THE LIMNOLOGY OF AN AFRICAN LAKE

by

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A. INTRODUCTION TO THE NAIVASHA BASIN

Lake Naivasha is a shallow freshwater lake which shares a common depression with two saline lakes, Elementeita and Nakuru, in the Eastern or Gregory Rift Valley of Kenya. The Nakuru-Naivasha basin is bounded,to the east by the Aberdare Range and the Kinangop Plateau, and by the Mau Escarpment to the west (Figure 1). The valley floor, extensively broken by secondary faulting, is still volcanically active. To the south of Lake Naivasha, Longonot and several smaller volcanoes form a barrier which is breached by the Njorowa Gorge , a former outlet of the lake. To the north, the Naivasha basin is partially separated from the Elementeita-Nakurubasin by the Eburu mountains.

The volcanic rocks of the Naivasha area consist of a mixed assemblage (facies) of acid and basic lavas. In the southeast and southwest of the basin fumaroles, hot-springs and steam vents are found and in the Njorowa Gorge these are being harnessed for geothermal power generation. Several of the craters within the basin can be seen along the western side of the lake (Figure 2) one of which contains standing water (Sonachi Crater Lake). The older lake sediments are composed of a mixture of volcanic ash, reworked volcanic strata and autochthonous organic matter. More recent deposits lack the volcanic component and form a semi-liquid ooze (gyttya) substratum.

The climate of the area is warm and semi-arid (East African Meteorological Dept., 1964). Air temperatures are moderate

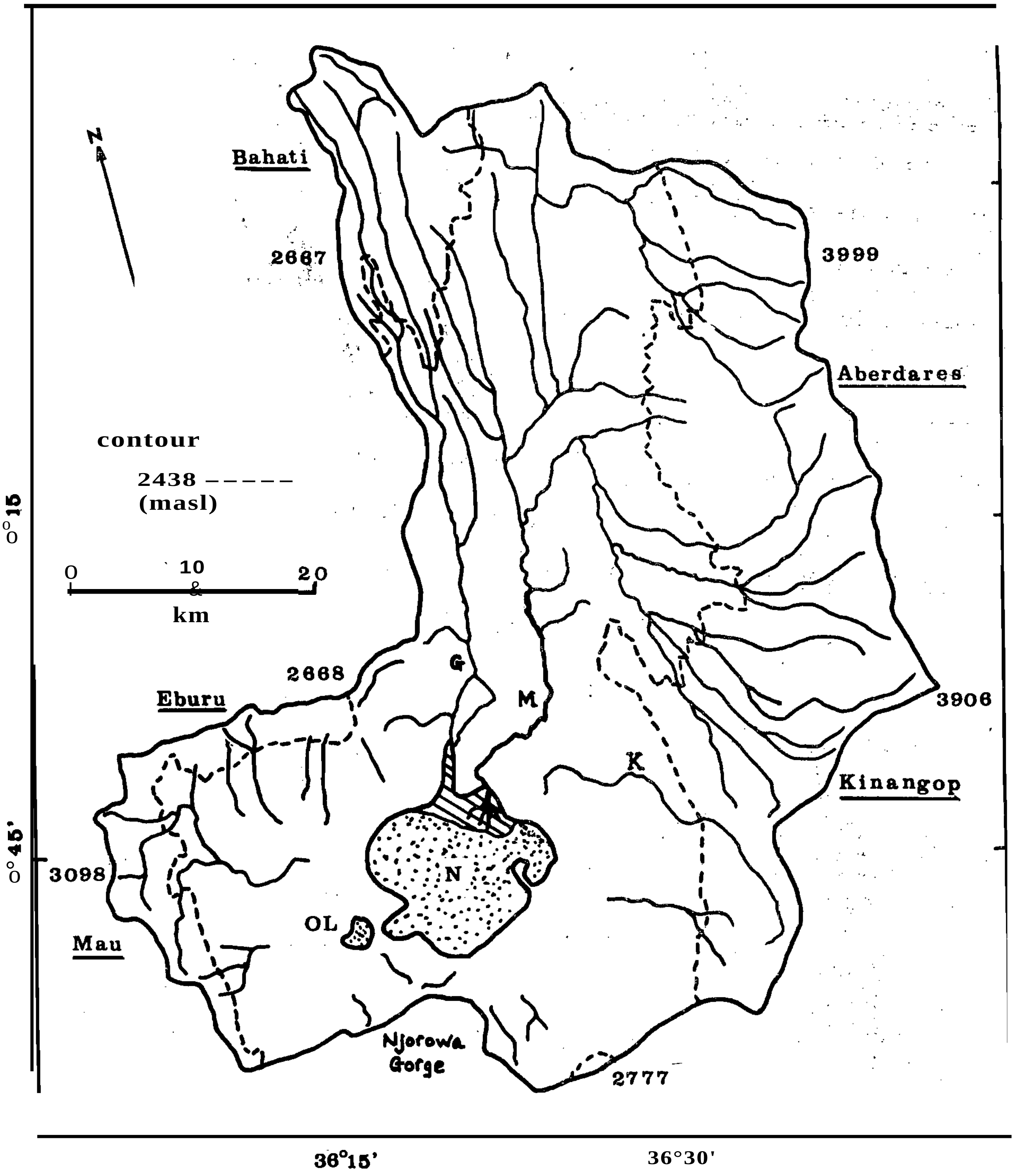


Figure 1. The Naivasha drainage basin.

M = Malewa River

G = Gilgil River

K = Karati River

N = Lake Naivasha

OL = Oloidien Lake

8L = Sonachi Crater Lake

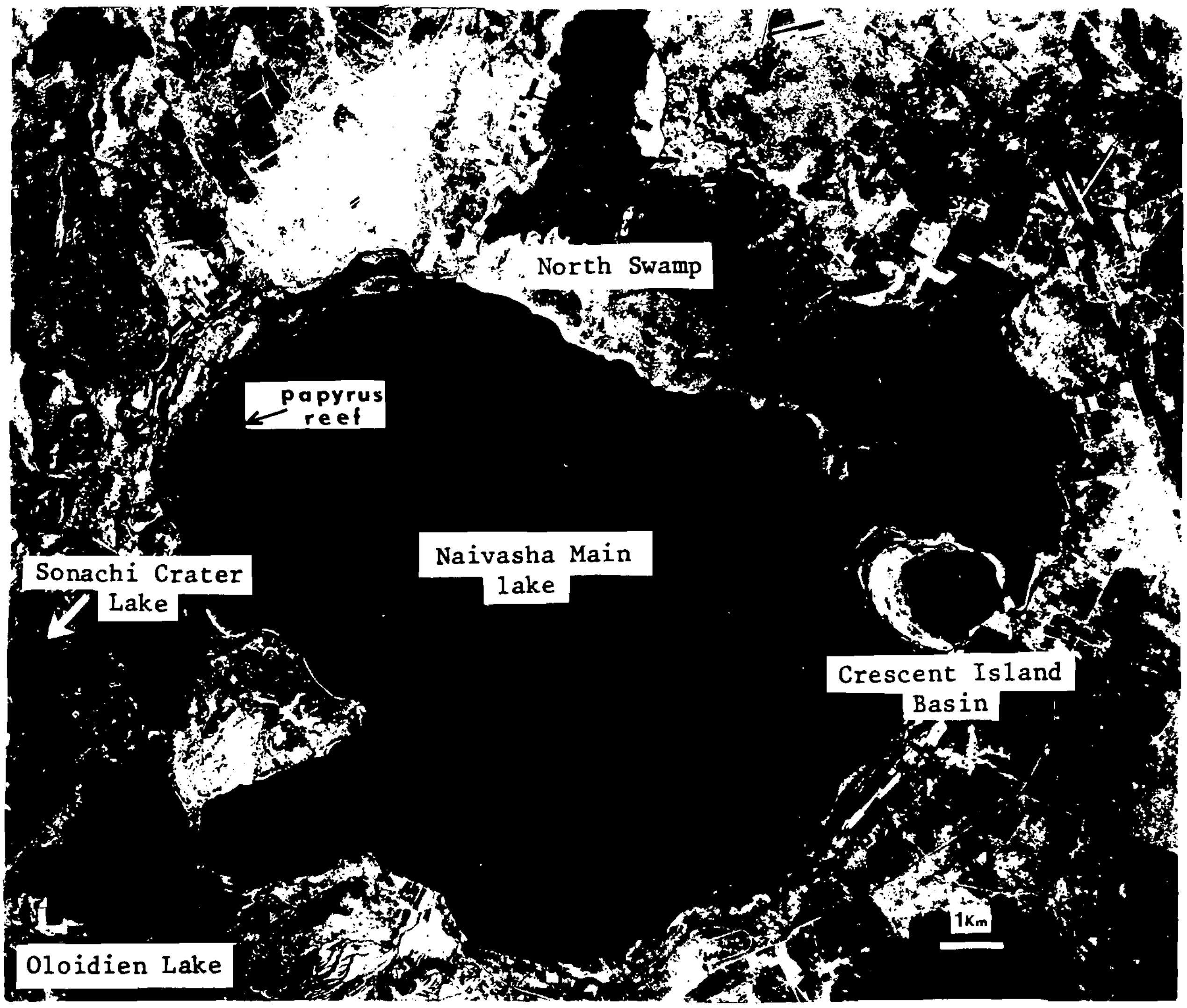


Figure2. The Naivasha basin showing local topography and the four major water bodies (Survey of Kenya 1968).

with monthly means varying little from 15.9 to 18.5 °C. Seasonal variations in water temperature. are also slight ranging from 19.5 to 23^{0} C the surface and from 19.2 to 21.5 near the bottom (Anon 1978). The combination of moderate temperature, low relative humidity and low rainfall make January and February the months with the highest evaporation. Only light breezes are common in the morning but stronger afternoon winds (11 to 15 kmh^{-1})are typical, and often produce violent storms on the lake. Winds usually come from the south with the importance of easterly and westerly components dependent on season. The stronger afternoon winds in conjuction with night-time cooling usually cause complete mixing in the main lake almost every day and well oxygenated water 5 mg 1-1) is present from top to bottom (Anon 1978, Melack 1979). Temporary thermal stratification developes however during periods of calm sunny weather and may persist for a day ·or more, particularly in the deeper waters of the Crescent Island basin (Litterick and Mavuti unpubl. data). Average rainfall near the lake has a muted bimodality with a main pulse in April and May and a minor pulse in November (Melack 1976). Irregularities from this pattern are common. The highlands surrounding the drainage basin receive more rain than the lakes and valley floor and provide most of the water that maintains the lake.

The Naivasha basin falls in the Ecological Zone IV of Pratt, Greenway and Gwynne (1966), a zone in which upland Acacia woodland is common. The northern parts of the basin, near the Malewa River source are bordered by sub-montane tropical evergreen forest dominated by Podocarpus spp. The slopes of the Rift Valley above Naivasha are covered by tropical Setaria spp. grassland which grades into the Tarchonanthus camphoratus L. bushland, typical of the Rift Valley floor. As the Malewa flows along the valley it passes through a riverine forest dominated by Salix hutchinsii Skan., and, about 5 km north of the main lake, it is bordered by papyrus (Cyperus papyrus L.) before finally entering North Swamp. The main lake lies directly in an Acacia Xanthophloea Benth. woodland, with trees up to 35 m tall. The lake-side flora is quite diverse and complicated (108 species) and has been described by Gaudet (1977).

Much of the drainage basin is used for ranchland with some forest clearance and farming in the north on the mountain slopes.. The lake basin has become an important area for vegetable production and supports a large vegetable drying factory. Cut flowers are grown on large plantations along the southern shore for export, and lucerne is grown under sprinkler irrigation (ten crops per year) to support an important dairy industry. This intensive agricultural production is made possible by the readily available irrigation water, good quality volcanic soil and tropical climate.

The Naivasha basin has no surface outlet (for discussion see page) and contains four topographically distinct water bodies viz. Lake Naivasha, Crescent Island basin of Lake Naivasha, Oloidien Lake and Sonachi (or Naivasha) Crater Lake (Figure 2). Details of the morphometry and geography of these sub-units are summarised in Table 1.

TABLE 1: Area, volume, mean depth ($\bar{z}$) and maximum depth (zm) of the Naivasha lakes. (December 1974 except Sonachi, July 74)

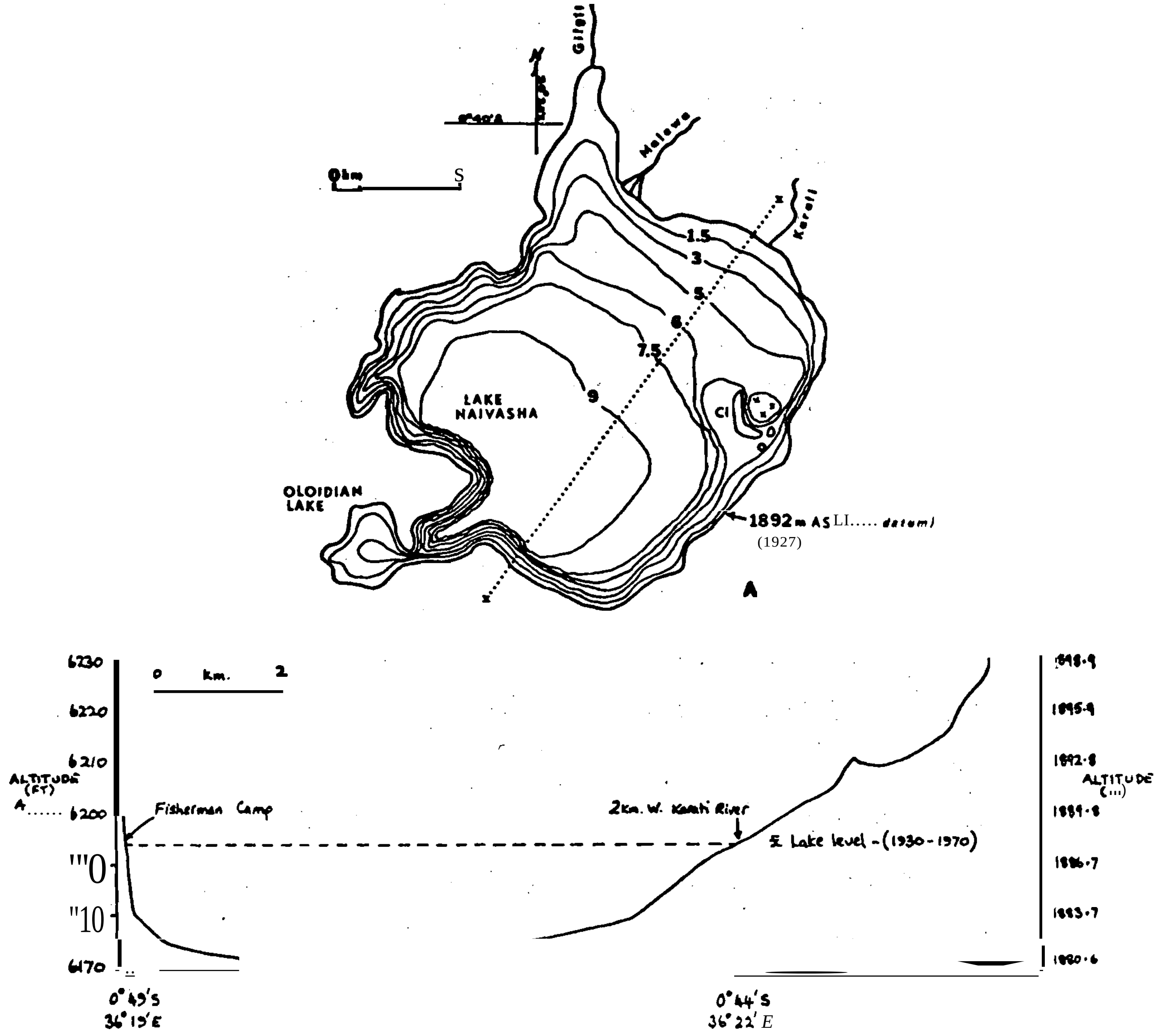
	Area (Km^2)	Volume (m^3 x 10.^{6})	$\bar{z}$ (m)	Zm (m)
Main Lake	145	680	4.7	7.3
Crescent Island Basin	2.1	23	11.0	17.0
Oloidien Lake	5.5	31	5.6	6.1
Sonachi Lake*	0.16	0.62	3.8	6.1

*data from Melack, 1976

The boundaries of the four water bodies were formed by the tectonic faulting and volcanic activity associated with the formation of the rift valley (Richardson and Richardson 1972).

