

CHANGES IN PHYTOPLANKTON PRIMARY PRODUCTIVITY AND BIOMASS  
IN LAKE VICTORIA (UGANDA)

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Submitted to the Faculty  
of  
Graduate Studies  
The University of Manitoba  
by  
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In Partial Fulfilment of the  
Requirements for the Degree  
of  
Master of Science  
Department of Botany

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CHANGES IN PHYTOPLANKTON PRIMARY PRODUCTIVITY AND  
BIOMASS IN LAKE VICTORIA (UGANDA)

BY

ROSE MUGIDDE

A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in  
partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

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## ABSTRACT

Mugidde, Rosemary. M. Sc., The university of Manitoba, 1992.  
Changes in phytoplankton primary productivity and biomass in Lake Victoria (Uganda). Major Supervisor; Dr. R.E. Hecky.

Phytoplankton primary productivity and biomass of Lake Victoria, Uganda were studied during 1989-91. The daily integral production (IPD) was between  $8-20 \text{ g O}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  offshore and  $8-43 \text{ g O}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  inshore, which is about a two fold increase over values obtained in a study conducted 30 years ago. The modern, maximum productivity per unit chlorophyll ( $P_{\text{max}}$ ) is lower than historic but still high when compared to literature values. Chlorophyll-a (Chl) ranged from  $8-40 \text{ mg} \cdot \text{m}^{-3}$  offshore and  $20-70 \text{ mg} \cdot \text{m}^{-3}$  inshore, and this high algal biomass causes rapid extinction of light. Integral photosynthesis is now light limited by self shading which causes low mean light intensities in the water column ( $I_{24}$ ) of  $(2-3 \text{ mEin} \cdot \text{m}^{-2} \cdot \text{min}^{-1})$ . The increases in productivity and biomass have been accompanied by phytoplankton taxonomic changes from diatoms to predominantly cyanobacteria, especially the filamentous heterocystous cyanobacteria which now seem to have a biological advantage in Lake Victoria.

The increases in photosynthesis over the historic values might be due to reduced herbivory because of fish community changes or increased nutrient loading. However, further increases in daily integral production will not be possible because of self-shading effects.

## FORWARD

Chapter II was formatted, submitted and accepted for publication in the Vern. Internat. Verein. Limnol. journal. The authorship is Mugidde. R.

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## LIST OF ABBREVIATIONS

Chl	chlorophyll-a concentrations ( $\text{mg} \cdot \text{m}^{-3}$ )
P	the rate of photosynthesis
IPH	hourly integral production per unit area ( $\text{g O}_2 \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ )
IPD	daily integral production per unit area ( $\text{g O}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ )
$nP_{\text{max}}$	maximum photosynthesis per unit volume $\text{mg O}_2 \cdot \text{m}^{-3} \cdot \text{h}^{-1}$ ) as in Talling (1965)
$P_{\text{max}}$	maximum rate of photosynthesis per unit of chlorophyll-a observed as in Talling (1965) ( $\text{mg O}_2 \cdot \text{mg}$ $\text{chl}^{-1} \cdot \text{m}^{-3} \cdot \text{h}^{-1}$ )
$P_{\text{opt}}$	maximum rate of photosynthesis per unit of chlorophyll at optimal PAR as in Fee 1990; ( $\text{mg O}_2 \cdot \text{mg chl}^{-1} \cdot \text{m}^{-3} \cdot \text{h}^{-1}$ )
$\alpha^B$	slope of the photosynthesis vs PAR curve at low PAR values, divided by chlorophyll ( $\text{mg O}_2 \cdot \text{mg chl}^{-1} \cdot \text{mEin}^{-1} \cdot \text{m}^{-2}$ )
$P_{\text{M}}^B$	the rate of photosynthesis at optimal PAR value, divided by chlorophyll ( $\text{mg O}_2 \cdot \text{mg chl}^{-1} \cdot \text{m}^{-3} \cdot \text{h}^{-1}$ )
PAR	photosynthetically available radiation ( $\text{mEin} \cdot \text{m}_2 \cdot \text{min}^{-1}$ )
k	total vertical light extinction coefficient ( $\text{ln} \cdot \text{m}^{-1}$ )
$I_k$	light intensity which measures the onset of light saturation of photosynthesis ( $\text{mEin} \cdot \text{m}^{-2} \cdot \text{min}^{-1}$ ).
$I_{24}$	mean light intensity in the water column over 24 hours ( $\text{Ein} \cdot \text{m}_2 \cdot \text{min}^{-1}$ )
$I_0$	light intensity just below the water surface
$z_m$	mixed depth layer (m).
SD	Secchi depth in metres



d/f day hour factor in hours (h)  
n number of observations  
std standard deviation

## INTRODUCTION

Phytoplankton photosynthesis, composition and abundance in relation to thermal and nutrient chemistry of Lake Victoria, near Jinja, Uganda were studied by limnologists in the 1950s and 1960s (Fish 1952, 1957; Talling 1957a, b; Evans 1962; Talling 1965; Talling and Talling 1965; Talling 1966). In the 1960s integral photosynthesis was 5-11 g O<sub>2</sub>.m<sup>2</sup>.d<sup>-1</sup> offshore and 10-11 g O<sub>2</sub>.m<sup>2</sup>.d<sup>-1</sup> inshore (Talling 1965). At that time the phytoplankton was composed primarily of colonial coccoid Myxophyceae during stratification, with a diatom community of Melosira and Stephanodiscus predominating during the mixing period of July-August.

Since those earlier studies, there have been changes in the catchment of Lake Victoria primarily caused by population increase and urbanization. The lake and its surrounding lands are heavily utilised by the local population for fishing, cultivation, water supply, woodfuel, grass cutting and animal grazing. Other changes in land use practices in the watershed include use of fertilisers, pesticides, herbicides and intense deforestation (Bugenyi and Balirwa 1989). The impacts of these activities remain to be assessed. The disturbances in the drainage basin, industrial influent and sewage disposal into the lake together with changing atmospheric chemistry (Hecky and Bugenyi 1992) may have led to markedly increased nutrient input into the lake. Nutrient enrichment from these sources could cause increased phytoplankton biomass and

productivity. Indeed, there are recent observations that the nutrient chemistry of Lake Victoria has changed (Hecky and Mungoma 1990; Hecky and Bugenyi 1992; Hecky 1993; Bootsma and Hecky, Submitted) and algal blooms are more prominent (Ochumba and Kibaara 1989).

Profound changes have also occurred in the food-chain relationships and energy flow patterns within Lake Victoria (Ligtvoet et al. 1989; Witte et al. 1992). Over-exploitation of the fisheries and the establishment of the introduced piscivore, Nile Perch (Lates niloticus) and algivorous, Nile Tilapia (Oreochromis niloticus L.) in Lake Victoria over the last three decades have been accompanied by reduction in fish species diversity (Ogutu-Ohwayo 1990a, b; Witte et al. 1992; Goldschmidt and Witte 1992). These introduced fish species along with the native, but now more numerous, Rastrineobola argentea currently dominate the fish community, having replaced the endemic haplochromines species flock (Ogutu-Ohwayo 1985; Ogari 1985; Wandera 1988; Witte et al. 1992). Lake trophic structure may have changed as a result of increased predator abundance at the top of the food web. It is believed that decline of the endemic planktivorous fish species has eased predation pressure on the invertebrate community such as the shrimp, Caradina nilotica, molluscs and insects (Mbahinzireki 1990; Witte et al. 1992) while increased zooplanktivory by the now abundant species R. argentea and large invertebrates (chaoborids, chironomids; Mbahizireki and

Ndawula 1990) may have reduced zooplankton abundance.

