A study of the macro-invertebrates of Lakes Naivasha, Oloidien and Sonachi, Kenya

Frank CLARK (1), Alan BEEBY (2) and Peter KIRBY (3)

ABSTRACT

Macro-invertebrates were sampled at Lake Naivasha in December 1982/83 and in July/August 1984. The adjacent Oloidien and Sonachi Lakes were sampled in 1984 only. There was a considerable difference between the faunal lists obtained on the two trips. Comparison with lists obtained by the Percy Sladen (1929) and Cambridge (1930-31) expeditions also showed major long-term changes, including a complete change in the Oligochaete and molluscan faunas. The short-term change between 1982/83 and 1984 is attributed to the large natural water level fluctuations. Additional factors which may be responsible for long term changes are the loss of submerged macrophytes through grazing by introduced Coypu Myocaster coypus *and crayfish* Procambarus clarkii, *the introduction of alien species, and farming practices involving the extensive removal of papyrus and increasing use of lake water for irrigation.*

KEY WORDS : Freshwater — Invertebrates — Littoral zone — Benthos — East Africa.

RÉSUMÉ

LES MACRO-INVERTÉBRÉS DES LACS NAIVASHA, OLOIDIEN ET SONACHI (KENYA)

Des prélèvements de macro-invertébrés ont été faits dans le lac Naivasha en décembre/janvier 1982/83 et en juillet/août 1984, et dans les deux lacs avoisinants, Oloidien et Sonachi, seulement en 1984. On a remarqué une différence considérable dans les listes faunistiques obtenues au cours des deux visites. La comparaison avec les listes obtenues par les expéditions de Percy Sladen (1929) et de Cambridge (1930-31) a aussi révélé un changement majeur à long terme, y compris un changement complet des faunes d'oligochètes et de mollusques. Le changement à court terme de 1982/83 à 1984 est attribué aux importantes fluctuations naturelles du niveau de l'eau. Parmi les autres facteurs qui ont pu causer les changements à long terme, on cite la disparition des macrophytes submergés, broutés par des espèces introduites, Coypou (Myocaster coypus) *et écrevisse* (Procambarus clarkii), *l'introduction des espèces étrangères et des pratiques agricoles entraînant l'enlèvement d'une grande quantité de papyrus et l'emploi toujours croissant de l'eau du lac pour l'irrigation.*

MOTS-CLÉS : Invertébrés — Eau douce — Zone littorale — Benthos — Afrique de l'Est.

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(1) *Department of Zoology, University of Leicester, Leicester LE1 7RH, United Kingdon.*
(2) *Department of Biotechnology, Polytechnic of the South Bank, London. S.E.1 OAA. United Kingdom.*
(3) *Nature Conservancy Council, Northminster House, Peterborough, PE1 1UA. United Kingdom.*

INTRODUCTION

Lake Naivasha is a slightly alkaline lake north-west of Nairobi in the Eastern Rift Valley of Kenya (0°45′ S and 36°20′ E; altitude 1890 m). It is fed by several rivers from the north and has an area of approximately 120 km², which changes with both seasonal and long term fluctuations in water level (Gaudet 1977). The adjacent Oloidien Lake is separated from the main lake by a papyrus (*Cyperus papyrus* L.) reef, though it is connected to the main lake at times of high water by a man-made channel cut through the reef. Oloidien has a much higher alkalinity and conductivity but is subject to the same fluctuations in water level as the main lake. Sonachi Crater Lake is a small (14 hectares) isolated lake, with high alkalinity and conductivity, located approximately 3 km west of Oloidien Lake. The physical and chemical characteristics of each lake are given in Table I.

The ecology of the macro-invertebrates in the Lake Naivasha basin is poorly documented. The 1929 Percy Sladen expedition (Jenkin, 1936) and the 1930-31 Cambridge expedition (Beadle, 1932) produced species lists for Lake Naivasha and other Rift Valley lakes. More recently Cox (1977) studied the ecology of chironomids in the main lake and Milbrink (1977) records a few macro-invertebrates.

Major changes have taken place in the main lake's ecology since these studies. The most notable are the almost complete disappearance of the blue water lily *Nymphaea caerulea* Savigny, which fringed much of the shore line up to the late 1970s, the decline of submerged macrophytes, and the spread of the water fern *Salvinia molesta* Mitch., an unintentional introduction which now forms dense mats in many of the bays.

Harper (1984) attributed the decline of *N. caerulea* and disappearance of submerged macrophytes to the presence of the coypu *Myocaster coypus* Molina and the crayfish *Procambarus clarkii* (Girard). Only a few plants of *Potamogeton* were found by Gaudet *(op. cit.)* in the early 1970s, yet there have been extensive beds of *Potamogeton octandrus* Poir around Crescent Island in recent years (Fig. 1). It is not clear why this species should be relatively unaffected.

Due to the prevailing east wind *S. molesta* is found predominantly on the western shore. The shade from this plant may inhibit the establishment and growth of submerged macrophytes. Large rafts of Papyrus which break away from the north swamp at times of high water are also blown onto the western shore. In shallow areas these rafts must disrupt submerged macrophyte communities.

Because of its higher alkalinity Oloidien Lake has no *C. papyrus* nor *S. molesta* but supports both *M. coypus* and *P. clarkii*. In this lake, there are extensive beds of *Potamogeton schweinfurthi* A. Bennett and *Potamogeton pectinatus* L., and smaller beds of *Naias pectinata* (Parl.) Magnus, *Nitella oligospora* Braun and *Nitella furcata* (Roxb. ex Bruz.) Agardth. This would suggest that the presence of *S. molesta* and *C. papyrus* is the main factor limiting submerged macrophyte growth in the main lake. Sonachi Lake, with the highest alkalinity of the three lakes, has no submerged macrophytes.