The deepest region (Crescent Island basin) lies in a volcanic crater in part bounded by an exposed rim called Crescent Island, but is normally confluent with the main lake. The distinctiveness of Oloidien Lake depends on the water level In the basin. During the first third of this century the width of the connection with Lake Naivasha proper varied from about 100 to 1000 m, and the region was called a bay. During the high' water levels in the 1960's a 100 m wide connection occasionally existed, and in 1965 a boat channel was dug which maintains contact with the main lake unless the water level falls below 1888.5 m above sea level.

Lake Naivasha proper contributes over 90% of the total water surface in the basin and because of the shallow depth (Figure 3a) and gently sloping sides (Figure 3b) its surface area and that of the fringing papyrus and littoral lagoons, is



Fegure 3. A) Bathymetric map of Lake Naivasha based on the survey of Kenya map 1957. B) Cross section of the lake showing the gentle, sloping eastern area.

extremely sensitive to changes in water level. A rise or fall of less than 0.5 m will alter the areas of these regions, particularly along the NE and NW shores, by many square kilometres.

Located about 2 km west of the main lake is Sonachi Crater Lake a small (14 ha) soda lake situated in a flooded volcanic vent. Although this lake lies within its own small catchment a hydrologic connection may exist between this lake and the other less saline waters of the Naivasha basin.

Daily recording of the main lake level was started in 1909 and shows repeated fluctuations (Figure 4) with an 8 m decline between 1931 and 1952 followed by a 5 m increase during the next 10 years. Superimposed on the year-to-year changes are oscillations usually ± 0.5 m resulting from a seasonally changing rainfall in the Aberdare range with lake maxima and minima in September - October and March - April respectively. The last major fluctuation was a 5.1 m increase between 1961 and 1964. Subsequently the level has remained high but had a net decline (Figure 4).

The Malewa River (1730 km^2 watershed) which obtains its water from the Aberdare range and Kinangop Plateau contributes about 90% of the discharge into Lake Naivasha. Most of the remainder is provided by the Gilgil River (420 km^2 watershed) which drains the Bahati highlands to the north of the Elementeita - Nakuru basin. Consumption of water for irrigation and natural losses, however, often eliminate flow in the Gilgil before the lake is reached. The two rivers enter the northern side of the lake after passing under North Swamp for several kilometres. The water under the swamp is diluted during the rainy season by river water and may receive inflow of lake water during the dry season. The major portion of the northern swamp consists of a floating mat of <u>Cyperus papyrus.</u> Interspersed among the papyrus and debris

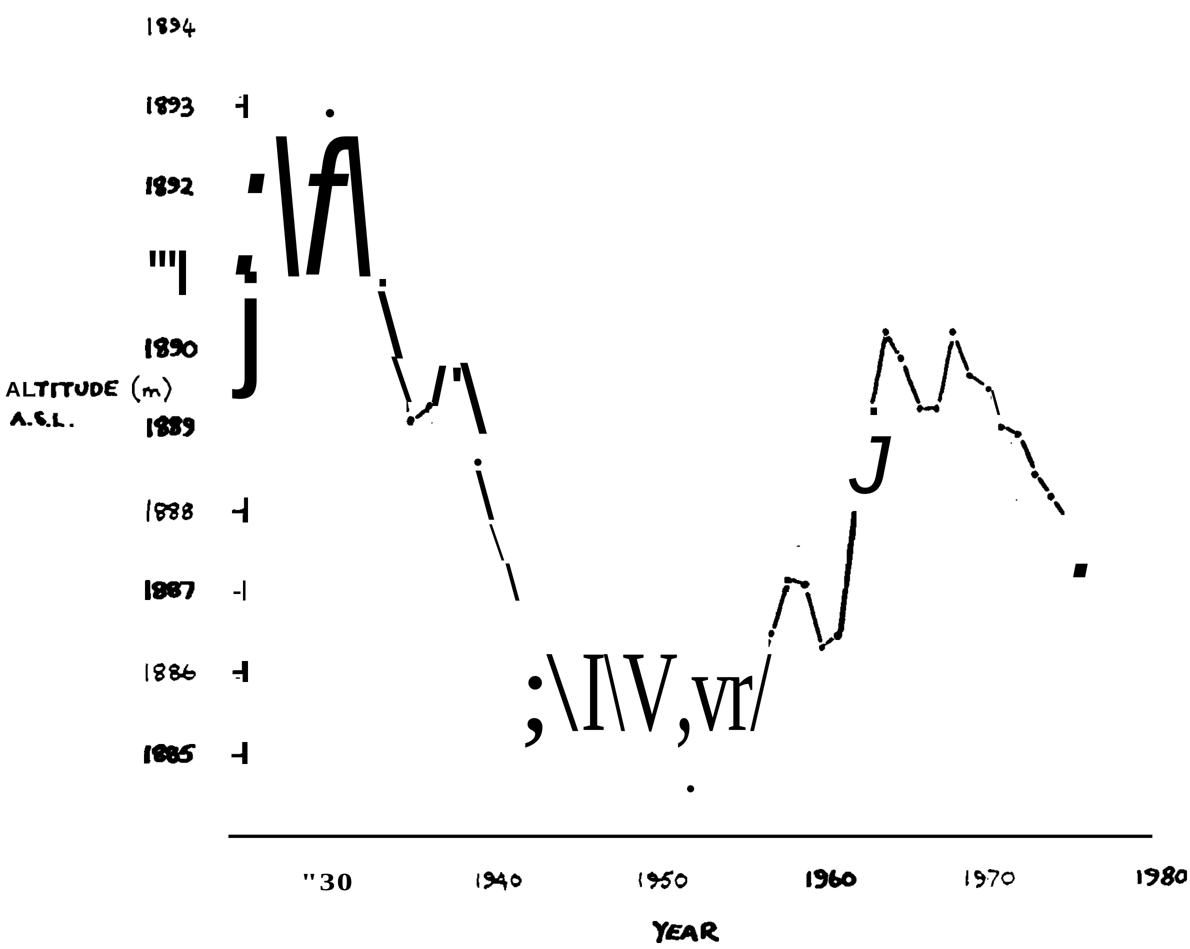


Figure 4. Annual mean lake levels in Lake Naivasha Cbasedon Sikes, 1963; Kenya Ministry of Works (Hydrology), 1958, 1964; Water Development Department, 1978).

are pockets of water that are isolated for most of the year but may be contiguous after heavy rain. Within the swamp, mixing of the surface and bottom waters occurs, but because the mixing is incomplete the upper water is usually chemically distinct from the water near the bottom.

B. THE GEOLOGICAL HISTORY OF LAKE NAIVASHA

The geological history of the Lake Naivasha basin has been explored and most recently documented by Richardson and Richardson (1972); the following account is based primarily on their work except where indicated.

Earth movements, vulcanism, and glacial activity have all played significant roles in the turbulent geological history of the Naivasha-Nakuru depression (Livingstone and Kendall 1969). Lakes Nakuru, Elementeita and Naivasha are mere remnants of the larger lakes which once filled their common basin to overflowing. The fluctuating water levels have left their mark as a series of raised strandlines (Washbourn 1967) on the hills within the Rift Valley (as for example on the sides of the Longonot and Menengai volcanoes), and also within the sediments deposited in the lakes themselves (Richardson and Richardson 1972). The causal factors producing these hydrological changes are not well resolved, but the possibility of the direct influence of tectonic activity in the Naivasha basin has been excluded by Livingstone and Kendal (1969) as Lake Naivasha occupies a closed depression ringed by almost horizontal strandlines. The evidence accumulated over the past few decades (Leakey 1931, Nilsson 1931, 1940) clearly indicates major changes in the climate of East Africa (and Africa as a whole) with periods in the past that were very much wetter than the present and largely responsible for the hydrological changes recorded in the lake sediments.

A recent 28 m core taken from the Crescent Island basin by Richardson and Richardson (1972) represents the past 9,200 years and is the longest sequence yet described in detail. Other cores from the Gregory Rift extend back to almost 30,000 BP but none have so far been studied in detail. The history of the lake inferred from the Crescent Island core is summarized in Figure 5.

It appears that the high lake levels at 9,200 BP had commenced about 3,000 years earlier and had been preceeded by a dry period and low lake levels that started 28,000 BP (Richardson 1972, Livingstone 1975)

1.) Stage I - The large lake stage - a large (c. 408 km^2) stable lake overflowing through the Njorova Gorge <Hells Gate) is indicated by the stratigraphic record and is thought to have existed from about 12,5000 BP, at which time the lip of the gorge was cut down to its present level (2089.4 metres). The basal 13 metres of the core contained a single variable diatom assemblage which persisted throughout this stable stage.

2.) Stage II - The shrinking lake stage - the evidence to date indicates that the drier phase following the large lake stage began rather abruptly and Lake Naivasha fell within 1,500 years (5,700 - 4,200 BP) to levels similar to today's. The water level thereby fell below the lip of the Njorowa Gorge and consequently the lake became a closed basin. Although these dates coincide with the worldwide Climatic Optimum,Richardson and Richardson (1972) believe that decreasing rainfall and not rising temperature caused this drying trend. After 4,200 BP only a small weedy lake existed in the Crescent Island basin which had became totally separated from the main lake and any extrapolation to the main lake subsequently becomes more speculative. The climate appears to have remained stable from 4,000 to 3,000 BP following which the Crescent Island Lake dried up completely, a fate probably shared by the main lake. It was dry for less than 100 years.

3.) Stage III - The rejuvinated lake stage - following the dry phase the Crescent

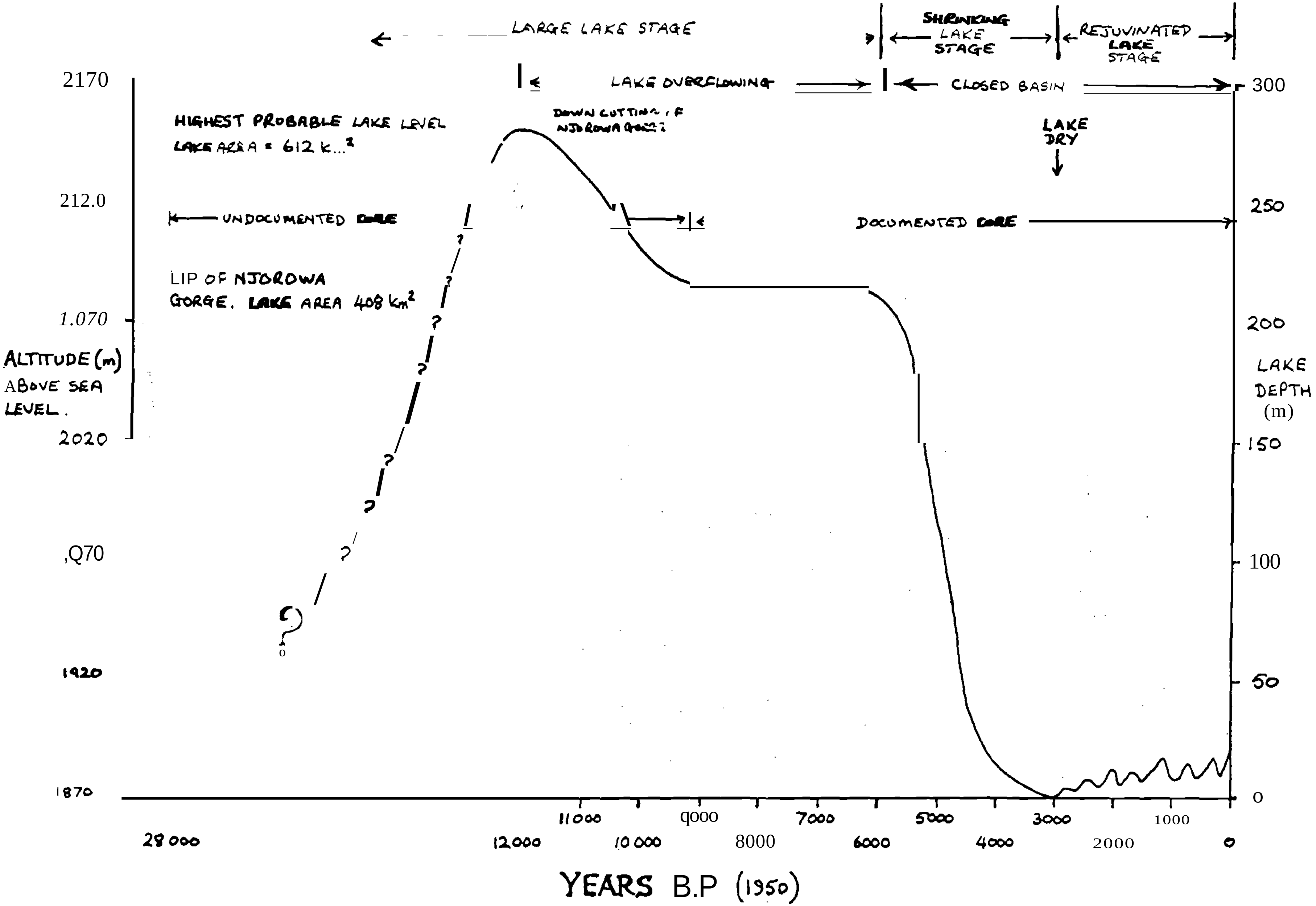


Figure 5. History of Lake Naivasha based on Richardson and Richardson (1972).

Island basin again contained a small weedy lake. In contrast to the stable lake previously occupying this basin the rejuvinated lake seems to have had a much more precarious and varied existence with water levels fluctuating near and below levels.

On the basis of the in the most recent deposits Richardson and Richardson (1972) [illegible] Jth century water levels may be the highest experienced in the last 3,000 years.

The microstratigraphy of the core also gives some indication of a change in climate during the final phase of the lakes history. The presence of this light and dark laminae (varves) in the sediment that were apparently deposited at the rate of one pair per radiocarbon year is suggestive of a change from a single wet and a single dry season per year prior to 2,500 BP, to the present two dry and two wet seasons each year.

Evidence is accumulating which indicates that Lake Naivasha may have dried out on other occasions since the 3,000 BP dry phase recorded by Richardson and Richardson (1972). Dale (1952) suggests that a period of significantly drier climate occurred less than 200 years ago which may have been sufficient to dry the lake again if, as the Richardsons state little change in the present day hydrologic balance would be needed to return Lake Naivasha to the lower levels experienced in the past 3,000 years or to dry the lake entirely.

Barton (pers. comm.) has found evidence in more recent cores that such a dry period has indeed occurred and in this he is supported by a Masai testament (E.A.F.F.R.O. Naivasha File) that Lake Naivasha was dry around 1894. An endemic fish fauna of only one species (see page) is in concordance with a recent drying and points to the importance of hydrological events in the biology and chemistry of shallow African lakes.

