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The inshore benthic macroinvertebrates of Lake Nabugabo, Uganda: seasonal and spatial patterns

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Lake Nabugabo, Uganda, is a lake of particular interest because of the unusual nature of its benthic macroinvertebrate community. In this study we quantified the spatial and temporal distribution of benthic macroinvertebrates within the lake with a focus on habitat associations in inshore areas. We focused on four inshore habitats: *Nymphaea lotus/Nymphaea caerulea* (water lily), *Miscanthidium violaceum*, *Vossia cuspidata* (hippo grass) and forest edge. The most notable characteristic of the Nabugabo fauna was the absence of bivalves and crustaceans and the scarcity of gastropods that made up only 1.8 % of the numerical abundance of the benthos. The numerically dominant taxa were ephemeropterans (77.7 %) and dipterans (11.1 %). Annelids (5.4 %), odonates (2.8 %) and trichopterans (1.3 %) comprised a much smaller component of the benthic assemblage. Total invertebrate abundance and the abundance of major taxa did not vary significantly across months, but habitat effects were evident. The water-lily habitat was very depauperate, which may reflect the low levels of dissolved oxygen near the sediments in this habitat. Lake Nabugabo is extremely poor in salts, mean conductivity in inshore sites ranging from 22.3 to 26.4 $\mu\text{S}/\text{cm}$ and 22.6 to 37.9 $\mu\text{S}/\text{cm}$ (K_{25}) for surface and bottom waters, respectively. The low conductivity (low concentrations of ions) in Lake Nabugabo may limit colonization by molluscs and crustaceans that, with their calcareous shells or exoskeletons, may require water with a higher mineral content.

Key words: aquatic invertebrates, East Africa, Ephemeroptera, macrophytes.

INTRODUCTION

The role of macroinvertebrates as natural food for fishes, in cycling nutrients and organic matter, and in exchanging dissolved gases with overlying water, has long been recognized. The macroinvertebrate community in the littoral zone of a lake is a crucial link in the transfer of energy from primary producers and detritus to fish, and fish biomass and production have been correlated with macroinvertebrate biomass and production (Matuszek 1978; Hanson & Leggett 1982; Boisclair & Leggett 1985). The spatial distribution of freshwater macroinvertebrates has thus been the subject of many investigations, most of which have been carried out in temperate regions. In temperate lakes, the habitat use of macroinvertebrates seems to be strongly influenced by vegetation characteristics, depth and/or complexity of the substrate (Karassowska & Mikulski 1960; Keast & Harker 1977; Dvorak & Best 1982; Hershey 1985; Hanson *et al.* 1989; Schmude *et al.* 1998). Substratum composition, complexity and particle

size seem to be very important factors affecting the distribution, structure and composition of macroinvertebrate communities in temperate running waters (Allan 1975; de March 1976; Rabeni & Minshall 1977; Williams & Mundie 1978; Grzybkowska & Witzak 1990; Ellsworth 2000). We understand far less about spatial patterns of macroinvertebrate assemblages in tropical regions than in temperate communities.

In East Africa, much of our knowledge of benthic macroinvertebrate communities derives from studies on lakes Victoria and George. These include works related to their biology, emergence, colonization of artificial substrata, biomass, standing crop and spatial distribution (e.g. Hartland-Rowe 1955, 1958; MacDonald 1956; Corbet 1958; Burgis *et al.* 1973; Mothersill *et al.* 1974; Greenwood 1976; Okedi 1971, 1990; Hare & Olisedu 1987; Balirwa 1998). Studies of smaller lakes in the region are few, yet these systems are often critical to local fisheries and water supply. One small lake in East Africa, Lake Nabugabo, has been a source of particular interest because of the unusual nature of its benthic macroinvertebrate community.

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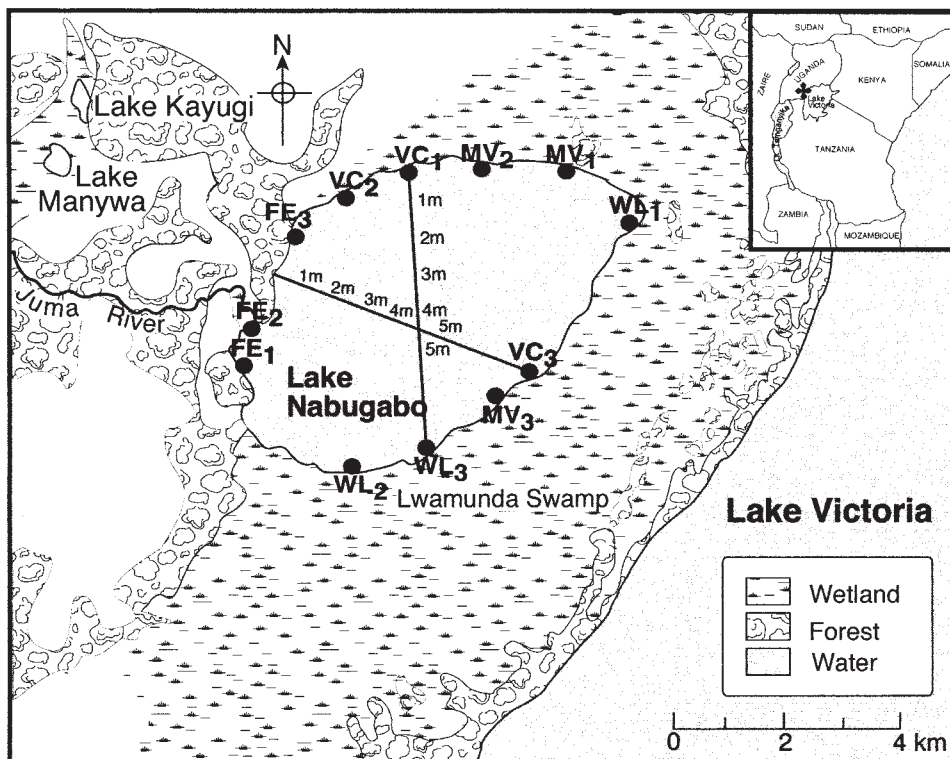


Fig. 1. Map of Lake Nabugabo and its location within the Lake Victoria basin indicating the sampling stations for the four inshore habitats (WL = water lily, MV = *Miscanthidium violaceum*, VC = *Vossia cuspidata*, FE = forest edge) and the transects for the offshore stations.

