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SUMMARY

A general investigation was carried out on Lake Liambezi to characterize
the limnological features of the lake. The lake, 101 km² in area and
situated within the tropics, was found to be shallow and bordered by reed
swamps, particularly on the south-western shore. It was polymictic and
consequently oxygen levels were high at all depths. Transparency was such
that photosynthesis occurred to the bottom. Conductivity ranged from 17,3
to 41,2 mSm^{-1} and the waters were moderately alkaline. Transfer of organic
detritus from the reed swamp into the open water has resulted in the
presence of high levels of organic nitrogen and phosphorus whilst ambient
levels of inorganic forms were low. Planktonic chlorophyll a concentra-
tions ranged between 1 and 104 µg ℓ^{-1} and *Microcystis* was the dominant
phytoplankter. The dominant zooplankter was *Bosmina*. The important
species of phytoplankton and zooplankton are listed and include two new
species of blue-green algae which are described. The lake was found to be
generally similar to most shallow tropical African lakes with a wide
diversity of food sources for fish. Progressive encroachment by *Salvinia*
appears to hamper access to fishing areas and the fishery potential is
threatened.

INTRODUCTION

The lack of limnological information on tropical
waters was recognized as an impediment to the
progress of limnology as early as 1925 by Thienemann
and Ruttner (Rodhe, 1974). Since that time more
information has become available on tropical
limnology, a large proportion of which is concerned
with Africa (Beadle, 1974). In addition, the
increasing economic importance of the fishery
potential of large water bodies in developing areas
has recently brought about a number of research
programmes (e.g. Regier, 1971).

A study of the Lake Liambezi area, Caprivi, was
initiated in 1973 with special attention devoted to
the development of the fishery potential of the area
(van der Waal, 1976). Since little was known about
the limnology of the lake at the time, an exploratory
study was proposed which included two visits to the
area, one in winter (July, 1974) and the other in
summer (January, 1975) to provide supporting
information on the physical, chemical and biological
characteristics of the lake. This paper presents
data collected during these two visits in addition to
data collected by B.C.W. van der Waal and discusses
their significance in relation to the fishery
potential of the lake.

DESCRIPTION OF AREA

The Caprivi region in which Lake Liambezi is found
(Fig. 1) is flat and characterized by numerous swamps
and slow-flowing rivers (Mackenzie, 1946). The swamp
system centred on Lake Liambezi comprises some 300
km² of which only 101 km² is open water (Fig. 1).
The lake has had an unstable modern history, since
maps prior to 1950 do not show the presence of an
open body of water, but merely that of a swamp. An
open body of water was formed after a drought during
which the local inhabitants burnt the accumulated
organic matter to clear the swamp area for agricul-
tural purposes (van der Waal, 1976).

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Lake Liambezi receives water from at least four
sources (van der Waal, 1976). The first source is
the Kwando-Linyanti River whose waters percolate
through the large Linyanti Swamp to the west of the
lake (Fig. 1). The second source is rainfall and the
third is run-off from the area north-west to north-
east of the lake. The fourth source is the flood
waters from the Zambezi River to the north which flow
southwards when the Zambezi bursts its banks. This
situation has occurred eight times during the last 23
years (van der Waal, 1976). Outflow from the lake
via the Chobe River is intermittent and depends on
lake level. The hydrology of the system is complex
and a fuller account of factors governing the inflow
and outflow of water for the lake is given by van der
Waal (1976).

The swamp area of Lake Liambezi is surrounded by
woodland savannah and lies in the Kalahari basin
where soils are mainly fine secondarily-deposited
aeolian sands with well developed secondary horizons
(du Toit, 1926). Bordering the lake, the soils
become more organic with sandy ridges and the lake
bottom is comprised of a fine organic ooze overlying
a thick peaty layer. The open water of Lake Liambezi
is bordered by a reed swamp comprised mainly of
Phragmites mauritianus Kunth. with patches of *Typha
capensis Rohrb*. The south-eastern shoreline does not
have reed growth as extensive as that of the south-
west where reed encroachment has created an almost
impenetrable maze of lagoons amongst which are
interspersed small islands.

Echo soundings revealed that the lake was shallow
(<5 m) and the depth fairly constant in the open
water. Extensive reed growth was encountered in
shallower water (<3 m) and in areas bordering
islands. In sheltered areas there were dense beds of
submerged macrophyte populations consisting of
numerous species such as *Ceratophyllum demersum* L.,
Lagarosiphon major (Ridl.) Moss and *Najas pectinata*
(Parl.) Magnus. In pools within the reedbeds,
Potamogeton pusillus L., *Nymphaea caerulea* Savigny,
Utricularia spp., and *Chara* spp., occurred. Free
floating plants such as *Salvinia molesta* Mitchell,
Pistia stratiotes L., and *Azolla pinnata* var. *pinnata*
R. Br., formed mats in certain places. *S. molesta* is
particularly important and van der Waal (1976)
reported that in April, 1974, approximately 12 per
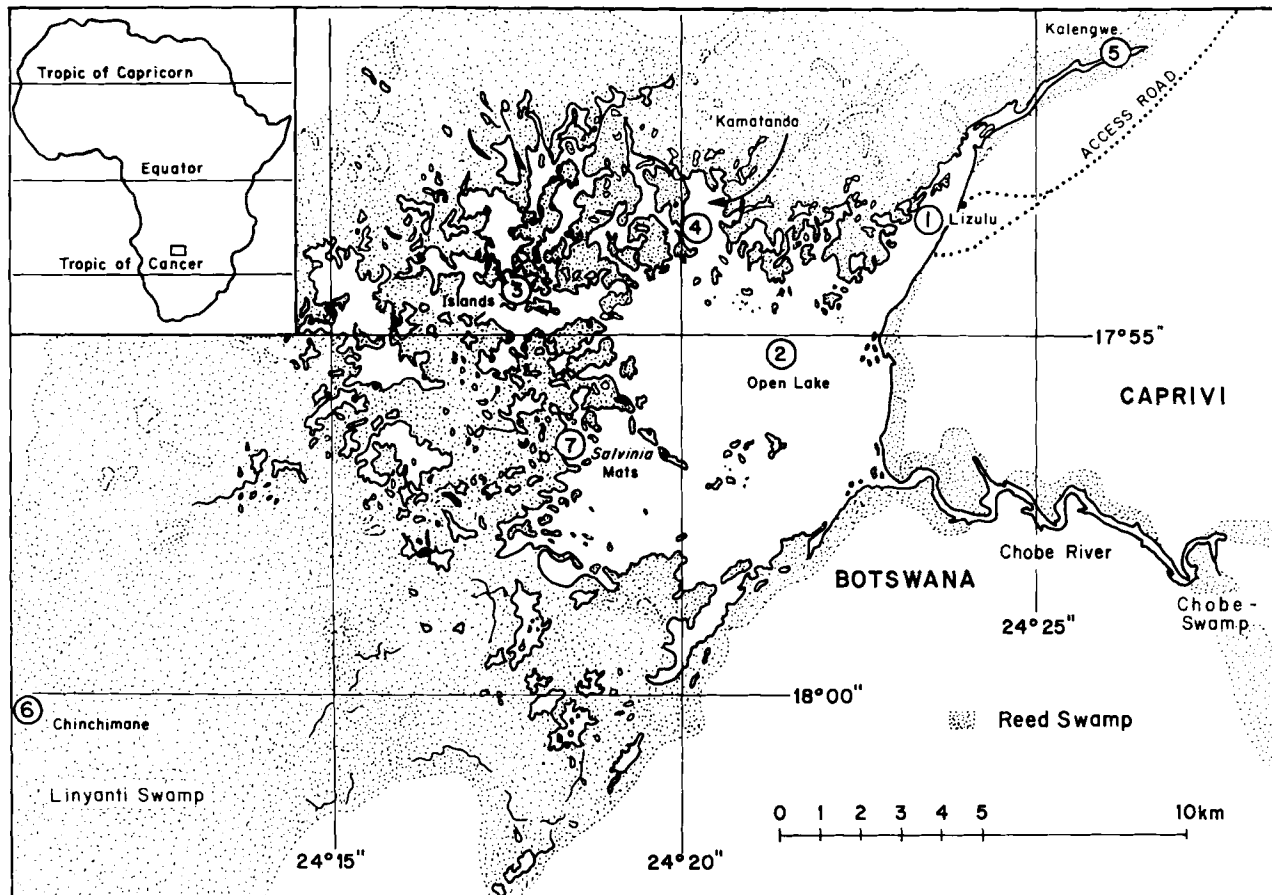cent of the open lake surface was covered by this

Figure 1.   A map of Lake Liambezi showing sampling stations.   The study area is outlined in the inset.

species. *Salvinia* cover had increased to 26 per cent by November 1975.

The lake shore is sparsely populated, largely because of the impenetrable reed swamp. Fishing of the lake waters provides a livelihood for a number of tribesmen who either live on the accessible eastern shore or migrate in small numbers for short periods to islands in the northern part of the lake. The lake is populated by 43 fish species of which twelve are large cichlids. *Clarias* spp, *Hydrocynus vittatus* Castelnau and *Mormyrus lacerda* Castelnau comprise the major part of the gill-net fishery on the lake (van der Waal, 1976). There are also populations of the genera *Barbus, Schilbe, Alestes, Hepsetus, Labeo, Marcusenius, Synodontis* and *Petrocephalus* that are not at present utilized by the fishermen.

MATERIALS AND METHODS

Seven sampling stations were selected (Fig. 1) in order to cover the different types of biotope. These included stations in the open water (stations 1 and 2), in secluded areas (stations 3, 4, 5, 6) and under a *Salvinia* mat (station 7). Most of these stations were visited during the two visits made to the lake in July 1974 and January 1975. The stations are briefly characterized as follows:

Station 1 (Lizulu) Near the fisheries research camp, water 4 to 5 m deep, 200 m from shore, no vegetation, bottom deposits consisting of coarse organic material and ooze.

Station 2 (Open Lake) Water 2,5 to 3,5 m deep, scant vegetation (*Lagarosiphon*), bottom consisting of layers of compact organic material covered by mud rich in organic matter.

Station 3 (Island area) Open channels and bays in reed swamp, water always clearer than open water with brown peat-stained colour, little vegetation (*Potamogeton*) and bottom deposits consisting of organic material and silt, water 2,5 to 3,5 m deep.

Station 4 (Kamatanda) Large bay connected to open lake, with dense stand of *Lagarosiphon major* forming thick mats on the surface, bottom muddy, water 2,0 to 3,0 m deep.