C. THE WATER BALANCE OF THE LAKE NAIVASHA BASIN

The hydrological equilibrium of a drainage basin is maintained by the dynamic balance between sources of water and water losses. Principal sources (or vectors) which bring water into a lake basin are affluent rivers, seepage-in and precipitation; while water may be lost through effluent/'rivers, seepage-out and evaporation. To construct a complete water balance for a lake basin reliable quantitative data. on each of these vectors must be available. These data are now being assembled for the Lake Naivasha basin.

In the present discussion a water budget for Naivasha main lake and Oloidien lake is presented below. Data for the Crescent Island basin are not included because during the study period (1973 to 1975 inclusive) lake levels were low (Figure 4) and the Crescent Island basin to a large extent was isolated from the main lake. It is thought that the exclusion of this basin would not greatly affect the overall budget for the Naivasha basin as this compartment has an area of less than 2% of the main lake.

1.) Sources of water

a). Precipitation - Maximum rainfall in the immediate vicinity of the lake occurs in April and allows a slight amount of recharge but is insufficient to offset losses by utilization (irrigation) and evaporation. The resulting annual deficit (Table 2) is offset primarily by river discharge originating in the elevated regions of the catchment (Aberdare Range and Kinangop Plateau), where there is a substantial annual surplus.

The seasonal peak of rainfall in the .upper Naivasha catchment is followed by run-off, principally into the Malewa River.

TABLE 2. Annual run-off for the Naivasha region compared to that for the Kinangop Plateau CSouth. Kinangop). Calculated by Nordell from East African Meteorological Dept. data (Nordell, unpublished).

	Naivasha Region (1938-1954]	 (1970)	South Kinangop 0960-66)
Water input Crrm)			
Precipitation	608	646	1142
Recharge.			
April	10	31	
Mar.-Apl.			92
Nov.			33
Total	618	677	1268
Water Output (rrm)			
Evapotrenspiretion	1328	1214	941
Utilization			
May	10	31	
Jul.-Oct.			61
Dec.-Feb.			64
Total	1338	1245	1066
Balance (rrm)			
Run-off	0	0	202
Deficit	720	568	0

Discharge from this river represents 8 to 18% of the total rainfall on the catchment (Table 3).

b.) River disCharge - Most of the surface water input to the lake comes from the Malewa River (90%). The other streams CGilgil and Karati) are either dry or flow intermittently during low reinfall periods. Maximum discharge normally occurs in September - October (Figure 6). Discharge during the 1973 - 1975 period was sufficient to fill the main lake basin in 2.7 years exclusive of evaporation losses.

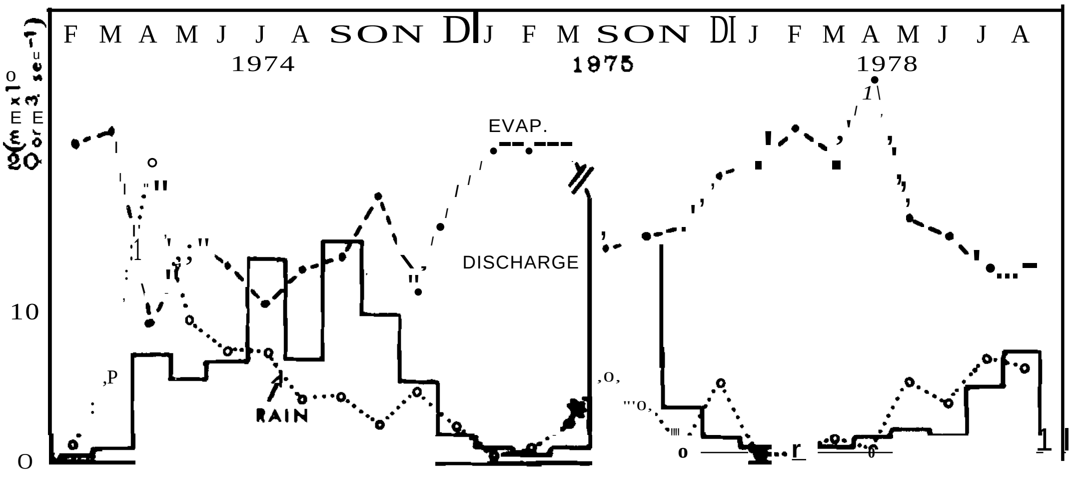


Figure 6. Evaporation, rainfall and discharge of the Malewa River over a 3 year period (After Gaudet 1978),

TABLE 3: Rainfall and runoff in Malewa River watershed of Lake Naivasha (after Gaudet and Melack, 1979).

	1973	1974	1975
Average rainfall on watershed (mm)*	693	836	789
Runoff from watershed via Malewa River (mm)	32	118	151
Runoff as percent of rainfall (%)	7.5	14.1	19.1

1:Calculated by two axis method (Bethlahmy 1976) based on 14 stations.

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c.) Seepage-in - Although Lake Naivasha lies in a topographic closed basin it is hydrologically a seepage lake because a portion of the inflow (and out flow) enters as groundwater. In the 1973 - 1975 period incoming seepage contributed 13 - 16% of the total annual input (Table 4) and entered mainly along the northeastern and northwestern shores. The lake has been described by Thompson and Dodson (1963) as a 'hydrographic window' because water can pass freely through the extremely porous volcanic rocks which form 80% of the lake basin. In addition the lava flows are usually well jointed and often vesicular, allowing free movement of water. According to Thompson and Dodson 'the absorbtivity of the Naivasha area is well known, within a few hours after rain most surface water has disappeared'.

Water input by seepage in the NE and NW sections and seepage-out in the S and SE sections of the main lake were earlier suggested by Thompson and Dodson (1963) from evidence based on differences in water level in lake-side boreholes compared to the level in the main lake. A detailed description of water tables and directions of flow in the NE section of the main lake based on recent work is provided by Gaudet and Melack (1979). They have also confirmed the above general directions of seepage with seepage meter readings. The meters showed that the rate of seepage-in is related to the amount of rainfall on the catchment. For example, in one seepage meter the usual daily

TABLE 4: Hydrologic balances for Lake Naivasha and 010idien Lake. Percentages of input and output shown in brackets for the main lake (after Gaudet and Melack, 1979).

	Lake Naivasha ($m^3 \times 10^6$)					
	1973	(%)	1974	(%)	1975	(%)
Surface run-off	0.6	(0)	0.7	(0)	0.4	(0)
River discharge	90.8	(39)	204.0	(56)	240.5	(67)
Rainfall	106.1	(45)	114.2	(32)	77.1	(20)
Seepage-in	37.0	(16)	42.3	(12)	50.8	(13)
Total Input	234.5		361.2		388.8	
Evapotranspiration (swamps)	14.3		13.2		13.3	
Lake evaproation	309.5		276.0		278.2	
Seepage-out and use for irrigation	24.6	(7)	50.6	(15)	93.3	(25
Total Output	348.4		339.8		304.8	
Change in Storage (Cal. by balance)	-113.9		+ 21.4		+4.0	
Change in Storage (cal. from level change)	-113.9		+21.4		+4.0	
	010idien Lake ($m^3 \times 10^6$)					
Surface run-off	0.0		0.0		0.0	
Rainfall	3.6		3.8		2.7	
Seepage-in	4.1		6.0		7.0	
	7.7		9.8		9.7	
Lake evaporation	11.3		10.1		10.1	
Seepage-out and use for irrigation	0.0		0.6		0.0	
Total Output	11.3		10.7		10.1	
Change in Storage (caL by balance)	-3.6		-0.9		-0.4	
Change in Storage (cal. from level change)	-3.6		-0.9		-0.4	

rate of seepage-in (237 ml d^{-1}) increased by 184% two days after a heavy rain storm in the hills to the west of the station. Seepage-in usually decreases logarithmically from lake shores towards deeper water (McBride and Pfannkuch 1975, Lee 1977 and Lock and John 1978), and Gaudet and Melack therefore assumed that most of the seepage on Lake Naivasha would occur in shallow water along the lake edge.

The annual rates of seepage were calculated using hydrologic balance. This balance (Table 4) was based on a simple model of inputs and outputs, and is discussed below.

2.) Water losses

a.) Evaporation - The climate in the Naivasha section of the Gregory Rift is hot:, dry and windy. After the April rains, evaporation increases each month (Figure 6) and generally results in an annual evaporation water loss almost twice that of local rainfall. The evaporation output is about 80% of the total output through all pathways.

b.) Seepage-out and utilization - Between 1973 and 1975 approximately 20% of the total water was lost from the main lake as seepage or was abstracted for lakeside irrigation (Table 4).

c.) Subt rranean outflow- Early theories to explain the continuing freslmess of Lake Naivasha postulated a subterranean river flowing southwords out of the lake which removed excess salts. These proposals were summarized by Beadle (1932) and Thompson and Dodson (1963) but have received no impirical support to date.

3.) Water balance

The three year water balance for the main lake and Oloidien Lake (Table 4) shows the relationship between inputs and outputs, and how they change through the years.

The two years following 1973 were wetter, river discharge and seepage-in were greater but evaporation from the lake was less and the level of Lake Naivasha rose. The use of lake water for irrigation was not monitored, but can be estimated from records of the maximum yearly allotments of water by the Water Development Department (Nairobi). The allotment for 1973 was 7 x 10^6 m^3 and this rose to 15 x 10^6 m^3 in 1975. The was likely accounted for by seepage-out. In 1974 and 1975, abrupt increases in lake level occurred during several moneths (e.g., 15 em in April 74,22 em in July 74, 50 em in August 75), and the net level changes for the two years were positive. Flooding of littoral regions and increased depth of water can both cause a lake to lose water through its bed, and this may well account for the increasesd outflow during 1974-75.

The water balance in Oloidien Lake is much simpler than in the main lake because there is no influent or effluent. Much of the input here comes from seepage and is most likely derived from the main lake. For example, it was noted that the largest water level differences between the two lakes occur during times of peak discharge from the Malewa River. Thus, the main lake fills first, the increase in volume creates a greater head of pressure, and the subsequent seepage-out gradually finds its way into Oloidien Lake reducing the difference in water level.

4.)Lake level fluctuations

Changes in the hydrologic balance, caused by variations in the climate of the catchment area, result in changes in lake volume and in lake level. The Naivasha basin, whether or not it is technically a closed basin, behaves hydrologiCally as if it were one and fluctuates in the manner of a closed lake (Richardson and Richardson 1972). Lake level changes occur continuously (the annual fluctuations from 1926 are shown in Figure 4).

Although these changes in level generally reflect periods of drought versus excessive rainfall there is no simple or direct correlation between anyone input vector on a monthly basis. In other words a month with high river discharge may result in lake levels other than those which would be predicted on the basis of discharge alone. This may be due to differences in climatic factors, as well as seepage effects which cause a delayed response to changes in the balance, and are of considerable importance in this basin (Gaudet and Melack 1979).

D. WATER CHEMISTRY

Until the recent studies by Gaudet and Melack no repetative, systematic chemical analyses of the waters in the Naivasha basin spanning a full year had been done. In their 1979 paper they quantify the chemical differences among the waters of the Naivasha basin. They also calculate solute and water balances for the basin and trace the origin and fate of the major ions within the boundaries of the Naivasha exosystem. These boundaries are normally defined laterally by the shoreline and vertically by the water surface and the maximum depth in the sediment utilized by organisms (Likens and Bormann 1975). Ions may be transported across these ecosystem boundaries as meteorologic, geologic and biologic inputs and outputs. -To be able to construct a complete chemical budget for aiake system it is necessary to quantify the ion exchanges along each of these routes. As yet this full analysis for the Naivasha basin is not available. Gaudet and Melack have quantified the exchanges by geologic vectors,viz. river discharge, seepage and sediment exchange, and have partially examined meteorologic inputs in their analyses of direct rainfall onto the lake. However, meteorologic inputs of dust and other windboume particulate matter have not been measured. Similarly, the potentially important effects of biologic vectors remain undocumented. This is particularly unfortuante in a lake system with large resident populations of aquatic birds, hippopotamus, and a commercial fishery.

A general summary of the water chemistry of the several compartments of the Naivasha basin is given in Table 5.

Kilham (971) considers the chemical composition of Naivasha water to be typical of that formed by leaching recent volcanic rocks, and the predominance of sodium and bicarbonate among the major dissolved ions typica

TABLE 5: Mean concentration of ions for each compartment (mg l^{-1}) from Gaudet and Melack (Sonachi Crater Lake from Kilham 1971).

Compartment	Na	K	Ca	Mg	HCO_3	CO_3	SO_4	Cl	F	SiO_2	K_{25}
Malewa River	19.0	4.3	8.0	3.0	70	0	6.2	4.3	0.4	17.2	88-179
Gilgil River	16.1	7.4	4.4	2.2	75	0	9.6	3.9	0.8	18.2	72-167
Main Lake	40	20	21	6.4	192	10.6	6.2	14	1.5	34	311-353
Crescent Island Basin	52	30	17	7.5	231	15	4.8	17	1.5	36	389-438
Oloidien Lake	125	82	9	6.9	496	43	7.1	32	8.0	44	768-892
Sonachi Crater Lake	1900	333	4.1	5.1	2837.4	960.2	36	1224	67.5	77	6270-17060

of East African waters. An unexpected and a typical feature of Lake Naivasha is the freshness of its water. For a closed basin lake, Naivasha is anomalously dilute when compared to neighbouring endorheic lakes in the Rift Valley. The continuing freshness can be attributed"to the long-standing balance between vector-s importing and exporting ions. The data presented by Gaudet and Melack make possible a quantitative evaluation of the relative importance of the various factors responsible for the freshening process. They show that the solute concentrations in the main lake fluctuate seasonally and interannually. These fluctuations are in part due to changes in the rate of transport of additional ions (i.e. 'new' ions) into the lake water from outside. The changes are also partly due to variation in the rates of uptake and release of 'old' ions which are recycled within the lake system principally between the water and the sediment.

The micro-ions which' are important as nutrients (particular'ly phosphate and nitrate) fluctuate in response to uptake and release from the biota, but very little is known of the cycling of these nutrients in Lake Naivasha. This is now beginning to receive some attention (J. Kalff pers. comm.).

1.) <u>Solute</u> <u>inputs</u>

Gaudet and Melack presented data from the main lake during 1974 and 1975 for five vector inputs; sediment release, seepage-in, river diSCharge, precipitation and surface run-off. These data are summarized in Tables 6 and 7.

a.) <u>Sediment</u> <u>release</u> - A very large amount of the ions coming into the lake is assumed to be taken up by the biota, or by inorganic and organic sediments. That taken up by the biota is lost from solution and can effectively be recycled within the lake system. Each year much of this material taken up by the sediment in the lake is thus recycled by decomposition, resuspension, etc. Over 65% of the annual solute input into the lake water is derived from the sediment in this way. The quantities of the various ions released from the sediment into the lake water are calculated by difference; the quantities coming in and going

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Table 6. Chemical balances for Lake Naivasha main lake during 1973 and 1974 (10^3 kg).