Benthic and littoral macro-invertebrates in the main lake and in Oloidien and Sonachi Lakes were investigated during two visits in December 1982/January 1983 and July/August 1984. The conditions prevailing at the lake were quite different between the two visits. In 1982/83 the short rains were prolonged and the lake level was high with much of the riparian farmland flooded. Floating islands of *C. papyrus* up to 2 km long drifted around the lake and much of the western shore line was fringed with mats of *S. molesta*. In 1984, due to successive failure of both the long and short rains, the lake level had fallen by at least 2 m, leaving large areas of exposed mud. The formerly mobile islands of *C. papyrus* were anchored and much of the *S. molesta* had dried out after stranding.

METHODS

The macro-zoobenthos was sampled quantitatively with a 15 cm × 15 cm Ekman grab. The grab was modified to close on impact with the substrate (Rawson 1947). Since the substrate in Lake Naivasha was found to be very soft, the top of the grab was covered with a fine (355 μ) stainless steel gauze to prevent animals in the top few centimetres passing out the top of the grab as it sank into the substrate. Each grab sample was sieved through a 355 μ sieve and then sorted by hand.

In 1982/83 between 10 and 20 grabs were taken along each of seven transects from shallow to deep water in the main lake, grab samples being at intervals of about 0.5 km. The positions of these transects are shown in Figure 1. In 1984 only 4 transects were sampled in the main lake at Mennell's Lagoon, Crescent Island, North Swamp and Hippo Point. In 1984 only, additional samples were taken along two transects in Oloidien Lake (25 grabs) and along one transect in Sonachi Lake (15 grabs).

Littoral samples were taken with a hand net at a number of points around the Naivasha and Oloidien

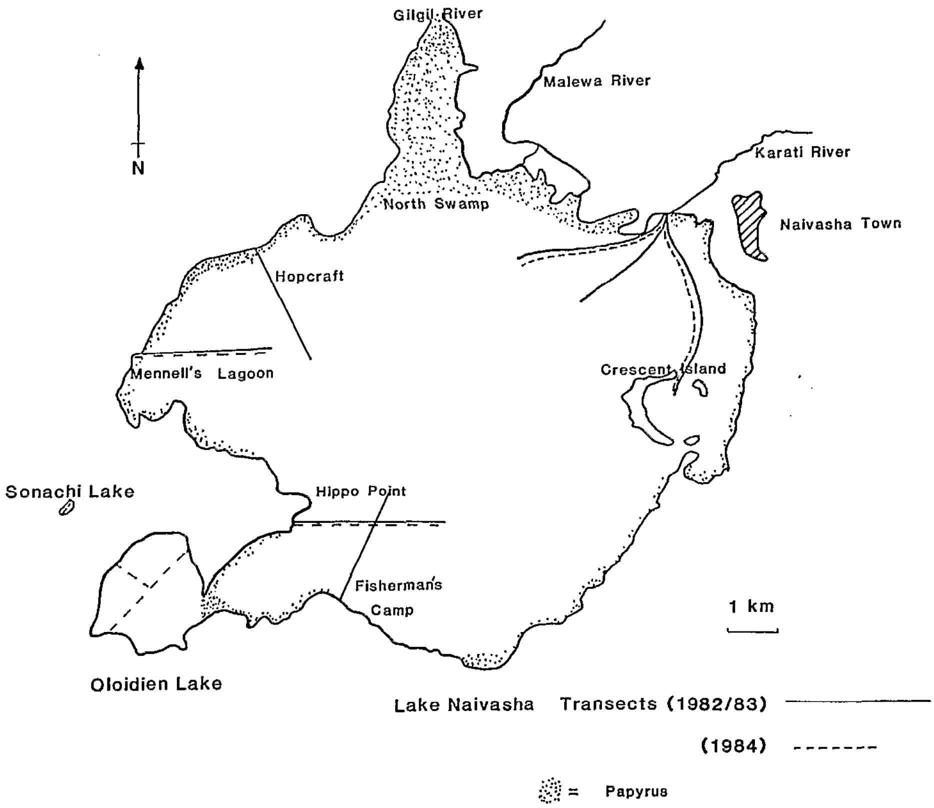

FIG. 1. — Map of the three lakes showing transects along which Ekman grab samples were taken
Carte des trois lacs indiquant les transects le long desquels les prélèvements à la benne d'Ekman ont été faits

Lakes in 1982/83 and all three lakes in 1984. Samples were preserved in 4 % Formalin.

Samples of the substrate from various points on the transects were analysed for organic material by loss on ignition from the main lake in 1982/83 and from all three lakes in 1984.

Oxygen concentration and temperature were measured at various points on the transects with a combined oxygen/temperature probe and meter. Oxygen concentration was also measured by micro-Winkler titration.

RESULTS

Environmental data

The physical and chemical characteristics of the 3 lakes are summarized in Table I.

Though there are patches of volcanic sand in the area around Crescent Island the substrate over much of the main lake comprised a disturbed layer of loose flocculent material, which, like that of Lake George, Uganda (VINER *et al.*, 1973) appears to be maintained by a wind-induced wave stirring regime. BURGIS

TABLE I

Physical and cheminal characteristics of the lakes.
Caractères physico-chimiques des trois lacs
N = Naivasha, O = Oloidien, S = Sonachi, HP = Hippo point, M = milieu du lac

	N 1982/83	1984	O 1984	S 1984
Alkalinity meq. -1	1.95	3.2	5.4	20.0
Conductivity µs cm^{-1}	259	350	620	3000.0
O_2 mg^{-1}	7-8	7-8	6-8	----
Temperature °C	19-21	19-21	19-21	19-21
Depth (meters)	HP	HP	M	M
	9.5	8.0	11.5	4.0
Organic content %	42-84	2-30	2-30	2-30

TABLE II
Densities of benthic macro-invertebrates (numbers m^{-2})
Densités des macro-invertébrés benthiques (individus m^{-2})

