatic ecosystems.

The development of an effective strategy of integrated control requires study of population dynamics of the intermediate hosts and their relation to environmental factors (El-Khayat *et al.* 2011; Hussein *et al.* 2011). Several factors can affect the ecology of snails and other intermediate disease hosts and therefore also their focal and seasonal distributions. These include physical factors such as water current, temperature, turbidity, transparency and distribution of suspended solids, chemical factors such as ion concentration and dissolved gases in water, and biological factors such as the availability of food, competition and predator–prey interactions (Williams 1970; Ofoezie 1999), as well as toxicological factors (Williamson *et al.* 2004; Chen *et al.* 2005; Gerard & Poullain 2005; Gerard *et al.* 2005; Zurawell *et al.* 2005) and reduced food web efficiencies (Gliwicz 1969; Hillbricht–Ilkowska 1977).

The importance of different ecological factors, however, can vary significantly from one ecological zone to the other, and even from one water body to another, suggesting local investigations to identify important factors in each zone or water bodies (Hussein *et al.* 2011). Thus, the purpose of the present study was to determine the spatial distribution and habitat characterization of schistosomiasis host snails in the lake and land habitats of western Kenya, as well as the possible influences of vegetation types, physicochemical parameters, phytoplankton and zooplankton on relative abundance of the snails.

METHODS

Study area and sampling

This study was conducted in the Kenyan Lake Victoria basin during the month of February 2010. The study area

is situated between longitude 24 350 and 34 551 E and latitude 00, 02′N and 00, 11′S. It has an equatorial type of climate, with the period between December and February being hot and dry. Temperatures in the area range between 17 and 34 °C. There are usually two rainy seasons, the long rains starting around March and continuing until June and the short rains beginning in October and lasting through November.

Perennial rivers flowing into Lake Victoria include Kuja, Miriu, Nyando, Nyamasaria, Nzoia and Yala. There also are numerous seasonal rivers flowing into the lake. The main water contact activities include bathing, doing laundry, swimming, fishing, playing in water (young children), fish mongers (washing fish) and car washers.

This study was carried out in certain areas within the Lake Victoria waters, specifically in the Nyanza Gulf and adjacent terrestrial areas within the basin. Sampling was performed in replicate sites throughout the study basin. The sampling site locations were marked using a GPS Garmin GPS II Plus. The in-lake sampling sites included Asembo Bay (9 sites), Homa Bay (8 sites), Kendu Bay (7 sites), Kisumu Bay (6 sites), Luanda Gembe (8 sites), Nyando Nyakach (9 sites), Sondu Miriu (6 sites) and Usoma point (6 sites). The on-land sampling sites included Ahero (3 sites), Asembo (5 sites), Auji (3 sites), Dunga (6 sites), Kendu/Homa bay (5 sites), Kisumu (3 sites), Luanda Gembe (4 sites) and Sondu Miriu (4 sites). The sampling sites were located within eight locations in the lake and also on land. The eight locations were chosen in the sampling design to ensure uniform statistical comparisons and also to ensure the replicate sampling sites within different locations or areas were distantly separated from one another. The sampled sites within the locations are identified in Table 1 (in-lake locations) and Table 2 (on land locations). The tables also highlight the number of replicate sites, GPS readings, elevations, habitats and vegetation types.

In-lake sampling sites within the Nyanza Gulf were accessed using boats. Habitat types were either in-shore or off-shore and characterized as follows: hippo grass, open lake waters, hippo grass/water hyacinth (HG/WH), water hyacinth or ambatch tree habitats. In-shore habitats were at the shoreline, while off-shore habitats were located about 500 m from the aquatic vegetation (macrophytes) or the shoreline.

On-land sampling sites were accessed using 4-wheel vehicles and on foot. Habitat types were broadly classified into four categories: dams, streams, swamps and ponds. On land, vegetation types in the sampled sites were hippo grass/other vegetation, water hyacinth/other vegetation and other vegetation alone. It is noted that Nyanza Basin non-aquatic plants on land habitats were simply categorized as 'Other Vegetation,' as they were numerous and classifying them to the species level would have been a challenging task. Identification of aquatic plants was carried out using the keys by Cook *et al.* (1974) and Sainty and Jacobs (1994).

Determination of the abundance of schistosomiasis snails in the sampling sites in the lake and land locations were carried out in open lake waters or in the vegetation types in either lake or land aquatic habitats (hippo grass, water hyacinth, ambatch tree, other vegetation or mixtures of some of the vegetation types) or in the different physical habitats in aquatic land habitats (streams, swamps, ponds and dams). Physicochemical parameters analysed in water were dissolved oxygen concentration, pH, alkalinity, hardness, turbidity, electrical conductivity, temperature, turbulence, depth and salinity. Presence and abundance of phytoplankton, and presence and abundance of zooplankton, all of which can influence abundance of the schistosomiasis snails in the aquatic habitats were also analysed.

Snail sampling and identification

Snail sampling was conducted by a trained field collector that searched each site, using a standard flat-wire mesh scoop (2 mm mesh size). The sampling period was fixed at ~30 minutes per site. At each collection point, snails from each site were labelled and transported in separate perforated containers to the Schistosomiasis laboratory at the Kenya Medical Research Institute (KEMRI) in Kisumu. Snails were identified to species level, based on shell morphological characteristics, using standard keys (Brown 1994; Danish Bilharziasis Laboratory & World Health Organisation 1998).

Physicochemical parameters

Physicochemical parameters measured at each in-lake and on-land sampling site, as appropriate, included water depth, pH, electrical conductivity, temperature, turbidity and dissolved oxygen concentration. Physicochemical parameters were measured with a YSI 556 MPS Handheld Multi parameter Instrument (YSI Incorporation, Yellow Spring, USA).

Phytoplankton presence and abundance

Phytoplankton samples were collected at the water subsurface. The water samples (25 mL) were preserved in acidic Lugol's solution. One ml water with a phytoplankton subsample was placed in a rafter cell chamber and left to settle. Representative numbers of strips were

Table 1. Sampling sites habitat/vegetation, replicate sites, elevation and GPS readings of in-lake study areas within Nyanza Gulf of Lake Victoria, Kenya