Crabs and gastropods have been reported as absent from the main lake, although a few isolated and very small colonies of *Biomphalaria sudanica* (Planorbidae) have been found in the depths of the reed and *Sphagnum* swamp on the eastern side of the lake (CNBS 1962; Olowo 1998). Whether this phenomenon has a seasonal component is unknown, because studies have been limited in duration. Schistosomiasis also seems to be absent from Lake Nabugabo, due to the lack of intermediate gastropod hosts. The unusual nature of the fauna may relate to the water chemistry of Lake Nabugabo. The lake seems to be acidic compared to the other lakes in Uganda, and the salt concentration is low (CNBS 1962; Beadle 1981); however, detailed study of the seasonal and habitat variation in pH and conductivity are lacking. In this study we provide a quantitative assessment of the spatial and temporal distribution of benthic macroinvertebrates within the lake with a focus on habitat associations in inshore areas and environmental correlates of abundance. This was achieved through (i) quantifying the species richness and

abundance of benthic macroinvertebrates in representative habitats within the lake, (ii) quantifying relationships between environmental factors and benthic invertebrate abundance and (iii) documenting seasonal variation in benthic macroinvertebrate abundance over a six-month period that covered one dry season-wet season cycle.

MATERIALS & METHODS

Study area

Lake Nabugabo is located off the western shores of Lake Victoria, Uganda, (31°50'E and 31°56'30"E to 0°20'S and 0°25'5"S) at an altitude of 3800 m above sea level. The lake is believed to have been formed when a sand bar separated a portion of Lake Victoria about 4000 years ago (Worthington 1932; Greenwood 1965; Beadle 1981). It is about 24 km² in surface area (Fig. 1), with an average depth of 4.5 m. The bottom of the lake is predominantly covered with a blanket of black liquid mud with the exception of the western shore, where it is sandy. The dominant fringing vegetation types

are *Vossia cuspidata* (hippo grass), *Miscanthidium violaceum*, *Nymphaea lotus*/*Nymphaea caerulea* (water lily) and swamp forest. Some patches of *Cyperus papyrus* (papyrus) are also found around the lake, but the plant is relatively scarce. The eastern and southern shores contain *Sphagnum* swamp.

The main influents to Lake Nabugabo are the Juma River and the Lwamunda Swamp (Fig. 1), and numerous small streams also discharge along the western lakeshore. Lake Nabugabo drains southeastwards via the Lwamunda Swamp, after which the water seeps underground through a sand bar into Lake Victoria. Mean annual rainfall ranges from 52 to 197 cm and is bimodal with maximum rainfall between April/May and October/November. Maximum yearly air temperatures range from 26.2–28.1 °C, and the minimum temperatures range from 14.1–16.2 °C (Meteorology Department, Masaka, Uganda).

Sampling stations

In this study we focused on the inshore macroinvertebrate fauna, but include offshore samples for comparison. The lake was divided into four major inshore habitat types based on aquatic vegetation characters. There are several other features on which habitat classification can be based (e.g. depth, type of bottom deposits), but vegetation type was selected in this study because it seemed to conform best with the observed distribution of the invertebrate fauna and has been shown in numerous studies to strongly affect benthic invertebrate distribution and abundance. Three sampling stations were randomly established in each habitat type in different parts of the lake to maximize variation in the magnitudes of physical and chemical attributes. All 12 stations were sampled at fortnight intervals for six months (June to November 1997), which covered one wet- and one dry-season period. The first habitat type (water lily, WL) was fringed by *Nymphaea lotus* and *Nymphaea caerulea*, and was populated by a submerged macrophyte (*Ceratophyllum* sp.). The bottom consisted of dark liquid mud and decaying vegetation. Three stations were established in this habitat: Stations WL₁ (1.8 m deep, in the northeastern part), and WL₂ (2.7 m deep) and WL₃ (1.2 m deep) in the southern part of the lake (Fig. 1). In the water-lily habitat, grabs were taken in between water-lily stems for stations WL₁ and WL₃ and at the edge of the water-lily bed at station WL₂. *Miscanthidium violaceum* dominated the fringing vegetation of the second habitat (MV), and the

bottom was composed of rotting macrophytic material of various size fractions and in different states of decomposition mixed with brown soil particles. Stations MV₁ (1.6 m deep) and MV₂ (1 m deep) were established on the northern part of the lake, and MV₃ (1.6 m deep) was established on the southern part of the lake (Fig. 1). Samples were taken approximately 1.5 m lake-ward from the edge of the stands of *M. violaceum*, because it was not possible to use a grab within the dense *M. violaceum* mats. *Vossia cuspidata* (VC, hippo grass) was the dominant fringing vegetation in the third habitat. Stations included VC₁ (1.1 m deep) and VC₂ (1.6 m deep) on the northern part of the lake and VC₃ (1.7 m deep) on the eastern side (Fig. 1). The bottom here also consisted of dead organic matter from fringing vegetation and dark brown, fine particles. Samples were taken within the *V. cuspidata*, but did not include live stems. The fourth habitat (forest edge, FE) was the swamp forest on the western lakeshore, and the bottom was sandy composed of brown, fine grains mixed with broken, dark, dead wood particles. Stations included FE₁ (1.2 m deep), FE₂ (1.8 m deep) and FE₃ (1.5 m deep, Fig. 1).