Taxa	Naivasha 1982/83	Naivasha 1984	Oloidien 1984	Sonachi 1984
Oligochaeta				
Tubificidae				
Branchiura sowerbyi Beddard	205	369	186	NF
Limnodrilus hoffmeisteri Claparede	587	784	430	NF
Potamothrix heuscheri/bavaricus	NF	NF	68	NF
Chironomidae				
Chironomus sp.	260	105	140	NF
Dicrotendipes sp.	20	54	40	NF
Cladotanytarsus sp.	120	102	22	NF
Procladius sp.	<5	<5	NF	NF
Tanypus sp.	<5	<5	NF	NF
Clinotanypus sp.	NF	NF	<5	NF
Nilodorum sp.	NF	98	62	NF
Endochironomus disparalis Goethebuer	NF	NF	NF	8000
Microtendipes sp.	NF	NF	NF	3000
Cladotanytarsus sp.	NF	NF	NF	2500

NF = not found, *non récolté*

et al. (1973) suggested the unstable nature of this type of substrate may limit colonisation by macro-invertebrates. The bottom of Oloidien Lake lacks the disturbed layer of the main lake and is comprised mainly of clay in deeper water and black muds in the shallows. The substratum in Sonachi Lake is comprised mainly of clays in the deeper water with soft muds in the shallows.

Four major substrate types may be distinguished:

1) A littoral, soft bottom.
2) A littoral, hard substrate of rocks and fallen acacia trees.
3) A profundal, soft bottom.
4) *C. papyrus* rhizome. This is not strictly littoral, since the fringe of the papyrus reefs were often over deep water.

The maximum depth recorded in the main lake in 1982/83 was 18 m in the middle of Crescent Island bay. This was atypical of the rest of the lake; the next highest was 9.5 m at Hippo Point. In 1984 the maximum depth recorded in the open lake was 8 m, again at Hippo Point. Neither Oloidien nor Sonachi Lakes were sampled for benthic invertebrates in 1982/83 and no depths were therefore recorded. In 1984 the maximum depth recorded in Oloidien was 11,5 m and in Sonachi 4 m.

The level of organic material in the main lake was high in 1982 but substantially lower in 1984. On both visits the highest levels were at the North Swamp and the lowest off Hippo Point. In both Oloidien and Sonachi Lakes the levels of organic material were comparable with those of the main lake.

Oxygen levels in 1982/83 were high in the water column but declined rapidly in the unstable loose substrate and were undetectable below this. In 1984 no distinct decline in oxygen levels was found in the loose substrate suggesting a higher rate of mixing in the main lake. Oloidien was well oxygenated down to the substrate where up to 6 mg^{-1} were recorded. No oxygen readings were taken in Sonachi Lake.

Water temperatures were similar in both lakes and on both visits. By the early afternoon the surface water temperature was usually 1-2 °C higher than the rest of the water column

Benthic macro-invertebrates

Macro-invertebrate densities are summarized in Table II.

In both the 1982/83 and 1984 collections the macro-benthos in both profundal and littoral soft bottom substrates was sparse and patchily distributed. It was comprised of tubificids (*Branchiura sowerbyi* (Beddard) and *Limnodrilus hoffmeisteri* (Claparede)) and chironomid larvae, a typical biota of many tropical lakes (see for example BURGIS *et al.* 1973, GREEN 1979, MARSHALL 1982). Little difference in the abundance of the tubificids was found between the two collections and there was little variation with depth. Their horizontal distribution in the lake did not appear to be correlated with the amount of organic material present.

Branchiura sowerbyi is widely distributed in the tropics, whilst *L. hoffmeisteri* is world-wide in distribution (BRINKHURST 1966). Both species occurred in the majority of grabs. *B. sowerbyi* has been shown to prefer a coarse substrate (MARSHALL 1973) where it positions itself so that the branchial part of its body is above the substrate and presumably in oxygenated water. No substrate preference is known for *L. hoffmeisteri*. SOROKIN (1966) showed that this species feeds on bacteria in a layer 2-3 cm below the surface. Examination of gut contents in cleared specimens of both species showed that *L. hoffmeisteri* takes in much smaller particles than *B. sowerbyi*. The two species may therefore occupy similar positions within the substrate without competing for the same food resource. They have often been recorded together in other tropical lakes (see for example MARSHALL 1983).

Mature and immature specimens of *L. hoffmeisteri* were taken in both collections. In the 1984 collection about 30% of the *B. sowerbyi* population was very small, recently hatched individuals; as only larger individiduals were found in 1982/83 this may indicate seasonality in the breeding cycle.

The grab samples in the profundal and littoral soft bottom of Oloidien Lake in 1984 yielded both *B. sowerbyi* and *L. hoffmeisteri* at similar densities to those found in the main lake. An addidional tubificid, *Potamothrix heuscheri/bavaricus*, was found at lower densities, associated mainly with the beds of submerged macrophytes. All the specimens recovered were immature and could not be identified to species. *P. heuscheri* has previously been recorded from the main lake (MILBRINK 1977). Its apparent disappearance may be connected with the decline of macrophytes. No oligochaetes were found in Sonachi Lake.

Prior to 1977 few records of oligochaetes from Lake Naivasha had been published. JENKIN (1936) records seven species of oligochaetes in Lake Naivasha, all belonging to the family Naididae. These were recorded from the littoral zone in submerged macrophytes, mud, or both. There seems therefore to have been a complete change in the Oligochaete fauna in Lake Naivasha over the past 50 years or so.