	Na		K		Ca		Mg		HCO_3		SO_4		Cl		F		SiO_2	
Year	73	74	73	74	73	74	73	74	73	74	73	74	73	74	73	74	73	74
Surface Run-Off	4	5	9	9	9	9	2	2	50	53	5	6	4	5	0.9	1.0	7	8
River Discharge	751	1615	242	478	664	1290	278	380	6852	12137	567	858	286	847	30.6	69.2	1070	3120
Rainfall	51	55	35	28	20	22	111	19	13	14	73	79	44	47				
Seepage-In	16211	1862	1147	1312	851	974	377	432	8399	9609	407	466	1036	1185	62.9	71.9	1739	[illegible]
Sediment Release	5853	94511	920	9278	2664	12432	445	1495	20792	17335	4714	5609	1682	6395	527.4	1006.1	12122	10678
Total Input	8287	12995	2353	11105	4208	14727	1120	2328	36106	39148	5766	7018	3052	8479	621.8	1148.2	149311	15796
Seepage-Out (+ Farm Use)	9112	2026	540	1114	540	1114	165	340	4986	10282	74	152	319	659	31.9	65.11	393	811
Sediment Uptake	5555	10759	3551	[illegible]	4576	16463	2091	1978	18990	77802	2847	7415	2818	6600	333.3	675.8	27058	17125
Total Output	6531	12785	4091	12132	5116	17577	2256	2318	23976	880114	2921	7567	3137	7259	365.2	741.6	27451	17936
Balance	+1750	+ 210	-1738	- 1027	- 908	- 2850	-1136	+ 10	+12130	-411936	+2845	- 549	- 115	+1220	+256.6	+ 406.6	-12513	- 2140
Change In Storage	+1750	+ 210	-1738	- 1027	- 908	- 2850	-1136	+ 10	+12130	-48936	+2845	- 549	- 85	+.1220	+256.6	+ 406.6	-12513	- 2140

TABLE 7: Total solute input (kg) into Lake Naivasha during 1974-1975 based on Gaudet and Melack (1979).

SOURCES OF LAKE WATER SOLUTES	TOTAL WEIGHT OF SOLUTE GAINED (1974-1975)	PERCENTAGE OF TOTAL
A. GAINS (INPUT)		
Sediment release	123,405	65.2
Seepage-in	33,549	17.7
River discharge	31,535	16.7
Rainfall	518	0.3
Surface run-off	189	0.1
TOTAL	189,196	100.0
B. LOSSES (OUTPUT)		
Sediment uptake	217,655	89.9
Seepage-out	24,594	10.1
TOTAL	242,249	100.0

out by other routes are assumed to balance, any difference causing imbalance is attributed to sediment exchange. This type of calculation leads to considerable accumulation and summation errors which are probably responsible for the apparent wide variation in sediment contribution between years.

b.) Seepage-in - Ions brought into the lake by seepage are 'new' ions which in the combined 1974-75 period represented 18% of the total input per annum. Variation between years was slight though the cause and significance of this apparent stabilitv is unknown.

c.) River discharge - The contribution of ions by river inflow was of a similar magnitude to that of seepage-in and again represented 'new' ions. The river input is much more variable for all ions, however, and was twice as much in 1975 as in the previous year. The Malewa and Gilgil rivers are dilute *t*

and contain a preponderance of bicarbonate with sodium and calcium as the major cations. The chemical canposition of the two rivers is similar to rivers draining other volcanic regions in eastern Africa such as the western slopes of the Mau escarpment and the Nkuruman escarpment (Jones et al. 1977) and Mount Elgon and Kararnoja in Uganda (Viner 1975). When compared to Meybeck's (1977) typology of transport by the major rivers of the world, the total dissolved load carried by the Malewa River is similar to the loads carried by rivers with low -runoff, medium relief and warm temperatures as expected from the characteristics of the Malewa watershed.

Gaudet and Melack point out that, as is typical for the incongruent solution of aluminosilicate rocks, the atmosphere and respiration of soil biota are probably the sources of the bicarbonate in the Malewa. Most of the sulphate, potassium and chloride and a portion of the other solutes would be derived from atmospheric precipitation.. When they distinguished denudation and non-denudation components, they found that only 22% of the mean weight of total dissolved solids carried by the Malewa River in 1973 and 1974 was derived directly from underlying rocks. Although this indicates that atmospheric precipitation is an important source of solutes to the Malwea watershed, a different result could emerge if longer term, more intensive data were available.

d.) Swamps -

Water entering Lake Naivasha from the Malewa and Gilgil rivers passes through North Swamp (Figure 2), a virtual monoculture of the giant sedge *Cyperus papyrus.* The effects of this swamp on the chemistry of water entering the main lake have been studied by Gaudet (1978). It is well known that emergent rooted aquatic macrophytes often act as phosphate pumps (McRoy et al. 1972) and this possibility exists within the swamp. Nitrogen is certainly fixed within the swamp (Gaudet 1979) and will probably find its way into the main lake. Suspended matter is generally filtered out by the papyrus and quantities of sediment and salts accumulate beneath the swamp in the inorganic clay bed. The effect of North Swamp on the salinity of the main lake is shown in the annual average of major ions trapped in detritus (Table 8). The effect

TABLE 8: Estimate amounts of major ions trapped in detritus in the North Swamp, based on an annual sedimentation rate in the swamp of 38 x 10^6 kg each year (from Gaudet 1978 and 1979).

	Present in Detritus[1] (%)	Estimated Amounts Sedimented	
		Total Amount (x 10^3kg.yr^{-1})	Percentage Retained of Annual Riverine Input
Na	0.225	86	7
k	0.175	67	19
Ca	0.033	13	1
Mg	0.110	42	13
Cl	0,020[2]	8	1
S04	2.88[2]	1094	153
SiO_2	1.20[3]	456	22

1. Gaudet, 1978.
2. Sulphate and chloride in detritus minus that present in interstitial water.
3. Silicate in whole plant only used here because silicate in sludge is supplemented by silt.

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on salinity (Na+, K+, Ca^{2}+, Mg2+, and Cl-) is minimal, but there is an effect on S04^{2}- and SiO_2, Although these results are tentative, they do indicate that generally the swamp would be most influential in altering water chemistry when flow rates in the influent rivers are low. Because of the large through-flow of water in the Malewa (e.g., during 1973-75) the effects of the swamp on Lake Naivasha must be minimal. The rate of inflow during that period would result in a fast replacement time, with an average of 2.7 years.

Changes in river water quality would be expected to dramatically affect the main lake system, particularly during wet periods. This can be seen for major ions but we do not know much about the fate of incoming minor ions. Since these often constitute the most important nutrient input, they must have an important influence on production rates in the main lake. However, the whole subject of nutrient inputs, budgets and recycling is still unknown for this lake. This is certainly one of the most interesting of the many problem areas yet to be studied in the Naivasha basin.

e.) Precipitation - Rainfall in the Naivasha basin supplies about 0.3 metric tons of solute per year to the lake (Table 7). Data relating to the ionic composition of rainwater in East Africa are rare. A few analyses are reported by Gaudet and Melack (Table 9). The origin of these ions is unknown but Visser (1978) who made extensive analyses of rainwater in Kampala concluded that there the solutes originated from both Lake Victoria and local dust and were not of oceanic origin.

f.) Surface run-off - The total input of ions in surface run-off amounts to less than **0.1** metric tons per year (Table 7). However, this water flows off rich agricultural land and may bring in significant amounts of plant nutrients especially in the E, SE and S regions of the lake.

g.) Biologic vectors -The introduction and removal of solutes by organisms frequenting the lake has not received much attention but forthcoming and ongoing studies of nutrient cycling in shallow water on the main lake will undoubtedly shed some light on the importance of nutrient import and exchange by birds, hippopotamus, crayfish and the commercial fishery.

2.) Solute losses

The principal route for solute loss is the uptake by sediment. During the two year period, 1974 through 1975, about 123 metric tons of solute were released from the sediment while at the same time over 240 metric tons was sedimented. The rate of sedimentation, therefore, exceeds the rate of release by a factor of two. Gaudet and Melack estimated that annually about 50 metric tons would be accumulated. This rate of accumulation is similar to rates calculated by Richardson and Richardson (1972) from the 28 metre core in the Crescent Island basin (i.e., 39 metric tons per year) and falls in the range calculated from another core taken in the main lake (15 - 65 metric tons per year, Richardson, pers. comm.). All these estimates, however, are subject to very large errors in calculation and should be treated with caution.

Barton (pers. comm.) noted a paucity of organic matter in recent cores taken from the main lake, Oloidien Lake and Sonachi Crater Lake. There was little organic matter in comparison to the amount accumulated in the sediment of the Crescent Island basin. This has led Barton to suggest that the organic matter originally deposited in the main lake, Oloidien Lake and Sonachi Crater Lake has been removed by deflation during very recent dry periods. This would involve the removal of large amounts of material by the wind and would profoundly influence the solute balance of the lake. What is needed is an accurate measure of sedimentation throughout the Naivasha basin to throw light on the accuracy of the chemical budgets and on the possible freshening mechanisms operating within this basin.

Tons lost in water seeping out of the basin represent irrevocable losses to which must be added losses due to abstraction for irrigation. These combined losses amounted to about 12 metric tons or 10% of the annual loss during 1974-75 (Table 7).

The freshness of the water of Lake Naivasha was explained by Gaudet and Melack. as due to several factors. A large fraction of the water supplied to the lake comes from very dilute rivers and rain. The lake does not lie in a closed basin, but loses water and solutes via seepage. Exchanges with sediments both in the pelagic and littoral regions of the lake are the major routes for solute movement, and the net accumulation of sediments removes solutes from the water. Previously Richardson and Richardson (1972) have suggested that Naivasha's freshness was owed to the burial and deflation of solutes, possibly removal by the papyrus swamps, intermittent seepage, recent increases in lake level and dilute river inflow. The effect of papyrus swamps has been discussed above, and is thought to have only a minor effect on. the solute content of the lake. Lake Chad is similar to Lake Naivasha in

TABLE 9: Ionic composition of rain in East Africa. Gaudet and Melack (1979) based on 27 samples in Kenya, Visser (1961) based on 78 samples in Uganda (Std. dev.+ in brackets).

	Na	K	Ca	Mg	Cl	S04	$HC0_3$*
Mean (Gaudet Melack)	0.48 (0.25)	0.33 (0.37)	0.19 (0.15)	0.14 (0.09)	0.41 (0.36)	0.69 (0.77)	0.12 (-)
Median (Visser)	1.7	1.7	0.05		0.9	1.8	
Range (Visser)	0.1 to 203.1	0.1 to 690			0.01 to 0.1	0.1 to 68.9	

*Estimated based on pH of 5.7 assuming equilibrium with $pC0_2$ at atmosphere.

that it also has no surface outflow, is situated in a semiarid region and contains fresh water. The low salinity of Lake Chad is attributed to the dilute inputs from the Chari River and rain, and outputs via seepage and sedimentation (Carmouze et al. 1977, Roche 1975). The removal of solutes by sedimentation is the result of clay diagensis, sorption by organic matter, clays and biota, and precipitation of carbonates and silica. The same processes may be operating in Lake Naivasha, but as yet, no direct measurements of pore water composition, sediment-water exchange and recent sedimentation rates have been made, and these are needed to test the validity of the chemical budget.

E. THE ECOLOGY OF LAKE NAIVASHA

1) THE HISTORY OF SPECIES INTRODUCTIONS INTO LAKE NAIVASHA

Prior to 1925 the fish fauna of Lake Naivasha consisted of a single endemic species, the small tooth carp Aplocheilichthyes antinorii (Vinc.), this paucity is highly unusual for a tropical freshwater lake and is undoubtedly related to the 100 year dry phase which occurred some 3000 years B.P. and to possible more recent dry periods (Richardson and Richardson 1972).

Between 1925 and 1970 eight (possibly nine) species of fish, one mammal, one invertebrate and one macrophyte were introduced into Lake Naivasha. Of these eleven species, seven were introduced intentionally, two unintentionally and two invaded the lake without man's involvement (Table 10).

As an apparent consequence of the increase in aquatic faunal diversity, the numbers and species of aquatic birds, particularly fish-eating birds, has likewise increased to include the white pelican (Pelecanus onocrotalus (Gmelin), the pink-backed pelican (Pe rufescens), the white-necked cormorant (P.halacrocorax carbo) and the long-tailed cormorant (P. africanus). Several other avian species notably the fisheagle (Haliaeetus vocifer) and the herons, probably already present on the lake, undoubtedly increased in numbers as a result of the increase in availability and variety of food (Diamond, pers. comm.)

The history of species introductions into Lake Naivasha began in 1925 when the mouth-brooding cichlid Tilapia nigra (Gunther) was introduced from the Athi River by Captain R.E. Dent of the Kenya Game and Fisheries Department followed by a further 450 fingerlings from Mr. Clays dam at Donyo Sabuk August 1926 (Elder et al. 1971). The purpose of this introduction was to provide a forage fish for the American largemouth bass (Micropterus sa'moides Lacepede) to be introduced later in at the suggestion

Table 10. The introduced species of Lake Naivasha

A. Intentional Introductions:

Sarotherodon spilurus nigra	1925 ••••• 1971
Micropterus salmoides	1929 ••••• mid 1940's, 1951 ••••• 1979
Tilapia zillii	1956 ••••• 1979 .
Tilapia nilotica	1965 ••••• 1969
Procambarus clarkii	1970 ••••• 1979
Gambusia sp.	Dates unknown; absent since 1977
Poecilia sp.	" " " " 1977

B. Unintentional Introductions:

Sarotherodon leucosticta	1956 ••••• 1979
Salvinia molesta	1962 ••••• 1979

C. Unaided Invaders:

Myocastor coypus	1968 ••••• 1979
Salmo gairdneri	Spasmodic reports

of U.S. President T. Roosevelt who believed that the sport fishing in East Africa needed improving (Robbins and Maccrimmon 1974). The largemouth bass (or Black bass) introduced 'from Europe in"1929 has thrived in the lake. They established readily and were immediately successful. This population must have been self-sustaining as there are no records of repeated introductions. Their success remained evident during the 1930's .and 40's but unfortunately coinciding with a long period of falling water level (Fig. 4). The bass population declined and presumably disappeared around 1950. Black bass were reintroduced in December 1951 (E.A.F.F.R.O. Lake Naivasha· File) and restocking continued at intervals at least until 1956 (Elder et ale 1971). *Tilapia nigra* the first cichlid introduced was not much in evidence in the early 30's, increased in the late 30's and 40's but had declined drastically by early 1950. A second cichlid, the herbivorous nest builder *Tilapia zillii* (Gervais), was introduced in 1956 (along with more bass) from ponds near Kisumu - presumably to establish a population for later commercial exploitation. Unfortunately (or perhaps fortunately as subsequent events revealed) "the Kisumu fish also contained some *Tilapia (nowSarotherodon) leucosticta* (Trewavas) and both species became successfully established in the lake (Elder et ale 1971).

Commercial fishing (using 10-14 em nets) began in 1959 and was initially based on *S.s. nigra,* supplemented with small numbers of *T. zillii.* *S. leucosticta* was not taken at this time but catches of an unidentified fish were noted. The presence of *S. leucosticta* was predicted by Trewavas and Greenwood (1960) and confirmed by Garrod and Elder (1960) when these aberrant fish were shown to be hybrids of *S.s. nigra* x *S. leucosticta.* number of hybrids increased in the early 60's and they constituted 57% of the total catch in 1962.

The second unintentional introduction", that of the aquatic fern, *Salvinia molestaMitch.,* occurred in 1962 (Gaudet 1976a) with the first specimens

2.) THE AQUATIC MACROPHYTES AND PAPYRUS SWAMPS

a) Lake-edge flora - The vegetation around the main lake has been described in detail by Gaudet (1977). He found that the number of families (43) and species (108) was high, but the impression is not one of diversity. The vegetation differs from zone to zone going away from the shore but it is quite monotonous going along the shore parallel to the water's edge. This is because the most common type of vegetation around the lake edge is papyrus. Pennanent papyrus swamp occupies 11 km^2 on Lake Naivasha. This swamp type occurs in four forms: small discrete clumps, elongated fringe swamps parallel to the shore, papyrus reefs in front of lagoons, and large floating swamps. The four forms differ from one another in several ways, for example: (a) the discrete clumps (2-10 m diam.) occur as free-floating or stranded islands; (b) the fringe swamp is larger (10-15 mwide) and firmly rooted on mud. Occasionally, the lake-side edge of the fringe swamp will float if the lake level permits, but otherwise it depends on ground water which is quite close to the surface around the lake edge. Fringe swamps are protected from drying by the large masses of wet peat and detritus which accumulate inside them; (c) the papyrus reefs present in this lake are large (500 m wide) elongated masses of papyrus aligned parallel to the shore and held in place by contact with small rock islands, detritus, old tree stumps, mud banks, etc. These reefs cut off large and small lagoons (Fig. 2) which occupy 25% of the shoreline; (d) the floating swamp is well illustrated by the large swamp in the north (NS in Fig. 3).