Station 5 (Kalengwe Channel) Upper reaches of channel, dense mats of *Ceratophyllum* on edges, 3,5 to 4,5 m deep, bottom consisting of mud and organic matter.

Station 6 (Chinchimane Channel) Channel with flowing water at the end of the Linyanti Swamp approximately 20 km south-west of the lake, water 2,0 to 4,0 m deep and very clear, bottom sandy, vegetation consisting of a variety of plants including *Ottelia, Lagarosiphon, Najas, Ceratophyllum* and *Nymphaea*.

Station 7 (*Salvinia* mat) Permanent mat of *S. molesta*, water 2,5 m deep, no submerged vegetation, rotting organic matter on bottom.

Water samples for chemical analysis were collected by means of a 2 ℓ Van Dorn water sampler, immediately below the surface and 0,5 m above the bottom.

Samples were frozen and transported in polyethylene bottles to the laboratory. After thawing and filtration, samples were analyzed for orthophosphate (PO_4-P, total dissolved phosphate (TDP), ammonium (NH_4-N), nitrate (NO_3-N), nitrite (NO_2-N), Kjeldahl nitrogen (Kj-N), sodium (Na), potassium (K), calcium (Ca), magnesium (Mg), sulphate (SO_4), chloride (Cl), reactive silicate (Si), alkalinity and conductivity, using methods described by Scott, Seaman, Connell, Kohlmeyer and Toerien (1977). The pH of water samples was determined in the field by means of a Lovibond comparator.

In July 1974, dissolved oxygen and temperature profiles at each station were recorded by means of a Hydro-Bios Grasshoff oxygen meter equipped with a thermistor probe. In January 1975, dissolved oxygen was determined using the Winkler technique (American Public Health Association, 1971) and temperature values were recorded using a standard mercury bulb thermometer which was inserted into water samples immediately after collection. Light penetration characteristics at each station were determined using a Lambda quantum photometer (model LI185) and a Secchi disc. An integrated water sample was collected at each station by means of a plastic hosepipe and analyzed for chlorophyll a by the method of Marker (1972). A portion of this sample was preserved with 4 per cent formaldehyde for a future microscopical investigation of the phytoplankton species present. A zooplankton sample was collected at each station by means of a vertical haul with a 100 µm mesh net, whilst the zoobenthos was sampled using an Ekman grab sampler. In all instances, samples were preserved with 4 per cent formaldehyde. Total zoobenthos and subsampled zooplankton samples were enumerated in the laboratory.

A diurnal study of temperature/oxygen profiles and the vertical distribution of zooplankton was conducted at station 1 over 22/23 July 1974 and 10/11 January 1975. Temperature and oxygen profiles were determined at 4-hourly intervals by the methods previously described, whilst a motorized pump was used to collect zooplankton samples from selected depths. The pumped water was passed through a 100 µm mesh zooplankton net. Subsamples of this concentrate were analysed as to species and numbers of individuals.

In January 1975, estimations of photosynthetic and respiratory rates were made at stations 1 (representing the open lake) and 5 (representing a protected bay). The light and dark bottle technique (Vollenweider, 1969) was employed and one dark and two light bottles were suspended at selected depths over a defined period of time. The decrease/increase in the oxygen content of each bottle was calculated after Winkler titration and the gross and net photosynthetic rates were estimated (Vollenweider, 1969).

RESULTS

TEMPERATURE

The weekly means of the surface water temperatures measured near station 1 in the early morning (08h00) and late afternoon (17h00) during the period 1973 to 1975 are shown in Figure 2. Surface water temperatures in Lake Liambezi ranged between a winter minimum of 15 °C and a summer maximum of 31 °C. Talling (1969) has compared the temperature ranges encountered in several African lakes and indicated that latitude plays an important part in determining seasonal temperature fluctuation. The predictive value of Talling's scale is confirmed by the observations on Lake Liambezi (18 °S) since the temperature range encountered, places it between Lake Bangweulu (11 °S), Florida Lake (26 °S), Lake Chad (14 °N) and the Aswan Reservoir (24 °N). On the basis of its temperature range, Lake Liambezi can be classified as a tropical water body (Hutchinson, 1957). However, it contrasts markedly with Lake George which is situated on the equator, and exhibits a negligible seasonal temperature variation (Talling, 1969).
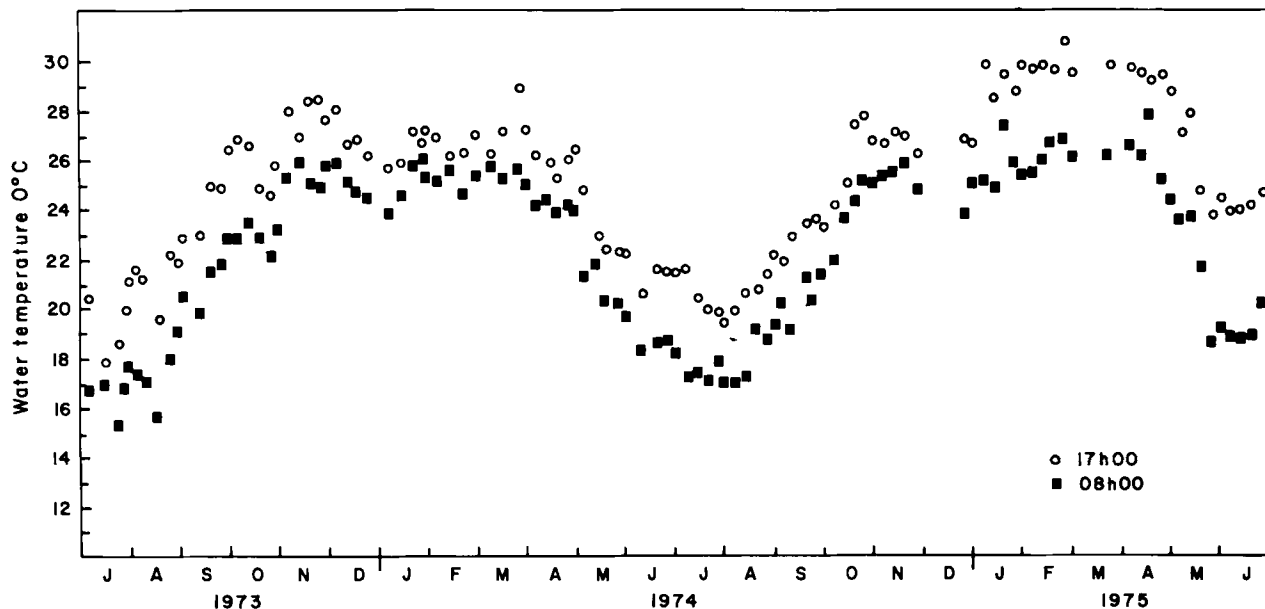

Figure 2. Maximum and minimum surface water temperatures (°C) in Lake Liambezi from July 1973 to June 1975. Each point is the mean value for one weet at station 1.

In the lake, temperature showed considerable daily variation and profiles were dependent on the time of day. Isotherms of the diurnal temperature readings taken at station 1 over 22/23 July 1974 and 10/11 January 1975 (Figs. 3 and 4) showed that during both winter and summer, a daily temperature cycle occurs in which thermal stratification develops during the day and becomes disrupted during the night. The system is therefore one in which polymixis occurs, possibly on a daily basis. This may be attributed to the shallow nature of the system which allows for rapid diurnal cooling and heating. Such a characteristic is a common feature of shallow tropical water bodies, e.g. Lake George (Viner, 1969), Lake Chad (Gras, Iltis and Lévêque-Duwat, 1967) and Lake Chilwa (Kalk, 1972).

OXYGEN

Dissolved oxygen concentrations in the surface and bottom waters at the six stations on 22 July 1974 and 12 January 1975 are presented in Tables 1 and 2. On these two visits, oxygen concentrations in the surface water were was always higher than in the bottom water. However, anaerobic conditions were not encountered. The relatively low surface oxygen values recorded throughout the lake in both visits (<120% saturation) indicated that photosynthetic activity in the waters was not particularly high. This contrasts markedly with oxygen values recorded in the water of Lake George, Uganda, where high photosynthetic activity results in consistently high
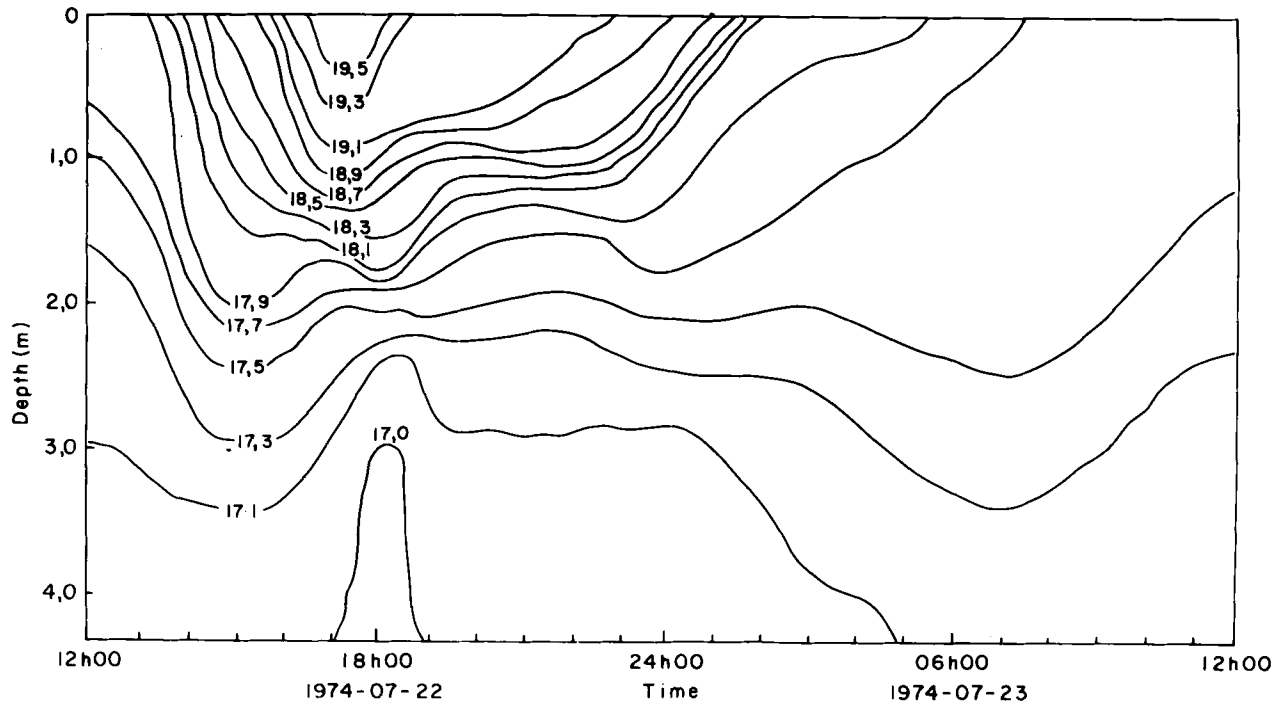

Figure 3.   Temperature isopleths (°C) at station 1, Lake Liambezi during a diurnal study in July 1974.