Environmental characters

A series of environmental parameters were measured during each sampling period at the surface of the water column and just above the sediments at each station. Water temperature and conductivity were determined *in situ* using a digital conductivity meter (HACH Model 44600). We report raw conductivity values (as per the water temperature at a particular site) in our summary table. In the text we also report conductivity values compensated to 25 °C. pH at each station was measured using a digital pH meter (Model pH21-AQUALYTIC). Dissolved oxygen concentration (mg/l) was measured with a YSI dissolved oxygen meter (Model 51B) and later converted to percentage saturation using standard tables (Wetzel & Likens 1991). Dissolved oxygen and water temperature measurements were made at the surface and just above the bottom using a long cable on the oxygen probe. Bottom samples for pH and conductivity were taken in water collected just above the sediments with a Lamotte water sampler. Secchi depth was used as a measure of water transparency. Percentage organic matter in the sediments was estimated from soil samples at each station heated to 100 °C, 200 °C and finally ignited at 550 °C for 8 h to determine ash weight.

Percentage organic matter was calculated on three occasions for all stations except the forest edge habitats where the bottom was composed primarily of sand with negligible organic material. Rainfall data were obtained from the Meteorology Department for Kamenyamigo DFI station in Masaka, Uganda.

Benthic macroinvertebrates

Macroinvertebrate samples were obtained from all the 12 stations using an Ekman grab with an opening of 225 cm² (length × width) and depth of 17 cm. The Ekman grab was used because the sampler adequately collected both submerged macrophyte- and sediment-dwelling invertebrates (Hanson *et al.* 1989). Submerged macrophytes in Lake Nabugabo are sparse and did not hinder the operation of the grab. Two grabs from each station were taken on each visit between 08:00 and 12:30, and stations were sampled twice monthly from June to November of 1997. Samples were washed through sieves of mesh size 3 mm, 1 mm and 0.25 μm to reduce the bulk, and organisms were sorted out alive and preserved in 10 % formalin. Invertebrates were identified to the lowest taxonomic category possible with available keys.

Invertebrates were also sampled on four occasions in the open water of Lake Nabugabo (June, July, October, November) using the same Ekman grab. Transects from the lake shoreline to inshore waters were established from different parts of the lake. In each transect, a total of four samples (two grabs on each occasion) were collected from the sediment at different depths along the transect at 1-m intervals up to 5 m (Fig. 1).

Statistical analyses

Macroinvertebrate densities were expressed as number per square metre of sediment surface area. Data for duplicate samples within each sampling station were averaged. To describe variation in invertebrate densities among taxa and sites, we calculated mean densities (±SE) for each taxon as an average of the 12 samples taken over six months. To examine seasonal trends, the two samples within a month were averaged to produce a monthly estimate of abundance of invertebrates for each of the 12 stations. Biotic richness was indexed as the total number of taxa within a particular habitat.

One-way repeated-measures analysis of variance was used to test for differences among

months in the total abundance of benthic macroinvertebrates and abundance of the six dominant taxa. We used the Mauchly's test of sphericity to verify a circular structure of the variance-covariance matrix of the dependent variables. When the sphericity assumption was violated, the Huynh-Feldt approximation was used to obtain a corrected significance level. No statistically significant seasonal differences in abundance were detected, so seasonal samples within a station were combined to describe habitat associations.

Because there was variation both within and among habitats in physico-chemical parameters, we used a stepwise multiple regression analysis to identify significant predictors of benthic invertebrate density among the 12 sampling stations. Predictor variables considered included: dissolved oxygen (% saturation), conductivity (K_{25}), pH, organic matter content of the sediments and depth. Percentage organic matter was given a value of 0 in the sand bottom habitats of the forest edge for this analysis. At these sites, bottom sediments consisted of 73 % sand, 17 % clay and 10 % silt with negligible quantities of organic matter. For dissolved oxygen, conductivity and pH, we used the bottom values collected just above the sediments. The following variables were log-transformed: invertebrate density (total and dominant taxa), conductivity, pH and depth.

RESULTS

Environmental features

During the sampling period in 1997, rainfall was low in June and July, averaging 23 mm and increasing to a peak level of 260 mm in November.

Water temperature varied little among stations (Table 1). Surface water temperatures averaged across sampling periods for each site ranged among stations from an average of 23.1–25.4 °C (Table 1). The water at the bottom ranged among stations from 22.4 °C to 25.4 °C. Seasonal variation was also modest: mean surface values averaged across habitats ranged from 23.4 °C in June to 25.3 °C in September. Bottom values varied from 23.5 °C in June to 24.6 in September.

Lake Nabugabo is extremely poor in salts, mean conductivity among sites ranging from 22.4–25.8 μS/cm (K_{25} = 22.3 to 26.4 μS/cm) and 22.3 to 36.7 μS/cm (K_{25} = 22.6 to 37.9 μS/cm) for surface and bottom waters, respectively (Table 1). Conductivity was higher in the bottom waters in all months except June, and notably higher in

Table 1. Variation in physical and chemical features (water transparency, organic matter, water temperature, conductivity, pH and dissolved oxygen) among three stations in each of the four major inshore habitats of Lake Nabugabo, Uganda. Each value represents the mean of 12 samples (\pm S.E.); samples were taken every two weeks between June and November 1997. WL = water lily; MV = *Miscanthidium violaceum*; VC = *Vossia cuspidata*; FE = exposed forest edge; S = surface; B = bottom (just above sediments).