The general zonation around the lake typically consists of a papyrus fringe (or other sedges in regions where papyrus has been cleared) with an area in front of the papyrus which is exposed during periods of low level (Fig. 7). In some areas, e.g. on the inner shore of Crescent Island volcanic sand supports a different flora (Table 11). Along the edge of Oloidien Lake

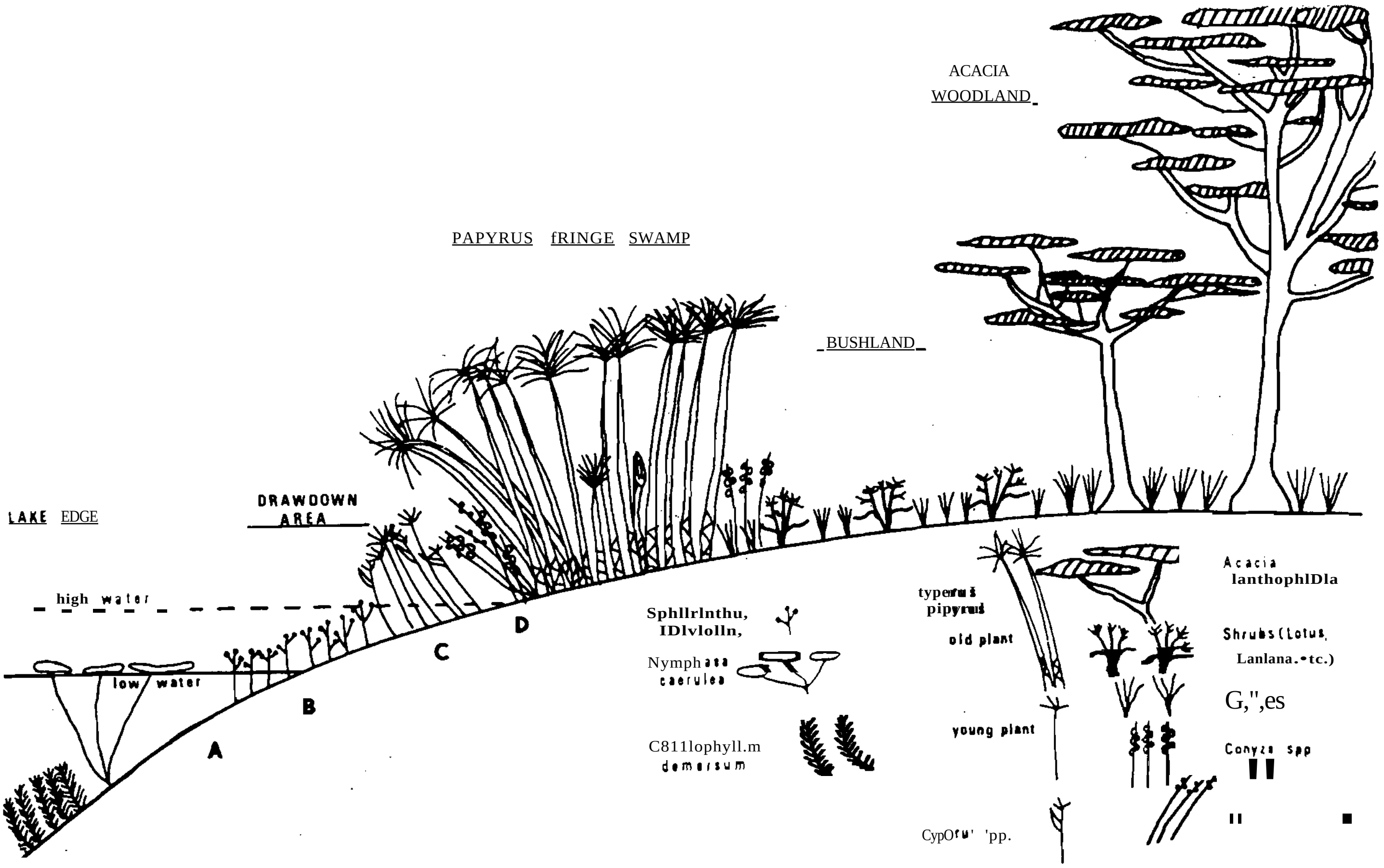

Figure 7. Lake-side communities and general zonation of the Lake Naivasha flora.

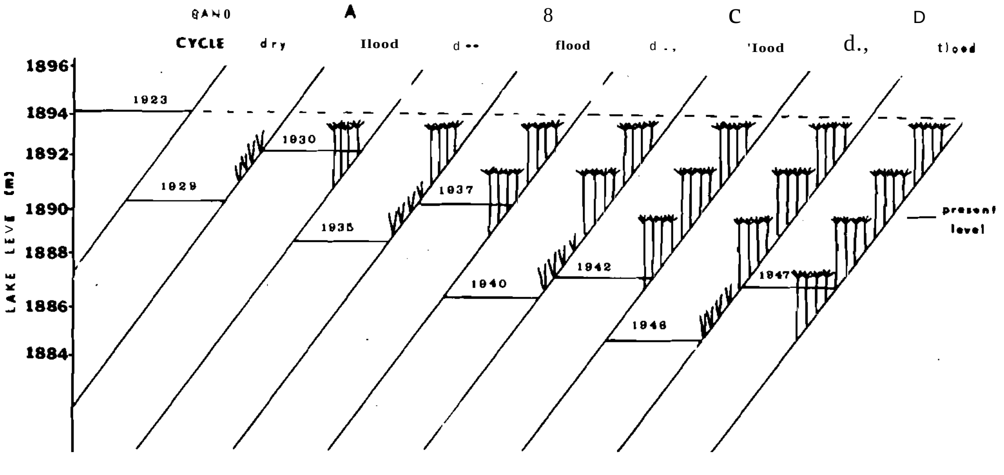

Figure 8. Schematic outline of the origin of four bands of fringe swamp (A, B, C and D). Peak lake levels and year indicated for each cycle.

Table 11 •. Species common on exposed shore (* = most common). (Based on Gaudet, 1977).

A. Volcanic sand

Seedling Zone

Cassia didymobotrya*
Sesbania sesban

Grass-Sedge Zone

Pennisetum. clandestinum*
Cyperus laevigatus*
Cyperus rigidifolius

Leguminous Zone

Cassia didymobotrya*
Hibiscus diversifolius*

Composite Zone

Tarchonanthus camphoratus*
Conyza hypoleuca*
Psiadia punctulata
Rhus vulgaris
Lantana camara

B. **Papyrus mud**

Seedling Zone

Senecio moorei*
Gnapbalium luteoalbum*
Sphaeranthus suaveolans*
Nymphaea caerulea (on very wet mud)
Cyperus spp.*

Sedge Zone

Cyperus papyrus*
Cyperus immensus*
Cyperus digitatus ssp. auricomus*
Scirpus inclinatus
Sphaeranthus suaveolans

Composite Zone

Conyza floribunda*
Conyza bonariensis
Gnaphalium luteoalbum*
Sphaeranthus suaveolans
Senecio moorei
Polygonum spp.*
Cyperus spp.

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and Sonachi Crater Lake the more 'alkaline' soils support a flora common to the soda lakes (e.g. Lake Nakuru) which is dominated by the salt sedge <u>Cyperus laevigatus.</u>

b) <u>Lagoons and papyrus reefs</u> - The general ecology of the lagoons on Lake Naivasha has been recently reported (Gaudet 1980).

Elder et ale (1971) explained the formation of these lagoons by a periodic growth of papyrus. Thus, during the period 1929 to 1956 while the lake level showed an overall tendency to decrease (Fig. 4) papyrus growth was common in shallow areas and on wet mud. From 1956 to 1959 the lake level began to rise creating extensive areas of open water between this papyrus and the shore. The water level then decreased and this papyrus was isolated for about 3 years on drying mud. During the floods of 1961 and 1962 these areas were re-flooded and remain today as lagoons. In addition to lagoon formation, papyrus could be spread by island formation. Small clumps of papyrus swamp are often seen around the lake edge and they clearly are stranded papyrus islands which are common in the lake during periods of high wind and rising water levels. Such patches can best be seen on the northeastern shores of Crescent Island. This portion of Crescent Island lies directly in the path of papyrus islands floating south from the extensive North Swamp (Fig. 2). After being stranded, the islands are slowly surrounded by young fringe swamps which gradually enclose the old islands.

During periods of high lake level, island formation would favor the spread of papyrus and during periods of low lake level, papyrus growth in shallow water would favor reef formation. But from Elder et ale it is not clear what sort of growth occurs during the formation of a papyrus reef; for example, is this growth from young seedlings? From the foregoing account of succession on exposed mud, it is obvious that a young papyrus swamp will be established whenever soil is exposed on the lake and this process requires approximately 1-3 years. The fringing swamp so established may remain distinct from the older papyrus fringe formed earlier especially if the lake level rises quickly, flooding the Composite Zone before papyrus colonizes this region.' Successive papyrus fringes would then present a "band effect" if, lake' level fluctuated over the years. 1948 aerial ,photographs recorded by the Survey of Kenya show four bands of papyrus near the southeastern shore close to the area referred to now as the East Lagoon. The 4 bands A, B, C and D must have undergone consolidation in the 20 years after 1948 because later aerial photographs (1968) show a more compact swamp which has persisted until the present. The origin of the four bands could be correlated With major periods of low lake level (Fig. 8) which were followed by sharp rises in lake level. But after each successive drying (D) and flooding (F) (= one D-F cycle) the water did not come back to its original level (1893 m in 1927). The term D-F cycle is used here as a period of general, progressive decrease in lake level followed by a general progressive increase. Such D-F cycles occurred during and after the formation of bands A, B, C and D. Gaudet (1977) found that the Width of each band was directly correlated and the area inversely correlated, with the duration of the drying portion of the D-F cycle. This indicated to him that a long drying period would allow more exposure of mud area for colonization and more papyrus seedlings would become established.

After 1947, the D-F cycles changed and for the next 20 years the drying periods were of shorter duration with longer floodings. During this 20 year period the formation of large bands apparently was not favored, but the, formation of smaller bands must have gone on possibly even during the shorter or secondary cycles which often occur during the major or primary cycles. For example, during 1962-1964 there ,were 5 secondary D-F cycles averaging ± 0.6 m which occurred during the primary 33D:36F cycle (33 months drying: 36 months flooding) during which the lake level went down 2.1, m and then up 5.2 m.

The succession on wet mud leading to a new papyrus fringe swamp described above (Fig. 8) occurred during a primary D-F cycle in which D started in September, 1971 (lake level at 1891.03 m) and ended in March, 1974 when F began (lake level at 1888.96 m). This new fringe swamp which has been produced along much of the shore area is not extensive enough to a band or a papyrus reef, but it did enclose several stranded papyrus islands on Crescent Island and extended the width of existing older fringe swamps by 2-4 m. It also occurred behind the mass of papyrus in the North Swamp and here it grew up between several large sections of older swamp.

It appears that the pattern of development of perennial emergent vegetation of African lakes varies considerably depending on many factors present during drawdown, such as soil water, soil chemistry (especially Salinity), grazing, vegetative growth, availability of species with a high reproductive capacity, etc. With re-flooding, further selection pressures are exerted because of water depth, water chemistry, grazing by amphibious animals, vegetative and sexual reproduction while inundated, water clarity which affects underwater germination, wind action, etc.

c) Submerged flora - In shallow areas around the lake edge, the bottom is almost completely covered by *Ceratophyllum demersum* interspersed with this is *Najas pectinata* which forms large clumps reaching almost to the water surface. The next most common plant is *Utricularia reflexa,* with scattered bladders, is locally common along with *Utricularia gibba,* a small plant with very small, scattered bladders. *Potamogeton thunbergii, P. pectinatus* and *Najas flexilis* are very common along with an occasional plant of *Potamogeton octandrus.* Three charophytes are locally common, *Nitella knightiae* (a large plant with a gelatinous matrix around the oogonia), *Nitella oligospira* (a smaller species), and *Chara braunii* (the smallest of the three).

d) Floating vegetation - The water lily, Nymphaea caerulea dominates the floating-leaved community in shallow water and does especially well close to shore where it shades out most species. Several free-floating duckweed species can be found especially confined to the inner edges of papyrus reefs or the front edges of papyrus fringe swamps along the shore. Here dense colonies of Lemna and Wolfiopsis are found growing. These quiet backwaters of the inner reef also provide ideal conditions for other species such as Ricciocarpus and Salvinia (Gaudet 1977). These free-floating and floating-leaved plants form an effective barrier against wind action on the water. In addition, the submerged plants hinder horizontal water movement and, because they often grow in masses which lie just 0-30 cm below the water surface, quickly dampen moving waves.

In the lagoons various types of floating sudd occur. Uprooted water lily 'is sometimes seen drifting in large clumps. These mounds are uprooted by hippos and include organic muck, roots, silt, rhizomes as well as leaves, and flowers, all turned upside-down, producing a small "mud island". On the edges of these mud islands Hydrocotyle can be seen in a small-leaved, young, or primary, form. Later, after the island becomes stranded against the inner reef or shore of the lagoon, the Hydrocotyle undergoes an expansive growth; producing larger leaves and rhizomes (Gaudet, 1980).

In 1977 and 1978 during a period of high lake level, all of the lagoons and most of the shallow water became infested with the floating weed, Salvinia molesta. Almost every day Salvinia disappears from the lagoons only to return again when the prevailing winds changed direction. These periodic movements of this weed depends mostly on prevailing winds, e.g., one day reveals an almost completely free lagoon surface, the next day finds 90% coverage. Thes'e overnight habitat changes have had enormous impacts on the lagoon eGology. The bird life, e.g., has changed from a cosmopoliton multispecies type to a specialized avifauna. Swimming and diving birds (ducks, coots, kingfishers) disappeared first, followed by the wading birds (herons, storks), leaving the lily-trotters (jacanas) and bee-eaters.

3.) THE DRAWDOWN ECOLOGY

The gently sloping shoreline of the main lake is ideal for the development of a wet mud flora. Recently a long period of low lake levels (1971-1973) revealed a wide band of exposed papyrus soil approximately 20 m Wide, in front of the lakeside papyrus fringe swamps. The total area exposed during this natural drawdown was 55 ha. The plants developing on this substrate are listed in Table 11.

The drawdown plant formation is dominated by forbs, whose seeds neither decay nor germinate while the bottom of the water body is inundated, but germinate and grow rapidly after the mud has emerged again. On this exposed mud one can find (a) hygrophilous terrestrial species which tolerate temporary submersion, (b) aquatic macrophytes which tolerate temporary drying, (c) amphibious perennials which seem to be more or less restricted to such habitats, and (d) hygrophilous annuals which quickly colonize open spaces but die immediately after flooding.