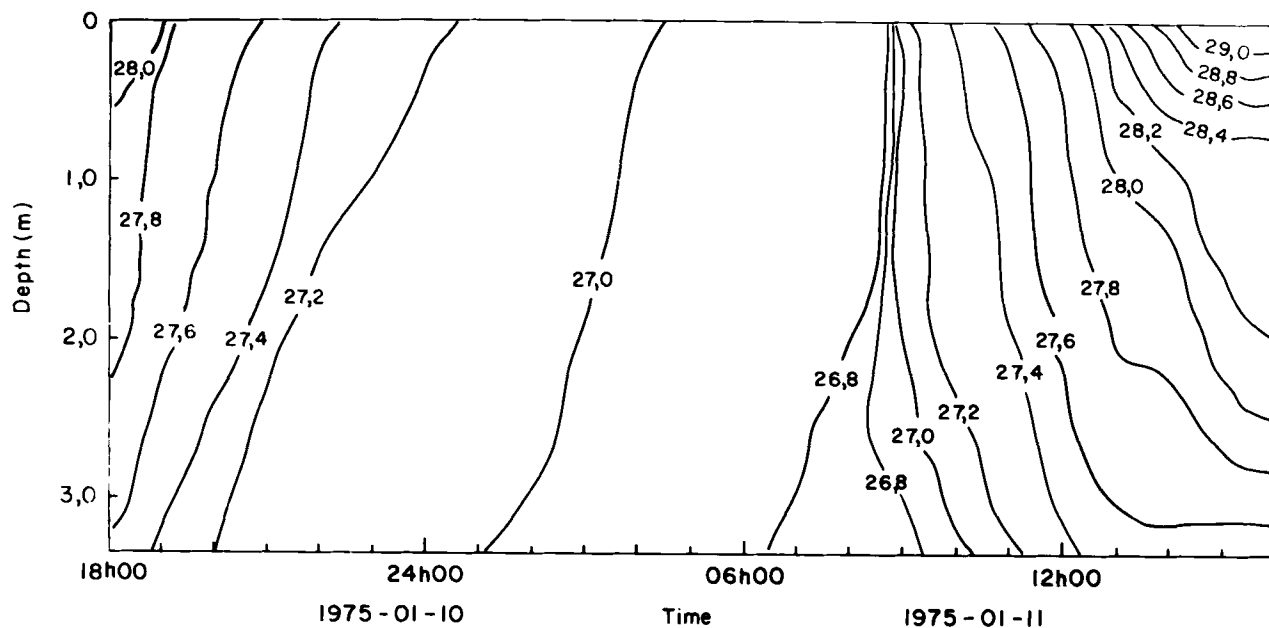Figure 4.   Temperature isopleths (°C) at station 1, Lake Liambezi during a diurnal study in January 1975.

Parameter	Station													
	1		2		3		4		5		6		7	
	S	B	S	B	S	B	S	B	S	B	S	B	S	B
$P - PO_4$ $(\mu g\ \ell^{-1})$	8	5	10	10	6	6	7	7	10	10	8	8	11	12
P - total	0,5	0,2	0,4	0,4	0,4	0,3	0,2	0,2	0,5	0,3	0,5	0,2	0,2	0,3
$N - NH_4$	0,3	0,2	0,2	0,2	0,3	0,2	0,2	0,2	0,2	0,2	0,2	0,2	0,2	0,2
$N - NO_2$ $(\mu g\ \ell^{-1})$	< 10	< 10	< 10	< 10	< 10	< 10	< 10	< 10	< 10	< 10	< 10	< 10	< 10	< 10
$N - NO_3$	0,2	0,2	0,2	0,2	0,3	0,2	0,3	0,2	0,2	0,2	0,2	0,2	0,2	0,2
N - organic	1,6	0,8	0,8	0,9	0,9	0,9	1,0	1,0	0,8	0,8	1,1	1,0	1,0	1,0
Na	16	14	14	16	12	12	14	14	12	10	9	8	12	12
K	9,1	8,4	9,1	9,4	7,2	6,8	8,0	8,4	6,8	5,9	5,6	5,0	8,2	7,8
Mg	6,0	5,0	6,0	6,0	5,0	8,0	6,0	6,0	5,0	5,0	3,0	3,0	7,0	5,0
Ca	24	25	27	34	27	27	24	29	25	24	16	17	29	28
SO_4	11	9	10	12	10	10	10	10	8	9	7	8	10	8
Cl	4	4	3	2	2	2	4	2	2	2	1	1	2	2
Si	8,4	8,5	12,9	13,4	10,8	10,6	11,8	13,0	5,5	7,2	11,7	11,2	11,9	13,5
Dissolved oxygen	8,8	8,7	10,1	9,7	9,1	7,8	10,3	10,0	10,0	9,7	7,9	10,7	8,7	4,6
Alkalinity (me ℓ^{-1})	1,06	1,06	1,12	1,47	1,06	1,01	1,00	1,16	1,00	0,90	0,63	0,64	1,11	1,04
Conductivity (mS m^{-1})	27,0	26,3	27,9	31,3	26,8	32,1	28,1	28,2	26,0	23,9	17,9	17,3	29,0	27,1

Table 1.   Chemical analyses of water samples (surface and bottom) collected from stations on Lake Liambezi (22 July 1974).   All values in mg/ℓ unless indicated otherwise.

Parameter	Station													
	1		2		3		4		5		6		7	
	S	B	S	B	S	B	S	B	S	B	S	B	S	B
$P - PO_4$ $(\mu g\ \ell^{-1})$	13	10	12	12	10	13	10	10	8	10	10	10	5	7
P - total	0,2	0,6	1,2	0,2	0,2	0,2	0,4	0,2	0,4	0,3	0,2	0,4	1,1	0,8
$N - NH_4$	0,5	1,0	0,3	0,4	0,4	0,6	0,5	0,5	0,9	1,0	0,6	0,4	0,9	1,0
$N - NO_2$ $(\mu g\ \ell^{-1})$	3	4	4	3	3	3	3	4	2	2	1	2	1	2
$N - NO_3$	0,2	0,6	0,3	0,3	0,3	0,3	0,2	0,2	0,2	0,2	0,3	0,3	0,2	0,2
N - Organic	2,4	1,7	3,2	1,4	1,0	1,3	1,3	1,1	1,1	1,0	1,4	1,7	1,4	1,0
Na	19	19	11	16	18	19	16	16	13	13	20	20	17	16
K	10	10	5,3	8,1	9,2	10	7,8	7,7	5,5	5,6	10	10	7,5	6,9
Mg	7,0	7,0	3,3	5,0	6,0	7,0	5,0	5,0	4,0	4,0	7,0	7,0	5,0	4,0
Ca	38	38	24	31	33	34	32	31	23	23	39	37	29	28
SO_4	8	7	5	5	9	10	8	8	5	6	9	9	7	5
Cl	4	5	4	5	4	5	4	5	4	3	4	3	5	5
Si	11,3	11,2	12,2	13,8	12,7	12,9	11,1	11,1	20,0	19,5	13,0	12,9	13,2	13,3
Dissolved Oxygen	6,4	4,3	6,5	3,5	4,0	1,9	6,3	5,9	5,6	5,3	-	-	2,10	1,15
Alkalinity (me ℓ^{-1})	1,60	1,61	1,03	1,29	1,41	1,46	1,31	1,29	,95	1,01	1,57	1,52	1,24	1,17
Conductivity (mS m^{-1})	41,2	39,4	23,8	31,3	35,7	36,5	32,2	32,2	20,8	19,5	39,1	38,2	30,4	28,0

Table 2.   Chemical analysis of water samples (surface and bottom) collected from stations on Lake Liambezi (12 January 1975).   All values in mg/ℓ unless indicated otherwise.

saturation values (>200% - Viner, 1969).   The lowest concentrations of dissolved oxygen were encountered beneath the *Salvinia* mat at station 6 on both sampling visits (4,6 mg $O_2\ \ell^{-1}$ and 1,15 mg $O_2\ \ell^{-1}$ in July 1974 and January 1975 respectively).   Additional observations made during the course of 1975 indicated that dissolved oxygen concentrations were extremely low under well-established *Salvinia* mats (< 1 mg $O_2\ \ell^{-1}$) in the north-western part of the lake (Table 3).   Under mats which were adjacent to open water, oxygen levels were usually high, presumably as a result of water movement under the mats.

Date	T °C	Type of *Salvinia* mat, or open water	D.O. mg ℓ^{-1}
29. 4.1975	22,0	Open water	6,3
		Medium dense mat, plants barely touching	2,2
		Dense mat, plants closely packed	0,2
24. 5.1975	20,0	Open water	7,6
		Medium dense mat	2,9
		Dense mat	0,29
3. 7.1975	20,0	Open water, *Lagarosiphon*	7,4
		Dense mat	0,7
		Medium dense mat, 100 m from open water with strong wind blowing from direction of open water	6,5
25.11.1975	25,0	Open water	9,5
		Dense mat on which secondary pioneer plants have become established	0,1

Table 3.   Dissolved oxygen values of water immediately below *Salvinia* mats of varying density, compared with values in adjacent open water areas of Lake Liambezi, on four separate sampling dates.