Station	Depth (m)	Mean Secchi depth (m)	Mean organic matter (%)	Temp (°C)		Mean		Mean pH conductivity (μ S/cm)		Mean dissolved oxygen (% saturation)	
				S	B	S	B	S	B	S	B
WL1	1.8 \pm 0.1	0.51 \pm 0.04	35.3 \pm 0.5	23.9 \pm 0.3	22.4 \pm 0.3	25.8 \pm 0.7	33.1 \pm 1.7	6.3 \pm 0.1	6.2 \pm 0.04	35.0 \pm 4.4	6.20 \pm 0.9
WL2	2.7 \pm 0.04	0.81 \pm 0.04	35.6 \pm 4.0	24.2 \pm 0.4	23.3 \pm 0.3	23.8 \pm 0.7	36.7 \pm 2.9	6.2 \pm 0.1	6.0 \pm 0.1	18.3 \pm 2.6	9.60 \pm 1.0
WL3	1.2 \pm 0.02	0.58 \pm 0.03	46.3 \pm 6.2	23.7 \pm 0.4	23.4 \pm 0.4	24.8 \pm 0.5	35.7 \pm 2.2	6.5 \pm 0.04	6.3 \pm 0.1	24.4 \pm 3.2	8.20 \pm 1.1
MV1	1.6 \pm 0.01	0.73 \pm 0.02	73.9 \pm 0.9	24.3 \pm 0.3	24.4 \pm 0.3	24.9 \pm 0.4	22.3 \pm 0.7	6.8 \pm 0.04	6.8 \pm 0.1	56.3 \pm 2.8	41.7 \pm 3.7
MV2	1.3 \pm 0.03	0.64 \pm 0.03	18.4 \pm 0.5	25.4 \pm 0.3	25.0 \pm 0.5	24.7 \pm 0.6	25.9 \pm 0.7	6.7 \pm 0.1	6.7 \pm 0.1	57.3 \pm 4.0	45.8 \pm 3.9
MV3	1.6 \pm 0.04	0.66 \pm 0.02	31.0 \pm 1.0	23.3 \pm 0.2	23.5 \pm 0.2	24.6 \pm 0.3	24.7 \pm 0.7	6.5 \pm 0.1	6.7 \pm 0.1	41.5 \pm 5.4	14.2 \pm 2.8
VC1	1.1 \pm 0.02	0.65 \pm 0.03	64.4 \pm 1.1	24.9 \pm 0.3	24.8 \pm 0.3	24.8 \pm 0.4	23.9 \pm 0.8	6.7 \pm 0.04	6.7 \pm 0.1	52.5 \pm 3.3	30.8 \pm 3.3
VC2	1.6 \pm 0.03	0.65 \pm 0.03	52.9 \pm 1.9	25.4 \pm 0.4	25.4 \pm 0.4	24.1 \pm 0.4	23.1 \pm 0.7	6.8 \pm 0.03	6.7 \pm 0.04	60.9 \pm 3.7	46.9 \pm 4.8
VC3	1.7 \pm 0.02	0.63 \pm 0.03	26.1 \pm 0.1	23.6 \pm 0.3	23.6 \pm 0.3	24.9 \pm 0.6	24.1 \pm 0.7	6.5 \pm 0.1	6.5 \pm 0.1	37.7 \pm 5.5	8.50 \pm 1.2
FE1	1.2 \pm 0.02	0.69 \pm 0.02	-	23.1 \pm 0.4	23.6 \pm 0.4	22.4 \pm 0.3	23.0 \pm 0.7	7.1 \pm 0.04	7.0 \pm 0.1	88.5 \pm 2.1	76.3 \pm 4.3
FE2	1.8 \pm 0.03	0.70 \pm 0.02	-	25.2 \pm 0.4	23.5 \pm 0.4	22.4 \pm 0.2	22.9 \pm 0.7	6.7 \pm 0.1	7.0 \pm 0.03	87.8 \pm 2.4	74.2 \pm 4.1
FE3	1.5 \pm 0.03	0.66 \pm 0.03	-	24.6 \pm 0.6	24.4 \pm 0.6	24.2 \pm 0.3	24.2 \pm 0.5	7.1 \pm 0.1	7.0 \pm 0.1	84.1 \pm 2.6	64.9 \pm 2.9

bottom waters of the water-lily habitat than in others (Table 1). Surface conductivity values averaged across habitats ranged from 22.4 μ S/cm (K_{25} = 23.4 μ S/cm) in July to 26.2 μ S/cm (K_{25} = 26.4 μ S/cm) in August while bottom values ranged from 21.6 μ S/cm (K_{25} = 22.4 μ S/cm) in June to 28.0 μ S/cm (K_{25} = 28.1 μ S/cm) in November.

The Lake Nabugabo water is acidic relative to that of many other lakes in Uganda; mean surface pH ranged among stations from 6.2 to 7.1, and mean bottom values ranged from 6.0 to 7.0 (Table 1). Except in June, the bottom pH was lower than the surface pH during the period of study, and pH was generally higher in the swamp forest sites than at the other stations (Table 1). Seasonal trends were modest, with surface values averaged across habitats ranging from 6.6 in October to 6.8 in July. Bottom values ranged from 6.5 in November to 6.7 in June.

Dissolved oxygen concentration in surface waters was higher than in bottom waters during all months. Surface mean values averaged across months ranged among stations from 18.3 % to 88.5 % saturation, while bottom values ranged from 6.2 % to 76.3 % saturation (Table 1). Oxygen content was higher at the swamp forest stations than at all other sites (Table 1). Dissolved oxygen concentration dropped sharply at the bottom, with near anoxic conditions occurring in some bottom habitats (water-lily stations, Table 1). Surface levels of dissolved oxygen (averaged across habitats) ranged from 44.5 % in September to 62.0 % in November, while bottom values ranged from 32.5 % in June to 41.8 % in August.

Water transparency varied among stations, ranging from 0.51 m to 0.8 m (Table 1). The highest Secchi depth was also recorded in the month of November (0.67 m) and the lowest in June (0.57 m, Table 1).

Organic matter concentration varied among the wetland ecotone sites from 26.1 % to 73.9 %.