In 1982/83 adults of only two species of chironomid, *Chironomus formosipennis* Kieffer and *Cladotanytarsus pseudomancus* Goetghebuer were found, but larvae of at least five species were present in grab samples. The majority of the larger red larvae were *Chironomus* sp. presumably *formosipennis*. A species of *Dicrotendipes* occurred at a lower density and was particularly frequent in the North Swamp. Larvae of *Cladotanytarsus*, presumably *pseudomancus* occurred in quite large numbers but were patchily distributed in areas of volcanic sand. Together with *Cladotanytarsus* were species of *Procladius* and *Tanypus*, both at very low densities. None of these were found on the softer substrates. DARLINGTON (1977) suggests that larvae of *Procladius* are unable to colonise unstable substrates, and the present results suggest that the same may be true of *Cladotanytarsus* and *Tanypus* in Naivasha.

In 1984 the most abundant chironomid adult was *Nilodorum brevipalpe* Kieffer with only a few *C. formosipennis* and *C. pseudomancus*. Of the larvae taken in the grab samples *Chironomus*, presumably *formosipennis*, was most abundant, with *Nilodorum*, presumably *brevipalpe*, almost equally so. With these two species were *Dicrotendipes* sp. which was again most abundant in the North Swamp area. *Cladotanytarsus*, *Procladius* and *Tanypus* were found at about the same density as in 1982/83 collections, and were found only in volcanic sand on the east shore.

Cox (1977) records seven species of chironomid from Lake Naivasha : *Chironomus formosipennis; Chironomus* (now *Dicrotendipes*) *pilosimanus quatuordecimpunctatus* Goetghebuer; *Cladotanytarsus pseudomancus; Clinotanypus claripennis* Kieffer; *Psectrocladius viridescens* Freeman; *Tanypus guttatipennis* Goetghebuer, and *Procladius brevipetiolatus* Goetghebuer. The larvae of *Dicrotendipes, Procladius* and *Tanypus* recorded in the present work may be the same species found by Cox, but without definite larval-pupal-adult associations positive larval identifications were not possible. MILBRINK (1977) found larvae of *Chironomus* sp., *Procladius* sp. and *Limnochironomus* sp. at a high density (4000 m^{-2}) in deep water at Crescent Island.

Nilodorum brevipalpe has not previously been recorded from Naivasha. Several species of *Nilodorum*, including *brevipalpe*, are found in association with the "Aufwuchs" of tropical and subtropical waters (see for example KALK *et al.*, 1979, MARSHALL 1982). Partly submerged trees are the favoured oviposition site for *N. brevipalpe* and the larvae are particularly abundant in newly flooded farmland (MARSHALL, *op. cit.*) It is a little surprising therefore that this species was not found in 1982/83 when large areas of farmland around the lake were flooded. In 1984 the formerly submerged fallen acacia trees were exposed and considerable numbers of chironomid eggs were found on them. If these eggs were *N. brevipalpe* it is possible that the absence of this species in 1982/83 was due to the lack of oviposition sites or as a result of seasonal differences.

The chironomid fauna of Oloidien Lake was similar to that of the main lake: larvae of *Chironomus* sp. were most abundant with *Nilodorum* sp. and *Dicrotendipes* sp. the next. *Cladotanytarsus* sp. was patchily distributed in areas with coarser sand substrates, as were small numbers of a species of *Clinotanypus*, not recorded from the main lake. The exposed trees in this lake in 1984 were also covered with chironomid eggs.

Sonachi Lake contained three species of chirono-

TABLE III
Coleoptera from lakes Naivasha, Oloidien and Sonachi, Kenya with records from previous expeditions
Coléoptères des lacs Naivasha, Oloidien et Sonachi récoltés au cours des diverses expéditions

Taxa	A, B	C, D, E	F	G
Dytiscidae (Adults)				
Rhantus capensis Aub	----	----	N.	----
Hydaticus galla Guerin	----	----	N.	----
Hydaticus capicola Aub	----	N.	----	----
Hydrocanthus impunctatus Gschw.	----	----	N.	----
Hydrovatus sp.	----	----	N.	----
Hydrocoptus koppi Wehn	----	----	N.	----
Canthydrus notula (Er.)	----	----	N.O.	N.O.S.
Canthydrus biguttatus Reg.	----	N.	----	----
Bidessus sharpi Reg.	----	----	N.O.	----
Bidessus sordidus Sharp	----	N.	----	----
Guinotus sordidus Sharp	----	----	N.	----
Philodytes umbrinus (Motschulsky)	----	----	N.	----
Cybister tripunctatus Ol.	----	N.	N.	----
Herophydrus sp.	----	----	N.	----
Methles cribratellus Fairm	----	----	N.	----
Laccophilus torquatus Guinot	----	N.	----	----
Copelatus aethiopicus Reg.	----	N.	----	----
Dytiscidae (Larvae)				
Cybisterinae	----	----	N.	----
Laccophilinae	----	----	N.	----
Colembetinae	----	----	N.	----
Hydrophilidae (Adults)				
Hydrophilus aculeatus Sol.	----	----	N.	----
Berosus furcatus Boh.	----	----	N.O.	N.O.S.
Sperchius gerardi d'Orchymont	----	----	N.	----
Sperchius sp.	----	N.	----	----
Helochares sp.	----	N.	N.O.	N.O.S.
Enochrus sp.	----	----	N.	----
Tropisternus sp.	----	----	N.	----
Amphiops sp.	----	N.	N.	----
Hydrophilidae (Larvea)				
Hydrophilinae sp. A	----	----	N.	----
Hydrophilinae sp. B	----	----	N.	----
Neohydrophilus sp.	----	----	N.	----
Berosus sp.	----	----	N.O.	N.O.S.
Sperchius sp.	----	N.	N.	----
Amphiops sp.	----	N.	----	----

N = Naivasha, O = Oloidien, S = Sonachi. ----- = no record, A = Percy Sladen Expedition (1929), B = Jenkin (1936), C = Cambridge Expedition (1930/31), D = Imms (1933), E = Balfour-Brown (1939), F = Leicester University (1982/83), G = Leicester University (1984)

mid. The most abundant was *Endochironomus disparalis* Goethebuer. This was the only species where a larval-pupal-adult association was established. This species has been recorded from similar high salinity lakes in other parts of Africa (FREEMAN *et al.*, 1980), but little appears to be known of its biology. *Microtendipes* sp. was the next most abundant with *Cladotanytarsus* sp. the rarest.