The diurnal variation in the oxygen content of the water at station 1 followed a pattern in which the oxygen content of the surface water increased during the daylight hours and decreased during the night (Figures 5 and 6). There was also evidence of circulation in the water column during the night of 22 July 1974 since oxygen in the bottom waters increased between 22h00 and 04h00. On 10 January 1975, little circulation was evident during the diurnal study (Figure 6). Despite evidence of daily destratification and polymixis there was always an oxygen gradient between the surface and the bottom. This gradient was more pronounced in the bottom layers indicating that the organic ooze on the bottom contributes to a large oxygen demand on the overlying waters.
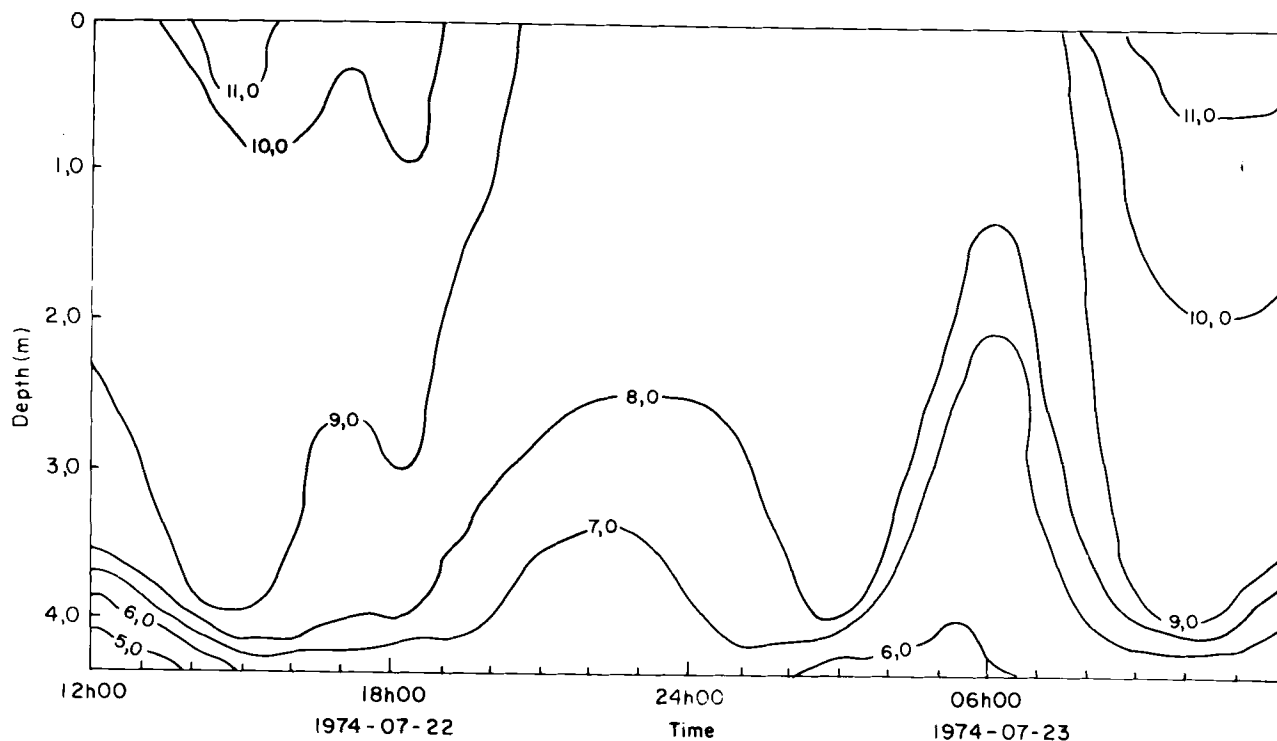
Figure 5.   Oxygen isopleths (mg O_2 ℓ^{-1}) at station 1, Lake Liambezi during a diurnal study in July 1974.
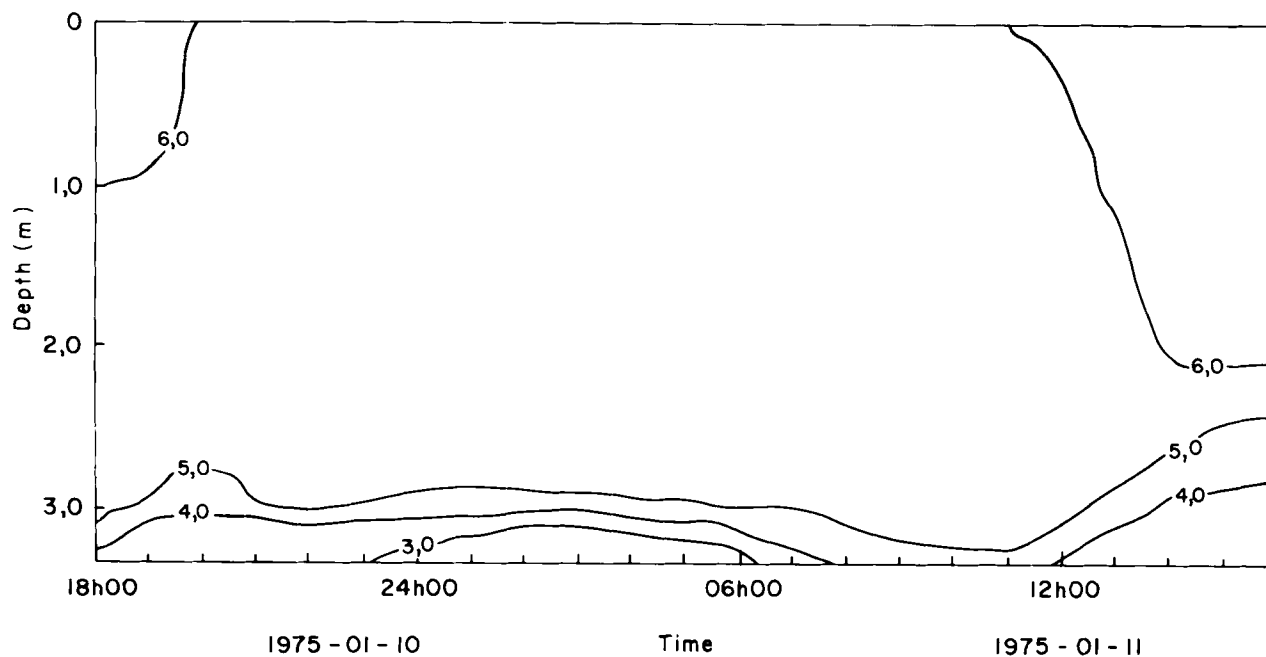
Figure 6.   Oxygen isopleths (mg O_2 ℓ^{-1}) at station 1, Lake Liambezi during a diurnal study in January 1975.

Profiles of photosynthetic and respiratory activity at stations 1 and 5 showed that there was no net photosynthesis below two metres at either station (Figure 7). Net photosynthetic rates were higher at the surface, with 0,15 mg O_2 ℓ^{-1} h^{-1} being the highest rate recorded. These rates of photosynthesis confirm that phytoplankton activity in the lake is low, particularly when compared to rates recorded for the highly eutrophic Lake George where net photosynthesis can exceed 1,0 mg O_2 ℓ^{-1} h^{-1} (Ganf, 1974). This experiment also serves to indicate that circulation of the water column in the lake is a frequent occurrence. For example, on the basis of the observed respiratory rates, the bottom waters at station 1 would lose approximately 0,6 mg O_2 ℓ^{-1} over a 12-hour period and would soon become anaerobic if there was no frequent circulation.

WATER TRANSPARENCY

Waters in the reed swamp were brown due to the presence of humic substances whilst those of the open lake were grey-green as a result of a higher algal and detrital content. It was also apparent that waters in the protected areas of the reed swamp had a greater Secchi disc transparency by comparison with the waters of the open lake (Table 4). In accordance with the above, light attenuation at open lake

Station	7.3.1974	10.6.1974	21/22.7.1974	8.10.1974	15.1.1975	24.4.1975
1	70	100	90	90	80	150
2	100	100	90	90	80	110
3	>280	200	200	180	>210	210
4	>230	>230	190	>220	>210	>220
5	-	>220	>230	210	190	210
6	-	-	220	-	-	-

Table 4. Secchi disc readings (cm) for 6 stations in Lake Liambezi, (- = NO DATA)

stations (stations 1 and 2) was greater than at stations in these protected areas (stations 3, 4, 5 and 6). However, at least 1 per cent of surface light penetrated to the bottom in the open lake and up to 10 per cent penetrated to the bottom in the sheltered areas (Fig. 8).
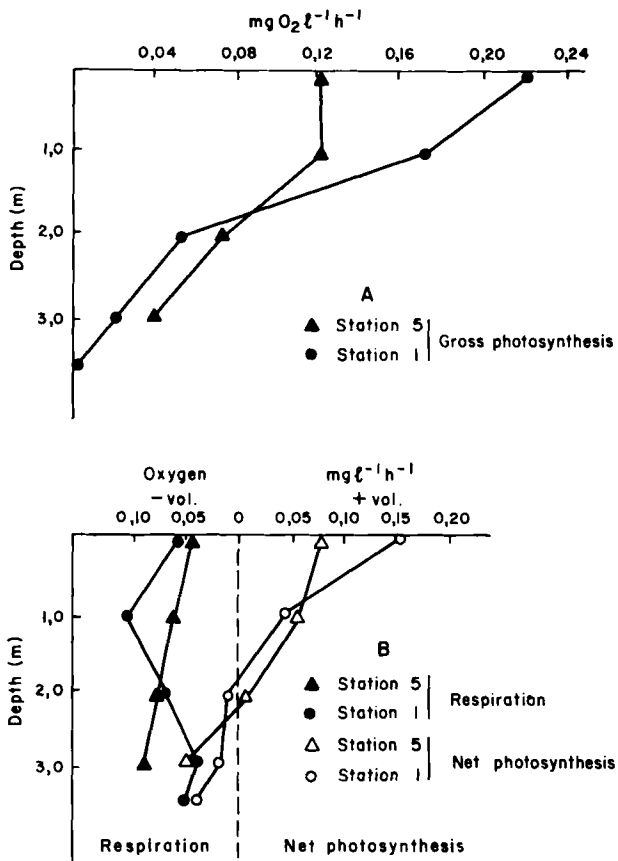

Figure 7. Profiles of (A) gross photosynthesis and (B) respiration and net photosynthesis at stations 1 and 5 in Lake Liambezi.
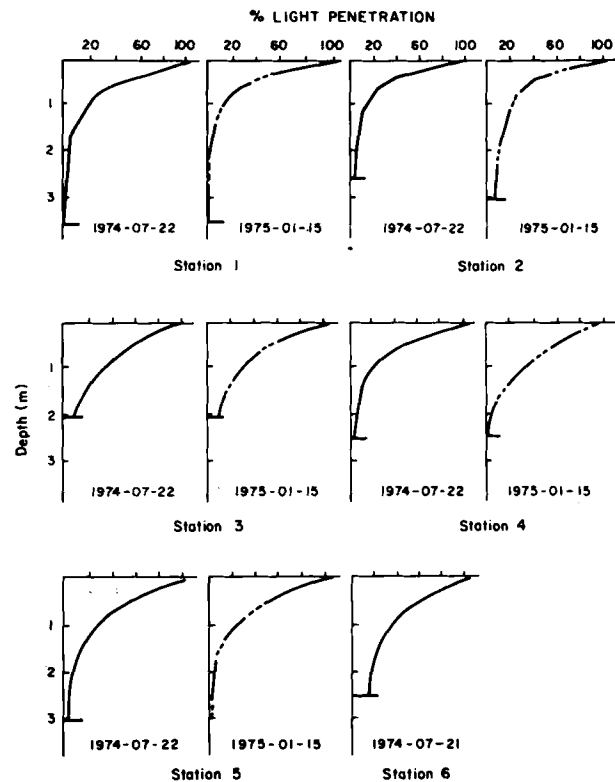

Figure 8. Light penetration profiles at six stations in Lake Liambezi for July 1974 and January 1975 (readings taken between 10h00 and 16h00).