According to the trophic cascade theory, increased planktivory would cause decreased zooplankton populations and decreased grazing pressure on the algae resulting in increased algal biomass and productivity (Carpenter et al. 1985). It seems possible that the increase in the abundance of introduced fish species into Lake Victoria and the reduction of many of the original trophic groups could have altered the energy flow in these lake communities and could cause increases in phytoplankton production and biomass. Alternatively, phytoplankton crop and production may have increased because more abundant invertebrates have enhanced internal nutrient regeneration from bottom detritus into the water column.

Given the significant changes occurring in Lake Victoria and its catchment, and evidence of eutrophication, a study of the current limnology of the lake was undertaken by researchers at the Uganda Freshwater Fisheries Research Organisation, Jinja to address concerns about future fish production. The purpose of this study was to determine the modern rates of phytoplankton photosynthesis and biomass (as chlorophyll-a) in Lake Victoria. The present condition was compared to the historic limnological data base of phytoplankton photosynthetic rates and biomass. The objective was to test the null hypothesis that phytoplankton productivity in Lake Victoria has increased. To examine this,

observations were done inshore and offshore in Lake Victoria using in situ methodology similar to that of Talling (1965).

The data were obtained and analyzed in a manner previously used by Talling (1965) in Lake Victoria to facilitate direct comparison of current observations to the historical limnological data base of phytoplankton productivity and abundance. The results obtained are discussed in the context of other changes in the lake that have occurred. In addition measurements were also made in Lakes Kyoga and Albert (Fig.1) to determine regional variability in phytoplankton photosynthesis.

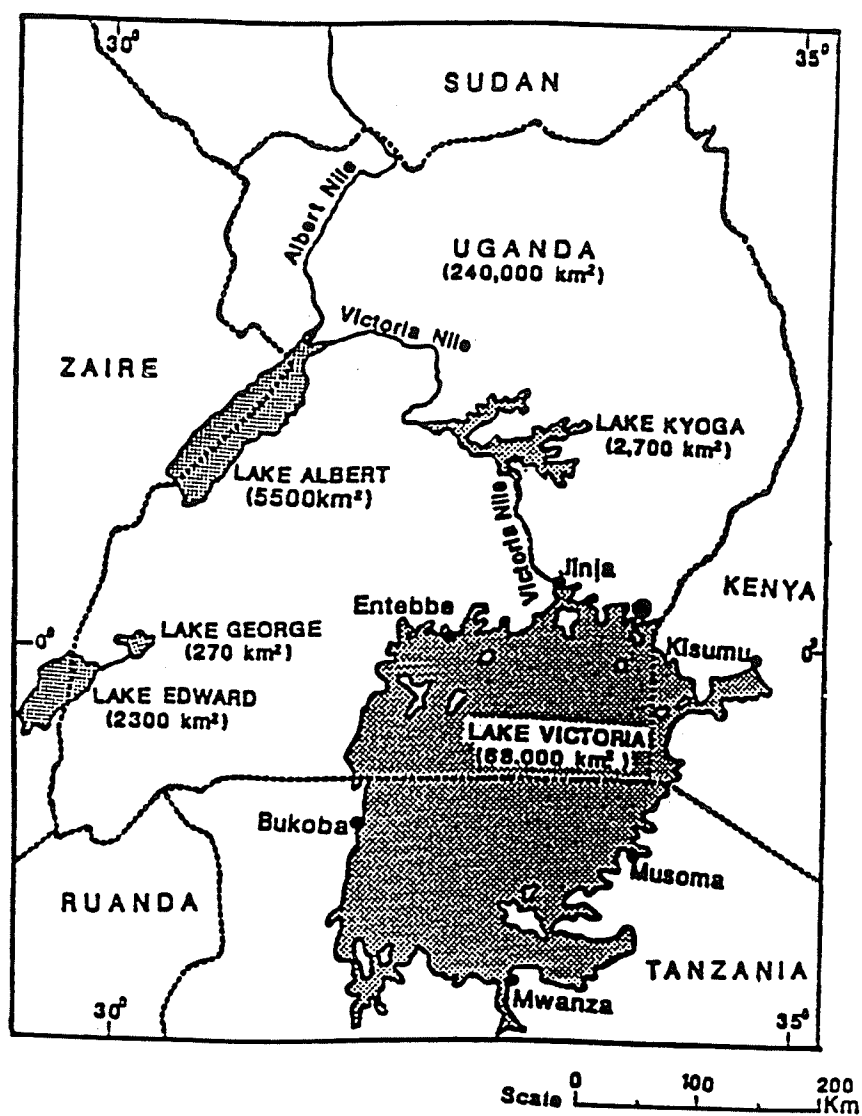


Fig. 1. Map of Uganda showing the location of Lakes, Victoria, Kyoga and Albert, which were sampled during this study.

## CHAPTER I

SEASONAL, SPATIAL AND INTER-LAKE VARIABILITY IN PHYTOPLANKTON  
PHOTOSYNTHESIS IN LAKES VICTORIA, KYOGA AND ALBERT (UGANDA).

## Abstract

Mean daily integral productivity in Lake Kyoga was 30% and 50% lower than in offshore and inshore regions of Lake Victoria respectively. The inshore integral production in Lake Albert approached levels of offshore Lake Victoria waters, while offshore Albert was 40% lower. Phytoplankton photosynthesis was less light limited in Lake Kyoga ( $I_{24}/I_k = 0.8$ ), but was severe and 50% more extreme in offshore Lake Albert than in Lake Victoria. In Lake Albert daily integral production was 40% higher in inshore than offshore and this corresponded to a 4x higher mean  $I_{24}/I_k$  ratio inshore.

In offshore Lake Victoria seasonality in phytoplankton photosynthesis and biomass were pronounced reflecting the effects of the annual mixing regime. Algal biomass maxima were in May and September to November, while production peaked in July and December. There was lower seasonal variance in chlorophyll concentrations and production at inshore regions than offshore Lake Victoria.

## Introduction

Few studies have examined seasonal, spatial and

inter-lake variability of phytoplankton photosynthesis and biomass in African lakes. Some of these lakes exhibit pronounced seasonal fluctuations that usually correspond with variations in rainfall, river discharges and vertical mixing (Talling 1965, 1966; Melack 1979; Hecky and Fee 1981; Hecky and Kling 1981, 1987; Bootsma 1993). The abiotic and biotic factors in regulation of phytoplankton productivity and biomass can vary within and between lakes so that extrapolation of causative factors can be difficult. Differential nutrient loading, underwater light availability and food web effects are recognised as potent regulators of biomass and primary productivity in lakes. One or more of these factors may be changing in the lakes of eastern Africa and especially Lake Victoria (Hecky 1993), Africa's largest lake and inland fishery.

The objective of this study was to examine seasonal variability in Lake Victoria. In addition, to measure and compare phytoplankton productivity and biomass in Lake Kyoga, which has gone through similar fish community changes as Victoria (Ogutu-Ohwayo 1990a,b) and Albert, the original habitat of the introduced species, but whose fish community has not been altered. The aim was to attempt to determine if increases in productivity and biomass were regional in scope or reflect recent alterations in the Victoria ecosystem only.



## MATERIALS AND METHODS

### Study areas

Victoria is the largest freshwater lake in Africa (69000 km<sup>2</sup>). It occupies a single basin at altitude 1135 m, with a bottom gently sloping to a maximum depth of 79 m. Much of the coastline is irregular, and shallow bays and gulfs are especially numerous on the northern and southern shores (Beadle 1981). Rainfall occurs throughout the year with a major wet season in March-April and a lesser one in October-November. The offshore regions are thermally stratified most of the year, but mix completely in July-August during the dry season when strong South-east trade winds blow across the lake (Talling 1966) causing increased cooling by evaporation. Phytoplankton measurements were done in the northern waters of Lake Victoria (Fig. 2) at sites for which historical data exist: inshore Pilkington Bay (Talling 1965; Kendall 1969; Stager 1984; Stager et al. 1986) and at a deep offshore station (Bugaia) (Talling 1965, 1966). Further measurements were made in Buvuma Channel, Napoleon Gulf and other areas covered by the ongoing bio-ecological studies on Lake Victoria.