No dry weight estimates of biomass were made for oligochaetes or chironomids as specimens from all three lakes were preserved in formalin, which makes accurate estimates impossible (HOWMILLER 1972).

Littoral macro-invertebrates

A total of 80 taxa for the two collections were recorded from the littoral region of Naivasha, Oloidien and Sonachi Lakes. These comprised Coleoptera 32; Hemiptera 20; Ephemeroptera 1; Diptera, Chironomidae 9; Culicidae 1; Ceratopogonidae 1; Odonata 3; Mollusca 5; Oligochaeta 4; Hirudinea 2; Hydracarina 1; Microturbellaria 1. The findings for the larger groups are summarized and compared with the published results of previous expeditions in Table III to VI.

COLEOPTERA (Table III)

Adults and larvae of 32 taxa and two families (Dytiscidae and Hydrophilidae) were recorded in 1982/83. In 1984 only 4 species were recorded. Only one species, *Canthydrus notula* (Er.) was found in association with *S. molesta*; in 1984 up to 100 m^{-2} were recorded. However, it was also taken in both Oloidien and Sonachi Lakes in similar numbers. In these lakes it was found mainly on submerged pieces of tree and in Oloidien in uprooted macrophytes that had accumulated at the waters edge. Two other species were abundant in this habitat, *Berosus furcatus* Boh. and *Helochares* sp. Fewer of both these species were found in 1982/83. In 1984 only *Helochares* was found with egg masses attached to the abdomen, suggesting a seasonal breeding cycle.

All of the genera and species recorded here are widespread in Africa (GUIGNOT 1958-1961).

HEMIPTERA (Table IV)

In 1982/83, 19 taxa of Hemiptera were recorded from the main and Oloidien lakes, and were confined mainly to the flooded farmland and lake margins. In 1984 only 6 taxa were recorded. No collection was made in Sonachi Lake in 1982/83, but in 1984 it yielded 8 taxa. All Heteroptera recorded in these and previous expeditions to Lake Naivasha are listed in Table IV, except for *Corixa mirandella* Hutch. of which there is only one record from the lake of 25 specimens collected in 1929 (HUTCHINSON 1930).

The most abundant heteropteran in all three lakes on both occasions, in habitats ranging from flooded farmland to open water, was *Micronecta scutellaris* (Stal.). In open water around rafts of *C. papyrus* and mats of *S. molesta* it often formed large shoals of up to 2000 m^{-2}. These rafts and mats appeared to provide resting places from which they would dive, presumably to feed on the bottom sediments of the lake. Analysis of the gut contents from a number of individuals revealed detritus, oligochaete chaetae and scales from the wings of Lepidoptera, presumably from individuals that had fallen into the lake. The range of items found suggests that *Micronecta*

TABLE IV
Hemiptera from lakes Naivasha, Oloidien and Sonachi, Kenya, with records from previous expeditions
Hémiptères des trois lacs récoltés au cours des diverses expéditions

Taxa	A, B, C	D, E	F	G
Belostomatidae				
Hydrocyrius columbiae Spinola	----	----	N.	----
Sphaerodema grassei Spinola	----	----	----	N.O.S.
Naucoridae				
Laccocoris limigenius Stal.	N.	----	----	N.O.S.
Notonectidae				
Anisops elegans Fieb	----	----	N.	N.
Anisops leesoniana Hutch.	----	----	N.	----
Anisops sardea Herrich-Schaffer	----	----	N.	----
Anisops varia Fieb.	N.	----	----	----
Anisops eros Hutch.	----	N.	----	----
Anisops nymphs	N.	N.	N.	N.O.S.
Corixidae				
Micronecta scutellaris (Stal.)	N.	----	N.O.	N.O.S.
Micronecta dimidiata Hutch. (Recorded as *M. piccanin*)	N.	N.	----	----
Micronecta jenkinae Hutch.	N.	----	----	----
Micronecta sp.	----	----	N.	----
Sigara pectoralis Fieb.	----	----	N.	----
Agraptocorixa gestroi Hutch.	----	----	----	S.
Sigara hieroglyphica kilimandjoronis (Kirk)	----	N.	----	----
Pleidae				
Plea pullula (Stal.)	N.	----	N.O.	N.O.S.
Plea piccanina (Hutch.)	N.	----	----	----
Hebridae				
Hebrus sp.	----	----	N.O.	----
Mesoveliidae				
Mesovelia vittigera Horvarth	----	----	N.O.	S.
Microvelidae				
Microvelia sp.	----	----	N.O.	----
Gerridae				
Limnogonus cereiventris (Signoret)	----	----	N.	----
Gerris swakopensis Stal.	----	----	N.O.	----
Nepidae				
Ranatra bottegoi Montandon	----	----	N.	----
Ranatra nymphs	----	----	----	S.
Laccotrephes ater Stal.	N.	----	----	----
Hydrometridae				
Hydrometra sp.	N.	----	----	----

N = Naivasha, O = Oloidien, S = Sonachi, A = Percy Sladen Expedition (1929), B = Hutchinson (1932), C = Jenkin (1936), D = Cambridge Expedition (1930/31), E = Jaczweski (1933), F = Leicester University (1982/83), G = Leicester University (1984)

are microphagous. Considerable numbers of *Micronecta* were found in open water of all depths, with no floating vegetation. This suggests that it may be a significant component of the bottom fauna, but cannot be effectively sampled using grabbing techniques. *Micronecta* have been reported as dominating the soft bottom littoral zone in other African lakes (COHEN 1986).