Water transparency in the open lake showed a dependency on water level since higher Secchi disc transparency (>100 cm) was recorded in 1974/75 when the lake level was high (Figure 9). During 1973 when the lake level was low, Secchi disc transparency was usually less than 60 cm. These differences can possibly be attributed to the presence of greater quantities of detritus in the water during 1973 as a result of increased turbulence in the shallower lake.

CHEMICAL CHARACTERISTICS

Lake Liambezi water was alkaline, with the pH usually ranging between 7,3 and 8,5 (Table 5). On one oc-

Kj-N>NH$_4$-N>NO$_3$-N>NO$_2$-N indicating that the nitrogen cycle is dominated by decomposition processes. The inorganic species of nitrogen and phosphorus (e.g.

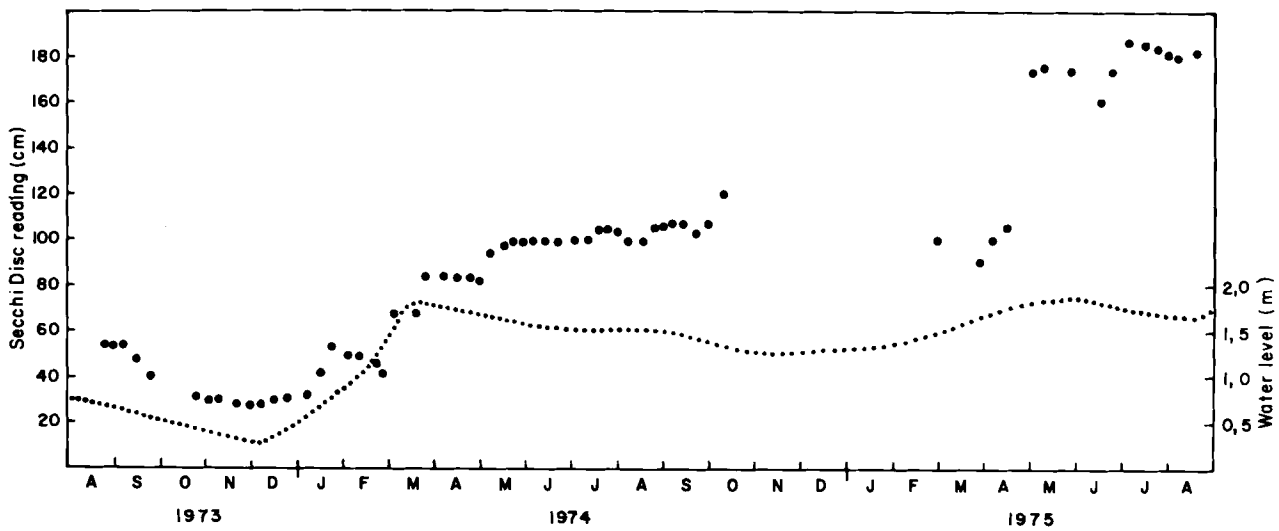| Date	Sampling station						
	1	2	3	4	5	6	7
23.3.1974	8,0	8,2	7,8	7,8	7,5	-	-
10.6.1974	8,0	8,1	8,0	7,5	7,2	-	-
21/22.7.1974	7,9	8,1	7,5	7,9	7,2	7,6	7,8
10.8.1974	8,2	8,2	7,6	8,0	7,8	-	-
22.1.1975	8,5	8,3	8,0	8,0	7,5	7,6	7,3
24.4.1975	7,5	8,4	8,0	-	6,5	-	-

Table 5.   pH values of water in Lake Liambezi

Figure 9.   Secchi disc readings (o) in the vicinity of station 1, Lake Liambezi, and water level (...) from August 1973 to August 1975.

casion (24 April 1975) a pH of 6,5 was recorded in the Kalengwe channel after a large inflow of Zambezi floodwater was experienced.

The results of the chemical analyses of water samples are presented in Tables 1 and 2. There was little difference between the chemical characteristics of the waters from the different stations and between summer and winter values of the individual constituents. Results showed that the waters were of moderate conductivity (17,3 to 41,2 mS m^{-1}) and alkalinity (0,6 to 1,4 me ℓ^{-1}) whilst the order of dominance of the major cations was Ca > Na > K > Mg. Levels of reactive silicate were also high (7,2 to 20,0 mg Si ℓ^{-1}) presumably as a consequence of the calcareous subsoils in the area. A dendrogram of similarity between the dissolved chemical constituents in the lake water is presented in Figure 10. The highest correlations existed between the conservative elements Na, K, Ca, Mg whilst little association was found between the nitrogen and phosphorus species. This pattern is consistent with the conclusions of Visser and Villeneuve (1974) that Na, K, Ca, Mg and SO$_4$ were the most reliable constituents in describing the chemistry of tropical waters since they were found to be the most frequently correlated.

Analyses of the phosphorus and nitrogen species showed that a large proportion of both these elements, was bound in the organic form. In the case of phosphorus, approximately 400 µg ℓ^{-1} existed as TDP whilst only 10 µg p ℓ^{-1} was recorded as PO$_4$-P. Nitrogen compounds predominated in the order of
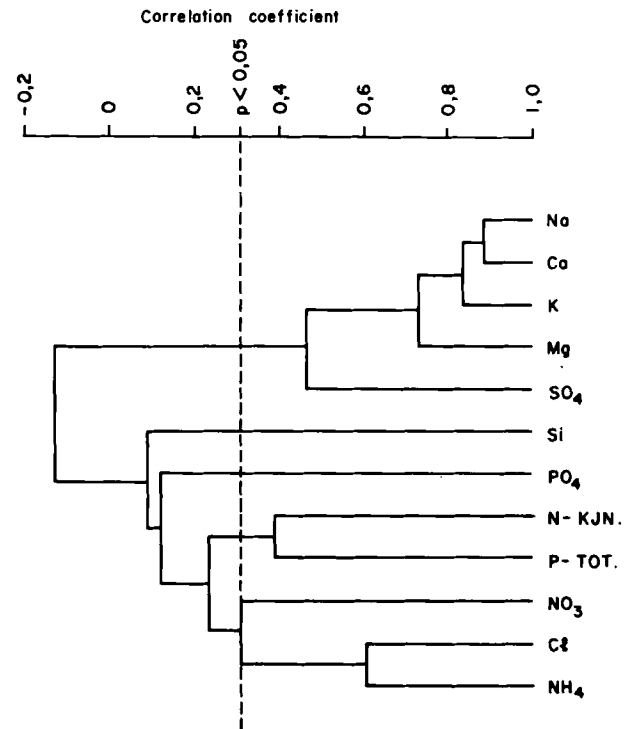

Figure 10.   A dendrogram of similarity (using group average sorting) between the dissolved chemical species in Lake Liambezi water.

NO$_3$-N, NH$_4$-N, NO$_2$-N and PO$_4$-P) are regarded as representing the forms which are available for algal growth and hence influence the productivity of the system (Vollenweider, 1968). In Lake Liambezi water, the quantities of available nutrients were generally low by comparison with levels recorded for eutrophic waters although the levels of total dissolved nitrogen and phosphorus were indeed indicative of eutrophic conditions (ccf. Vollenwieder, 1968). It is therefore apparent that the supply of the available forms of these two nutrients is rapidly utilized as it becomes available through recycling. Such a situation has been observed in Lake George, Uganda, where inorganic phosphate and nitrogen are usually undetectable whereas considerably quantities of total nitrogen and phosphorus are present (Ganf and Viner, 1973). This has been attributed to rapid recycling of the two nutrients at the high ambient temperatures. Under such circumstances nutrient dynamics are more relevant to production than are nutrient concentrations (Brylinsky and Mann, 1973).

PHYTOPLANKON

The open water phytoplankton of Lake Liambezi was found to be dominated by *Microcystis* spp. during the two sampling visits in July 1974 and January 1975.

Following Komárek (1958), these species were identified as *M. aeruginosa* forma *aeruginosa*, *M. aeruginosa* forma *flos-aquae* and *M. wesenbergii*. The phytoplankton was identified to species level using the following literature: Smith (1916); Frémy (1929); Hustedt (1930); Geitler (1932); Rich (1935); Fritsch and Rich (1937); Huber-Pestalozzi (1938); Cleve-Euler (1951); Tomasson (1957); Komárek (1958); Desikachary (1959); Prescott (1962); Skuja (1954); Welsh (1965); Rino (1969, 1971, 1972); Taft and Taft (1971); Fott (1971) and Iltis (1972).

The species recorded are shown in Table 6. The list (Table 6) contains two new species of blue-green algae; conventional descriptions of which, follow:

Gloecapsa laeta W.E. Scott, sp. nov. cells oval to' spherical, blue-green with granular content; cells with or without sheath usually laminated; cells 7-10-13 µm broad, 11-18-24 µm long (without sheath); 1-4 cells per sheath.

Gloecapsa laeta W.E. Scott, sp. nov., cellulis ovalibus vel sphaericis, cyaneo-viridibus contento granulato; cellulae cum vel sine vagina plerumque lamellata; cellulae 7-10-13 µm latae, 11-18-24 µm longae (sine vagina); cellulae 1-4 in quaque vagina.