Lake Kyoga lies on the Nile down stream of Lake Victoria, between longitude 32°E and 34°E and latitude 1° N and 2° N (Fig. 3). It has an area of 2700 km<sup>2</sup>, and an average depth of 3.5 m and a maximum of about 4 m. Sampling on Lake kyoga was done

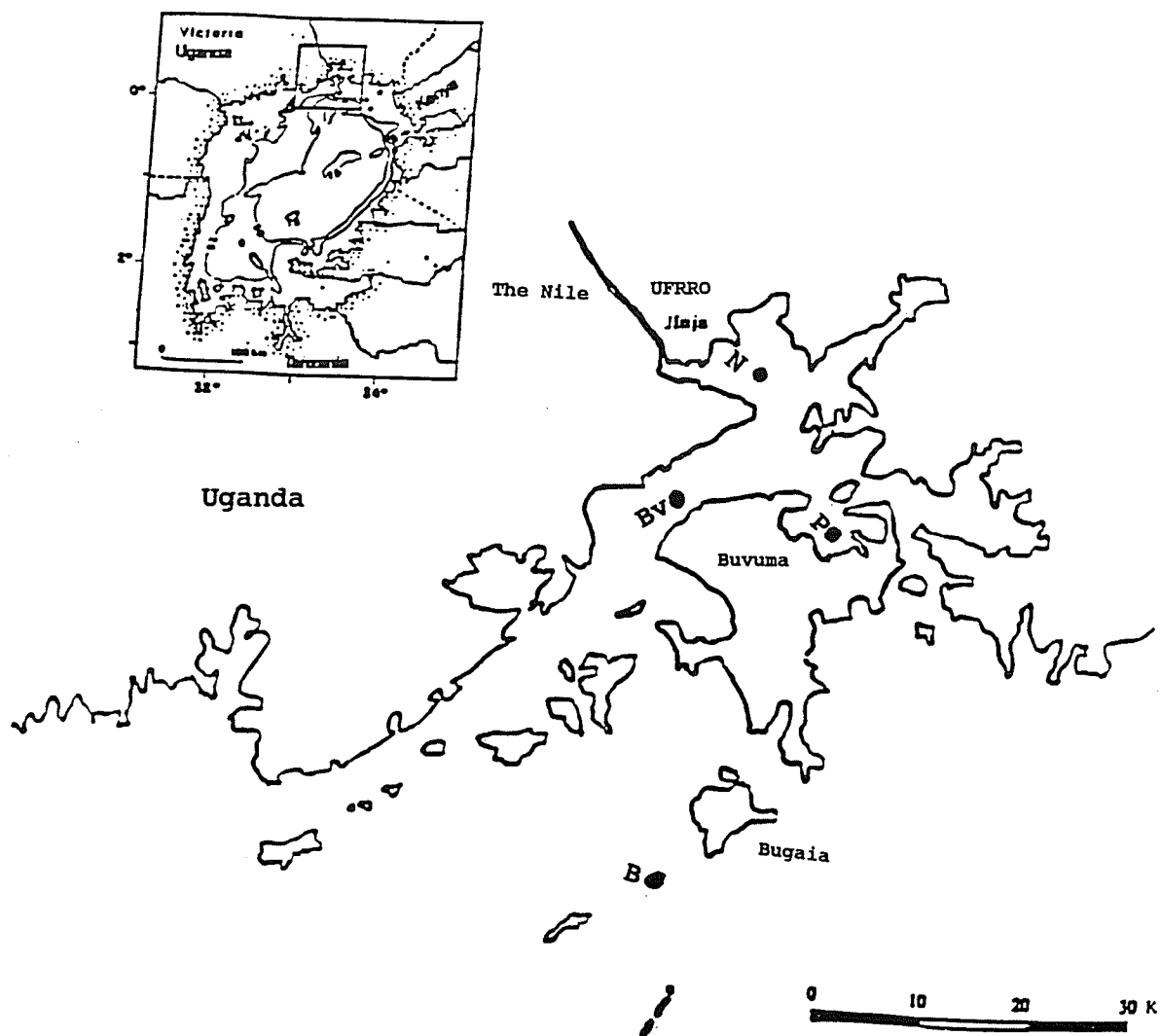


Fig. 2. Map of Northern Lake Victoria, near its mouth flow at Jinja. The sampled area are: Bugaia (B), Buvuma Channel (Bv), Pilkington Bay (P) and Napoleon gulf (N).

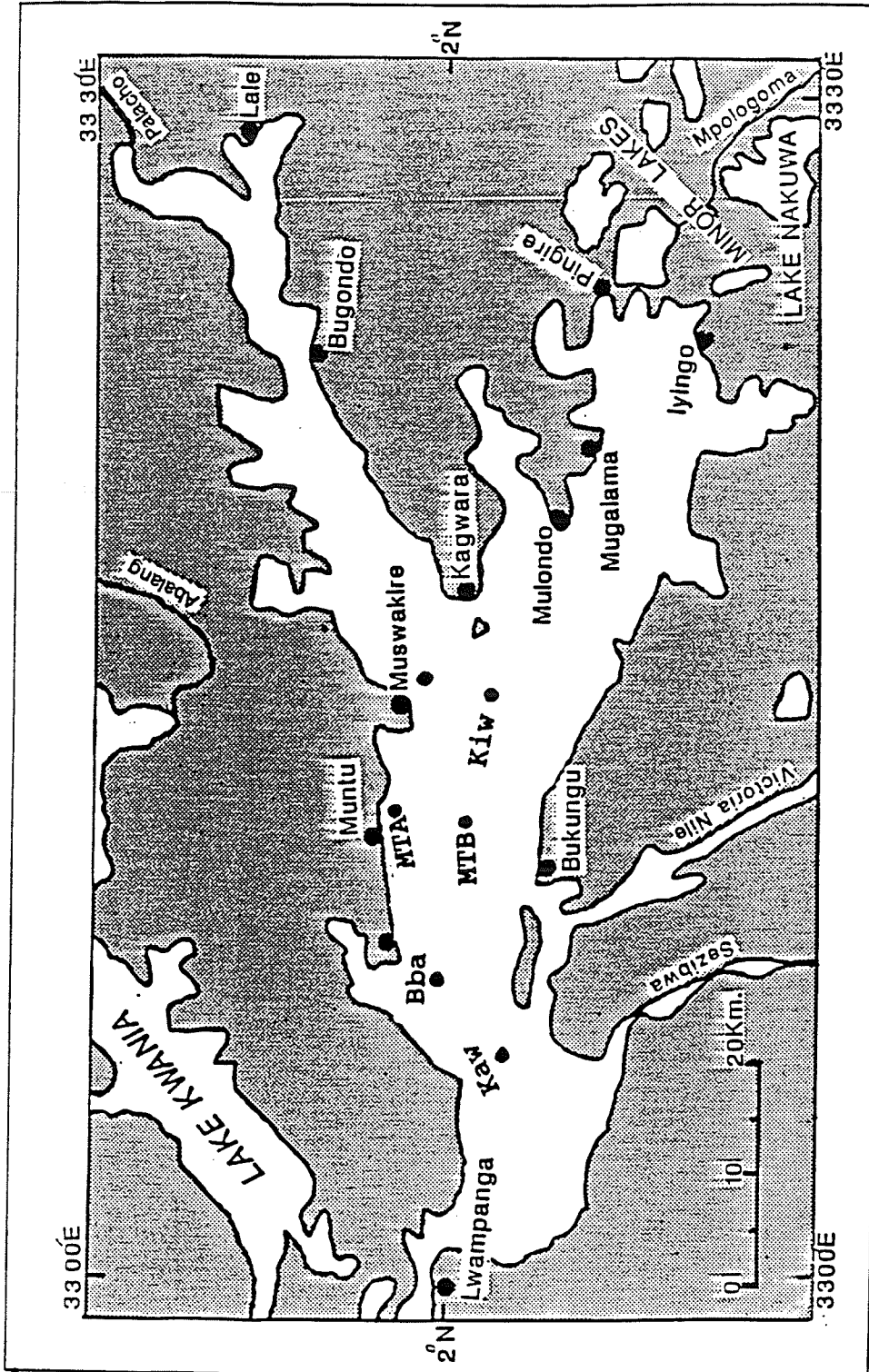


Fig. 3. Lake Kyoga basin showing the main stations sampled: Bbangala (Bba), Muntu A (MTA), Muntu B (MTB), Muswakire (Mus), Kiwantama (Kiw), and Kawongo (Kaw).

at six locations (Fig. 3). These areas were chosen because of accessibility from the main fish landings.