Benthic macroinvertebrate fauna

The major components of the inshore benthic fauna were Ephemeroptera (77.7 %), Diptera (11.1 %), Annelida (5.4 %),

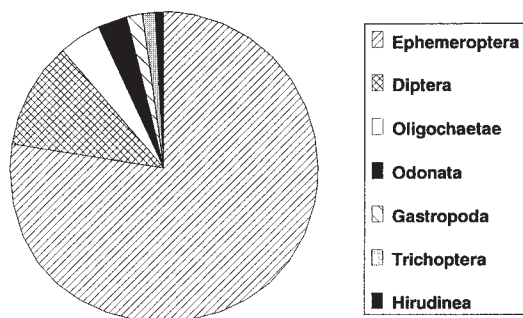


Fig. 2. The relative abundance (%) of benthic macro-invertebrate taxa in the inshore habitats of Lake Nabugabo. Data represent relative abundance of taxa averaged across all inshore sampling stations for all six months of sampling.

Odonata (2.9 %), Gastropoda (1.8 %), and Trichoptera (1.3 %, Fig. 2). Total invertebrate abundance did not vary significantly across months ($F = 0.60$, $P = 0.530$, $n = 6$). Therefore all months were combined to describe variation among stations and habitats. Invertebrate abundance was lowest in the water-lily habitat and highest in the *M. violaceum* and *V. cuspidata* habitats (Table 2). In fact, only chironomids (Chironominae) and a few trichopterans were found in the water-lily habitat, and at only one of the water-lily stations (Table 2). Taxa richness was highest in the *M. violaceum* and *V. cuspidata* habitats (Table 2). Stepwise multiple regression identified conductivity as the only significant predictor of total invertebrate abundance among stations ($r^2 = 0.71$, $F = 24.07$, $P = 0.001$, $n = 12$). Sites with lower conductivity values were characterized by higher invertebrate abundance.

Offshore areas exhibited a much lower density and richness of invertebrate taxa than most of the inshore sites, and both richness and abundance decreased at depths greater than 3 m (Table 3). Chironomids, chaoborids and oligochaetes were the most abundant taxa in offshore waters (Table 3).

There were two species of Ephemeroptera present in the bottom fauna of Lake Nabugabo. *Povilla adusta* was the dominant species, while the second species, *Caenis* sp., was much less common (Table 2). *Povilla adusta* dominated not only the Ephemeroptera, but also the total bottom fauna by density and percentage (Table 2). The density of ephemeropteran nymphs averaged across sampling periods and habitats was 1519 individuals per m^2 . There was no significant seasonal variation in ephemeropteran abundance ($F = 0.36$,

$P = 0.700$, $n = 6$), but abundance differed among inshore stations. Ephemeroptera were absent from the water-lily stations, and most abundant in the *M. violaceum* and *V. cuspidata* habitats (Table 2) and at one of the swamp forest sites (Table 2). The high abundance of ephemeropterans at the one forest edge site was probably related to the presence of rotting pieces of wood that offered suitable habitats for the burrowing nymphs of *Povilla adusta*. At station FE₃, on one sampling occasion, a piece of wood (5 cm long) contained 22 ephemeropteran nymphs. Nymphs were mainly found burrowing in pieces of wood or dead vegetation material accumulated at the bottom of vegetated shoreline habitats or they were found moving freely on the surface of the bottom substrata. Stepwise multiple regression identified conductivity as the only significant predictor of ephemeropteran density among all inshore stations ($r^2 = 0.41$, $F = 6.84$, $P = 0.026$, $n = 12$). Ephemeroptera were more abundant in habitats with lower conductivity. *Povilla adusta* nymphs were also found up to 300 m offshore, although they were rare, and mostly young nymphs (Table 3).

The chironomids were the most abundant dipterans in Lake Nabugabo, represented by Chironominae (9.3 % of the Insecta), Tanypodinae (1.9 %) and Chironominae (0.6 %, Table 2). Chaoborids were rare, but occasionally found in the *M. violaceum* habitat and at the forest edge (Table 2). There was no significant seasonal variation in dipteran density ($F = 1.06$, $P = 0.368$). However, inshore stations varied in dipteran abundance. Dipterans were extremely rare at the water-lily stations, limited to a few specimens of Chironominae at one station (Table 2). Dipterans were found at all other stations but were most abundant at one of the *V. cuspidata* sites (VC₁) and one of the *M. violaceum* sites (MV₁, Table 2). Stepwise multiple regression identified conductivity as a significant predictor of dipteran abundance among inshore stations ($r^2 = 0.74$, $F = 28.04$, $P < 0.001$, $n = 12$). Dipterans tended to be more abundant in sites with lower conductivity. Chaoborids and chironomids were also well represented at offshore stations (Table 3).

Annelids in Lake Nabugabo were represented by two families of oligochaetes (Tubificidae and Lumbriculidae, Table 2) and Hirudinea. There was no significant variation in annelid abundance across the months sampled ($F = 0.93$, $P = 0.371$), but, annelid density varied among inshore sta-

Table 2. Density of benthic macroinvertebrate taxa (number per m²) at three stations in each of the four major inshore habitats of Lake Nabugabo. Each value represents the mean (±S.E.) of 12 samples; samples were taken every two weeks between June and November 1997. WL = water lily; MV = *Miscanthidium violaceum*; VC = *Vossia cuspidata*; FE = exposed forest edge.