Class	CYANOPHYCEAE	Family	Ankistrodesmaceae
Family	Chroococcaceae		*Ankistrodesmus falcatus* (Corda) Ralfs
	Aphanocapsa elachista W. et G.S. West		*Selenastrum minutum* (Näg). Collins
	A. pulchra (Kütz.) Rabenh.		
	Aphanothece stagnina (Spreng.) A. Braun	Class	CONJUGATOPHYCEAE
	Coelosphaerium kützingianum Näg	Family	Desmidiaceae
	Gloecapsa laeta sp. nov.		
	Merismopedia glauca (Ehrenb.) Kütz.		*Closterium acutum* var. *variabile* (Lemm.) Krieger
	M. punctata Meyen		*Staurastrum excavatum* var. *planctonicum* Krieger
	Microcystis aeruginosa forma *aeruginosa* (Kütz) Elenkin		
	M. aeruginosa Forma *flos-aquae* (Wittr.) Elenkin	Class	EUGLENOPHYCEAE
	M. wesenbergii Komárek	Family	Euglenaceae
	Synechococcus cedrorum Sauvageau		*Phacus orbicularis* Hübner
Family	Oscillatoriaceae		
	Lyngbya limnetica Lemm.	Class	DINOPHYCEAE
	Spirulina liambeziensis sp. nov.	Family	Glenodiniaceae
Family	Nostocaceae		*Glenodinium pulvisculus* (Ehrenb.) Stein
	Anabaena cylindrica Lemm.	Family	Ceratiaceae
	A. solitaria Kleb.		
	A. solitaria forma *planctonica* (Brunnth.) Komárek		*Ceratium hirundinella* (O.F. Müll.) Schrank.
	A. torulosa (carm.) Lagerh.		
	Aphanizomenon flos-aquae forma *gracile* Lemm.	Class	BACILLARIOPHYCEAE*
		Family	Coscinodiscaceae
Class	CHLOROPHYCEAE		*Melosira fennoscandica* Cleve-Euler
Family	Hydrodictyaceae		*M. granulata* (Ehrenb.) Ralfs
	Pediastrum boryanum (Turp.) Meneghini		*M. granulata* var. *augustissima* O.F. Müll.
	P. duplex var. *clathratum* (A. Br.) Lagerh.	Family	Fragilariaceae
	P. simplex (Meyen) Lemm.		*Fragilaria brevistriata*
	P. tetras var. *tetraodon* (Corda) Rabenh.		*F. construens* (Ehrenb.) Grunow
Family	Botryococcaceae		*F. fonticola* Hustedt
	Botryococcus braunii Kütz.		*F. pinnata* Ehrenb.
Family	Oocystaceae	Family	Naviculaceae
	Lagerheimia subsala Lemin.		*Cymbella cistula* (Hemprich) Grunow (cf. Hustedt, 1949)
	Tetraedron minimum (A. Br.) Hausgirg		*Navicula cryptocephala* Kütz.
	T. muticum (A. Br.) Hausgirg		*N. viridula* Kütz.
	T. regulare Kütz.		
Family	Scenedesmaceae	Family	Epithemiaceae
	Crucigeria apiculata var. *truncata* (G.M. Smith) Ahlstrom et Tiffany		*Epithemia zebra* (Ehrenb.) Kütz.
	Scenedesmus abundans (Kirchner) Chodat		*Rhopalodia gibba* (Ehrenb.) Kütz.
	S. acuminatus (Lagerh.) Chodat	Family	Nitzschiaceae
	S. bijuga (Turp.) Lagerh.		
	S. perforatus Lemm.		*Nitschia amphibia* Grunow
	S. quadricauda (Turp.) Bréb.		*N. confinis* Hustedt

Table 6. A list of algal species recorded in Lake Liambezi. *Kindly identified by R.E.M. Archibald

G. laeta has been isolated into culture and it has been given the NIWR culture number WR20. A culture has been sent to the Cambridge Culture collection, United Kingdom. The alga is illustrated in Plate 1.
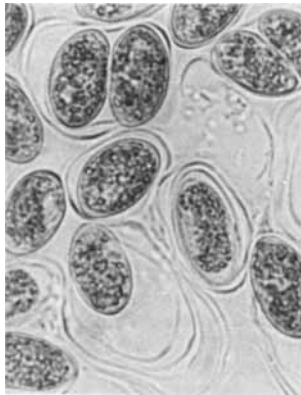

Plate 1. A Photomicrograph of <u>Gloeocapsa laeta</u> sp. nov.

Spirulina liambeziensis W.E. Scott, sp. nov. trichomes 1,2 μm broad; regularly coiled; distance between the turns 4-6 μm; diameter of coil 5,1-6,3-7,5 μm; filaments short with 3-5 spirals; sheath absent.

Spirulina liambeziensis W.E. Scott, sp. nov. trichomata 1,2 μm lata; ordinatim circinata; distantia 4-6 μm inter anfractos; anfractus 5,1 - 6,3 - 7,5 μm diametro; filamenta brevia anfractibus 3-5; vagina absenti.

S. liambeziensis was present in the euplankton on both sampling trips albeit in small numbers. A type specimen has been sent to the Albany Museum in Grahamstown, South Africa. The alga is illustrated in Plate 2.

Plate 2. A Photomicrograph of <u>Spirulina liambezien-sis</u> sp. nov.

As in the cases of Lake Chad (Iltis and Compére, 1974) and Lake Bangweulu (Thomasson, 1957), the waters of Lake Liambezi support a varied phyto-plankton assemblage. The dominance of the waters by *Mycrocystis* spp. can be attributed to the high temperatures and pH which favour the growth re-quirements of such blue-green algal species (Fogg, Stewart, Fay and Walsby, 1973). However, the si-tuation is not as extreme as that encountered in Lake George, Uganda where the phytoplankton consists exlusively of blue-green algae (Ganf, 1974).

On the basis of chlorophyll a concentrations, the standing crop of algae in the lake was not high (Table 7). Chlorophyll a concentrations were higher in January 1975 than July 1974 and the only evidence of an excessively high phytoplankton population was encountered at station 3 in January 1975 where a diatom bloom was present (104 μg chl $a\,\ell^{-1}$).

Station	July 1974	January 1975
1	7	19
2	10	14
3	3	104
4	2	5
5	-	4
6	2	1

Table 7. Chlorophyll a values in Lake Liambezi (All values in μg chl $a\,\ell^{-1}$, - = no sample collected).

Zoobenthos

It was not possible in the time available to make a thorough study of the zoobenthos due to the large number of samples required to obtain a statistically reliable estimate of populations. However, from the samples collected during the July 1974 visit, it is possible to obtain some indication of the nature of the benthos in the different areas (Table 8).

All benthic samples contained large amounts of organic matter. The greatest numbers of benthic invertebrates were found in the Chinchimani channel (station 6) where the sandy bottom was strewn with *Hippopotamus* dung. Most benthic samples were dominated by Chironomids, Ceratopogonids and various Oligochaetes. There were also some Ephemeroptera, Zygoptera and Trichoptera. One of the Trichoptera was identified as the rare Hydroptilid *Tricho-leiochiton* (K.M.F. Scott - personal communication).

Taxa	1	2	3	4	6 Sandy	6 Muddy
Chironomids	1 583	1 333	417		4 667	4 000
Ceratopobonids	83	83	83		667	
Chaoborus	333					
Ephemeroptera		83			333	167
Trichoptera						167
Zygoptera						167
Hirudinea						167
Ilyodrilus	1 000	500	167		667	
Limnodrilus	83	83			1 333	
TOTAL	3 082	2 082	667	0	7 667	4 668
Mollusc Shells:						
Mutela				167		
Bulinus		83		1 500	33	
Biomphalaria				667		
Lymnaea				583		

Table 8. Zoobenthos numbers m^{-2} at 5 stations in Lake Liambezi from samples collected in July 1974.

Molluscs were the dominant invertebrates in the North-Central part of the lake, but particularly so at station 4 where a luxurious growth of the sub-merged macrophyte *Lagarosiphon* was present. The molluscs included the large *Mutela* bivalve and two operculates *Bellamya* and *Lanistes*. Shells of Bulinus, Lymnae and Biomphalaria, found at stations 2, 3 and 4 indicate shallower conditions in the lake's history. Their presence also suggest the possibility of the mammalian trematode diseases paramphistomiasis, fascioliasis and schistosomiasis

(for which trematodes they are intermediate hosts respectively) being found in the vicinity of the lake.

Zooplankton

The dominant zooplankter of the lake was *Bosmina longirostis* (O.F. Müller) whilst the dominant rotifers were various *Brachionus* species, including *Brachionus calyciflorus* Pallas, *Brachionus falcatus* Zacharias, *Brachionus caudatus* f. *provectus* Ahlstrom and *Brachionus quadridentatus* Hermann. Other zooplankters included the copepods *Diaptomus congruens* Sar and *Thermocyclops* spp., the cladocerans *Ceriodaphnia reticulata* (Jurine), *Moina dubia* Richard, *Diaphanosoma excisum* Sars, *Chydorus* sp., *Alona* sp., *Macrothrix* sp. *Pleuroxus* sp., the rotifers *Tetramastix opoliensis* Zacharias, *Filinia pejleri* Hutchinson, *Trichocerca* cf. *insignis*, *Anureopsis fissa* Gosse, *Mytilina ventralis* Ehrenberg, *Trichocerca chattoni* de Beauchamp, *Asplanchna* sp., *Keratella tropica* Apstein, *Keratella cochlearis* Gosse, *Hexarthra* sp., *Epiphanes* sp., and *Lecane luna* O.F. Müller, and the coelenterate medusoid *Limnocnida tanganyicae* Günther.

The zooplankton community composition appeared to be similar at all stations although numbers of the individual species were always highest at stations 1, 2 and 3 (Fig. 11). These stations represent the open water situation in the lake (stations 1 and 2) and
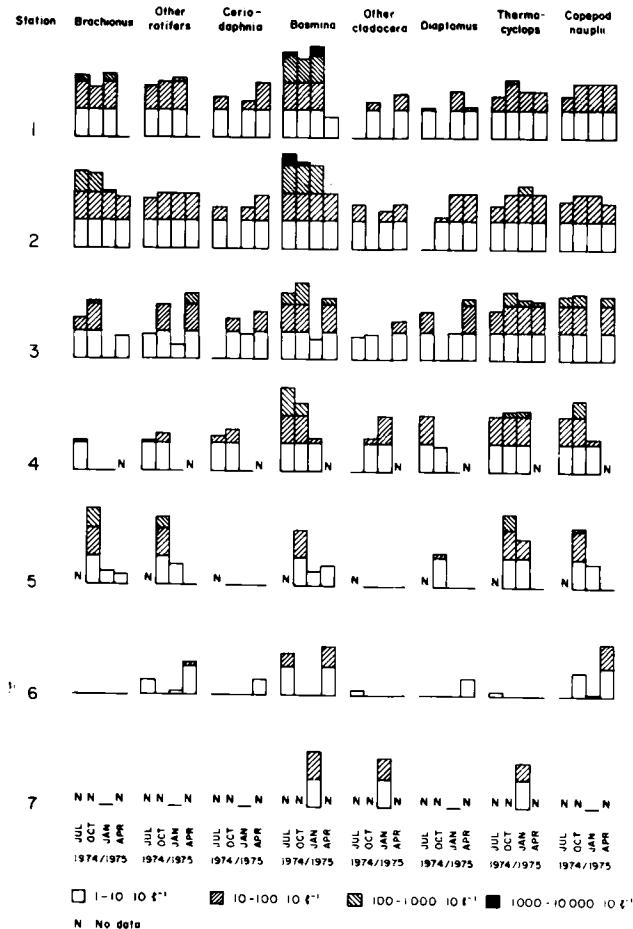