Lake Albert, Uganda is a characteristic Rift valley lake (5500 km<sup>2</sup>; maximum depth 58 m; mean depth 25 m). It lies between latitude 1°0' N and 2°20'N and longitude 30°20'E and 31°20'E. The Victoria Nile enters its northeast corner, but almost immediately turns away, making a variable contribution to the lake proper (Talling 1957c). All samples were taken in the north-eastern part of this lake Albert (Fig. 4). Sampling areas included a 45 m deep offshore station (B1) where previous surveys were done by Talling (1965), and inshore regions: Wanseko, Butiaba, Bugoigo, Panyamur, Walukuba and Waki.

#### Sample collection, treatment and analysis

##### Field (in situ) measurements

The method of Talling (1965) was used to estimate *in situ* gross phytoplankton production. At all stations water samples were drawn from discrete depths within the euphotic zone with a Van Dorn plastic sampler of 2 L capacity. Water was siphoned into either clear or blackened 120 ml glass bottles. The light and dark bottles were suspended without shading at several depths in the euphotic zone (0 to 6 m). All bottles were filled with water taken from the depth of exposure and incubation lasted usually two hours at or around midday. At the end of the incubation samples, were fixed using manganese

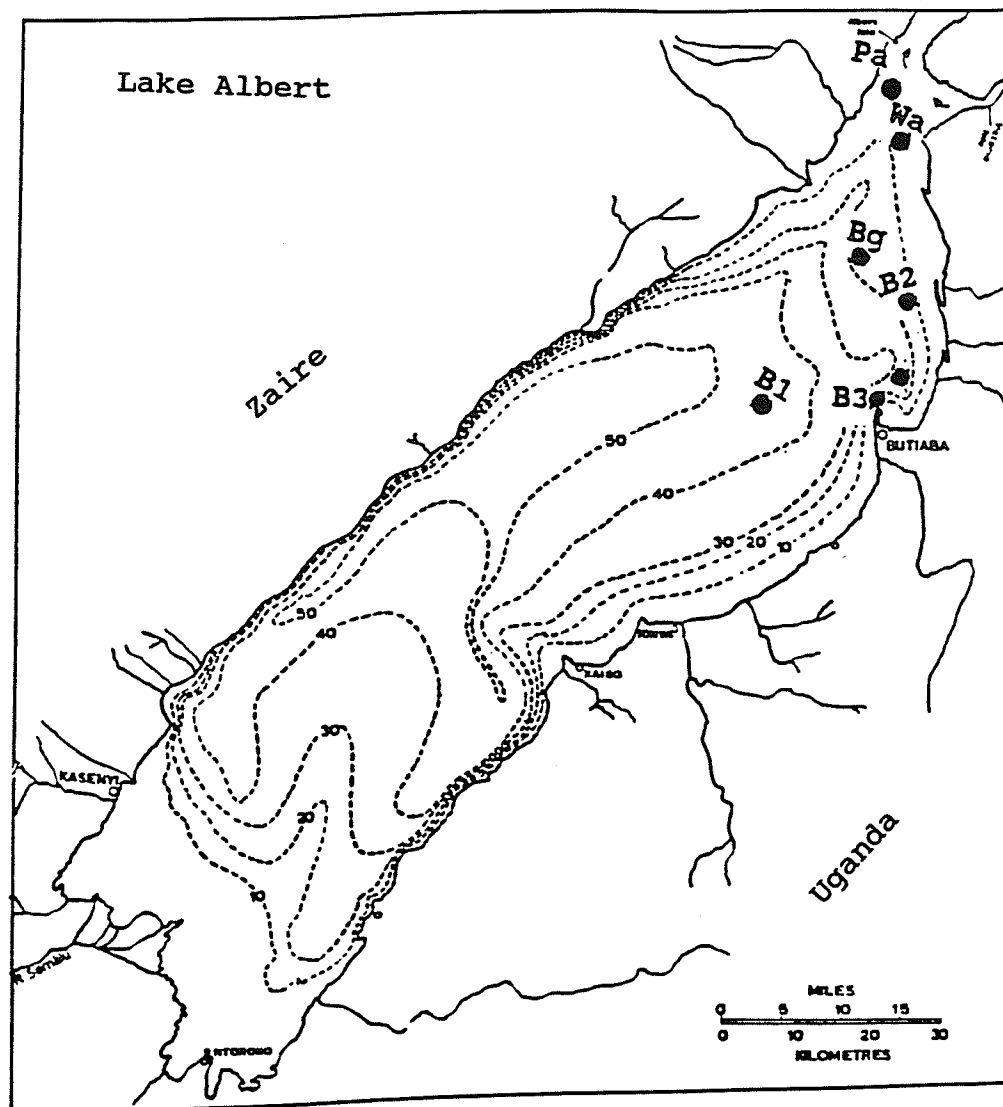


Fig. 4. Map of Lake Albert showing the main stations sampled: B1 (Butiaba 1), B2 (Butiaba 2), B3 (Butiaba 3), Bg (Bugogo), Wa (Wanseko) and Panyamur (Pa).

chloride or sulphate and potassium iodide (with sodium azide added). Gross photosynthesis at each depth was estimated by changes in the dissolved oxygen in light and dark bottle using the Winkler method. Approximately 0.1 N thiosulphate was used to titrate the whole volume of the light or dark bottle (about 120 mls) with 1% starch as the end point indicator. Initial oxygen concentrations were also measured at each sampled depth, prior to incubation.

#### Light and Temperature measurements

Light attenuation, Secchi transparency and temperature profiles were measured at all sites during sample collection. Water column temperatures were measured as a function of depth using a resistance thermometer and/or a Hydrolab (SVR2- Sonde Unit). Secchi disc measurements, defined as the average of the depth of disappearance and reappearance of the disc, were made using a 25 cm diameter white disc. These readings were made on the shaded side of the boat. Underwater light attenuation was measured at 0.5 or 1.0 m intervals throughout the water column using a Li-Cor 1000 quantum sensor and meter which measures the total quanta of photosynthetically available (PAR). These measurements were used to calculate the total vertical light extinction coefficient ( $k$ ) and the mean light intensity in the water column over 24 hours ( $I_{24}$ ). The natural logarithm of irradiance (with surface illumination as 100%) was used to calculate the total vertical light

extinction coefficient ( $k$ ), (Hutchinson 1957). The extinction coefficient was determined by using linear regression to estimate the slope of the logarithm of measured light versus depth. The mean light intensity over 24 hours ( $I_{24}$ ) was calculated as in Hecky and Guildford (1984) with the following equation:

$$I_{24} = \frac{I_0 (1 - e^{-kz_m})}{kz_m}$$

where  $I_0$  is the surface light and  $z_m$  is the mixed depth layer depth.  $I_0$  was obtained from a cloudless solar irradiance (Fee 1990).