Location	Habitat/Vegetation	Replicate	Elevation	GPS reading
Nyando Nyakach	Open water	5	3738	S:00′ 16.742′ E: 034′ 49.688′
Nyando Nyakach	Hippo grass/Hyacinth	2	3727	S:00′ 16.935′ E: 034′ 51.027′
Nyando Nyakach	Hyacinth	2	3729	S:00′ 17.525′ E:034′ 51.039′
Sondu Miriu	Open water	3	3741	S:00′ 18.947′ E: 034 45.191′
Sondu Miriu	Hippo grass	3	3736	S:00′ 19.619′ E: 034′ 45.642′
Kendu Bay	Open water	3	3725	S:00′ 20.604′ E: 034′ 38.743′
Kendu Bay	Hippo grass/Hyacinth	2	3721	S:00′ 20.919′ E: 034′ 38.786′
Kendu Bay	Hyacinth	1	3733	S:00′ 20.848′ E: 034′ 38.089′
Kendu Bay	Ambatch tree	1	3736	S:00′ 20.512′ E: 034′ 37.783′
Homa Bay	Hippo grass	1	3799	S:00′ 27.706′ E: 034′ 29.957′
Homa Bay	Hyacinth	1	3793	S:00′ 27.730′ E: 034′ 30.068′
Homa Bay	Hippo grass/Hyacinth	1	3746	S:00′ 27.715′ E: 034′ 30.210′
Homa Bay	Hyacinth	1	3713	S:00′ 27.719′ E: 034′ 30.226′
Homa Bay	Open water	2	3724	S:00′ 27.793′ E: 034′ 30.191′
Homa Bay	Open water	1	3726	S:00′ 31.042′ E: 034′ 25.254′
Homa Bay	Hippo grass/Hyacinth	1	3727	S:00′ 30.910′ E: 034′ 25.182′
Luanda Gembe	Open water	3	3723	S:00′ 27.707′ E: 034′ 17.321′
Luanda Gembe	Hyacinth	2	3732	S:00′ 27.462′ E: 034′ 16.924′
Luanda Gembe	Hippo grass/Hyacinth	1	3730	S:00′ 27.925′ E: 034′ 16.880′
Luanda Gembe	Hyacinth	2	3730	S:00′ 28.141′ E: 034′ 18.380′
Asembo Bay	Hippo grass	2	3742	S:00′ 12.688′ E: 034′ 20.617′
Asembo Bay	Open water	3	3761	S:00′ 12.208′ E: 034′ 20.859′
Asembo Bay	Hippo grass/Hyacinth	1	ND	S:00′ 12.798′ E: 034′ 20.640′
Asembo Bay	Hyacinth	1	3738	S:00′ 12.818′ E: 034′ 20.651′
Asembo Bay	Ambatch tree	2	3735	S:00′ 12.059′ E: 034′ 20.920′
Usoma Point	Open water	3	3739	S:00′ 06.420′ E: 034′ 43.110′
Usoma Point	Hippo grass/Hyacinth	3	3728	S:00′ 06.412′ E: 034′ 43. 185′
Kisumu Bay	Open water	3	3720	S:00′ 05.706′ E: 034′ 44.890′
Kisumu Bay	Hippo grass/Hyacinth	3	3731	S:00′ 05.793′ E: 034′ 44.883′

counted for quantification of algal abundance. Phytoplankton species identification and enumeration were carried out with an inverted microscope (400× magnification). Phytoplankton taxa were identified with the methods of Huber-Pestalozzi (1968). Phytoplankton densities were estimated by counting all the individuals, including single cells, colonies and filaments.

Zooplankton presence and abundance

Zooplankton samples were collected at the water subsurface, using a cone-shaped Nansen net in open water areas. The integrated sample was then stirred, and a subsample was filtered through a 60-μm plankton net. The contents were washed into a 300 mL vial, fixed in a 4% formaldehyde solution and analysed in the laboratory. The samples were made to the appropriate volume, depending on organism density. Samples were stirred for uniform distribution and subsamples poured into a counting tray for analysis with an Olympus dissection microscope (50× magnification). The number of individuals per litre was computed as follows:

$$D = N/V \quad (1)$$

where: N = number of organisms in sample (=number in subsample X volume of sample/subsample volume); V = volume of lake water filtered ($=\pi r^2 d$, where r = radius of mouth of net (25 cm) and d = depth of haul).

Copepoda was grouped into immature copepod (nauplii and early copepodid stages), Cyclopoida and Calanoida. Cladoceran and Rotifera were identified to species level using the identification keys of Smirnov (1996) and Korovchinsky (1992), respectively.

Table 2. Sampling sites (showing elevations and GPS reading) on-land habitats within Nyanza Gulf of Lake Victoria basin, Kenya

Location	Vegetation type	Replicate	Elevation	Habitat	GPS reading
Auji	Hippo grass/Hyacinth	1	3749	Stream	S:00′ 07.524′ E: 034′ 44.700′
Auji	Hippo grass/Hyacinth	2	3749	Stream	S:00′ 07.524′ E: 034′ 44.700′
Auji	Hippo grass/Hyacinth	3	3749	Stream	S:00′ 07.525′ E: 034′ 44.701′
Dunga Beach	Other vegetation	1	3720	Swamp	S:00′ 08.688′ E: 034′ 44.277′
Dunga Beach	Other vegetation	2	3720	Swamp	S:00′ 08.688′ E: 034′ 44.277′
Dunga Beach	Other vegetation	3	3727	Stream	S:00′ 08.664′ E: 034′ 44.279′
Dunga Beach	Hippo grass/Other vegetation	4	3730	Stream	S:00′ 08.657′ E: 034′ 44.282
Dunga Beach	Hippo grass/Other vegetation	5	3734	Stream	S:00′ 08.649′ E: 034′ 44.289′
Dunga Beach	Hippo grass/Hyacinth	1	3735	Pond	S:00′ 08.775′ E: 034′ 44.136′
Asembo	Hippo grass/Other vegetation	1	3758	Pond	S:00′ 10.756′ E:034′ 23.564′
Asembo	Hippo grass/Other vegetation	2	3755	Stream	S:00′ 10.759′ E: 034′ 23.564′
Asembo	Other vegetation	3	3756	Stream	S:00′ 10.761′ E: 034′ 23.564′
Asembo	Other vegetation	4	3757	Pond	S:00′ 10.766′ E: 034′ 23.512′
Asembo	Other vegetation	5	3757	Swamp	S:00′ 10.773′ E: 034′ 23.512′
Kisumu	Hyacinth/Other vegetation	1	3790	Dam	S:00′ 05.957′ E: 034′ 09.092′
Kisumu	Other vegetation	1	3849	Dam	S:00′ 04.728′ E: 034′ 46.373′
Kisumu	Other vegetation	1	3716	Stream	S:00′ 05.637′ E: 034′ 42.447′
Luanda Gembe	Other vegetation	1	3824	Swamp	S:00′ 28.634′ E: 034′ 17.366′
Luanda Gembe	Other vegetation	2	3745	Swamp	S:00′ 28.633′ E: 034′ 17.363′
Luanda Gembe	Other vegetation	3	3761	Swamp	S:00′ 28.638′ E: 034′ 17.366′
Luanda Gembe	Hyacinth/Other vegetation	1	3741	Stream	S:00′ 29.069′ E: 034′ 17.854′
Kendu/Homa Bay	Hippo grass/Other vegetation	1	3757	Pond	S:00′ 29.504′ E: 034′ 31.218′
Kendu/Homa Bay	Hippo grass/Other vegetation	2	3768	Pond	S:00′ 29.514′ E: 034′ 31.201′
Kendu/Homa Bay	Other vegetation	1	3786	Pond	S:00′ 29.541′ E: 034′ 31.651′
Kendu/Homa Bay	Other vegetation	2	3724	Pond	S:00′ 29.534′ E: 034′ 31.661′
Kendu/Homa Bay	Hippo grass/Other vegetation	1	3960	Dam	S:00′ 25.550′ E: 034′ 35.765′
Sondu Miriu	Other vegetation	1	3999	Dam	S:00′ 20.703′ E: 034′ 48.047′
Sondu Miriu	Other vegetation	2	3759	Dam	S:00′ 20.682′ E: 034′ 48.149′
Sondu Miriu	Other vegetation	1	3764	Pond	S:00′ 20.682′ E: 034′ 48.109′
Sondu Miriu	Other vegetation	1	3748	Swamp	S:00′ 20.810′ E: 034′ 47.615′
Ahero	Other vegetation	1	3760	Dam	S:00′ 10.368′ E: 034′ 55.404′
Ahero	Hyacinth	2	3827	Dam	S:00′ 10.590′ E: 034′ 56.115′
Ahero	Hyacinth	1	3776	Stream	S:00′ 10.306′ E: 034′ 54.634′