	Habitat: Taxa/Site:	Water lily			<i>Miscanthidium violaceum</i>			<i>Vossia cuspidata</i>			Exposed forest edge		
		WL ₁	WL ₂	WL ₃	MV ₁	MV ₂	MV ₃	VC ₁	VC ₂	VC ₃	FE ₁	FE ₂	FE ₃
INSECTA	Odonata	0	0	0	107 ± 19	30 ± 11	4 ± 4	384 ± 22	111 ± 12	4 ± 4	0	0	26 ± 12
	Diptera	0	0	0	570 ± 288	41 ± 21	30 ± 14	1106 ± 353	115 ± 62	22 ± 8	30 ± 22	78 ± 41	15 ± 9
	Chironominae	0	0	0	44 ± 22	59 ± 35	4 ± 4	141 ± 47	59 ± 47	11 ± 11	22 ± 15	41 ± 19	44 ± 30
	Tanytopodinae	0	0	0	26 ± 26	4 ± 4	7 ± 7	70 ± 45	11 ± 11	0	0	4 ± 4	0
	Chironomii	0	0	0	4 ± 4	4 ± 4	0	0	0	0	7 ± 7	12 ± 11	4 ± 4
	Chaoboridae	0	0	0	9454 ± 1204	2497 ± 471	4 ± 4	1936 ± 356	3733 ± 689	0	0	11 ± 5	355 ± 170
	Ephemeroptera	0	0	0	70 ± 41	30 ± 21	4 ± 4	44 ± 25	85 ± 55	0	0	0	0
	<i>Povilla adusta</i>	0	0	0	4 ± 4	18 ± 11	0	26 ± 16.6	74 ± 32.3	0	63 ± 23	52 ± 18.5	59 ± 15
	<i>Caenis</i> sp.	0	0	4 ± 4	52 ± 23	0	63 ± 34	23 ± 21	0	0	0	0	0
	Trichoptera	0	0	0	111 ± 48	4 ± 4	0	162 ± 63	0	0	0	0	0
MOLLUSCA	Gastropoda	0	0	0	4 ± 4	0	0	0	0	0	0	0	0
	<i>Biomphalaria pfeifferi</i>	0	0	0	0	0	0	0	0	0	0	0	0
ANNELIDA	<i>Bulinus ugandeyi</i>	0	0	0	4 ± 4	0	0	0	0	0	0	0	0
	Oligochaeta	0	0	0	4 ± 4	0	0	0	0	0	6 ± 4	48 ± 20	19 ± 9
	Tubificidae	0	0	0	758 ± 161	137 ± 58	0	0	7 ± 7	0	11 ± 11	44 ± 33	22 ± 22
	Lumbriculidae	0	0	0	71 ± 13	18 ± 12	0	63 ± 34	26 ± 9	0	13 ± 11	15 ± 11	7 ± 7
	Hirudinea	0	0	0	11275	2842	116	3955	4221	37	152	405	551
Total			15										

tions. No annelids were recovered from water-lily stations. Annelids were most abundant at two of the *M. violaceum* stations (Table 2). In a stepwise multiple regression, annelid density was positively related to both dissolved oxygen and percentage organic matter ($r^2 = 0.84, F = 22.90, P < 0.001$: dissolved oxygen partial $r = 0.91, t = 6.76, P < 0.001$; percentage organic matter partial $r = 0.78, t = 3.79, P = 0.004, n = 12$). Annelids were also present in offshore stations at all depths (Table 3).

Among the Odonata nymphs, anisopterans were more abundant and comprised of two families: Aeschnidae and Libellulidae. Odonate abundance did not vary significantly over the months of the study ($F = 0.82, P = 0.479, n = 6$). However, habitat effects were evident. No odonates were recovered from the water-lily stations, and odonates were found at only one of the forest-edge stations (FE₃, Table 2). Odonates were most abundant at two of the *V. cuspidata* stations (Table 2). In a stepwise multiple regression, odonate density was negatively related to conductivity and positively related to percentage organic matter ($r^2 = 0.70, F = 10.45, P = 0.005$: conductivity partial $r = -0.76, t = 3.50, P = 0.007$; percentage organic matter partial $r = 0.73, t = 3.23, P = 0.010, n = 12$). No odonates were recovered in offshore samples (Table 3).

Two species of gastropods were encountered in the inshore areas of Lake Nabugabo: *Bulinus ugandeyi*, which was the more abundant species, and *Biomphalaria pfeifferi* (Table 2). Overall, gastropods were rare, and there was no difference among months in gastropod abundance ($F = 1.69, P = 0.562$). Gastropods were only found in two habitats, *V. cuspidata* and *M. violaceum*, and limited to only one of the three *M. violaceum* stations (Table 2). Stepwise multiple regression revealed percentage organic matter as the only significant predictor of gastropod abundance among inshore sampling stations. Gastropod density was higher in areas where the substrata contained

Table 3. Density of benthic macroinvertebrates (number per m²) in open waters of Lake Nabugabo, Uganda, at stations ranging from 1–5 m in depth.

Taxa	Density of invertebrates				
	1 m	2 m	3 m	4 m	5 m
Chaoboridae	133	311	355	33	0
Chironominae	455	78	255	67	144
Tanypodinae	0	0	11	11	0
<i>Povilla adusta</i>	44	122	78	0	0
Corixidae	64	44	22	0	0
Hirudinea	67	0	11	11	0
Oligochaeta	33	67	222	78	44
Total	3285.6	2486.4	3818.4	799.2	754.8

large amounts of organic material ($r^2 = 0.61$, $F = 5.81$, $P = 0.037$, $n = 12$). Neither species of gastropod was encountered in offshore samples (Table 2).

Trichopterans were rare in Lake Nabugabo and represented by a single species, *Limnophilus politus*. Seasonal variation in trichopteran abundance was not statistically significant ($F = 1.06$, $P = 0.373$). The highest densities occurred at one of the *V. cuspidata* stations (VC₂) and one of the forest-edge stations (FE₁, Table 2). Stepwise multiple regression indicated dissolved oxygen concentration as a significant predictor of trichopteran abundance among all inshore stations ($r^2 = 0.88$, $P < 0.001$, $n = 12$). Densities were higher in areas characterized by higher dissolved oxygen availability. Trichopterans were not encountered at offshore stations (Table 3).