The oxygen produced per unit volume at optimal irradiance for photosynthesis was normalised, by dividing it by the chlorophyll concentration; This parameter is referred to as  $P_{max}$  by Talling (1965) and  $P_M^B$  by Fee (1990). The light intensity at the onset of light saturation of photosynthesis ( $I_k$ ) was calculated using the computer programme of Fee (1990);  $I_k$  defined as  $P_M^B / \alpha^B$  where  $\alpha^B$  is the slope of the light limited chlorophyll-specific photosynthesis vs PAR curve at low PAR (Fig. 5).

The ratio of the solar radiation integrated over the whole day to that received during the incubation period was used to estimate *in situ* daily gross production as detailed in Talling (1965), but cloudless weather was always assumed (and often observed) during incubations. Talling (1965) usually reported near cloudless conditions on his dates of

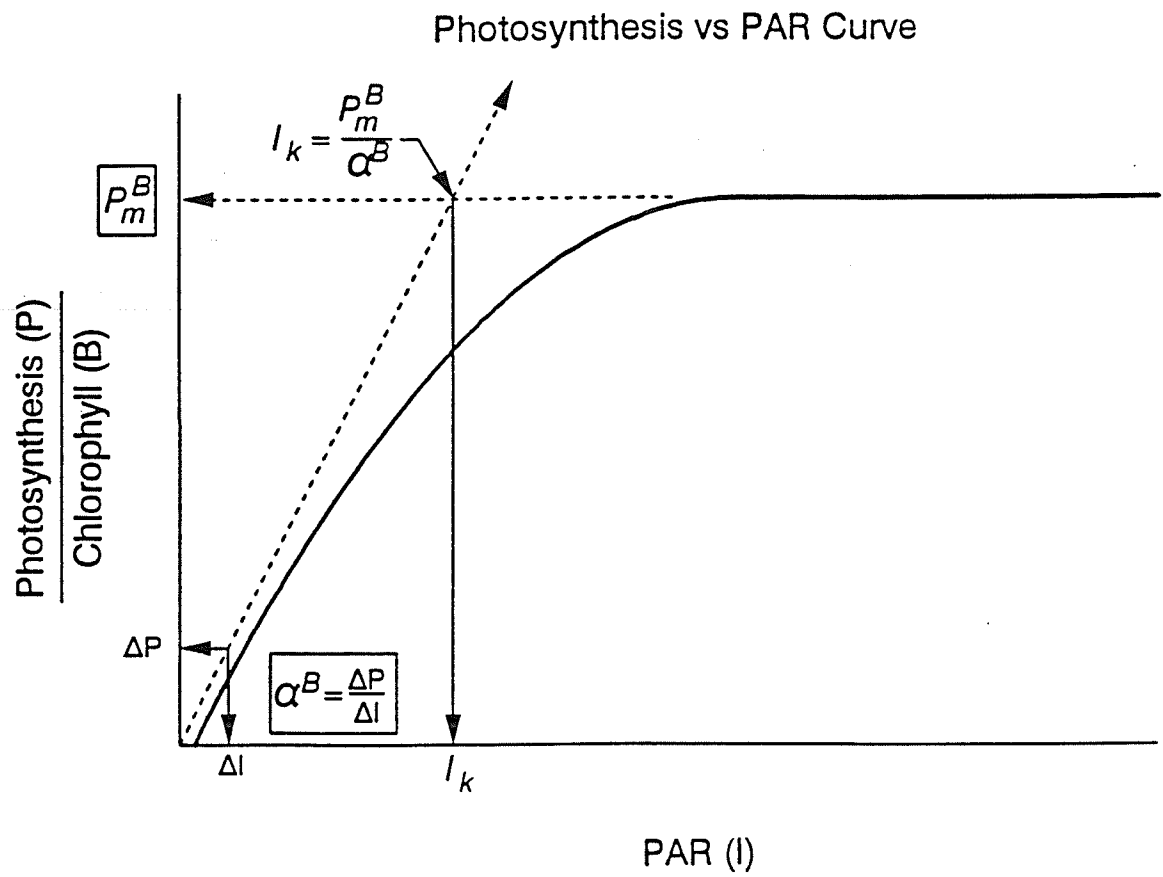


Fig.5. Photosynthesis vs PAR Curve



measurements.

Phytoplankton chlorophyll concentrations (Chl) (n in notation of Talling 1965) was determined by filtration of 100 mls of sample water on to a GF/C filter; the filter was immersed in 10 mls of 95% methanol for approximately 20 hours at 4°C and in dark. This extract was read on a Turner fluorometer which was calibrated using standard chlorophyll-a solutions calibrated using a spectrophotometer (Stainton et al. 1977).

## Results and discussions

### Photosynthesis and biomass offshore

The *in situ* photosynthesis versus depth profiles of Lake Victoria were shallow, reflecting the rapid underwater light attenuation typical of eutrophic lakes (Fig. 6). Most profiles showed a decline in photosynthesis at the surface. Maximum photosynthesis per unit volume ( $nP_{\max}$ ) was in the range 235-600  $\text{mg.O}_2\cdot\text{m}^{-3}\cdot\text{h}^{-1}$  with a mean of 400  $\text{mg.O}_2\cdot\text{m}^{-3}\cdot\text{h}^{-1}$  offshore (Fig. 6 and Table 1). The highest photosynthetic rates occurred between 0.5-4 m below the water surface in 7-29 m euphotic zone.

At the offshore station, seasonality in phytoplankton, with a biomass was pronounced with a maxima in September to November and in May (Fig. 7a). Lower chlorophyll-a concentrations occurred during mixing periods (June to August) and during the period of pronounced and prolonged