Statistical analysis

All generated data were stored in Microsoft Excel, normalized by log transformation using $\log_{10}(n + 2)$ (Reisen & Lothrop 1999), although only non-transformed means are reported in this study. Data were analysed using MSTAT-C and Excel data analysis software to determine whether or not there were significant variations between the sampling sites, habitats, organisms or vegetation types. One-way analysis of variance (ANOVA) was used to compare the differences in snail abundance between different locations, habitats and vegetation types on land and in the lake. A Student's *t*-test was used to compare the differences in means between *Bulinus* spp. and *Biomphalaria* spp. in different locations, habitats or vegetation types on land and in the lake. Regression analysis was used to determine associations between the abundance of schistosomiasis snails versus physicochemical parameters, phytoplankton and zooplankton abundance. Levels of significance were accepted at 95% confidence limits ($P < 0.05$).

RESULTS

There were more *Biomphalaria sudanica* snails than *Bulinus africanus* snails in the lake and land locations/habitats (Tables 3–7). Significantly more *Biomphalaria* and *Bulinus* spp. were found in Asembo Bay, Kisumu, Usoma

Table 3. Snail abundance (Mean ± SD) in different in-lake locations

	Mean (±SD) No. of snails	
Locations (No. of sites)	*Biomphalaria sudanica*	*Bulinus africanus*
Asembo Bay (9)	39.4 ± 40.6	9.6 ± 9.3
Homa Bay (8)	0	1.3 ± 3.5
Kendu Bay (7)	0	0
Kisumu (6)	39.5 ± 41.5	5.33 ± 5.5
Luanda Gembe (8)	3.88 ± 6.3	1.5 ± 2.8
Nyando Nyakach (9)	0	0
Sondu Miriu (6)	0	0
Usoma Point (6)	21.67 ± 24.31	4 ± 4.6
ANOVA	<0.0001	0.0003

Point and Luanda Gembe (One-way ANOVA, $P < 0.001$; Table 4). No schistosomiasis host snails, however, were found in Kendu Bay, Nyando Nyakach and Sondu Miriu (Table 3). The abundance of *Biomphalaria sudanica* and *Bulinus africanus* snails was significantly different in different locations on land (Student's *t*-test, $P = 0.026$). There were no significant variations, however, in the snail abundance in different locations on land (One-way ANOVA, $P > 0.05$; Table 4).

Significantly more *Biomphalaria* spp. than *Bulinus* spp. were observed in different physical habitats (dams, swamps, ponds and streams) on land (Student *t*-test, $P = 0.005$), with relatively more *Biomphalaria* spp. being observed in ponds (8.8 ± 13.8), streams (4.7 ± 6.9) and swamps (4.1 ± 9.2), compared with dams (1.7 ± 4.5). *Bulinus africanus* were however slightly more abundant, in ponds (1.5 ± 4.2) and streams (1.1 ± 2.1) than in swamps (0.4 ± 1. 1), and dams, being absent in the latter (0.0 ± 0.0; Table 5).

Table 4. Snail abundance (Mean ± SD) in different on-land locations

	Mean (±SD) No. of snails	
Location (No. of sites)	*Biomphalaria sudanica*	*Bulinus africanus*
Ahero (3)	0	0
Asembo (5)	2 ± 4.5	0
Auji (3)	9.3 ± 2.3	0.7 ± 1.2
Dunga (6)	12.2 ± 12.7	1.7 ± 2.9
Kendu/Homa Bay (5)	9.4 ± 15.2	2.4 ± 5.4
Kisumu (3)	1 ± 1.7	1 ± 1.7
Luanda Gembe (4)	0.5 ± 1	0
Sondu Miriu (4)	0	0
ANOVA	0.072	0.714

With respect to aquatic vegetation, *Biomphalaria* spp. and *Bulinus* spp. abundance varied significantly in different vegetation habitats in the lake (One-way ANOVA, $P = 0.002$ and $P = 0.0002$ respectively), with more schistosomiasis host snails being found in the ambatch tree zone, hippo grass/water hyacinth zone, hippo grass zone and water hyacinth zone, compared with open water (Table 6). There also were significantly more *Biomphalaria* spp. than *Bulinus* spp. in different vegetation habitats in the lake (Student's *t*-test, $P = 0.005$).

There was no significant variation in the relative abundance of *Biomphalaria* spp. and *Bulinus* spp. in different vegetation habitats on land (One-way ANOVA, $P = 0.228$ and $P = 0.290$). In land aquatic habitats, however, more *Biomphalaria sudanica* snails were associated with hippo grass/other vegetation, compared with water hyacinth/other vegetation, and other vegetation alone, while more *Bulinus africanus* were associated with other vegetation than water hyacinth/other vegetation or hippo grass/other vegetation (Table 7).

Table 5. Snail abundance (Mean ± SD) in different physical on-land habitats

	Mean (±SD) No. of snails	
Habitats (No. of sites)	*Biomphalaria sudanica*	*Bulinus africanus*
Dam (7)	1.7 ± 4.5	0.0 ± 0.0
Swamp (7)	4.1 ± 9.2	0.4 ± 1.1
Pond (8)	8.8 ± 13.8	1.5 ± 4.2
Stream (11)	4.7 ± 6.9	1.1 ± 2.1
ANOVA	0.6415	0.6435

Table 6. Snail abundance (Mean ± SD) in different in-lake vegetation habitats

	Mean (±SD) No. of snails	
Habitats (No. of sites)	*Biomphalaria sudanica*	*Bulinus africanus*
Hippo grass (6)	17.7 ± 29.4	5.7 ± 9.0
Open water (26)	1 ± 2.8	0.2 ± 0.8
Hippo grass/Hyacinth (14)	33.1 ± 38.5	6.9 ± 7.3
Hyacinth (10)	10.8 ± 29.4	1.7 ± 4.1
Ambatch tree (3)	17.0 ± 15.1	4.7 ± 4.0
ANOVA	0.002	0.0002

Regression of physicochemical parameters and abundance of *Biomphalaria sudanica* and *Bulinus africanus* snails

All the physicochemical parameters analysed (DO, pH, alkalinity, hardness, turbidity, electrical conductivity, temperature, turbulence, depth and salinity), varied significantly between different locations in the lake (One-way ANOVA, $P < 0.001$; Table 8). Regression analyses revealed that some physicochemical parameters, namely, DO ($R^2 = -0.659$; $n = 8$; $P = 0.014$), pH ($R^2 = 0.728$; $n = 8$; $P = 0.007$) and turbulence ($R^2 = -0.616$; $n = 8$; $P = 0.02$), were predictive of *Biomphalaria* spp. abundance. However, pH ($R^2 = 0.610$; $n = 8$; $P = 0.02$) and turbulence ($R^2 = -0.578$; $n = 8$; $P = 0.028$) were predictive of *Bulinus* spp. abundance in different locations in the lake. Turbulence, however, showed a negative relationship with both *Biomphalaria* spp. and *Bulinus* spp., whereas DO exhibited a negative relationship with *Biomphalaria* spp.