Figure 11. The composition and seasonal abundance of zooplankton at seven sampling stations in Lake Liambezi.

that of an enclosed bay where little submerged macrophyte growth was present. In areas where flowing water and/or macrophyte growth was present (stations 4, 5, 6 and 7) zooplankton populations appeared to be consistently low. In general, the most notable aspect of the zooplankton is that the species were ubiquitous forms i.e. they were as likely to be found in the littoral zones as in the open water. The lake, being shallow, can be considered as an extended littoral zone where the large variety of zooplankton species thrive on the decaying organic debris in the water column. The zooplankton composition differs from that of other shallow tropical African lakes, mainly by the dominance of *B. longirostris*. In the more eutrophic lake George, Uganda, *Thermocyclops* dominates almost to the exclusion of other species (Burgis, Darlington, Dunn, Ganf, Gwahaba and McGowan, 1973). In Lake Chilwa, Malawi, which has a large conductivity range, periodic flooding and low fish populations, large Cladocerans (*Diaphanosoma*, *Moina* and *Daphnia*) and Copepoda dominate (Kalk and Schulten-Senden, 1977). The zooplankton community composition of Lake Liambezi appears to be intermediate between that of Lake George and that of eutrophic Transvaal impoundments (Kruger, Mulder and van Eeden, 1970; Seaman, 1977). In these impoundments the zooplankton was dominated by *Daphnia*, *Bosmina* and *Thermocyclops*.

Effective fish predation probably plays an important role in determining the zooplankton community composition. In this respect, larger Cladocerans will be preyed on preferentially until only the smallest (*Bosmina*) survive, as in Lake Liambezi. Under heavier grazing pressure, even *Bosmina* becomes eliminated leaving the elusive *Thermocyclops* as dominant. The shallowness of Lake Liambezi ensures that fish populations do not concentrate along the edges, but are well distributed (van der Waal, 1976). This situation leaves the zooplankton with no safe refuge in the system.

The diurnal vertical distributions of the dominant zooplankters in the water column at station 1 on 22/23 July 1974 and 10/11 January 1975 are presented in kite diagrams (Figs 12 to 15). There did not appear to be a consistent pattern of zooplankton distribution during these two studies, which may possibly be attributed to the shallowness of the system. However, there were indications of vertical migration, but the individual species behaved differently. The factors causing these migrations cannot in the present context be discussed in detail due to the lack of information. However, the mass movement of zooplankton is usually caused by certain stimuli, e.g. light, pH, food availability and competition (Hutchinson, 1967). In Lake Liambezi, where probably the most important zooplankton food is detritus, food availability and competition can be ruled out as factors since the polymictic nature of the lake results in the uniform distribution of food. It appears more likely that the stimuli could be related to physical factors such as light, pH or temperature. However, these observations do indicate that the zooplankton as a food source for fish is well distributed throughout the water column during the day and night.

Fish

According to van der Waal (1976), most of the 43 fish species in the lake are to be found in the open water where populations are highest. Gut analyses showed that the larger cichlid species feed on algae and zooplankton whilst the smaller fish species (which are numerically dominant) feed on water insects. It was found that only one fish species (*Tilapia rendalli*) feeds exclusively on macrophyte material whilst *Haplochromis giardi* and *H. codringtoni* are more selective and feed on molluscs and water lily
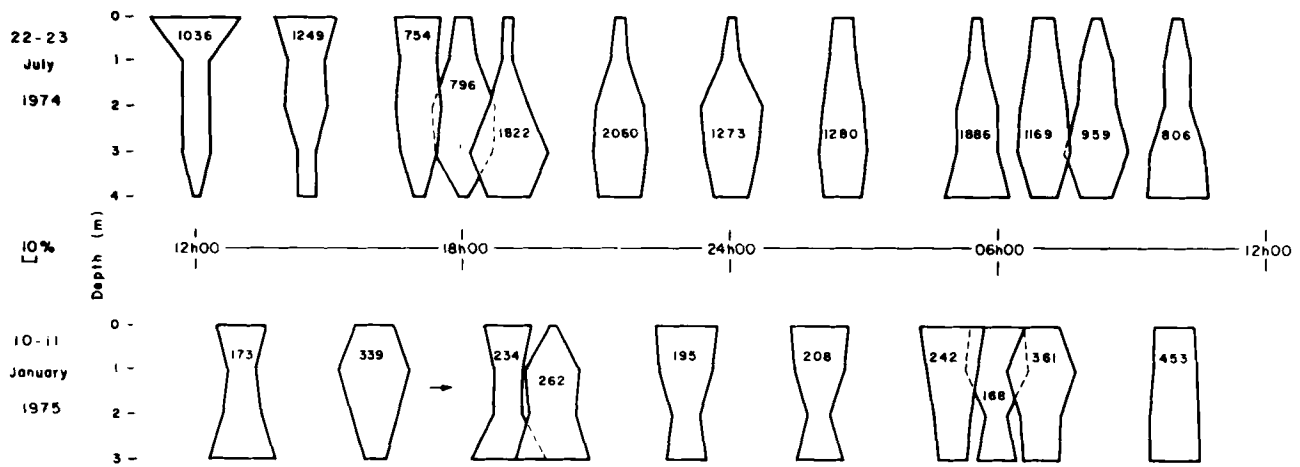
Figure 12.   The vertical distribution of *Bosmina longirostris* in Lake Liambezi during diurnal studies in July 1974 and January 1975.
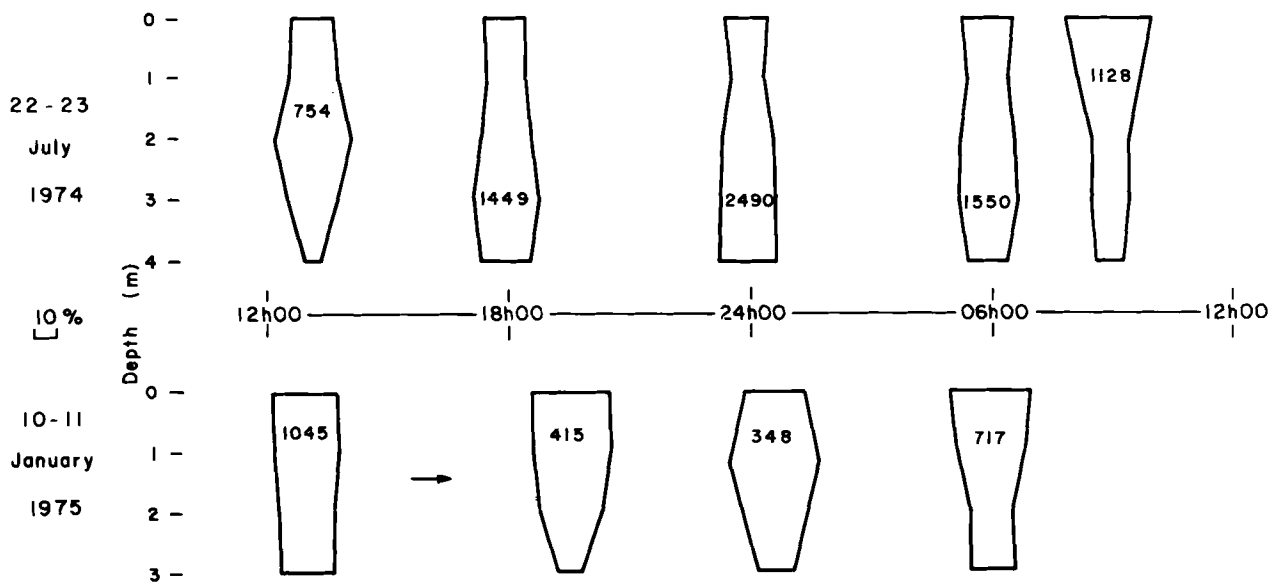
Figure 13.   The vertical distribution of rotifers in Lake Liambezi during diurnal studies in July 1974 and January 1975.

seeds respectively. Three mormyrid species and *Synodontis* live on zoobenthos. A large number of predatory species are found in the lake giving an indication of the stability of the food pyramid in the system.

DISCUSSION

Lake Liambezi can essentially be divided into two zones. The first is the open expanse of water in which water transparency is low and populations of biota high, and the second consisting of the network of lagoons and channels contained within the *Phragmites* reed swamp. In this latter zone, water transparency is higher and larger populations of submerged and floating macrophytes are present.