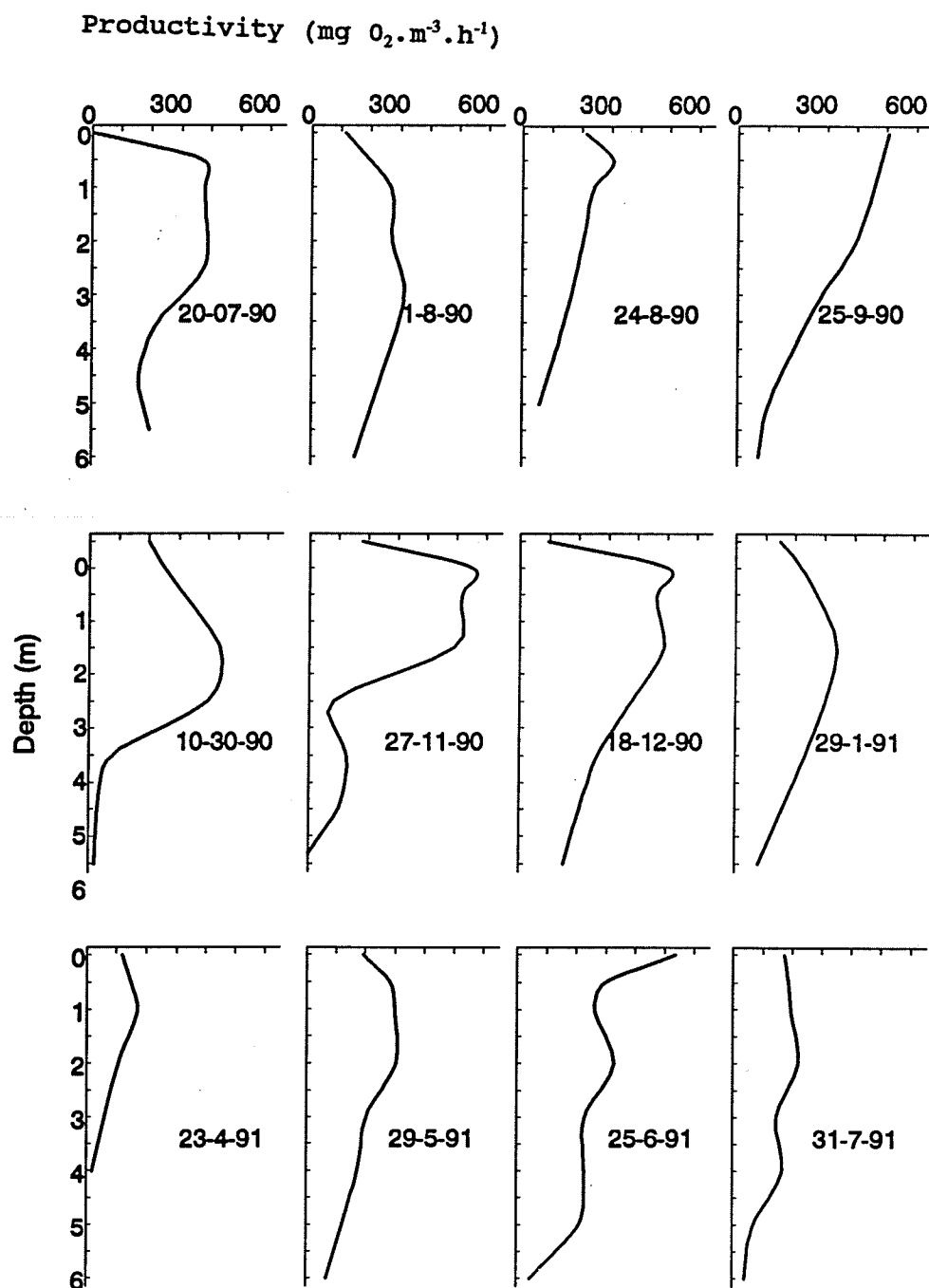


Fig. 6. The depth distribution of the photosynthetic rates per unit volume offshore (Bugaia) Lake Victoria during 1990-91.

Table 1. Means and standard deviation of photosynthetic parameters and integral productivity per unit area of Lake Victoria during 1989-91. Chl, chlorophyll-a ( $\text{mg}\cdot\text{m}^{-3}$ );  $nP_{\text{max}}$ , maximum productivity per unit volume ( $\text{mg O}_2\cdot\text{m}^{-3}\cdot\text{h}^{-1}$ );  $P_{\text{max}}$ , maximum productivity per unit chlorophyll ( $\text{mg O}_2\cdot\text{mg chl}^{-1}\cdot\text{h}^{-1}$ );  $nP_{\text{max}}/k$ , ratio of  $nP_{\text{max}}$  to  $k$ , the vertical light extinction coefficient ( $\text{ln}\cdot\text{m}^{-1}$ ); IPH, hourly integral productivity ( $\text{g O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ ); IPD, daily integral production per unit area ( $\text{g O}_2\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ )

Station		Chl	$nP_{\text{max}}$	$P_{\text{max}}$	$nP_{\text{max}}/k$	IPH	IPD
Bugala	mean	25	401	19	889	1.4	13
	std	10	125	6	366	0.4	4
Pilkington	mean	47	765	17	744	2	22
	std	11	234	6	210	1	8
Buvuma	mean	38	738	19	955	2	20
	std	8	279	6	345	1	8
Napoleon	mean	41	752	19	797	2	18
	std	12	231	4.9	229	0.5	5

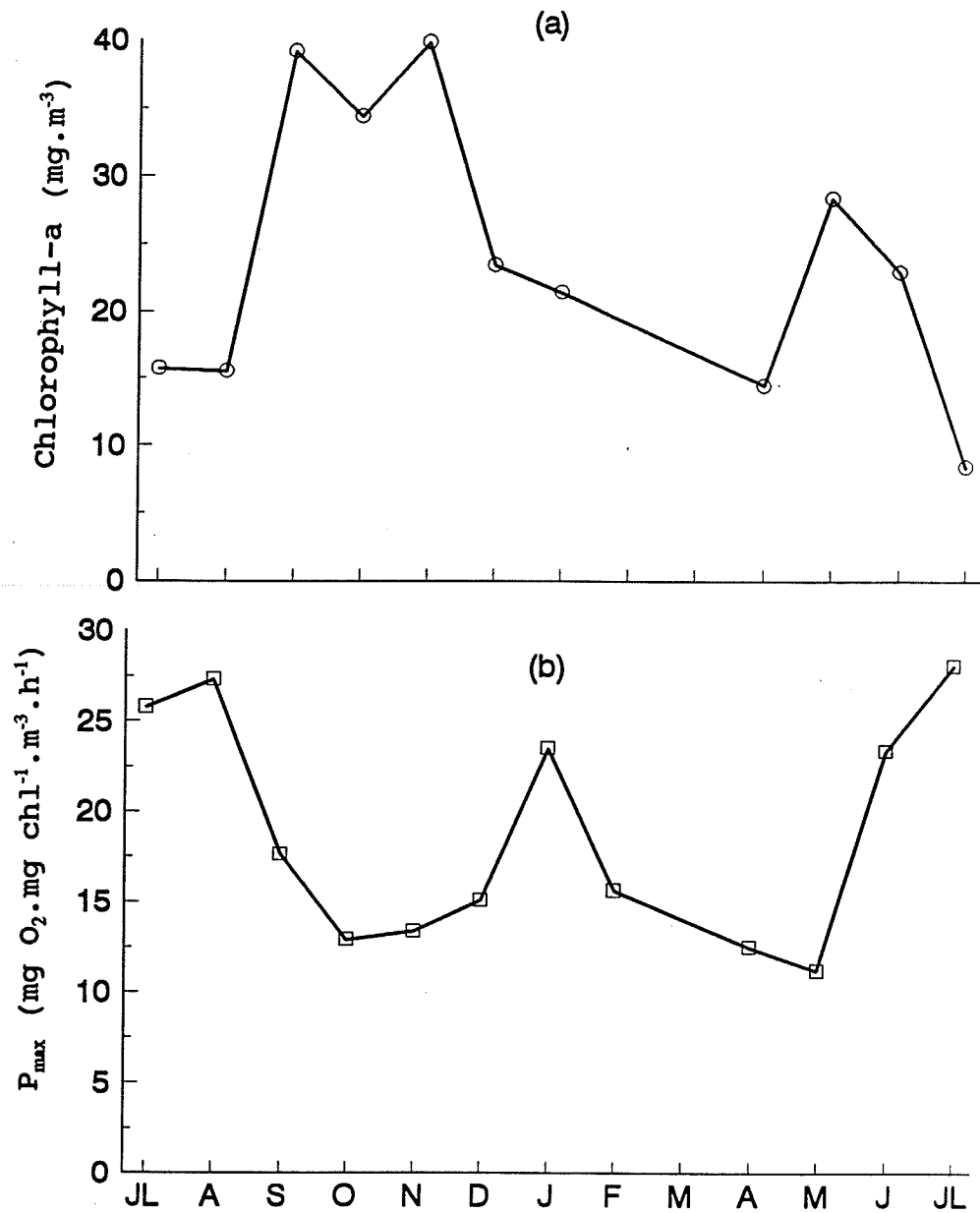


Fig.7. Seasonal (a) chlorophyll concentrations and (b) maximum specific productivity ( $P_{\text{max}}$ ) at the offshore (Bugai) region of Lake Victoria during 1990-91

stratification (December to April). Chlorophyll-a concentrations varied five fold ( $8\text{--}40\text{ mg.m}^{-3}$ ) with a mean of  $25.0\text{ mg.m}^{-3}$  for the entire period (Table 1).

Seasonal changes in the maximum photosynthetic activity per unit chlorophyll ( $P_{\text{max}}$ ) are indicated in Fig 7b.  $P_{\text{max}}$  showed a two fold range ( $11\text{--}28\text{ mg O}_2\text{.mg chl}^{-1}\text{.h}^{-1}$ ) and was highest during July-August. It varied inversely with chlorophyll-a, especially so during the biomass maxima (Fig. 7a & b). Daily integral production per unit area (IPD) varied between  $8\text{--}20\text{ g O}_2\text{.m}^{-2}\text{.d}^{-1}$  (Fig. 8) and the mean was  $13.0\text{ g O}_2\text{.m}^{-2}\text{.d}^{-1}$  (Table 1). Production declined sharply in August and January and peaked in July and December (Fig. 8). Lower values were maintained during January to April, but there was a minor peak in June that was synchronous with the minor biomass maxima (Fig. 7a & 8).