There were no significant variations in dissolved oxygen concentration, pH, alkalinity, hardness, turbidity, electrical conductivity, temperature, turbulence, salinity and depth between different aquatic habitats on land (One-way ANOVA, $P > 0.05$; Table 9). Significant variations in dissolved oxygen, alkalinity, hardness and depth, however, were observed between the different in-lake habitats (One-way ANOVA, $P < 0.05$; Table 10). Only the electrical conductivity varied significantly in different vegetation habitats on land (One-way ANOVA, $P < 0.05$), while all other physicochemical parameters showed no significant variation (One-way ANOVA, $P > 0.05$; Table 11).

Regression of phytoplankton presence and abundance with *Biomphalaria* spp. and *Bulinus* spp. abundance

Among the phytoplankton observed in this study (cyanobacteria, chlorophyceae, diatoms, euglenoids, zygnematids and dinoflagellates), only the diatoms and dinoflagellates varied significantly between different in-lake sites (One-way ANOVA, $P < 0.05$; Table 12). There were significant variations, however, among different phytoplankton taxa at each of the in-lake sampling sites (One-way ANOVA, $P < 0.01$). Regression analyses revealed cyanobacteria ($R^2 = 0.638$; $n = 8$; $P = 0.02$) and chlorophyceae ($R^2 = -0.50$; $n = 8$; $P = 0.05$) were predictive of *Biomphalaria* spp. abundance in different locations in the lake. Likewise, cyanobacteria ($R^2 = 0.682$; $n = 8$; $P = 0.01$) and chlorophyceae ($R^2 = -0.575$; $n = 8$; $P = 0.03$) were predictive of *Bulinus* spp. abundance in different locations in the lake. Chlorophyceae exhibited negative relationships with both *Bulinus* spp. and *Biomphalaria* spp. (Table 13).

With respect to aquatic habitats on land, significant variations were observed between different phytoplankton taxa abundance in streams (One-way ANOVA, $P < 0.001$), but not in ponds, swamps or dams. Furthermore, different phytoplankton taxa abundance in different in-lake habitats exhibited significant variations (One-way ANOVA, $P < 0.001$; Table 14). Phytoplankton abundance in the aquatic habitats between different vegetation types on land did not exhibit any significant variations (One-way ANOVA, $P > 0.05$; Table 15). There were significant variations, however, within or among the phytoplankton taxa in hippo grass/other vegetation habitats (One-way ANOVA, $P = 0.03$) and in aquatic habitats with other vegetation on land (One-way ANOVA, $P < 0.001$).

Regression of zooplankton presence and abundance and *Biomphalaria* spp. and *Bulinus* spp. abundance

Zooplankton abundance (*Cyclopoid* spp., *Calanoid* spp., *Daphnia* spp. and *Keratella* spp.) varied significantly between different locations in the lake (One-way ANOVA, $P < 0.001$; Table 16). Furthermore, there were significant variations among different zooplankton taxa abundance in different locations in the lake (One-way ANOVA, $P < 0.01$). Regression analyses indicated that the zooplankton taxa *Bosmina* spp. were predictive of *Biomphalaria* spp. abundance ($R^2 = -0.627$; $n = 8$; $P = 0.01$), as well as *Bulinus* spp. abundance ($R^2 = -0.50$; $n = 8$; $P = 0.05$), in different locations in the lake, although the relationship was negative.

There were significant variations among different zooplankton taxa abundance in the open water habitat, ambatch tree zone, hyacinth zone and hippo grass/hyacinth zone (One-way ANOVA, $P < 0.05$), but not in hippo grass zone in the lake. Zooplankton abundance, however, did not exhibit any significant variation between different vegetation habitats in the lake (One-way ANOVA, $P > 0.05$; Table 17).

Table 7. Snail abundance (Mean ± SD) in different on-land vegetation habitats

	Mean (±SD) No. of snails	
Vegetation (No. of sites)	*Biomphalaria sudanica*	*Bulinus africanus*
Hippo grass/Other vegetation (10)	9.2 ± 12.3	0
Hyacinth/Other vegetation (5)	1.6 ± 3.6	0.4 ± 0.9
Other vegetation (18)	3.5 ± 7.5	1.4 ± 3.2
ANOVA	0.228	0.290

Table 8. Variations (Mean ± SD) of physicochemical parameters in different in-lake locations

	Mean (±SD) Values of the physico-chemical parameters								
Location (No. of sites)	DO (mg L^{-1})	pH	Alkalinity (mg L^{-1})	Hardness (mg L^{-1})	Turbidity (NTU)	Electrical conductivity (μS cm^{-1})	Temperature (°C)	Turbulence (m s^{-1})	Depth (m)
Asembo Bay (9)	4.7 ± 1.8	8.2 ± 0.4	70.2 ± 7.0	48.7 ± 5.5	99.5 ± 27.6	164.9 ± 3.3	27 ± 0.5	0.04 ± 0.03	1 ± 0.5
Homa Bay (8)	8.0 ± 1.5	7.6 ± 0.5	56.0 ± 10.8	45.8 ± 5.4	103.9 ± 68.3	154.6 ± 0.9	27.8 ± 0.5	0.1 ± 0.05	1.4 ± 0.6
Kendu Bay (7)	6.1 ± 1.6	7.6 ± 0.2	58.6 ± 5.4	48.3 ± 8	108.5 ± 40.4	165.6 ± 2.9	26.2 ± 0.5	0.07 ± 0.2	0.8 ± 0.1
Kisumu (6)	1.6 ± 1.2	8.4 ± 0.2	92 ± 18.4	56 ± 9.2	197.1 ± 47.2	220.2 ± 23.5	27.5 ± 0.1	0.02 ± 0.01	1.28 ± 0.4
Luanda Gembe (8)	6.7 ± 0.5	7.6 ± 0	53.3 ± 7.6	42.3 ± 3.8	29.4 ± 13.1	133.9 ± 0.6	26.4 ± 0.4	0.09 ± 0.03	1.9 ± 1.1
Nyando Nyakach (9)	5.7 ± 0.9	7.8 ± 0.2	76.4 ± 12.3	64.4 ± 10.3	181.8 ± 46.9	213.2 ± 8.8	27.3 ± 0.5	0.17 ± 0.1	0.7 ± 0.1
Sondu Miriu (6)	6.9 ± 0.8	7.7 ± 0	45 ± 10.2	37.3 ± 7.2	54.8 ± 10.6	184.2 ± 7.3	28 ± 0.3	0.23 ± 0.1	0.7 ± 0.1
Usoma Point (6)	5.6 ± 1.5	7.7 ± 0.4	74 ± 10.4	54.3 ± 6.1	153 ± 43	174.1 ± 6.2	27.8 ± 0.2	0.05 ± 0.02	1.45 ± 0.7
ANOVA	<0.001	<0.001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

DO, dissolved oxygen concentration.