DIPTERA

Diptera belonging to three families were recorded: Chironomidae; Ceratopogonidae and Culicidae. Chironomid larvae from handnet samples did not include any species additional to those from the Ekman grab samples.

Ceratopogonids were found around the rhizomes of *C. papyrus*, where they were abundant. Members of this family have been recorded in swamps of other tropical lakes, for example Lake Sonfon, Sierra Leone, (GREEN 1979).

Larvae of Culicidae were generally scarce in spite of the very large numbers of adults that swarmed around the lake. Adults caught at light on the west shore at Korongo Farm were all *Mansonia africana* Theobald. The larvae of this species respire by "tapping" the vascular system of aquatic macrophytes such as *Pistia* and *Eicornia*. A few *Pistia* plants were seen on Naivasha, but it is unlikely that so many adults could have come from larvae on so few plants. A few culicid larvae were taken from *S. molesta* and even fewer pupae were seen. The main breeding site of *M. africana* in Naivasha remains unknown.

TRICHOPTERA

During each visit several adult and larval specimens of a new species of *Ecnomus* were collected, together with specimens of *Ecnomus thomasseti* Mosely, both species belonging to the *natalensis*-group. The new species has been named *Ecnomus mennelli* : for a full description and account of its ecology see BARNARD and CLARK (1986). In 1982/83 only 3 adults were caught of *E. mennelli* at light at Korongo Farm, together with a single female of *E. thomasseti*. Three further adults of *E. mennelli* were caught on the east shore of the main lake and at Oloidien Lake between 1100 and 1300 hr during August 1984. In 1984, larvae of both species were found in both lakes, usually by searching partly submerged rocks and fallen trees. No larvae were found in water deeper than 2m. No larvae were found on the 1982/83 visit, either because large larvae were not present at that time of the year or because high water levels in both lakes made the favoured habitat inaccessible. No Trichoptera have been previously recorded from any of the three lakes.

EPHEMEROPTERA

Cloeon perkensi Barnard was the only species found. In both visits nymphs were frequently encountered amongst *S. molesta* and in flooded farmland, and amongst submerged macrophytes in Oloidien. DEMOULIN (1965) also found this species in Naivasha. JENKIN (1936), found Ephemeroptera nymphs but was unable to identify them.

Odonata

Adults and nymphs of Aeshnidae, Libellulidae and Coenagriidae were common in all three lakes. Nymphs were found mainly on pieces of submerged wood and amongst submerged macrophytes. All specimens of Odonata collected have been deposited at the British Museum (Natural History) but due to the uncertain state of East African Odonate taxonomy, no positive identifications have yet been made.

Mollusca (Table V)

The molluscan faunas of both Naivasha and Oloidien Lakes were poor, totalling only 5 species. No molluscs were found in Sonachi. Of the recorded species only *Physa acuta* Drap. and *Ferrisia* sp. could be considered as common in the lakes. *P. acuta* occurred in beds of *S. molesta, C. papyrus* rhizomes and submerged macrophytes. *Ferrisia* sp. appeared to be confined to *C. papyrus* rhizomes. The other species encountered were *Succinea* sp., *Lymnaea natalensis* (Krauss) and *Ceratophallus natalensis* (Krauss) and each was represented by only a few individuals. All Mollusca collected from Lake Naivasha are widely distributed in Africa (Brown 1980, *L. natalensis* p. 136, *P. acuta* p. 212, *C. natalensis* p. 158-159, *Ferrisia* p. 148, *Succinea* p. 22). Jenkin (1936) recorded 3 species of mollusc from Naivasha, but all were different species to those encountered in the present study. Milbrink (1977) found an unidentified clam (Sphaeridae) in great abundance (8000 m^{-2}) at Crescent Island, but no sign of any living or empty shells of Sphaeridae were found in this study.

Oligochaeta (Table VI)

In addition to *B. sowerbyi*, *L. hoffmeisteri* and *P. heuscheri/bavaricus*, which were encountered in grab samples from the soft littoral substrate, the swamp worm *Alma emini* (Michaelson) was also found. It was rare in the soft littoral substrate, but was common though patchily distributed where *S. molesta* formed tightly compacted mats. Its presence could be detected by casts deposited on the surface of the mats. In 1984 where *S. molesta* had been stranded on mud as the water level receded *A. emini* was found at a high density. In 1982/83 many cocoons containing small *A. emini* were found amongst *S. molesta*, but none were seen in 1984. Clearly breeding was taking place in 1982/83, but whether this was due to particularly favourable conditions or to definite seasonality could not be determined. *A. emini* is widely distributed in East Africa (Brinkhurst *et al.* 1971, p. 778) in swamps, also in farmland prone to seasonal flooding (Wasawo *et al.* 1959).

Table V

Mollusca recorded from the three lakes, with records from the previous expeditions

Mollusques récoltés dans les trois lacs au cours des diverses expéditions

Taxa	A, B	C	D	E
Mollusca				
Lymnaeidae				
Lymnaea elmeteitensis Smith	N.	----	----	----
Lymnaea natlensis (Krauss)	----	----	N.	----
Planorbidae				
Bulinus baringoensis (Prest.) (now *tropicus* group)	N.	----	----	----
Ceratophallus natalensis (Krauss)	----	----	N.	----
Planorbis gibbonsi Nelson	N.	----	----	----
Physidae				
Physa acuta Drap	----	----	N.O.	N.O.
Succineidae				
Succinea sp.	----	----	N.	----
Ancylidae				
Ferrisia sp.	----	----	N.	N.
Sphaeridae	----	N.	----	----

N = Naivasha, O = Oloidien, S = Sonachi, A = Percy Sladen Expedition (1929), B = Jenkin (1936), C = Milbrink (1977), D = Leicester University (1982/83), E = Leicester University (1984)