The first phase of drawdown succession begins just after the water recedes, at that time a bare, wet mud is revealed With bits of Nymphaea flowers, fruits, and leaves. This detritus is left over from the eating activity of the coypus, Myocastor coypus Molina. In addition, many crayfish (Procambarus clarkii Girard) are active on the wet mud. From November 1973 to April 1974 they constructed burrows in which they breed. Later, when the water level begins to rise, they remain active in and around the inundated wet mud flora. With advanCing age they die or moult and their bleached carapaces are found scattered amongst the other detritus. In addition to the detritus, a few recently germinated seeds and a few seedlings are found, but the fresh mud is generally bare. Later a large number of seedlings grow up on the drying mud. This region is referred to at this stage as the Seedling Zone. Nymphaea seedlings are found in profusion here, but do not survive the drying which progressed as the water level decreased.

Proceeding inland from here, young Cyperus plants are found in large numbers. At this stage it is impossible to distinguish between the three major species (C. papyrus L., C. digitatus Roxb. and C. immensus C.B.Cl.). This region constitutes the Sedge Zone during this early stage of succession. Further inland the Composite Zone is found. Here Conyza, Gnaphalium and Sphaeranthus are found.

Following the dry phase (Le.,the drawdown period) a period of re-flooding begins when the drawdown flora is inundated. In some cases aquatic species are present which *grow* up quickly as the water level rises. Good examples are Ludwigia and Nymphaea.

The majority of tropical drawdown plants are not aquatic, however, and are better described as hygrophilous ephemerals. These are short-lived plants which die during the high water period. Many plants along the shore on Lake Naivasha, such as Conyza, Gnaphalium and sedge seedlings, fall within this class. These plants die leaving behind a thick root mass which does not decompose easily since inundation once more imposes anaerobic conditions on the mud and slows decomposition. Many of the species within the wet mud area show a tolerance of dry conditions, and are also found inland from the shore.

In general then, the wet mud supports a flora that is mostly composed of annual weeds, the Composite Zone is a more selective environment and lastly, the Sedge Zone is qUite specialized allowing growth of mostly rhizomatous emergents, such as sedges and Typha spp.

In intriguing question is how does papyrus survive this re-flooding? Here there seems to be a compromise in that seedlings and young plants of papyrus resemble hygrophilous emphemerals in that they do not survive flooding but older plants are more tolerant and survive for a few years. The lighter color of the surviving plants suggests, however, that they may eventually suffer from nitrogen deficiency. Nitrogen has been suggested as the most obvious limiting factor in a papyrus swamp (Gaudet, 1976b) since these swamps rely heavily on nitrogen fixation. Fixation in a young swamp may not be at a sufficiently high rate if the plants remain rooted to the soil as they are after re-flooding. In mature fringe swamps the plants grow up on top of a large accumulation of waterlogged detritus, while in floating swamps and papyrus reef swamps the plants grow on top of a dense, thick floating mat. In both cases the plant does quite well. So, at least at some stage of development, papyrus does have an option and obviously can adapt to flooding, whereas some species, such as Sphaeranthus, adapt to a limited extent and most others cannot adapt at all. It is also interesting to note that papyrus along the White Nile is restricted to sites where the range of flooding is 20 cm (between 130 and 150 cm; Anon., 1954). But on Lake Naivasha bands of papyrus originate in areas with a larger range in water level, i.e. 130 cm (70-200 cm). The difference is most likely due to the swamp origin, since the bands of fringe swamp on Lake Naivasha originate from seedling growth on exposed mud. On the other hand, mature papyrus as in the Nile study produces new growth by propagation from older rhizomes.

What then is the function of drawdown in tropical water bodies? In Lake Kariba, McLachlan (1971) pointed out that drawdown functions as part of the lake-edge nutrient cycle. Many animals graze on the drawdown flora during the drying phase. Subsequently the grass and dung in the drawdown region when re-flooded produce an increase in inshore conductivity, alkalinity and potassium with concurrent decrease in pH and oxygen. In addition to providing food for terrestrial grazers on Lake Naivasha the drawdown flora also provides for aquatic grazers such as the hippo which wallow and defecate in shallow water, thus adding to the nutrient load inshore. After re-flooding the drawdown region on Lake Naivasha experiences an explosive development of ostracod populations (M. Mendes, pers. comm). This also occurs under laboratory conditions when containers of young papyrus transplanted directly from the lake are flooded (Gaudet, unpublished results). The rapid build-up of ostracods is accompanied by death and decay of the drawdown flora, increases in other invertebrates, appearance of juvenile fish, increase in fishing bird feeding activity, etc. Offshore primary production increases as the water level rises (Melack, 1979). In short, the reflooding phase coincides with a period of increased production in this lake.

It should be obvious from this discussion that in the tropics drawdown and reflooding are fruitful topics for future research. Much work has yet to be done on the details, but the general impression one gets is that each year the cycle is repeated in water bodies where drawdown exposes hydrosoil which undergoes oxidation. There then follows a period in which ephemerals experience fast growth to maturity and become involved in both terrestrial and aquatic food chains. The last part of the cycle, re-flooding, results in an increase in offshore production. In summary, it must be said that drawdown in Lake Naivasha must have an appreciable effect on the whole main lake ecosystem.

4.) THE PHYTOPLANKTON

Lake Naivasha is shallow ($\bar{z}$ = 5 m) and eutrophic with a chlorophyll a concentration of between 20 and 50 mg m^{-3} (Anon 1978) and secchi values of 0.5 to 1.5 m (Melack 1979). However, among lakes of the region, many of which are characterised by high(er) salinity, Lake Naivasha is among the most oligotrophic. Only the deeper Crescent Island basin ($\bar{z}$ = 11m), largely separated from Lake Naivasha proper during periods of low water levels, has less chlorophyll a per unit volume. However, this smaller basin has a deeper photic zone resulting in similar values to the main lake on an areal basis. Although nearby Oloidien Lake, with its typical surface bloom of blue-green algae, appears much more eutrophic (secchi 0.5 - 1.0 m) it is only marginally so when viewed on an areal basis (Kalff, unpublished data) because in contrast to Naivasha most of the biomass is concentrated near the surface.

The even distribution of algal biomass (Chl.a) in Naivasha (Anon 1978) must be attributable to its algal species composition and the night-time cooling and daily circulation of the water column (Melack 1979). Nevertheless, the algal biomass is sufficiently high to restrict gross primary production to about the top three metres (Melack 1979, Anon 1978). With an inverse relationship between depth of eutrophic zone and photosynthetic rates per unit volume of water, the roughly extrapolated and averaged daily gross productivity of lakes in the Naivasha basin varied only from a low of about 5 g O_2 m^{-2} in the main lake, the Crescent Island basin and Sonachi Lake, to a high of 8 g O_2 m^{-2} in Oloidien lake (Melack 1976, 1979). These rates again characterise Lake Naivasha as eutrophic by world standards.

In contrast to the considerable information on gross primary production and chlorophyll a concentrations, little is known about the algae responsible, apart from some information on the relative abundance of major species. The use of nets and formalin as preservative in all but one study, the variable taxonomic competence of the investigators and the different taxonomic keys used do not enhance the possibility of detecting patterns. However, both Melack in 1973 - 1974, and Kallquist in 1976 - 1977 (Anon 1978)noted the relative abundance of blue-green algae. Their lists and comments further suggest that Lyngbya contorta, Spirulina laxissima and an Aphanocapsa species were important during both periods. Other important taxa noted in 1973 - 1974 were Anabaenopsis tanganyikae, Microcystis sp., Merismopedia sp. Chroococcus sp. In 1976 - 1977 additional Lyngbya species were noted as being abundant. The diatoms appear to have been more abundant in 1973 - 1974 than in 1976 - 1977 with Synedra acus, Surirella linearis, Nitzschia sp. and Melosira ambigua fairly abundant, whereas during the latter period only Synedra acus was abundant and then only in February. Lind's December 1964 data (Lind 1968) are difficult to compare as they were collected during one short period and with a very coarse meshed net (140 µm). However, she noted the relative abundance of what she refers to Synedra ulnae, Melosira ambigua and two large desmids as well as the presence of Microcystis sp. and r

based on both the temperate and tropical literature.

5.) THE FISH AND FISHERIES OF LAKE NAIVASHA

Four species are exploited commercially in Lake Naivasha; the crayfish (Procambarus clarkii), Sarotherdon leucosticta, Tilapia zillii and the largemouth bass (Micropterus salmoides). The bass is also taken by sport fishermen.

The commercial fishery is a canoe-based industry using monofilament nylon gillnets. These are set parallel to the shore in shallow water particularly near the papyrus reefs and inside the littoral lagoons that both tilapia and bass favour (Elder et ale 1971, Siddiqui 1979).

A summary of some biological and ecological features of the three fish species is presented in Table 11.

Commercial fishing began in 1959 exploiting what was though to be a pure population of Sarotherodon spilurus nigra with a small number of Tilapia zillii (Elder et ale 1971). Sarotherodon leucosticta was not taken in the 13 (5'/8") and 14 (5^1/2") centimetre nets used at the time but a few fish, which later proved to be hybrids of S.s. nigra and S. leucosticta (Garrod and Elder 1960) began to enter the commercial fishery in 1960. By 1962 the hybrids had greatly increased in abundance and contributed 57% of the total catch in experimental nettings (Elder et ale 1971). The balance was made up of S.s. nigra and S. leucosticta (Table '2).

Eleven centimetre (4^1/2") nets were in general use by 1961 and catches of tilapia increased throughout the early 60's to a peak of 500 metric tons in 1966 (Fig. 9). This mesh net was made the legal minimum size in 1966 but the number of nets per boat remained unrestricted. During this period the sport fishery for bass was reported to be good (Malvestuto 1974). Despite the rejection in 1967 of the request by local fishermen to have the legal minimum mesh size reduced to 10 em (4"), the smaller mesh size was used extensively in 1968. Mann and Ssentongo (1969) report that 250 illegal nets out of 544 in use (46%) were

Table 12. A comparison of the composition of the Naivasha tilapia population taken in different years during experimental fishing trials.

	(%)				
	S.s. nigra	S. leucosticta	T. zillii	Hybrids	N
Year					
1962 1)	27.2.	15.3	0.9	56.7	1664
1972-73 2)	0	79.8	20.0	0	1568
1975 3)	0	54.4	40.5	**5.1**	880

After:-

1) = Elder et ale 1971
2) = MaJ.vestuto 1974
3) = Siddiqu 1977, 1979

confiscated in May 1969. The smaller nets used did not lead to greater catches and between 1966 and 1968 fish landings fell. The 10 cm net was legalized in 1970, the number of fishermen increased and the tilapia catch for the year rose to its highest level since 1959 (1 131 metric tons). This record yield was followed in the next two years by greatly reduced catches, 465 t and 109 trespectively. The fishermen responded to the declining yield by using still smaller mesh nets (8.9 cm - 3½", and 7.6 cm - 3"). The Fisheries Department restricted the humber of nets to 10 per licenced boat. Catches, however, continued to decline and by the end of the year the fish filleting factory in Naivasha was forced to close down (Malvestuto 1974) and the fishery effectively collapsed.

From 1973 to 1977 the tilapia fishery remained depressed and annual catches averaged a mere 49 t (maximum 67, minimum 34). The 10 cm minimum was enforced during this period by patrols of Fisheries Scouts. Since 1977, however, catches have steadily improved reaching 212 t in 1978. The projected total for 1979 is expected to approach 400 t, a figure still far short of the 1970 peak.

The data available for the commercial landings of black bass from 1968 onward show a generally similar pattern to that of the tilapia fishery (Fig. 9). The commercial yield for 1979 is expected to be about 40, t. The offtake by the sport fishery from 1968 to 1970 varied from 98 to 190 t per year, i.e. about 5 to 10 times the commercial yield at that time; it is therefore, unfortunate that the collection of sport yield data ceased after 1970.

The gillnet fishery at Lake Naivasha has caused major changes in the exploited fish populations. The steady decrease in the size of the nets from 1959 onwards has reduced the abundance of the larger-sized fish, the inevitable effect seen in most other fisheries. This reduction in larger-sized fish is acceptable so long as sufficient mature breeding

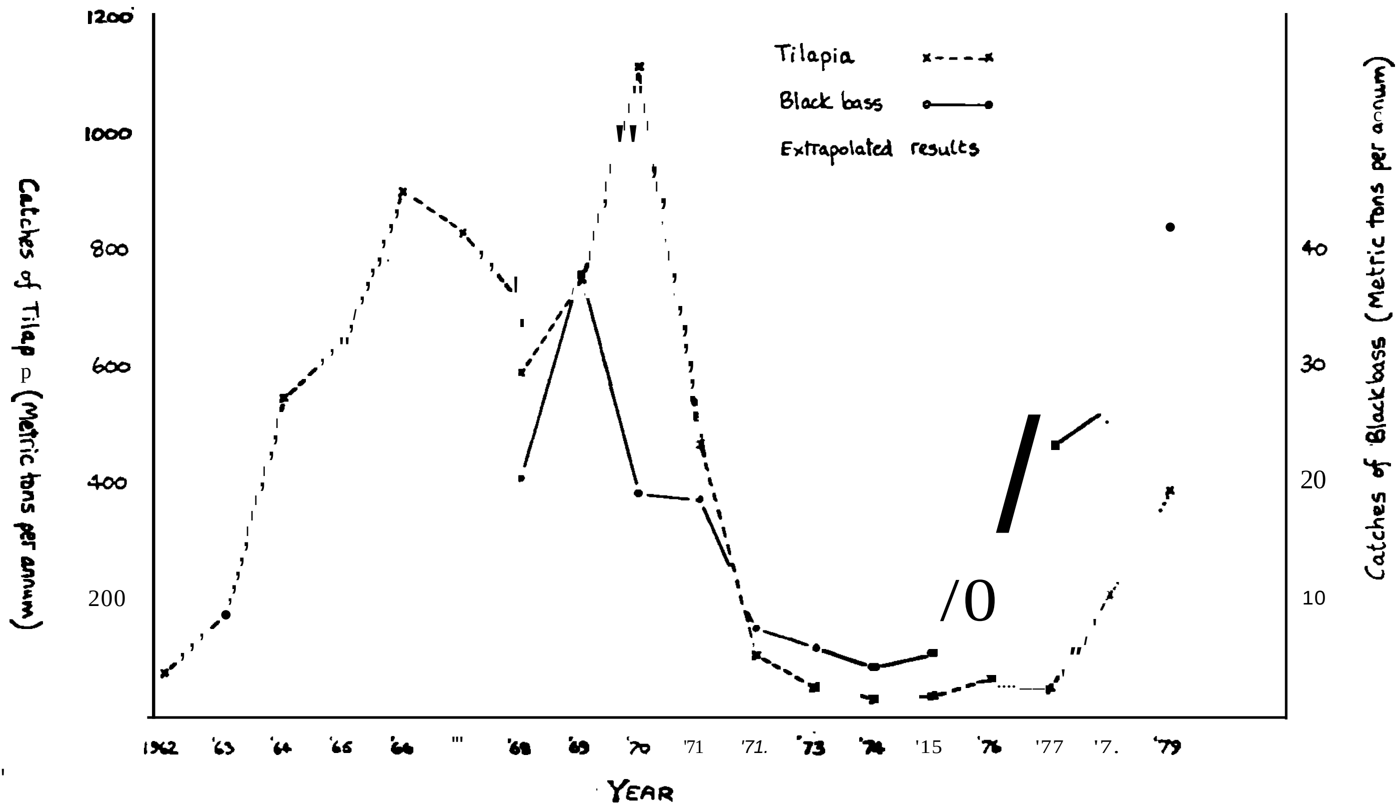

Figure 9. Annual commercial catches of Tilapia and black bass from 1962 to 1979.

From: Malvestuto (E.A.F.F.R.O. Naivasha File) 1962–1968.

Fisheries Department, Statistical Abstracts 1968-1979.

fish remain to maintain recruitment into the fishery (Malvestuto .1974).