Table 9. Variations (Mean ± SD) of physicochemical parameters in different on-land habitats

	Mean (±SD) Values of the physico-chemical parameters									
Habitat (No. of sites)	DO (mg L^{-1})	pH	Alkalinity (mg L^{-1})	Hardness (mg L^{-1})	Turbidity (NTU)	Electrical conductivity (μS cm^{-1})	Temperature (°C)	Turbulence (m s^{-1})	Salinity (mg L^{-1})	Depth (m)
Dam (7)	5.3 ± 2.3	7.5 ± 1.1	119.1 ± 75	84.9 ± 48	225.6 ± 231.5	209.9 ± 126.4	28.6 ± 4.1	0.16 ± 0.13	0.1 ± 0.2	0.4 ± 0.1
Swamp (7)	4.0 ± 2.3	7.3 ± 0.7	306 ± 279.4	140.9 ± 198.4	216.4 ± 153.5	178.6 ± 70.7	26 ± 2.9	0.09 ± 0.07	0.47 ± 0.39	0.3 ± 0.1
Pond (8)	5.7 ± 1	7.7 ± 0.7	126.4 ± 73.5	185.4 ± 222.2	197.7 ± 150	252.4 ± 161.3	25.7 ± 3	0.15 ± 0.11	0.2 ± 0.3	0.5 ± 0.3
Stream (11)	4.6 ± 2.1	7.9 ± 0.7	152.5 ± 0.90	102.4 ± 85.4	105.7 ± 165.5	262 ± 193.6	25.5 ± 1.7	0.12 ± 0.14	0.22 ± 0.28	0.7 ± 0.5
ANOVA	0.415	0.488	0.575	0.823	0.069	0.825	0.171	0.882	0.178	0.082

DO, dissolved oxygen concentration.

Table 10. Variations (Mean ± SD) of physicochemical parameters in different in-lake habitats

	Mean (±SD) Values of the physico-chemical parameters								
Habitat (No. of sites)	DO (mg L^{-1})	pH	Alkalinity (mg L^{-1})	Hardness (mg L^{-1})	Turbidity (NTU)	Electrical conductivity (μS cm^{-1})	Temperature (°C)	Turbulence (m)	Depth (m)
Hippo grass (6)	5 ± 2.1	7.7 ± 0.7	56.3 ± 22.7	41.7 ± 11.1	61.4 ± 27.1	171.3 ± 9.9	27.4 ± 0.8	0.2 ± 0.1	0.8 ± 0.2
Open water (26)	6.4 ± 1.7	7.7 ± 0.3	66.4 ± 14.0	50.1 ± 8.9	104.7 ± 55.6	179.4 ± 30.4	27.1 ± 0.8	0.1 ± 0.1	1.5 ± 0.9
Hippo gr./Hya. (14)	4.3 ± 2.4	8 ± 0.3	75 ± 19.7	55.6 ± 13.2	149.5 ± 77.4	182.6 ± 30.7	27.5 ± 0.6	0.1 ± 0.1	0.9 ± 0.3
Hyacinth (10)	6.1 ± 2.0	7.8 ± 0.4	55.6 ± 11.2	48.2 ± 8.4	119.9 ± 84.4	160.3 ± 30.7	27.1 ± 0.7	0.1 ± 0.1	0.8 ± 0.5
Ambatch tree (3)	6.9 ± 1.1	8.2 ± 0.5	66.7 ± 3.1	44.7 ± 3.1	135.3 ± 7.6	163.3 ± 4.0	27.3 ± 0.4	0.07 ± 0.02	0.6 ± 0.1
ANOVA	0.033	0.092	0.02	0.047	0.134	0.285	0.511	0.389	0.01

DO, dissolved oxygen concentration.

Table 11. Physicochemical parameters (Mean ± SD) in different on-land vegetation habitats

	Mean (±SD) Values of the physico-chemical parameters									
Vegetation (No. of sites)	DO (mg L^{-1})	pH	Alkalinity (mg L^{-1})	Hardness (mg L^{-1})	Turbidity (NTU)	Electrical conductivity (μS cm^{-1})	Temp (°C)	Turbulence (m s^{-1})	Salinity (mg L^{-1})	Depth (m)
Hippo gr./Other veg. (10)	5.3 ± 1.8	7.8 ± 0.7	136.4 ± 72.1	162.4 ± 185.9	108.1 ± 146.9	308.9 ± 222.1	25.6 ± 1.9	0.11 ± 0.14	0.3 ± 0.3	0
Hyacinth/Other veg. (5)	5.2 ± 1.5	7.9 ± 0.7	136.4 ± 50.1	112.4 ± 48.4	284.2 ± 251.8	298.8 ± 107.9	27.8 ± 4.3	0.18 ± 0.16	0.06 ± 0.05	0.05 ± 0.1
Other veg. (18)	4.6 ± 2.3	7.5 ± 0.9	201.1 ± 202.4	124.8 ± 148.7	185.3 ± 158.4	168.7 ± 66.5	26.2 ± 3.1	0.12 ± 0.1	0.31 ± 0.35	0.2 ± 0.4
ANOVA	0.504	0.578	0.943	0.713	0.340	0.049	0.374	0.552	0.292	0.093

DO, dissolved oxygen concentration.

Table 12. Variations (Mean ± SD) of phytoplankton abundance in different in-lake locations

	Mean (±SD) Phytoplankton abundance					
Location (No. of sites)	Cyanobacteria	Chlorophyceae	Diatoms	Euglenoids	Zygnematids	Dinoflagellates
Asembo Bay (9)	83.6 ± 21.0	7.1 ± 8.5	3.08 ± 3.9	5.7 ± 10.5	0.27 ± 0.5	0.23 ± 0.4
Homa Bay (8)	68.3 ± 29.5	19.6 ± 26.8	6.9 ± 7.1	2.5 ± 3.5	1 ± 1.9	1.6 ± 1.8
Kendu Bay (7)	51 ± 42.5	23.9 ± 19.7	10.5 ± 13.3	8.1 ± 9.5	3.42 ± 4.3	3.2 ± 6.8
Kisumu (6)	81.4 ± 18.1	11 ± 15.8	4.6 ± 5.6	2.9 ± 5.6	0.13 ± 0.2	0.07 ± 0.07
Luanda Gembe (8)	62.8 ± 25.5	17.5 ± 18.9	13.5 ± 9.7	3.5 ± 4.8	1.44 ± 3.2	1.24 ± 1.7
Nyando Nyakach (9)	67.2 ± 35.6	14.3 ± 14.4	12.9 ± 18.6	2.7 ± 5.5	1.02 ± 2.0	1.94 ± 2.7
Sondu Miriu (6)	55.8 ± 28.6	19.30 ± 14.2	10.4 ± 7.1	6.5 ± 7.6	0.5 ± 0.7	7.57 ± 7.3
Usoma Point (6)	96.6 ± 2.8	2.3 ± 2.8	0.8 ± 0.7	0.19 ± 0.19	0.2 ± 0.4	0.01 ± 0.02