Table VI

Oligochaeta recorded from Lakes Naivasha and Oloidien, Kenya

	A, B	C	D	E
Oligochaeta				
Naididae				
Nais communis Piguet	N.	----	----	----
Naidium jenkinae Stephenson	N.	----	----	----
Pristina longiseta Ehrenberg	N.	----	----	----
Pristina aequiseta Bourne	N.	----	----	----
Aulophorus tonkinensis (Vejd.)	N.	----	----	----
Aulophorus flabelleger Stephenson	N.	----	----	----
Dero sp.	N.	----	----	----
Tubificidae				
Branchiura sowerbyi Beddard	----	----	N.	N.O.
Limnodrilus hoffmeisteri Claparede	----	----	N.	N.O.
Potamothrix heuscheri (Bretscher)	----	N.	----	----
Potamothrix heuscheri / bavaricus	----	----	----	O.
Glossoscolecidae				
Alma emini (Michaelsen)	----	----	N.	N.O.

N = Naivasha, O = Oloidien, S = Sonachi, ----- = No record.
A = Percy Sladen (1929), B = Jenkin (1936),
C = Milbrink (1977), D = Leicester University (1982/83),
E = Leicester University (1984)

Hirudinea

Two species of Hirudinidae have previously been recorded from Lake Naivasha, *Glossiphonia stuhlmanni* Blanchard by Moore (1932) and Jenkin (1936) and *Hirudo* sp., by Moore *(op. cit.)*.

In 1982/83 no Hirudinidae were found, although according to local farmers leeches abounded in the lake earlier in the year. In 1984 a single specimen of *G. stuhlmanni* was found under a stone at the edge of Oloidien Lake. Twenty specimens of another species, as yet unidentified, were found in clumps of *S. molesta* in the North Swamp. The apparent erratic occurrence of Hirudinea in the lakes may be linked to seasonal fluctuations or changes in water level.

Microturbellaria

These were occasionally encountered in the sediments and plankton of both Naivasha and Oloidien. These have not been identified and there appear to be no previous records for any of the three lakes.

Hydracarina

These were abundant throughout the littoral zone of Naivasha and Oloidien lakes, particularly on flooded farmland, and have previously been recorded from Naivasha (Lundblad 1934). None were found in Sonachi Lake. Identification has not been possible.

Macro-Crustacea

The only macro-crustacean found was the introduced *Procamburus clarkii*, the Louisiana red crayfish. This species was introduced into Lake Naivasha in about 1970, (Lowery *et al.* 1977), and now forms a well-established local fishery. It was found in shallow water in both Naivasha and Oloidien Lakes, where it digs burrows in the mud. Examination of gut contents from a number of specimens revealed a mass of quite finely ground detritus, suggesting a generalised detritus feeder.

Although not strictly aquatic it is worth mentioning here the Isopod *Eubelum instrenuum* Fer. This was often encountered around the rhizomes of *C. papyrus* and has only been recorded from Kenya.

DISCUSSION

The considerable difference in the organic content of the substrate between 1982/83 and 1984 may be due to the difference in the water levels between the two occasions. Gaudet (1976) showed that water movement through papyrus swamp washed out large quantities of sludge and other materials and deposited them beyond the swamp. This may have occurred in Naivasha in 1982/83, when prolonged short rains increased the flow of water through the north swamp via the Gilgil and Malewa rivers. The importance of swamps in the input of organic material has been shown for a number of tropical lakes. In Lake Chilwa, McLachlan (1979), found that the benthic fauna was largely dependent upon the organic input from fringing *Typha* swamps. In Naivasha the large mobile rafts of *C. papyrus* and mats of *S. molesta* in 1982/83 may also have contributed to the organic material in the substrate.

Decomposition in tropical lakes is very rapid (McLachlan 1974a). After a long period of low input resulting from the failure of the rains in 1983/84, the large quantities of organic material in the main lake could have been utilised by macro-invertebrates and micro-organisms. Oloidien and Sonachi Lakes have no major inputs of organic material and levels may always be low. However, the distribution of macro-invertebrates did not appear to be correlated with the amount of organic material.

The benthic macro-invertebrates of the main and Oloidien Lakes are typical of soft, unstable deoxygenated mud. The margins, and in particular the flooded farmland around the lakes, provide more diverse and benign habitats, reflected in the increased diversity of macro-invertebrates.

The diversity of macro-invertebrates is low when compared with other tropical lakes, for example Volta Lake (Petr 1970). The trichopteran genus *Orthotrichia*, for example, is the commonest Afrotropical genus of the Hydroptilidae but has never been recorded from Naivasha. There are two probable reasons for this low diversity. First, the lake has dried up on a number of occasions in the past (Sikes 1936, Edmonson 1977). Secondly, the nearest lakes are alkaline, support a low diversity of macro-invertebrates, and probably dried out at the same time as Naivasha, so that there has been limited scope for re-colonisation. After re-filling colonisation would rely on species persisting in the catchment, capable of flying considerable distances or with eggs able to withstand dessication. Less mobile taxa such as oligochaetes and molluscs may have reached the lake on fishermen's nets, or aquatic birds (Darwin 1859). In other tropical lakes that have dried out, for example Lake Chilwa (McLachlan 1974b) the first colonisers in the re-filling stage were Diptera, (Chironomidae and Ceratopogonidae), Coleoptera, Hemiptera and Trichoptera all of which presumably were capable of flying some distance or whose eggs were able to withstand dessication. During and after re-colonisation the macro-invertebrate community structure would be affected by fluctuations in water level.