In the open lake zone, there is a regular circulation of the water column as a consequence of wind action and nocturnal cooling of the surface waters. As a result of this circulation, dissolved oxygen in the water column appears to be always present at levels not detrimental to the well-being of zooplankton and fish. It should be noted, however, that even in shallow tropical systems the occurrence of extended calm periods can produce the depletion of oxygen and a mass mortality of fish and other aquatic life (Greenwood, 1976). It is also evident that circulatory and mechanical processes in the reed swamp area are not as vigorous as those in the open lake, hence the low oxygen levels under *Salvinia* mats in this zone and the higher water transparency. The reed swamp area thus provides an ideal habitat for
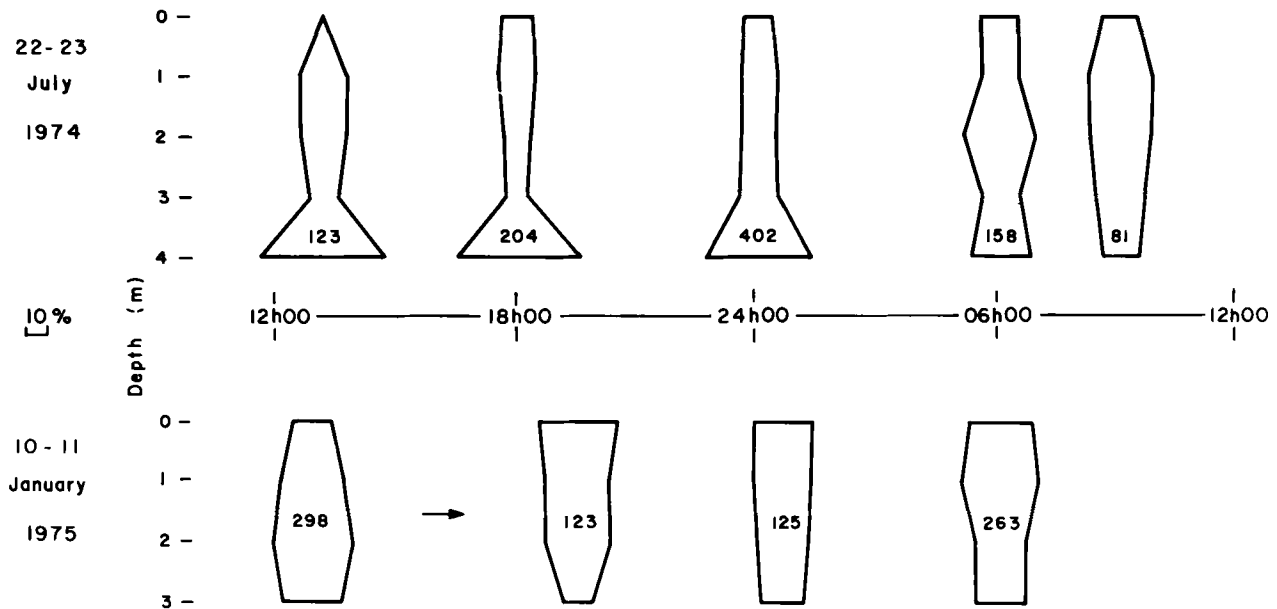
Figure 14.   The vertical distribution of Cyclopoids in Lake Liambezi during diurnal studies in July 1974 and January 1975.
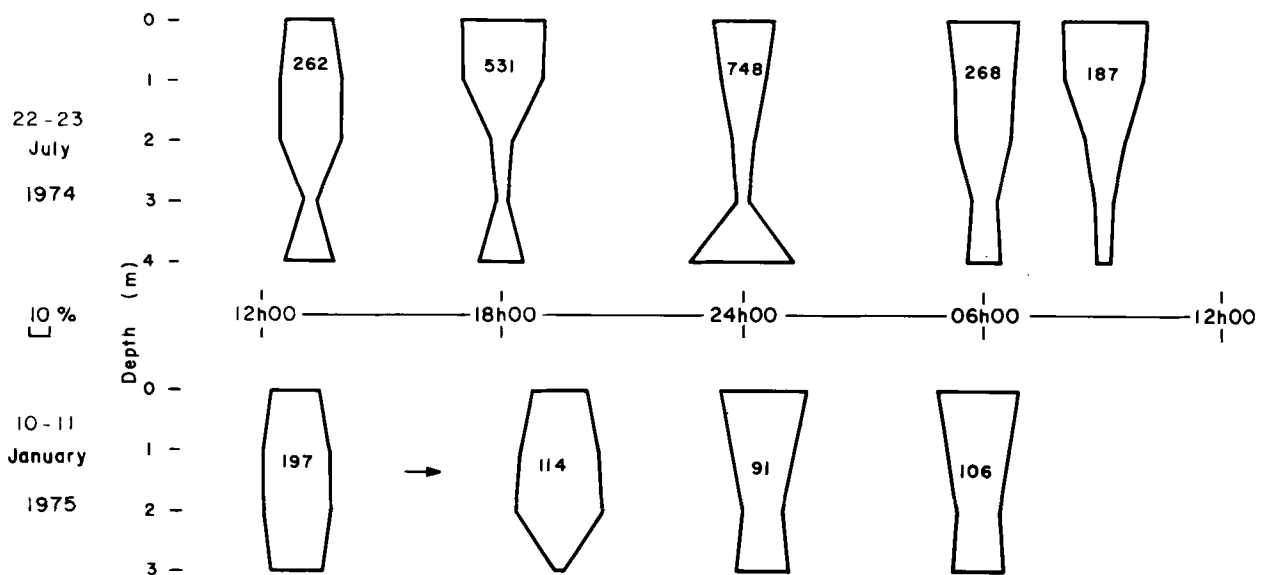
Figure 15.   The vertical distribution of Copepod nauplii in Lake Liambezi during diurnal studies in July 1974 and January 1975.

other rooted macrophytes which are able to thrive in secluded bays and channels.

Wind direction over Lake Liambezi is westerly to south westerly (van der Waal, 1976). This appears to play a significant role in the distribution of *S. molesta* in the system since plants tend to be blown into the reed swamp were the most dense mats are found. In some instances, it was observed that secondary colonization of *Salvinia* mats was in progress indicating the stability of these mats in the reed swamp. It is also envisaged that wind direction will play a considerable role in changing the morphometry of Lake Liambezi. This is because the winds stir up the water of the open lake and

drive the sediment-laden water into the reed swamp to the west and south-west. As a result of decreased turbulence within the swamp system, a considerable amount of this material is deposited. The net effect is thus one in which the lake bottom is raised in the west and south-west and eroded in the east and north-east. As a consequence, it is postulated that the reed swamp will encroach on the open water which will itself encroach on to its eastern and north-eastern shoreline. Weisser (1978) reports that a similar situation has occurred in the Neusiedler See, Austria, where the lake has shifted its geographical position within recent history. The situation for Lake Liambezi is depicted in Figure 16. However, these processes do not preclude
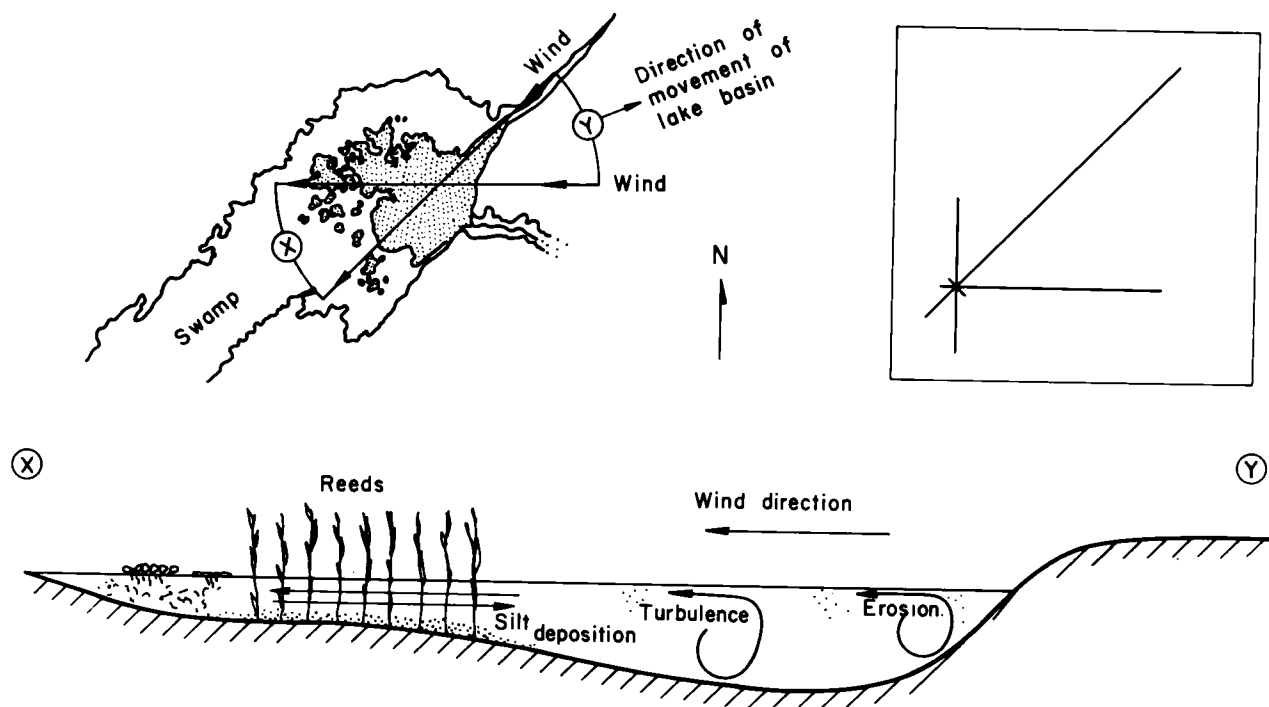
Figure 16. A schematic representation of the effect of wind on the direction of movement of the Lake Liambezi basin (inset the 1974 windrose for the lake based on daily data).

the complete coverage of the open water by reeds during extended periods of low water content. Such a situation has occurred in the past, after which reopening was facilitated by a long drought period and burning of the dry reed material (van der Waal, 1976).

Nutrient input into the lake is mostly via slow-flowing rivers which take approximately 6 months to reach the lake from their origins in Angola (van der Waal, 1976). The surrounding reed swamp appears to act as a nutrient sponge which absorbs available nutrients and releases nutrients in detrital form into the open lake. The availability of nutrients to algae is therefore dependent on recycling, and on the rates of decomposition of detritus in the water. Since most of the ichythyomass is dependent on the quantities of zooplankton and algae in the water, it follows that the reeds are the most important primary producers in the system since all levels of the food chain in the open lake depend on them for the availability of organic material.

Lake Liambezi has a great fishery potential, but this depends on the maintenance of a large open body of water and on direct access to it.   At present, access has been from two directions, the south-east where no swamp exists, and the north-west where fishing is carried out from protected islands in the channels of the reed swamp. The fishing areas in the north-west are being threatened by the encroachment of *Salvinia* mats which, as has been shown, result in habitats unsuitable for fish or zooplankton populations. Because of its floating nature, *Salvinia* can rapidly colonize new areas and therefore poses a threat to the open water of the lake.   It has been demonstrated that the growth of *Salvinia* in Lake Liambezi can be curbed by the application of selective herbicides without detrimental effect (Edwards and Thomas, 1977). It is therefore imperative that populations of the weeds be monitored and action taken if the open water area becomes threatened.

CONCLUSIONS

1. Polymixis and wind-assisted circulation ensure that oxygen concentrations in Lake Liambezi are high at all depths in the open water.

2. Water transparency is higher in the lagoons and channels of the more protected swamp area than in the open water. However, photosynthesis occurs throughout the water column at all parts of the lake.

3. Primary production in the open water is low and the reeds appear to be the most important primary producers in the system. The transfer of energy and nutrients from the reeds to the open water in the form of detritus appears to be the most important fact in maintaining high populations of invertebrates and fish.

4. The open water supports the largest populations of phytoplankton, zooplankton and fish.

5. Future management of the system should involve the careful monitoring of encroaching *Salvinia* mats as they appear to have a detrimental effect on the fishery potential.

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KEY WORDS: Shallow tropical lake, limnology, water quality, biological characteristics, phytoplankton, zooplankton, Gloecapsa laeta sp. nov., Spirulina liambeziensis sp. nov., Salvinia infestations.