Table 13. Variations (Mean ± SD) of phytoplankton abundance in different on-land habitats

	Mean (±SD) Phytoplankton abundance					
Habitat (No. of sites)	Cyanobacteria	Chlorophyceae	Diatoms	Eugleniods	Zynematids	Dinoflagellates
Dam (5)	14.7 ± 21.0	30.1 ± 17.1	30.6 ± 26.4	8.4 ± 10.2	8.9 ± 8.7	7.3 ± 10.9
Swamp (7)	8.9 ± 16.6	13.6 ± 16.1	17.1 ± 19.8	2.2 ± 3	2.9 ± 5.9	3.9 ± 9.4
Pond (8)	17.9 ± 30.2	19.5 ± 28.5	16.7 ± 24.9	5.7 ± 12.9	1.7 ± 3.5	0.9 ± 2.7
Stream (11)	35 ± 34.5	29.5 ± 26.7	22.2 ± 26.9	5.9 ± 10.6	2.7 ± 5	1.2 ± 2

Table 14. Variations (Mean ± SD) of phytoplankton abundance in different in-lake habitats

	Mean (±SD) Phytoplankton abundance					
Habitats (No. of sites)	Cyanobacteria	Chlorophyceae	Diatoms	Euglenoids	Zygnematids	Dinoflagelletes
Hippo grass (6)	47.4 ± 32.5	34.9 ± 23.3	11.1 ± 6.0	10.8 ± 10.8	0.4 ± 0.6	4.7 ± 6.5
Open water (26)	80.4 ± 17.9	9.8 ± 11.4	4.8 ± 6.2	1.9 ± 3.0	1 ± 2.3	2 ± 3.8
Hippo gr./Hy (14)	60.3 ± 37.4	16.6 ± 15.9	13.0 ± 16.3	7.3 ± 9.7	1.0 ± 2.4	1.9 ± 4.9
Hyacinth (10)	73.2 ± 31.5	15.6 ± 23.3	9.8 ± 11.5	3.3 ± 4.5	1.2 ± 3	0.8 ± 1.4
Ambatch tree (3)	74.3 ± 30.9	8.4 ± 13.7	2.2 ± 3.3	1.0 ± 1.7	1.0 ± 1.7	0.04 ± 0.07

Table 15. Variations (Mean ± SD) of phytoplankton abundance in different on-land vegetation habitats

	Mean (±SD) Phytoplankton abundance					
Vegetation (No. of sites)	Cyanobacteria	Chlorophyceae	Diatoms	Eugleniods	Zynematids	Dinoflagellates
Hippo gr./Other veg.(10)	32.4 ± 38.5	20 ± 26.6	16.1 ± 20.2	9.8 ± 15	2.8 ± 4.6	1.3 ± 2.7
Hyacinth/Other veg. (5)	6.4 ± 14.4	23.6 ± 24.4	49.5 ± 40.3	0.8 ± 1.3	3.6 ± 5.7	6.2 ± 11.4
Other vegetation (18)	17 ± 23.2	20.3 ± 23	22.4 ± 16.3	3.8 ± 6.4	3.2 ± 6.4	2.3 ± 6

Table 16. Variation (Mean ± SD) of zooplankton abundance in different in-lake locations

	Mean (±SD) Zooplankton abundance					
Location (No. of sites)	Cyclopoid spp.	Calanoid spp.	*Daphnia* spp.	*Bosmina* spp.	*Keratella* spp.	Other zooplankton
Asembo Bay (9)	12.8 ± 15.9	8.2 ± 7.1	8 ± 11.4	0.27 ± 0.8	1.4 ± 4.1	0.6 ± 1.7
Homa Bay (8)	9.8 ± 8.5	8.4 ± 8.5	5.7 ± 4.8	0.6 ± 0.7	8.6 ± 11.6	0.8 ± 1.1
Kendu Bay (7)	6.4 ± 4.3	7.4 ± 5.3	3.5 ± 3.4	0.6 ± 1.3	0.14 ± 0.37	0.2 ± 0.4
Kisumu (6)	0.04 ± 0.1	0.1 ± 0.1	0.08 ± 0.1	0.01 ± 0.01	0.0	0.02 ± 0.04
Luanda Gembe (8)	1.2 ± 0.9	1.05 ± 0.9	0.5 ± 0.5	0.05 ± 0.14	0.06 ± 0.2	0.3 ± 0.4
Nyando Nyakach (9)	8.5 ± 11.0	4.7 ± 4.6	2.7 ± 3.3	0.47 ± 0.8	0.0	0.8 ± 1.4
Sondu Miriu (6)	2.9 ± 3.9	4.7 ± 7.7	2.2 ± 4.1	0.77 ± 1.4	0.4 ± 1.1	0.0
Usoma Point (6)	1.7 ± 2.2	2.5 ± 2.0	2.7 ± 2.3	0.1 ± 0.2	0.5 ± 1.1	0.4 ± 0.6

DISCUSSION

The results of the present study indicated more *Biomphalaria sudanica* than *Bulinus africanus* snails in the lake and on land locations and habitats within the Lake Victoria basin of Kenya. There were significantly more *Biomphalaria* and *Bulinus* species in Asembo Bay, Kisumu, Usoma Point and Luanda Gembe. Previous studies of Ofulla *et al.* (2010) also indicated no host snails were present in the Nyando and Sondu Miriu regions. The present study also found no schistosomiasis host snails in Nyando Nyakach, Sondu Miriu and Kendu bay. Significantly more *Biomphalaria* spp., however, were found in Dunga, Kisumu, Kendu/Homa bay and Auji in land habitats (One-way ANOVA, $P < 0.001$), although they were absent in Ahero.

Although no schistosomiasis host snails were found in the lake and land aquatic habitats in Ahero region, health records (data not shown) highlighted a high prevalence of schistosomiasis in Ahero and Nyando regions. This probably is attributed to sampling of snails being carried out in dams, ponds and lake waters, rather than in rice fields and canals where schistosomiasis intermediate host snails have previously been reported to be abundant around Ahero and Nyando regions (WHO/FAO/UNEP 1988).

Different physical habitats on land: ponds, streams and swamps in that order, were found to favour *Biomphalaria* and *Bulinus* snails, as compared to dams. Similarly, significantly more *Biomphalaria* spp. than *Bulinus* spp. were sampled on different locations on land (Student's *t*-test, $P = 0.026$). The results of the present study are similar to those reported by Opisa *et al.* (2011), who also reported that *Biomphalaria* spp. were more abundant than *Bulinus* spp. in different terrestrial aquatic habitats in the Kisumu rural region of Lake Victoria basin of Kenya.