Fig 8 shows the seasonal changes in the Secchi depth (SD, metres) which is used here as an index of the underwater light availability offshore. Production tended to increase when there was an increase in Secchi transparency (Fig. 8). However, once, in July 1991, this was not observed because of the unusually deep euphotic depth ( $29.2\text{ m}$ ) and low biomass ( $8.4\text{ mg.m}^{-3}$ ) associated with a phytoplankton crash. There was a high correlation between chlorophyll-a and the inverse of the secchi transparency ( $R^2 = 0.85$ ) which was significant ( $p < 0.01$ , Fig. 9).

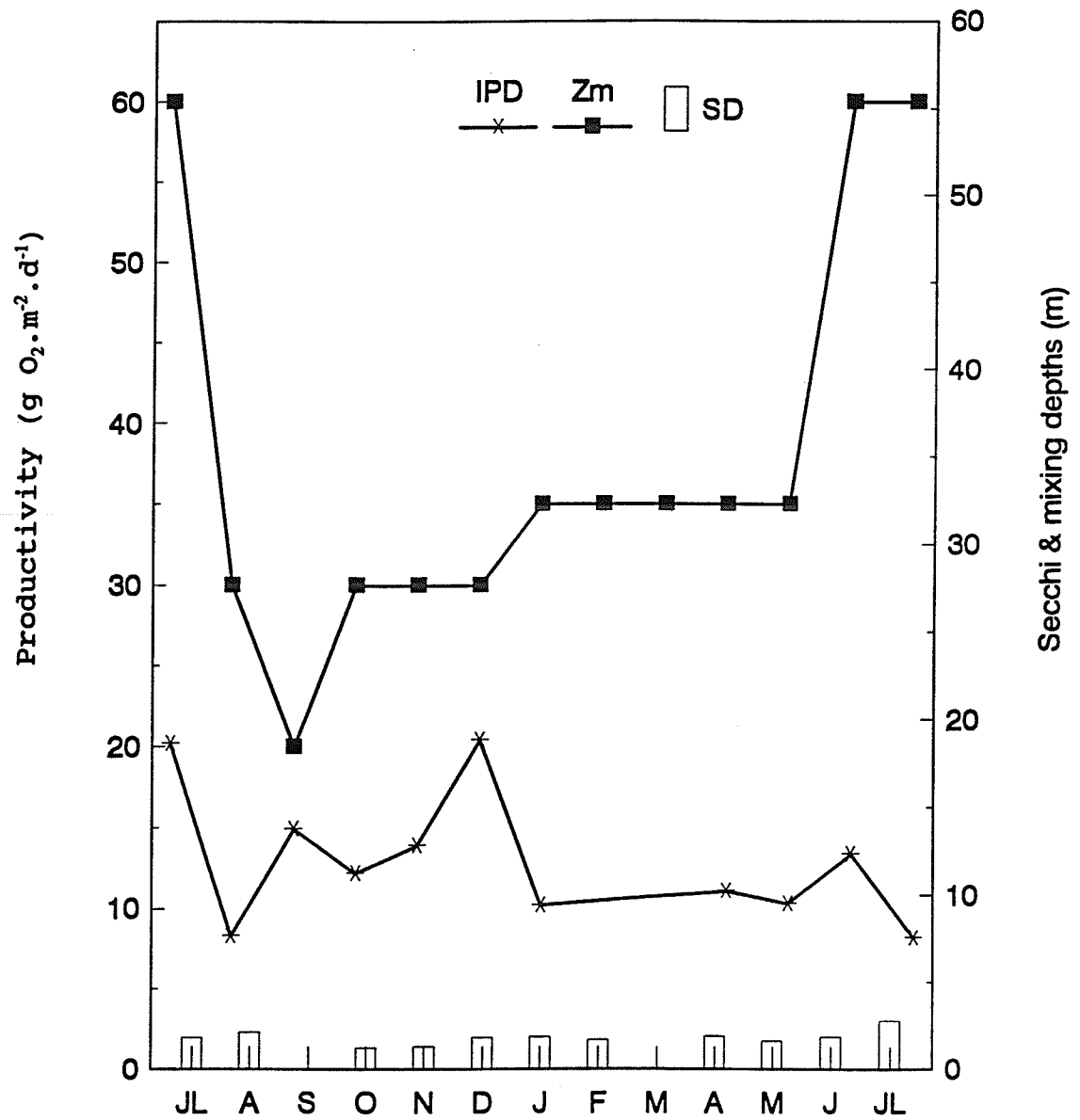


Fig. 8. Seasonality of daily integral production (IPD), Secchi depth (SD) and mixing depth (Zm) at the offshore station of Lake Victoria during 1990-91.

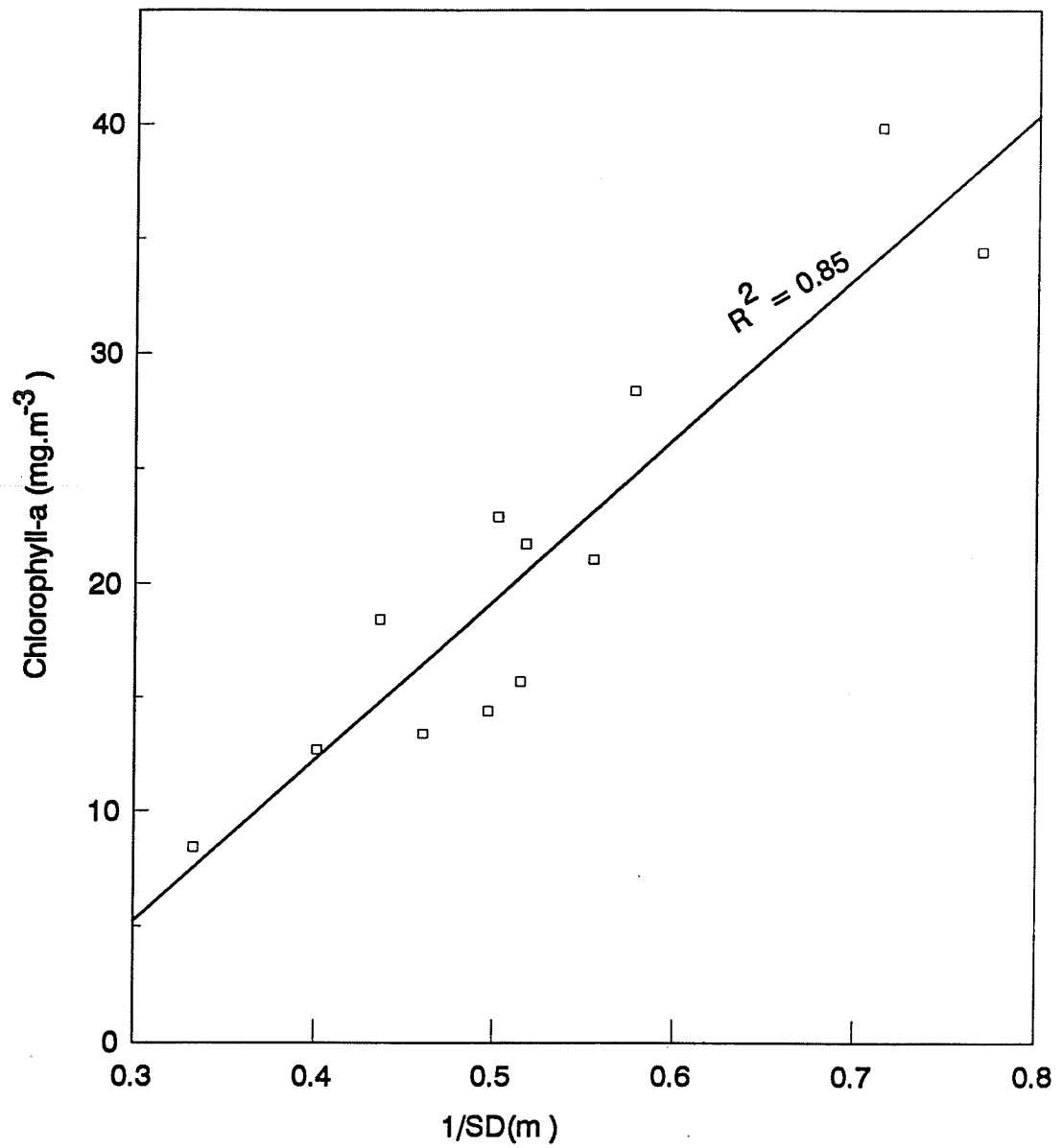


Fig.9. The correlation between chlorophyll-a concentrations and the inverse Secchi disc transparency offshore, Bugaia during 1990-91.