DISCUSSION

Lake Nabugabo is an unusual lake because of its extremely low conductivity and both depauperate and scarce mollusc fauna. Conductivity was generally low but did vary among inshore stations, ranging from 22.3 to 26.4 $\mu\text{S}/\text{cm}$ and 22.6 to 37.9 $\mu\text{S}/\text{cm}$ (K_{25}) for surface and bottom waters, respectively. The low conductivity values reflect the low salt content of the lake and surrounding wetlands and are very low relative to many other East African lakes. Beadle (1981) reported conductivity values in open surface waters (at 20 °C) of 735 $\mu\text{S}/\text{cm}$ for Lake Albert and 925 $\mu\text{S}/\text{cm}$ for Lake Edward. At 25 °C, this would be approximately 813 $\mu\text{S}/\text{cm}$ and 1023 $\mu\text{S}/\text{cm}$, respectively. Even Lake Victoria, which lies only 4 km from Lake Nabugabo, has much higher conductivity; Talling & Talling (1965) reported a value of 96 $\mu\text{S}/\text{cm}$ at 20 °C (approximately 106 $\mu\text{S}/\text{cm}$ at 25 °C) for a

sample of surface water from Lake Victoria.

Conductivity is generally low in waters throughout the Lake Nabugabo area due to insoluble rocks in the catchment and the fact the waters drain into the lake through dense swamp channels. Water entering the lake passes over rocks that are very old, and soils have been leached and minerals carried to deeper layers. Beadle (1981) noted that many of the small lakes, streams and swamps within about 20 km of the northwest coast of Lake Victoria from the Katonga River to the south of Bukoba are characterized by a low mineral content and are generally free of molluscs. In addition to the insoluble rocks in the catchment, the low conductivity may reflect, at least in part, passage through the extensive Lwamunda swamp where ions are likely to be removed through absorption and accumulation by the swamp vegetation. Talling & Talling (1965) discussed the ionic composition of African lakes. One group of lakes with particularly low ionic concentration was characterized by inflow that enters the main lake through a swamp, as is the case in Lake Nabugabo.

With the exception of swamp forest habitat, most of Nabugabo sites were slightly acidic. This acidity of the water can be attributed, at least in part, to the presence of *Sphagnum* in the swamps (Beadle 1981). The decomposing plant material acts as a cation exchange system, releasing hydrogen ions, hence the acidity (Wetzel 1975). The acidic waters of Nabugabo contrast with those of many other lakes in East Africa where pH is higher. Beadle (1932) reported pH values in open surface waters of 10 East African lakes as ranging between 8.8 in Lake Baringo to 10.5 in Lake Maseche.

The low conductivity in Lake Nabugabo may be responsible for the small number of molluscs (1.8 % of the numerical abundance) and absence

of crustaceans which, with their calcareous shells and exoskeleton, have great need for the divalent cations, especially calcium (Beadle 1981). Beadle & Heron (unpubl. data reported in Beadle 1981) reported a very low calcium concentration in Lake Nabugabo of 0.060 meq/l. In addition, Beadle (1981) noted that low conductivity is often associated with low pH, which accelerates calcium loss from organisms. Several studies have noted a correlation between the calcium content of the water and the calcium content, density and/or distribution of some molluscs in both temperate (e.g. McKillop & Harrison 1972; Dussart 1976, 1979; Mackie & Flippance 1983) and tropical (e.g. Williams 1970a,b) waters. Lac Tumba, situated in the central Congo basin, is another example of an African lake with a low mineral content for which there are chemical and biological data. The lake water has a conductivity of 26.5–35.4 $\mu\text{S}/\text{cm}$ (K_{25}), a pH ranging from 4–5 to 5–0, and a calcium concentration of 0.03 meq/l (Marlier 1958; Dubois 1959 as cited in Beadle 1981); and molluscs and crabs are absent (Marlier 1958; Beadle 1981). In Uganda, lakes with higher conductivity and pH tend to show a greater richness of gastropod and crustacean taxa and a greater relative abundance of these taxa. For example, in his study of the benthos of Murchison Bay, Lake Victoria, Okedi (1990) found that gastropods and bivalves made up 21 % and 47 % of the biomass of the benthic invertebrate fauna, respectively. With respect to numbers, gastropods and bivalves comprised 11 % and 9 % of the benthos, respectively. In their study of the macroinvertebrate fauna in northwestern Lake Victoria, Mothersill *et al.* (1980) found the gastropod *Melania tuberculata* to be the dominant taxon with respect to number of stations occupied. In a later study of the Jinja area of Lake Victoria, Balirwa (1998) reported an average mollusc density of 136 individuals per m^2 at the wetland ecotone, 1054 individuals per m^2 20 m off the wetland ecotone, and 301 individuals per m^2 in open-water stations, a dramatic contrast to our average density of 35 individuals per m^2 in our inshore survey and the absence of molluscs in open-water stations. In their study of Lake George, Uganda, Burgis *et al.* (1973) found that gastropods made up approximately 22 % of the dry weight biomass of the benthic mud fauna in the inshore areas.

Although we found gastropods to be rare in Lake Nabugabo, two species were encountered: *Bulinus ugandyei* and *Biomphalaria pfeifferi*. These

two snail genera are important secondary hosts of *Schistosoma haematobium* and *S. mansoni*, respectively (Beadle, 1981). A survey of fishermen in Lake Nabugabo (G.R. Barnley, as quoted in CNBS 1962), found that few of the fishermen on Lake Nabugabo carried the bilharzia parasite, and the few who did have the disease had at one time worked on Lake Victoria, where the disease has a high frequency of occurrence. The distribution of the two snails within Lake Nabugabo was largely confined to some parts on the shallow vegetated northern lakeshores that may limit their availability as intermediate hosts. The presence of snails in these particular areas of Lake Nabugabo may be explained by the large amount of organic matter and the dense macrophytes at these sites.