In the lake habitats, significantly more *Biomphalaria sudanica* and *Bulinus africanus* snails were found in the ambatch tree zone, hippo grass/water hyacinth zone, hippo grass zone and water hyacinth zone, compared to open water (One-way ANOVA, $P < 0.002$ and $P = 0.0002$), clearly indicating aquatic vegetation plays a vital role in harbouring these snails, as was also previously reported by Ntiba *et al.* (2001) and Plummer (2005). In the recent past, water hyacinth, an alien plant (Strayer 2010) that was almost eradicated in the 1990s within the Nyanza

Table 17. Variation (Mean ± SD) of zooplankton abundance in different in-lake vegetation habitats

	Mean (±SD) Zooplankton abundance					
Habitat (No. of sites)	Cyclopoid	Calanoid	*Daphnia sididae*	*Bosmina*	*Keratella*	Other zooplankton
Hippo grass (6)	9.4 ± 20.4	4.8 ± 8.2	6.1 ± 15	0.8 ± 1.1	2 ± 5	1.1 ± 2.1
Open water (26)	5.6 ± 6.7	5.7 ± 6.7	3.3 ± 3.4	0.3 ± 0.8	1.6 ± 7	0.4 ± 0.8
Hippo grass/Hyacinth (14)	4.7 ± 7.4	4.3 ± 6.0	2.5 ± 4.2	1.1 ± 1.4	1.7 ± 3.8	0.4 ± 0.9
Hyacinth (10)	7.1 ± 9.8	3.7 ± 3.7	2.5 ± 3.3	0.1 ± 0.4	1 ± 2.1	0.4 ± 1
Ambatch tree (3)	4.8 ± 1.6	4.3 ± 3.1	5.9 ± 4	0.0	0.3 ± 0.6	0.0

gulf has resurged. It is now accompanied by other aquatic weeds as well, including *Vossia cuspidata* (hippo grass), *Phragmites mauritanius*, Ambatch tree and *Cyperus papyrus* (Ofulla *et al.* 2010). Water hyacinth also has spread to smaller water bodies in the marginal terrestrial areas of the Lake Victoria basin, probably creating even more suitable habitats for optimal development of schistosomiasis or bilharzia-transmitting host snails, which was one of the subjects of investigation in the present study.

More snails were generally found in the ambatch tree zone, hippo grass/water hyacinth zone, hippo grass zone and water hyacinth zone, compared with the open water in the lake. *Biomphalaria sudanica* and *Bulinus africanus* snail abundance exhibited significant variations in different vegetation habitats in the lake (One-way ANOVA, $P = 0.002$ and $P = 0.0002$). Furthermore, there were significantly more *Biomphalaria* spp. than *Bulinus* spp. in different vegetation habitats in the lake (Student's *t*-test, $P = 0.005$). These findings are consistent with previous study findings illustrating that many schistosomiasis host snails were associated with water hyacinth, followed by hippo grass, although others were free-floating, especially after heavy storms in the lake which probably dislodges the snails from their attachment to aquatic vegetation (Ofulla *et al.* 2010). The results of the present study also are consistent with the findings of Kariuki *et al.* (2004), who reported that the abundance of snails was significantly associated with different vegetation types. Thus, it is clear that schistosomiasis host snails are clearly associated with different aquatic macrophytes. In fact, it is surprising that Opisa *et al.* (2011), in their malacological survey and geographical distribution of vector snails for schistosomiasis within informal settlements of Kisumu city, western Kenya, never found any association between vegetation cover and snail abundance, even though the most common vegetation cover identified in their sampling areas was floating macrophytes (i.e. water hyacinth; *Eichhornia crassipes*) and water lily (*Nymphaea* spp.).

All the physicochemical parameters analysed varied significantly between different locations in the lake (One-way ANOVA, $P < 0.001$). Regression analyses revealed that DO ($R^2 = -0.659$; $n = 8$; $P = 0.014$) and turbulence ($R^2 = -0.616$; $n = 8$; $P = 0.02$) were predictive of *Biomphalaria* spp. although negatively, while pH ($R^2 = 0.728$; $n = 8$; $P = 0.007$) exhibited a positive relationship with *Biomphalaria* spp. in different locations in the lake. Furthermore, pH ($R^2 = 0.610$; $n = 8$; $P = 0.02$) and turbulence ($R^2 = -0.578$; $n = 8$; $P = 0.028$) were observed to be predictive of *Bulinus* spp. abundance in different locations in the lake, although turbulence exhibited a negative relationship. These findings indicate that both *Biomphalaria* spp. and *Bulinus* spp. are not found in highly turbulent habitats, most likely because the turbulent water dislodges them from aquatic vegetation or substratum.

Mean dissolved oxygen concentrations ranged between 1.6 and 8.0 mg L^{-1} in different locations in the lake. The temperature levels, however, exhibited a negative relationship with *Biomphalaria* spp. in different locations in the lake. In the studies of Opisa *et al.* (2011) in the Kisumu region of Lake Victoria basin, the water temperature appeared to be the key determinant of snail abundance among the range of measured physicochemical variables. The positive association between snail abundance and water temperature is in agreement with observations from Uganda that snail distributions were restricted in the north and north-eastern parts of the country exhibiting high temperatures (Stensgaard *et al.* 2006). It also had previously been demonstrated that *B. pfeifferi* grew and survived better at 25 °C than at 19 °C (Sturrock 1966). In contrast to the results of Opisa *et al.* (2011), however, Kariuki *et al.* (2004) did not find any association between snail abundance and water temperature, suggesting this observation might have been attributable to the narrow range of temperature in their study.

Although Opisa *et al.* (2011) reported encountering snails in habitats exhibiting a wide pH range (6.7 and >11), it is suggested that pH might not have much impact on snail abundance. No habitat with a pH value below 7.3 existed in the present study. Furthermore, pH exhibited a positive relationship with both *Biomphalaria* spp. and *Bulinus* spp. in different locations in the lake. These findings were consistent with those of Abdel Malek (1958), who reported that high pH is a survival advantage to snails, as lower pH values are known to be harmful and might cause mucus coagulation on exposed snail surfaces. It has been suggested that high pH values might be caused by human contaminants such as cleaning products or might be attributable to the acquisition of H^+ ions as a consequence of the normal process of photosynthesis during daylight hours in the aquatic habitats (Standley 2008).

Among the phytoplankton phyla, only the diatoms and dinoflagellates varied significantly between different locations in the lake (One–way ANOVA, $P < 0.05$). Cyanobacteria ($R^2 = 0.638$; $n = 8$; $P = 0.02$) and Chlorophyceae ($R^2 = -0.50$; $n = 8$; $P = 0.05$) were found to be predictive of *Biomphalaria* spp. abundance in different locations in the lake, although the correlation was negative for Chlorophyceae. Likewise, Cyanobacteria ($R^2 = 0.682$; $n = 8$; $P = 0.01$) and Chlorophyceae ($R^2 = -0.575$; $n = 8$;

$P = 0.03$) were predictive of *Bulinus* spp. abundance in different locations in the lake, although the correlation was again negative for Chlorophyceae. Cyanobacteria exhibited a positive relationship with *Biomphalaria* spp. and *Bulinus* spp., while Chlorophyceae showed a negative relationship with the same in different locations in the lake. These findings, however, were contradictory to those of Williamson *et al.* (2004), who reported that secondary metabolites from Cyanobacteria are harmful to *Biomphalaria* spp. It is possible, however, that there could have been toxicological factors (Williamson *et al.* 2004; Chen *et al.* 2005; Gerard & Poullain 2005; Gerard *et al.* 2005; Zurawell *et al.* 2005) in this study, as well as food web efficiency factors (Gliwicz 1969; Hillbricht–Ilkowska 1977), all of which could have influenced these positive and negative relationships with snails abundance. This suggestion warrants future research, as highlighted in following paragraphs.