Hart (1985) points out that in tropical lakes the seasonality of zoobenthic communities is intimately associated with hydrographic characteristics. Changes in the species composition of macro-invertebrates would be expected with continually fluctuating conditions. This is demonstrated particularly well by a comparison of Coleoptera and Heteroptera recorded in 1982/83 with those found in 1984. The majority of those recorded in 1982/83 were found in the flooded farmland. The reduction in both these taxa in 1984 was almost certainly due to the loss of the flooded farmland habitat. Fluctuating water levels may also interrupt breeding cycles. It appears that other species of *Alma*, for example *A. nilotica* (GRUBE) in the Nile, (KHALAF EL-DUWEINI 1951), breed continuously which is certainly not the case for *A. emini* in Naivasha.

It would seem likely that changes in waterlevel, both seasonal and otherwise, may account for much or all of the observed short-term changes in the fauna of the lake. Fluctuating water levels and changes in the type and extent of available littoral habitats may also have played a part in the long-term changes apparent from a comparison of recent faunal lists with those made by past expeditions 50 or more years ago. They are, however, unlikely to have been responsible for the complete change in Oligochaete and molluscan faunas.

Three other ecological changes are worthy of consideration as possible causes of long term faunal change.

These are :

1) Changes in agricultural practices in the surrounding land.
2) Loss of macrophytes.
3) Introduction of fish species.

The riparian farming practice of extensive removal of papyrus may have affected nutrient levels in the lake. It has been shown that *C. papyrus* swamp acts as a nutrient filter (GAUDET 1976) and since it is one of the most productive of the emergent macrophytes (THOMPSON 1975) may significantly contribute to the levels of organic material.

Increasing use of lake water for irrigation will decrease water levels below those of natural draw down. Such changes may exacerbate the effects of natural fluctuations in water level on the fauna.

Land in the area bordering Lake Naivasha is approximately 50 % cultivation, 40 % range/ranching and 10 % forest/bush. The use of pesticides and herbicides over a long period of time in the catchment may have resulted in residue accumulation in the biota of the lake and contributed to some of the observed changes. Results so far available suggest that this is unlikely, however. The most widely used pesticides in the Naivasha basin are organochlorine based. LINCER *et al.* (1981) measured organochlorine levels (DDE) in various aquatic macrophytes, invertebrates, fish and birds from Lake Naivasha; they found only very low levels of DDE in algae and Diptera (mainly chironomids) ($0{,}007 \pm 0{,}20$ and $0{,}034 \pm 0{,}76$ mgl^{-1} (OD)[1] respectively) with only a trace in leeches and molluscs. The highest levels recorded were in *S. molesta* ($0{,}107 \pm 0{,}035$ mgl^{-1}), *Micropterus salmoides* Leceped ($0{,}016 \pm 0{,}019 mgl^{-1}$) and Pygmy cormorant *(Phalacrocorax africanus)* ($2{,}10 \pm 4{,}01 mgl^{-1}$). Polychlorinated biphenyls were also present but were never found in high enough concentrations to allow for accurate analysis. Herbicides are rarely used in the catchment; there is a large inexpensive local labour force, and weeding is done manually.

The loss of aquatic macrophytes might be expected to adversely affect many invertebrate species. Their decline would, for example have de-stabilised the substrate and de-oxygenated the water. The change in the oligochaete fauna from one dominated by naidids, a family which tend to be associated with submerged macrophytes and higher oxygen levels, to a fauna dominated by tubificids, which are tolerant of unstable low-oxygen habitats, might occur with the loss of macrophytes. However, only tubificids were found in Oloidien Lake where extensive beds of submerged macrophytes occurred. No information on the oligochaete fauna of Oloidien appears in the literature, and it is hence not known if similar changes to those in the main lake have taken place.

Some vertebrate populations certainly appear to have been affected by the loss of macrophytes. There has been a dramatic decrease in the number of duck and coot on Naivasha since the 1970s. As recently as 1981, 35,000 were censussed (VAN SOMEREN 1982), but in 1982/83 and 1984, in the absence of submerged macrophytes, they could only be counted in tens over the whole lake (HARPER *op. cit.*). There is no evidence that these changes in the birds have in themselves affected invertebrate populations.

A number of fish species have been introduced into Naivasha during the last fifty years. The Large-Mouthed Bass *M. salmoides* was introduced in 1929 and 1949, largely as a sporting fish, (LITTERICK *et al.* 1979). In Naivasha, juveniles of between 150 mm and 190 mm feed mainly on aquatic insects and adults feed on insect larvae, fish and crayfish, (MUCHIRI, *pers. comm.*). The preferred diet of adults of this species is crayfish, (MALVESTUTO 1974; SIDDIQUI 1979). *Tilapia zilli* Gervais was introduced into Naivasha in 1956 for commercial exploitation. This and *Oreochromis leucostictus* Trewavas are the major fish species on which the gill net fishery is based. Examination of the gut contents of a number of individuals of *T. zilli* in 1982/83 and 1984 revealed detritus, planktonic algae, fragments of crustacea and insect larvae. This is in broad agreement with other investigations of this species in Lake George, Uganda (MORIATY *et al.* 1973), and Naivasha (SIDDIQUI 1977, MUCHIRI, *pers. comm.*).

Barbus amphigramma Blgr. is another recent introduction to the lake's fauna, (HARPER *op. cit.*). It appears to feed mainly on zooplankton in the lake. It enters the rivers to spawn, and is then insectivorous, (MUCHIRI, *pers. comm.*). *Lebistes reticulata* Peters, *Poecilia* sp. and *Gambusia* sp., all were introduced in an attempt to control mosquito larvae, (LITTERICK *et al.*, *op. cit.*), but will presumably take other similar-sized aquatic invertebrates.

The introduction of so many potential predators to the lake clearly may have had an effect on the abundance and distribution of macro-invertebrates, but the extent of such effects cannot be determined.

These data show that Lake Naivasha has undergone considerable long-term changes. Some of the short term differences observed may be due to sampling in different seasons. Only regular sampling (e. g. monthly samples) can future faunal changes be effectively monitored.

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