Although seasonal variation in dissolved oxygen concentration was modest, dissolved oxygen varied among sites and also declined with depth. This was more dramatic in the heavily vegetated swamps on the southern part of the lake (water-lily sites) where dissolved oxygen concentration often reached extremely hypoxic levels in the waters above the sediments. The waters of heavily vegetated swamps are often characterized by reduced oxygen levels due to low level of incident light, minimal mixing of water beneath the vegetation and a high rate of organic decomposition (Carter 1955; Chapman & Liem 1995; Chapman *et al.* 1998). The low levels of oxygen in the bottom waters of the water-lily sites probably reduced the volume of the available substratum for invertebrates, contributing to the near absence of macroinvertebrate taxa on the bottom of the heavily vegetated water-lily habitats. The density of two taxa in our study, trichopterans and annelids, was positively correlated with dissolved oxygen that may limit their use of water-lily sites. The most abundant taxon in the water-lily habitat was the Chironominae. Among aquatic insects, haemoglobin is restricted to some species of chironomids and notonectids. The chironomids are the best known of the insects with respiratory pigments, which facilitates their use of extremely hypoxic waters (Merritt & Cummins 1996)

Water in the water-lily habitat was also characterized by higher conductivities than other inshore areas. Among inshore stations, the density of the benthic invertebrates (all taxa combined), as well as the density of some specific taxa, were negatively correlated with conductivity. It is possible that the invertebrate taxa that survive in Lake Nabugabo and other low-conductivity lakes in

East Africa represent a fauna that does particularly well under low ion concentrations and may select habitats with lower levels of conductivity. However, the negative relationships that we observed between low conductivity and invertebrate abundance may also mean that some variable correlated with conductivity (like dissolved oxygen) is driving the relationship. It is difficult to separate the effects of dissolved oxygen and conductivity on habitat use by invertebrates in Lake Nabugabo because stations characterized by low oxygen were often also characterized by relatively high conductivity (all WL sites). However, what is clear is that the water-lily zone is extremely depauperate, and given the expansion of this habitat that has been observed over the past decade (L.J. Chapman, pers. obs.), the low densities of macroinvertebrates may have implications for inshore macroinvertebrate feeders.

Concentrations of organic matter were much higher within substrates of *M. violaceum* and *V. cuspidata* than in the forest-edge habitats where the bottom was predominantly fine sand. In exposed forest sites, habitat structure was limited to deadfall and overhanging branches, while the other three habitat types had muddy bottoms with the upper layers consisting of decomposing vegetation of varying size and structure. This provided a diversity of suitable microhabitats, and may have contributed to the coexistence of a higher richness of invertebrates at the *M. violaceum* and *V. cuspidata* sites. Although the per cent organics was also high in the water-lily habitat, other features of these stations (low dissolved oxygen) may have limited colonization and survival. We found the densities of two taxa, the annelids and the gastropods, were positively correlated with the percentage organic material in the sediments; both taxa were most abundant in the *V. cuspidata* sites. The importance of organic materials to the distribution of benthic macroinvertebrates is supported by earlier work. Egglisshaw (1964) found a positive correlation between the amount of plant detritus and the numbers of several species of invertebrates in a temperate stream. In their study of the microdistribution of stream-dwelling benthic insects, Rabeni & Minshall (1977) found evidence to support Egglisshaw's findings. Their findings suggested that the effect of substratum particle size on the microdistribution of the insects related to the capacity of certain substratum conditions to more efficiently collect detrital materials.

It is also possible that differences in the relative

abundance of macroinvertebrates (all taxa combined) among the habitats reflected differences in protection from predators afforded by the various plant species. Some studies in temperate lakes have linked fish predation to the structure and distribution of benthic invertebrate assemblages (Gilinsky 1984; Hershey 1985). Several species of fishes in Lake Nabugabo feed on benthic invertebrates at some life history stage (Greenwood 1965; Ogutu-Ohwayo 1993; Olowo 1998; Schofield & Chapman 1999). For some macroinvertebrate predators like juvenile Nile perch, wetland habitats are far less utilized than open-water sites (Schofield & Chapman 1999) and may therefore afford protection to benthic invertebrate prey.

Numerically, the ephemeropterans were the dominant taxon, and this may reflect an abundance of suitable habitats for *P. adusta* in Lake Nabugabo. As filter feeders (Hartland-Rowe 1953), they facilitate energy flow from primary producers to secondary consumers, and are very important prey for several fish species (Petr 1969, 1970). They also play an important part in the destruction of bark and wood of flooded forests (Petr 1969, 1970). *Povilla adusta* selects substrata into which it can burrow (Petr 1969, 1970). In the Volta Lake, they burrow primarily into submerged bark and wood (Petr 1970), while in Lake Victoria and Lake George, *Povilla* are mainly found in dead stems and rhizomes of *Cyperus papyrus* fringing these lakes. The results of our study are consistent with this previous work on *Povilla* in East Africa, the only difference being that papyrus is not the dominant plant in Lake Nabugabo, so they tend to burrow into other substrata.

Seasonal variation in density was not significant for the six major benthic macroinvertebrate taxa in Lake Nabugabo. This may relate to the fact that seasonal change in most environmental characters was modest and did not incur strong seasonal trends in macroinvertebrate numbers. In addition, the heavy rainfall of 1996 and 1997 created conditions whereby the differences between the dry and wet seasons were less distinct than in many other years. Finally, the high variance within and among habitats may have obscured the seasonal trends from manifesting, and a larger sample size may have permitted a more powerful analysis and revealed more subtle seasonal trends in macroinvertebrate densities.

In summary, the benthic macroinvertebrate fauna of Lake Nabugabo represents an unusual community characterized by low taxa richness, a

depauperate gastropod assemblage and the absence of crustaceans. This seems to relate to the extremely low conductivity of the system driven by the geological history of the region and drainage through the extensive Lwamunda Swamp. Inshore habitat effects on the invertebrate fauna were dramatic, ranging from the depauperate water lilies to areas near *M. violaceum* with rich organic sediments colonized by all major invertebrate taxa in the lake. The expansion of the waterlily habitat in Lake Nabugabo that has occurred over the past decade may limit the availability of food for macroinvertebrate-feeding fishes in inshore regions of the lake.

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