The catch per unit effort (CPUE) has also declined and reflects the decline in abundance of mature fish below the level required to maintain the stock (Malvestuto 1974). Results of gill-net selectivity and length at maturity (Table 13) show that the legal 10 em nets now in general use exploit only mature Micropterus salmoides and tilapia. These mature fish are, however, being exploited very soon after they mature. S. leucosticta, for example, is caught at 20 cm Ls (standard length), only 3 cm greater than the length at maturity which, at their estimated growth rate of 0.5 cm per month, leaves only about 6 months in which they can breed before entering the exploited stock (Malvestuto "1974). Most individuals of S. leucosticta appear to breed at six montl1 intervals and consequently most have only a single chance to breed before being subjected to fishing mortality. This exploitation of the adult stock so soon after maturity has reduced fecundity to a lOW, uneconomical level (Malvestuto 1974).

The decline in the Naivasha fishery since 1971 is not, in the opinion of Malvestuto, entirely attributable to overfishing and the use of nets below the legal (10 cm) limit. His results (Figure 10) have shown that tilapia yields in Lake Naivasha, like those in Lakes Chilwa (Morgan 1971), Victoria (Fryer and lIes 1972), Mweru and Mweru wa Ntipa (Williams 1972) are strongly dependent on lake level fluctuations.

Rising water levels correlate well with increased fish production while catches increase approximately two years later when the increased stock has grown to a commercially exploitable size. Catch per unit effort, therefore, correlates most strongly with lake levels experienced two years previously (Malvestuto 1974). This increase results from the additional area of inundated land made available for breeding and perhaps also to an increased food supply when nutrients, released from

Table 13. Length at maturity and length of fish retained by gillnets on Lake Naivasha (after Malvestuto 1974; figures in brackets from Siddiqui, 1979).

	Length at maturity	Mean standard length, ($\bar{L}s$) retained by 10 cm nets (cm)
S. leueostieta	17.4	20.2 (23.0)
T. zillii	13.0	18.0 (22.0)
M. salmoides	22.6	30.5

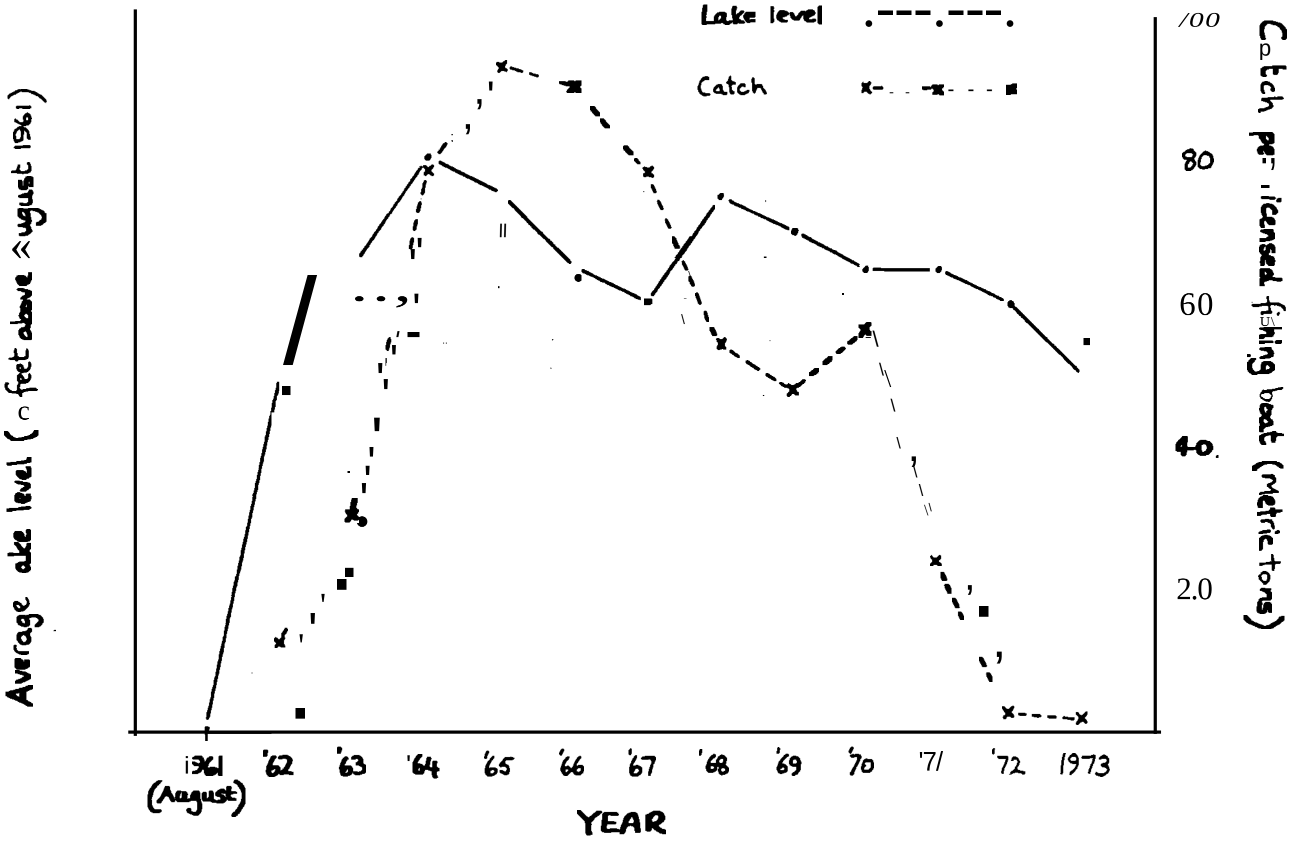

Figure 10. Lake level fluctuation and catch per licensed fishing boat from 1961 to 1973. (After Malvestuto 1974).

the decaying terrestrial vegetation and soil,enhance aquatic primary production.

The increase in tilapia production associated with rising water levels is temporary; as the inundated land quickly becomes choked with aquatic weeds its usefulness for breeding soon diminishes (Malvestuto 1974).

Falling water levels are immediately and dramatically accompanied by declining catches as water level effects on fish populations are more direct. The 1.2 metre drop in lake level between 1971 and 1975 undoubtedly contributed to the collapse of the fishery during this same period along with overfishing.

Salvinia molesta has also been implicated as a possible causative factor in the decline of the Naivasha fishery by Siddiqui (1977). Since the introduction of this weed in 1964 it has encroached on the shallow water spawning and nursery grounds of the tilapia. A preliminary investigation by Siddiqui revealed no brooders, fry or fingerlings in areas heavily infested with Salvinia, a situation similar to that reported by Donnelly (1969) in Lake Kariba.

The introduction of the crayfish (Procambarus clarkii) in 1970 and the subsequent build-up of a large population in the NE sector of the lake (see page) may also have contributed to the decline in the gillnet fishery.' The crayfish is a shallow water benthic scavanger (Oluoch, pel's. comm.) and may well seriously disturb Tilapia zillii and Sarotherodon leucosticta during the 'nesting' phase of their spawning activity and possibly they feed on the nest-bound eggs of T. zillii. They also play a deleterous role in feeding on the fish trapped in gillnets (Oluoch, pel's. comm.) greatly reducing their commercial value, and in damaging the nets when fishermen attempt to disentangle them from the nets.

The Lake Naivasha fishery is ess'entially unstable and unpredictable because of the close association between fish production and lake level fluctuations which results from the almost exclusively littoral distribution of the exploited fish species. The intermittent use of various illegal sized nets has added to the difficulty of predicting yields.

To reduce the degree of unpredictability and stabilize catches Malvestuto(1974) cautiously advocates the introduction of other species of fish which will utilize the more stable open water regions of the lake. Such management procedures are at best risky and the Fisheries Department should perhaps, as Malvestuto also suggests, devote its efforts toward more effectively enforcing the current fisheries management policies regarding net size, number of nets per boat and the number of licenced fishermen. To which might be added that some attempt to explain the basics of fisheries biology to the fishermen may assist in this endeavour if the fishermen understand more clearly the effects of gill netting on the fish populations.

6. The Ecology of the Invertebrate Fauna

Of all the communities in the Naivasha basin the ecology of the invertebrates communities are the most poorly documented. Short-term collections from the main lake, Crescent Island basin, Oloidien Lake and Sonachi Crater Lake have been made, starting with the Percy Sladen Expedition in 1929 (Jenkin 1936) and the 1930-31 Cambridge Expedition (Beadle 1932). More recently studies have been undertaken on the ecology of the chironomids (N. Cox), the crayfish (A. Oluoch) and the limnetic zooplankton (K. Mavuti).

a) Chironomids - Seven species have been found in the Naivasha basin as follows: Chironomus formosipermis* Kieffer; C. pilosimanus* subsp. quatuordecimpunctatus Geotghebuer; Cladotanytarsus pseudomancus Goetghebuer; Tanypus guttatipenriis Goetghebuer; Procladius brevipetiolatus Goetghebuer; Clinotanypus claripennis Kieffer; Psectrocladlus viridescens (N. Cox pers. corum.) with the first two* being the most common (75% of total).

The great abundance of chironomids is found in the western part of the main lake (Table 14).

Table 14. Percentage occurence of Chironomidsin the Naivasha basin (N. Cox, pers. comm.)

AREA	%
Main Lake	
East	1.7
West	42.3
South	29.2
Crescent Island basin	19.8
Oloidien Lake	6.9

The distribution pattern of chironomids is of interest when compared to that of the crayfish. The crayfish is most abundant in the eastern area of the main lake and is virutally absent in all of the regions most favoured by chironomids.

b) Crayfish - After its introduction there was a rapid, initial spread of the crayfish throughout the eastern basin until 1974. Since then the distribution appears to have remained static and confined within the eastern area of the main lake (Fig. 11). Isolated populations have been established in the western basin by local farmers but these show little sign of expansion, in fact experimental translocation of crayfish between areas of high density - continuous distribution (e.g. the eastern area) and low density - patchy distribution (western area) indicated reduced rates of growth and survival of specimens moved from east to west (Oluoch,pers. comm.). This suggests that the western area of the lake is a less satisfactory habitat for Procambarus. In the eastern region a maximum density of 67,000 crayfish per hectare was recorded in 1976, but declined to less than 15,000 per hectare by early 1978. The extent to which commercial exploitation precipitated this decline is unknown.

Crayfish density decline with increasing depth resulting in a strictly littoral distribution, with breeding going on in shallow water or in burrows along the shore. Breeding continues throughout the year with two slight peaks of activity which coincide with rising water levels associated with the rainy season. The fecundity of the Naivasha crayfish is high with a mean egg number of 459, compared to fecundity of crayfish in Louisiana, where 313 eggs are found per individual (Oluoch pers. comm.).

The crayfish population in Lake Naivasha,is heavily predated by a wide range of aquatic and semi-aquatic predators including marabou stork, sacred ibis, herons and cormorants. The stomachs of 50-70% of Micropterus salmoides from the Orescent Island basin contained only Procambarus clarkii; whereas only 1.9% of the bass from the main lake contained crayfish.

The spoiling of 10-40% of the commercial gill-netted fish, by crayfish predation causes serious financial losses to the local fishermen which counters the benefits to the gill-net fishery of the crayfish as food for Micropterus.

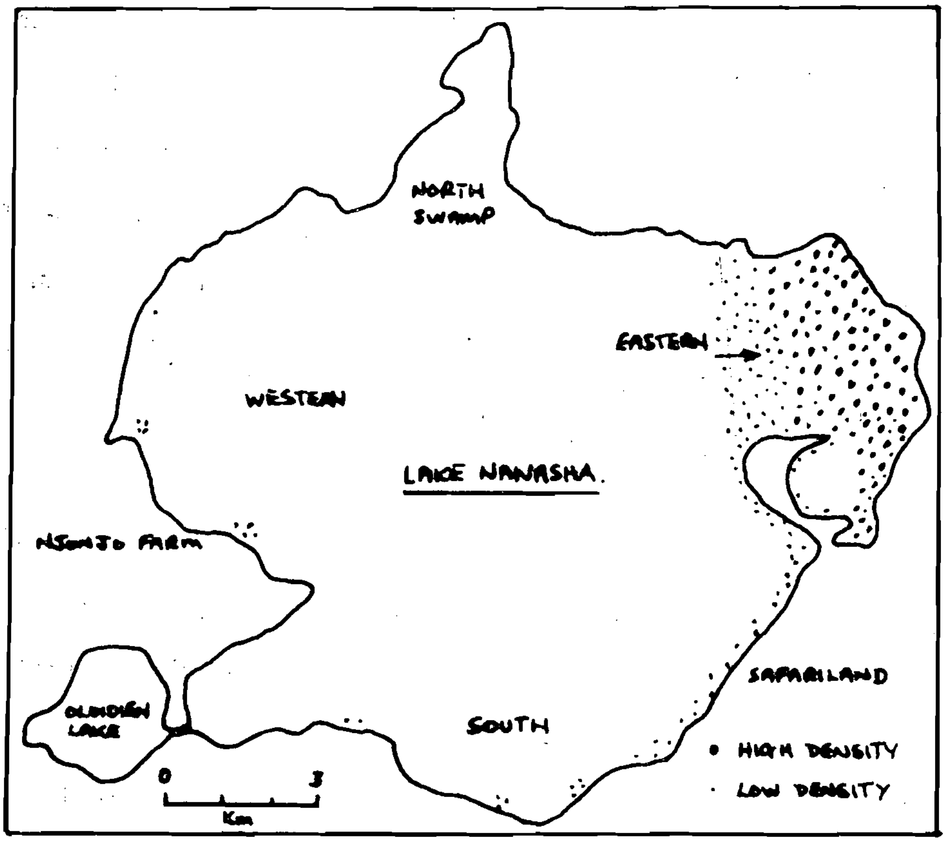

Fig. 11. Distribution of crayfish in Lake Naivasha 1977-78 (Oluoch, pers. comm.).

c) Zooplankton - The limnetic net (105 μ mesh) zooplankton of Lake Naivasha is dominated by six species:-

Diaphanosoma excisum Sars	CLADOCERA
Simocephalus vetulus Schødler	
Thermocyclops schurmanni	COPEIDDA
Mesocyclops leuckarti (Claus)	
Brachionus calyciflorus	ROTIFERA
Brachionus caudatus	

Fluctuations in numbers (Fig. 12a) and biomass (Fig. 12b) show a distinct seasonal periodicity (Mavuti, pers. comm.)

The copepods are numerically dominant throughout the year and are the major contributor to biomass during the first half of the year (Jan-July). The cladocerans are the second most numerous and dominate the biomass from July through November. The rotifers contribute a small fraction to numbers and biomass throughout the year.

Zooplankton density decreases from July through December, increases steadily from January to early April,and maintains a stable population until July. The period of minimum population density (December-January) coincides with the long dry season, while the peak period of increase from March through April coincides with the long rains.

Changes in total biomass show a complex seasonality with two major peaks (September-November and April-July.Fig. 12b) each of which is bimodal. It increases markedly and rapidly during August to reach a major peak in early September. From early September to early November biomass and population density decline. A second, minor peak occurs in November coincident with the short rains after which biomass and density decline sharply during the dry season (December-mid February). Towards the end of the dry season the zooplankton populations begin to increase in both numbers and biomass.