Cyanobacteria become increasingly dominant as TP and TN concentrations increase with increasing eutrophication of lakes, rivers and estuaries. Temporal dynamics of cyanobacteria blooms are variable. Persistent blooms occur in summer to fall in some water systems, whereas blooms are more sporadic in other systems. Cyanobacteria blooms have a wide range of possible biological impacts, including potential toxic effects on other algae, invertebrates and fish, impacts to plants and benthic algae due to shading, and impacts to food web function as large inedible algae produce a bottleneck to C and energy flow in the plankton food web (Karl E. Havens, Cyanobacteria blooms: Effects on aquatic ecosystems; from a book chapter accessed from the internet, 20th April, 2013). In lakes with dense cyanobacteria blooms, the accumulation of organic material in lake sediments and increased bacterial activity might also lead to anoxic conditions that alter the structure of benthic macroinvertebrates. In addition to potential toxic effects, cyanobacteria blooms also might affect grazing zooplankton by mechanical interference with the filtration apparatus (Gliwicz & Lampert 1990). It has been suggested that the high C/P ratios that occur during algal blooms might lead to growth limitation of zooplankton taxa such as *Daphnia*, the latter having a high P requirement (Hessen *et al.* 2005).

It is of interest to note that large *Daphnia*, generally considered the most effective grazers of algae, and the taxa responsible for such things as the spring clear water phases in eutrophic lakes, are most sensitive to chemical stressors, including cyanobacterial toxins (Fulton 1988), and most sensitive to mechanical interference. As a result of this differential sensitivity, smaller zooplankton (e.g. *Bosmina* and rotifers) become increasingly dominant as lakes progress from a mesotrophic to eutrophic condition. At the same time, the average size of phytoplankton increases. This convergence of zooplankton and phytoplankton size leads to an energetic bottleneck in the grazing food chain that restricts C and energy flow to higher trophic levels (Havens & East 1997). Microbial pathways become relatively more important, and overall food web efficiency is reduced in eutrophic lakes exhibiting cyanobacterial blooms (Gliwicz 1969; Hillbricht–Ilkowska 1977). The loss of *Daphnia* might to a certain extent be due to increased predation, as the biomass of planktivorous and omnivorous fish increases with increasing eutrophication (Jeppesen *et al.* 2000).

The last two decades have been marked by an increasing occurrence of toxic cyanobacterial blooms in aquatic ecosystems, which pose an expanding threat to the environment and to the human health. Microcystins (hepatotoxins) are the most frequent and widely studied of the intracellular toxins produced by cyanobacteria. As a ubiquitous herbivore living in eutrophic fresh waters, the freshwater snail *Lymnaea stagnalis* (Gastropoda: Pulmonata) is particularly exposed to cyanobacteria. The toxic filamentous *Planktothrix agardhii* is common in temperate lakes, therefore being a potential food resource for gastropods (Lance *et al.* 2006). Contamination of organisms can occur by exposure to soluble toxins, direct consumption of cyanobacterial cells, and by consumption of contaminated prey. Microcystins have been recognized to accumulate and induce extensive damage in some organisms, including zooplankton, bivalves and fish, after ingestion of cyanobacterial cells (see Zurawell *et al.* 2005 for a review).

Freshwater gastropods have rarely been considered in toxic cyanobacteria studies. These organisms, however, represent an important part of the freshwater macroinvertebrate biomass. They are important links between primary producers and higher consumers and often play key roles in structuring aquatic communities (Habdija *et al.* 1995). Pathogenic effects of dissolved microcystin-LR on life traits have recently been demonstrated in laboratory experiments on two gastropod species. The prosobranch *Potamopyrgus antipodarum* has exhibited a decrease in survival, growth and fecundity (Gerard & Poullain 2005), whereas the pulmonate *Lymnaea stagnalis* has exhibited a decreased fecundity (Gerard *et al.* 2005).

As cyanobacteria can dominate phytoplankton community and colonize littoral waters during bloom periods, it is relevant to ask whether or not these grazers would consume large quantities of toxic cyanobacteria, and whether they would be affected by this consumption

(Chen *et al.* 2005). If toxic cyanobacteria densities can become very high in shallow waters, and with the filaments trapped and accumulating in dense macrophytes, on rocks and littoral sediments increasing the probability of grazing by snails, it is therefore possible that the snail populations, and the populations of other grazers, will be affected. Accordingly, future research should also focus on determining whether or not such effects of toxic cyanobacteria can be used in control programs directed to eliminating schistosomiasis snails or other aquatic disease vectors.

The zooplankton abundance varied significantly between different locations in the lake (One-way ANOVA, $P < 0.001$), while *Bosmina* spp. was shown to be predictive of *Biomphalaria* spp. abundance ($R^2 = -0.627$; $n = 8$; $P = 0.01$), as well as *Bulinus* spp. abundance ($R^2 = -0.50$; $n = 8$; $P = 0.05$) in different locations in the lake, with the relationship being negative. This could imply that *Bosmina* spp. is either a major food item for the snails or they could be exhibiting secretions that keep the snails away from their habitats. As previously stated and suggested for future study, there also could have been toxicological factors and food web efficiency factors that could influence these relationships. *Cyclopoid* spp., however, were the most prominent zooplankton taxa in different locations in the lake, followed by *Calanoid* spp. and *Daphnia* spp. in that order. This is consistent with the results of Green (2009) who reported that the zooplankton were dominated by cyclopoid copepods in Lake Kyoga, Uganda.

A number of schistosomiasis snails were also found in the ambatch tree zones in the lake locations, especially in Asembo. *Biomphalaria* spp. and *Bulinus* spp. abundance varied significantly in different vegetation habitats in the lake (One-way ANOVA, $P = 0.002$ and $P = 0.0002$), with more schistosomiasis host snails being found in the ambatch tree zone, hippo grass/water hyacinth zone, hippo grass zone and water hyacinth zone, compared with open water. These findings indicate the need for further studies, as colonization of the lake shores by ambatch tree could pose a future risk of increased incidences of schistosomiasis along the Kenyan Lake Victoria Basin.

ACKNOWLEDGEMENTS

This work has been made possible with the help of colleagues from Maseno University, Kenya Medical Research Institute (KEMRI), Division of Vector Borne Diseases (DVBD) – Ministry of Public Health and Sanitation and Kenya Marine and Fisheries Research Institute (KMFRI). Too many to individually mention, our sincere thanks are hereby expressed to all of them. The skilful and competent assistance of Mr. Jondiko Eric for carrying out data analysis also is highly acknowledged. Sincere thanks are due to all the technicians from DVBD, KMFRI, KEMRI and Maseno University who helped in the sampling and sample analysis and to colleagues for suggestions to improve this manuscript. This research received financial aid and authorization for publication from EAC-Lake Victoria Basin Commission.

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