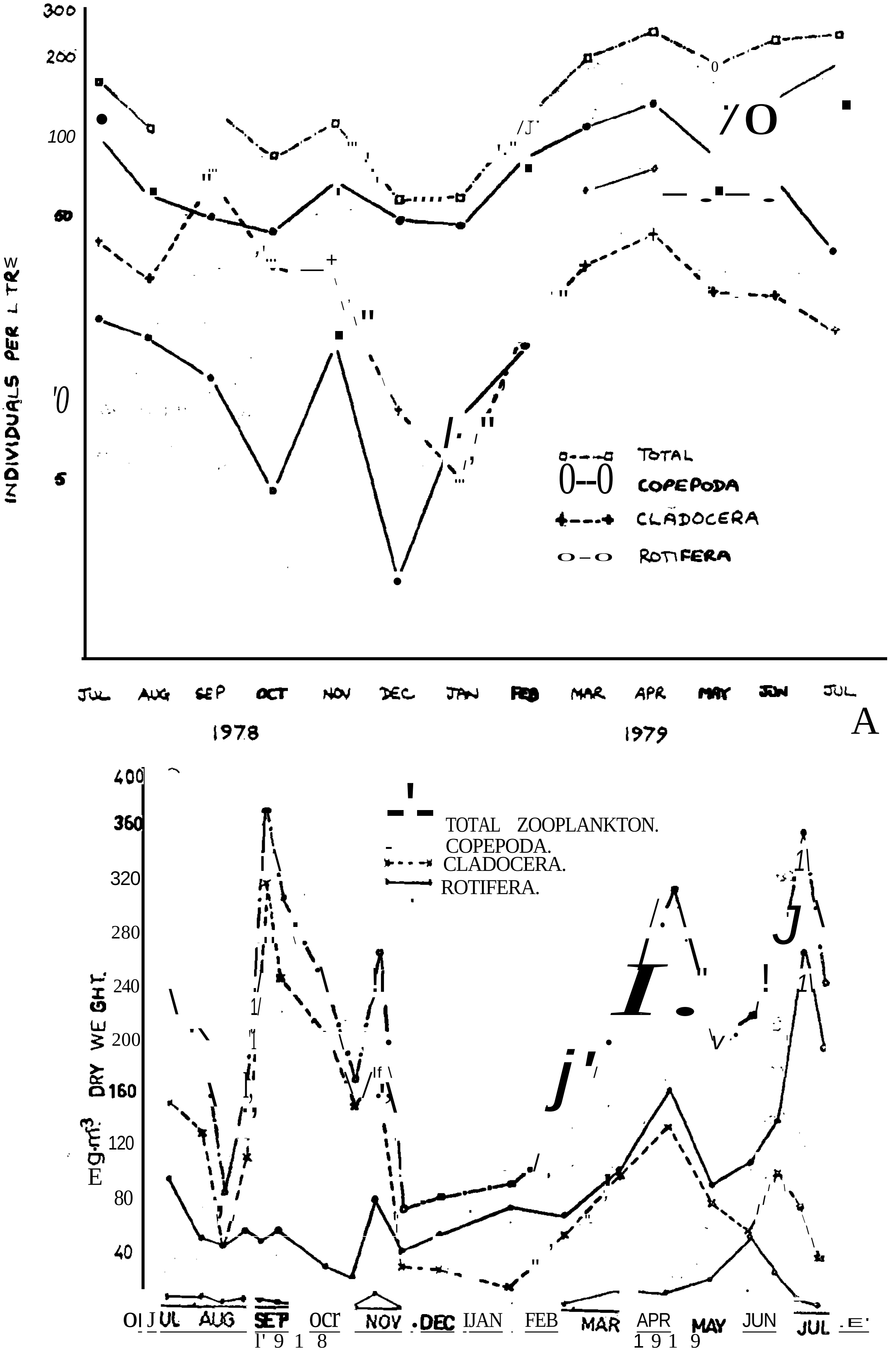

Fig. 12. Seasonal variation in (A) numbers and (B) biomass of zooplankton 1978-79 (Mavuti, pers. comm.).

This growth continues to a peak in mid-April and represents the main period of recruitment and growth of individuals. Following the onset of the long rains in the Aberdare Range (March-April) the biomass is significantly reduced. Numbers remain steady through JUly wheras biomass increases to a major peak, presumably representing a phase of rapid individual growth.

H.) SUMMARY

The Naivasha drainage basin has no surface outlet and contains four morphometrically distinct bodies of water of varying salinity (Fig. 13). The main lake of Lake Naivasha and the Crescent Island basin are the most dilute, and Oloidien lake and Sonachi Crater lake are appreciably more concentrated.

The lakes lie in the floor of the Gregory Rift Valley at an altitude of 1888 metres, where the climate of the area is warm (monthly mean air temperatures range from 15.9 to 18.5^{0}C) and semi-arid. Rainfall near the lake has a muted bimodality with the main rains in April and May and short rains in November.

The geological history of the lake basin determined from core samples records substantial changes in climate during the past 30,000 years. From 12000 BP to 9200 BPa large (612 km^2) lake over:flowed southward cutting the Njorora Gorge. By 9200 BP the gorge was downcut to its present day level (2089.4m) and a 400 km^2 lake occupied the Naivasha basin until 5700 BPo Decreasing rainfall reduced the size of the lake and closed the basin. In 3000 BP the lake dried out completely and remained dry for 100 years. During the past 3000 years a small fluctuating lake has existed in the basin which may have dried up on more than one occasion in the very recent past.

Lake Naivasha is an alkaline bicarbonate water with sodium and calcium as the major cations. Differences in the chemical composition of the water

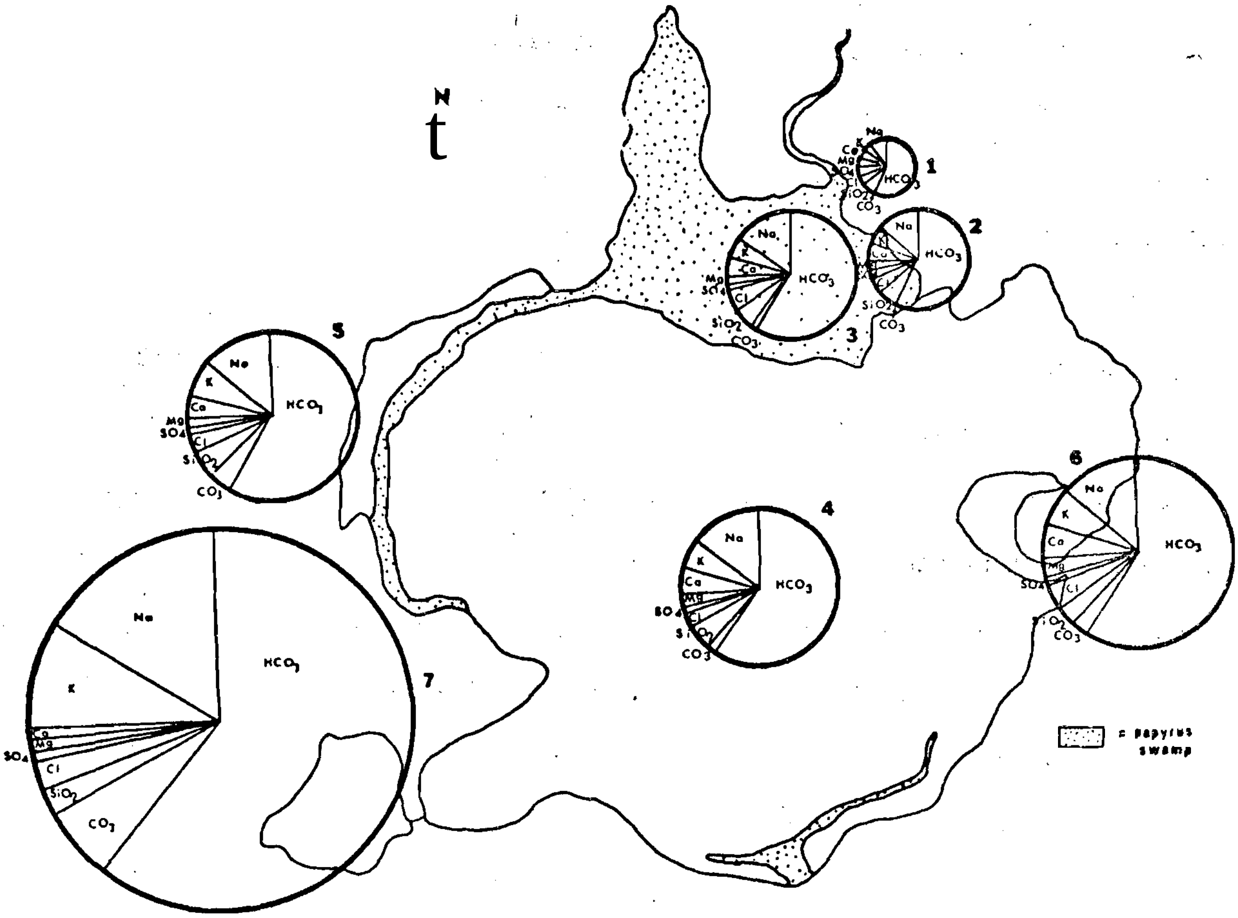

Fig. 13. Variation in ionic composition and total ionic strength in the Naivasha basin.

in various parts of the lake (Fig. 13) may have influenced species distribution especially of the phytoplankton. A chemical budget for the major ions has been constructed which indicates that exchanges With the sediments are the major routes of solute flux in L. Naivasha.

The majority of the water entering the contiguous waters of the Naivasha basin (main lake, Oloidien Lake & Crescent Island basin) comes from the Malawa River which drains the Aberdare and Kinangop Plateau. Direct precipitation and seepage-in account for the balance. Evaporation accounts for 80% of the water loss from the Naivasha basin, seepage-out and abstraction make up the balance. No evidence of discrete underground outflows has been found. Such outflows were once proposed to explain the anomalous freshness of L. Naivasha. The dilute nature of Lake Naivasha water can be explained by a combination of freshening factors, principally the inflow of very dilute water coupled with the outflow of more concentrated seepage water, the burial of 'solutes in the sediments and deflation.

Ecologically L. Naivasha is an unusual and incomplete ec.osystem. It is unusual because it combines freshness With fluctuating water levels a situation more usual of man-made impoundments and is incomplete because its excessively impoverished native fauna leaves several important niches unoccupied. Only one species of fish existed in the Naivasha basin prior to further introductions by man. It is tentatively suggested that the desiccation of the lake in the recent and more distant past, coupled with the relative isolation of the lake from suitable waters containing potential replacement species, is responsible for the improverished nature of the fish fauna.

The flora of L. Naivasha, by comparison, is diverse but with only a few dominant species including Cyperus papyrus (emergent), Salvinia (floating), and Ceratophyllum (submerged). The reasons for this diversity have yet to be explored, but the effects of lake level fluctuations on the littoral flora in the drawdown zone are now well documented.

Naivasha main lake is eutrophic and supports a wide variety of phytoplanktonic species including Microcystis, Lyngbya, Oscillatoria, Melosira, etc.

The phytoplankton is cropped by an abundant zooplankton community which includes Diaphanosoma, Simocephalus, Mesocyclops, Thermocyclops and two species of Brachionus. The zooplankton show a seasonal modality with a dry season low (December-January) followed by a steep increase in. numbers and biomass of copepods. This is followed by a second low in biomass (August) and a second high following the rainy season.. The second high is a result of cladocerans.

The almost total absence of zooplanktivorous predators reflects one major "gap" the Naivasha food web (Fig. 14), and in consequence, nearly all zooplankton production is unutilized by the higher trophic levels. Instead it enters the decomposer chain.

The Naivasha gillnet fishery is based on three species introduced during the last century. Presently the mainstay is Sarotherodon leucosticta supplemented by Micropterus salmoides. Commercial fishing began in 1959, butoverfishing and fluctuating water levels resulted in its collapse in 1971. It is now slowly recovering.

The introduced Louisiana crayfish is also commercially -exploited, but is having an adverse effect on the gillnet fishery. Trapped. fish are spoiled and nets damaged by the cray:fish with considerable economic loss to the fishermen. The general biology of this species is now under investigation.

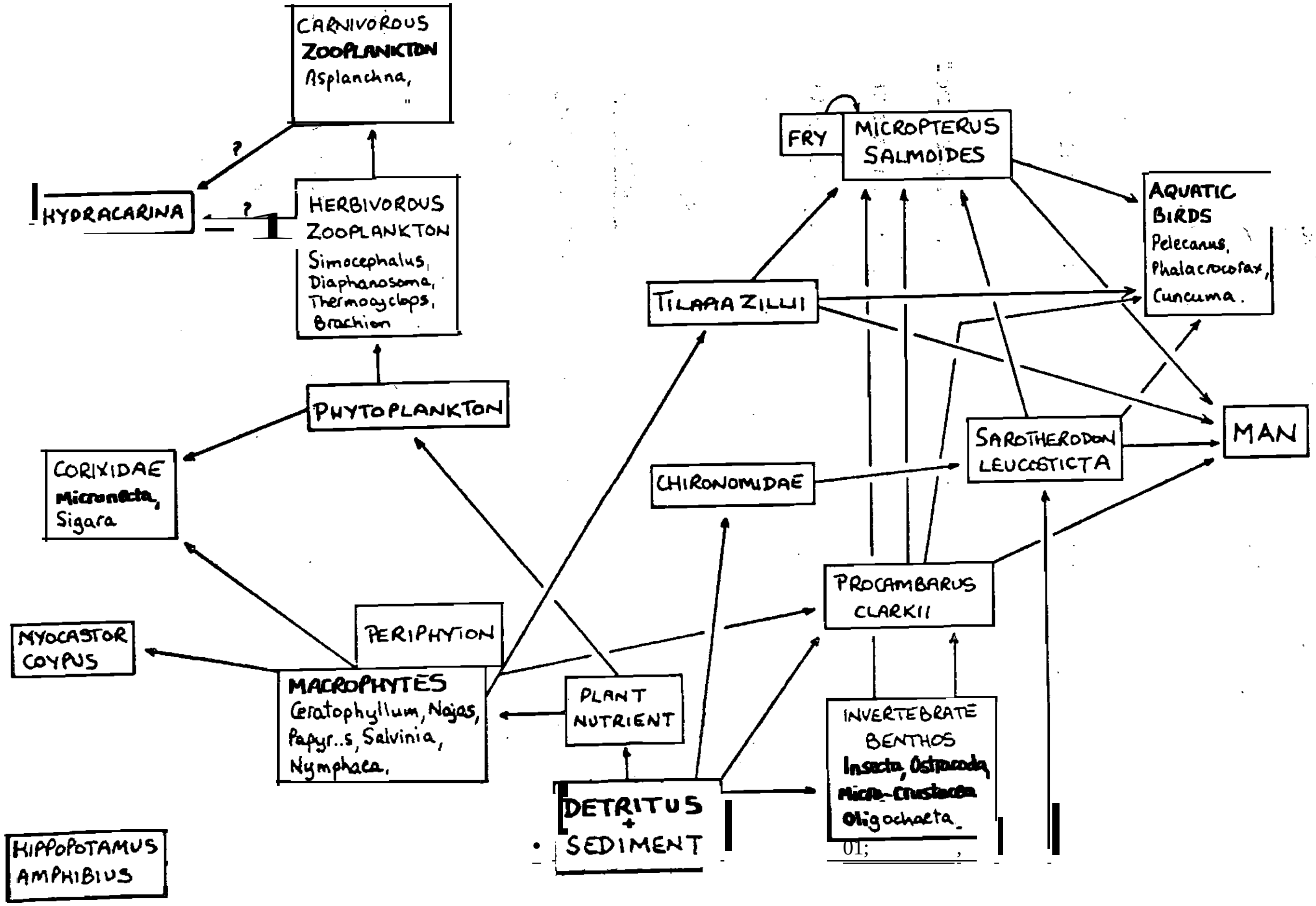

Fig. 14. Lake Naivasha food open water.

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