### Phytoplankton photosynthesis and biomass inshore

Photosynthetic depth profiles inshore were shallower, reflecting the more rapid underwater light attenuation inshore than offshore (Fig. 10). The highest  $nP_{\max}$  occurred between 0.5-3 m in a euphotic zone of 5-6 m mean depth that was shallower than offshore waters (Table 2). Maximum photosynthesis per unit volume was higher in the inshore areas, with mean estimates in the range of 738-765  $\text{mg O}_2 \cdot \text{m}^3 \cdot \text{h}^{-1}$  (Fig. 10 & Table 1). Surface photo-inhibition was as frequent as offshore.

There were minimal differences in areal productivity and biomass among the inshore regions of Lake Victoria (Table 1). As offshore, the trends in  $P_{\max}$  were not associated with trends in chlorophyll-a concentration (Fig. 11a, b & c). All the inshore regions had chlorophyll-a concentrations of the same order of magnitude but these were higher than offshore. Mean chlorophyll-a concentrations in Pilkington bay, Buvuma channel and Napoleon gulf were 47.0  $\text{mg} \cdot \text{m}^{-3}$ , 38.0  $\text{mg} \cdot \text{m}^{-3}$  and 41.0  $\text{mg} \cdot \text{m}^{-3}$  respectively (Table 1). The correlation between the inverse Secchi transparency and chlorophyll was lower than offshore reflecting the low seasonal variance, ( $R^2=0.3$ ) but significant at  $p<0.05$  (Fig. 12). Fluctuations in hourly integral production with the Secchi transparency and light extinction coefficient inshore showed no obvious trend (Fig. 13a, b,) However, a slight tendency for increased production was observed in September and November in Pilkington bay and



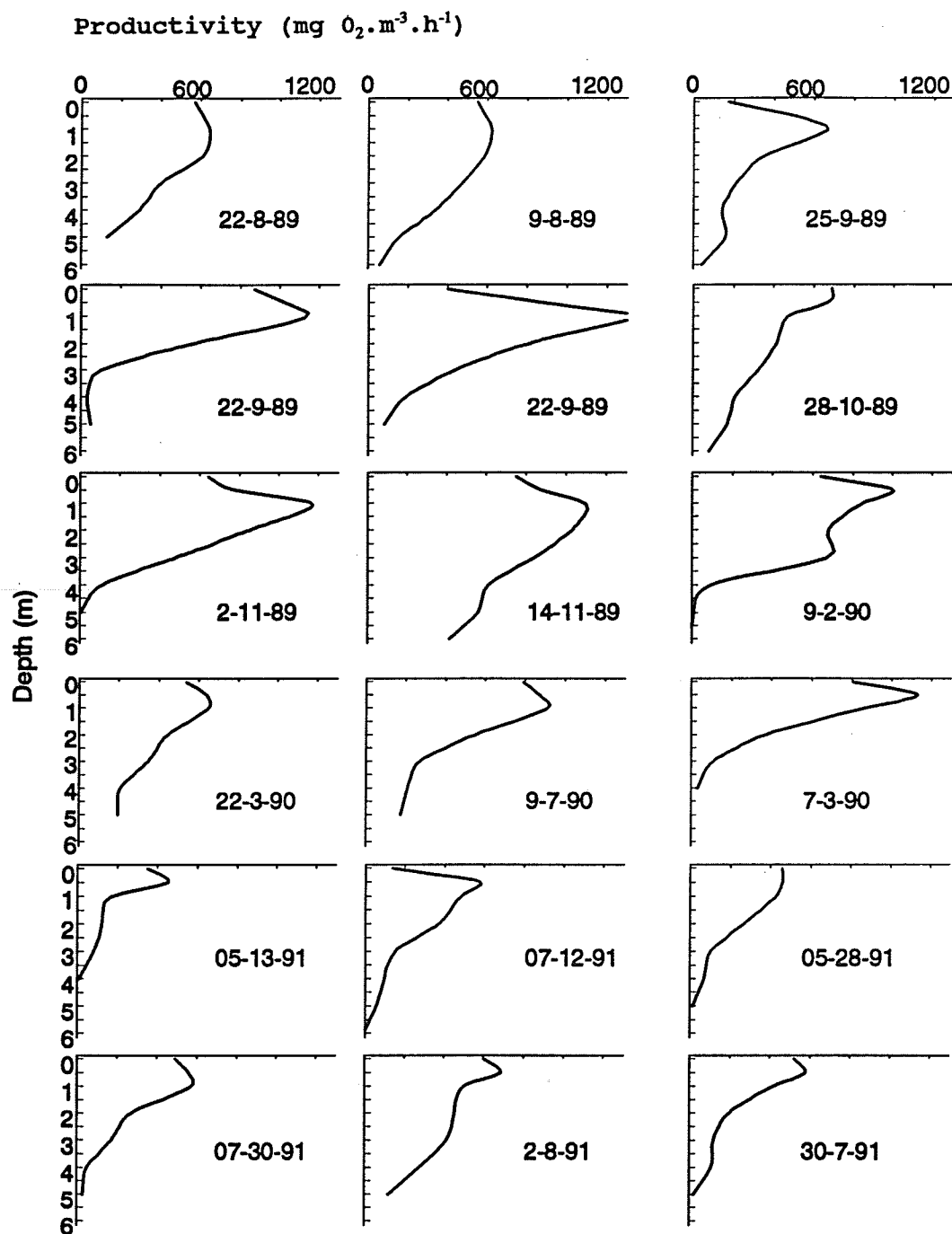


Fig. 10. Selected profiles of the depth distribution of photosynthetic rates per unit water volume at inshore stations: Pilkington Bay, Buvuma Channel and Napoleon gulf during 1989-91.

Table 2. Light characteristics of Lake Victoria during 1989-91. SD, Secchi depth (m); k, vertical light extinction coefficient ( $\ln.m^{-1}$ ); Zeu, euphotic depth (m);  $I_k$ , irradiance at the onset of light saturated photosynthesis ( $mEin.m^{-2}.min^{-1}$ );  $I_{24}$ , mean light intensity in the water column integrated over 24 hours ( $mEin.m^{-2}.min^{-1}$ );  $I_{24}/I_k$ , the ratio of  $I_{24}$  to  $I_k$ .

STA		SD	k	Zeu	$I_k$	$I_{24}$	$I_{24}/I_k$
BUG	mean	2.0	0.5	14.0	11.0	2.0	0.2
	std	0.4	0.2	9.0	1.0	0.3	0.04
PLK	mean	1.0	1.0	5.0	10.0	3.0	0.3
	std	0.2	0.1	1.0	2.0	0.5	0.06
BUV	mean	1.6	1.0	6.0	11.0	2.1	0.2
	std	0.2	0.1	1.0	2.0	0.3	0.07
NAP	mean	1.3	1.0	5.0	11.0	3.0	0.2
	std	0.2	0.1	1.0	2.0	1.0	0.09

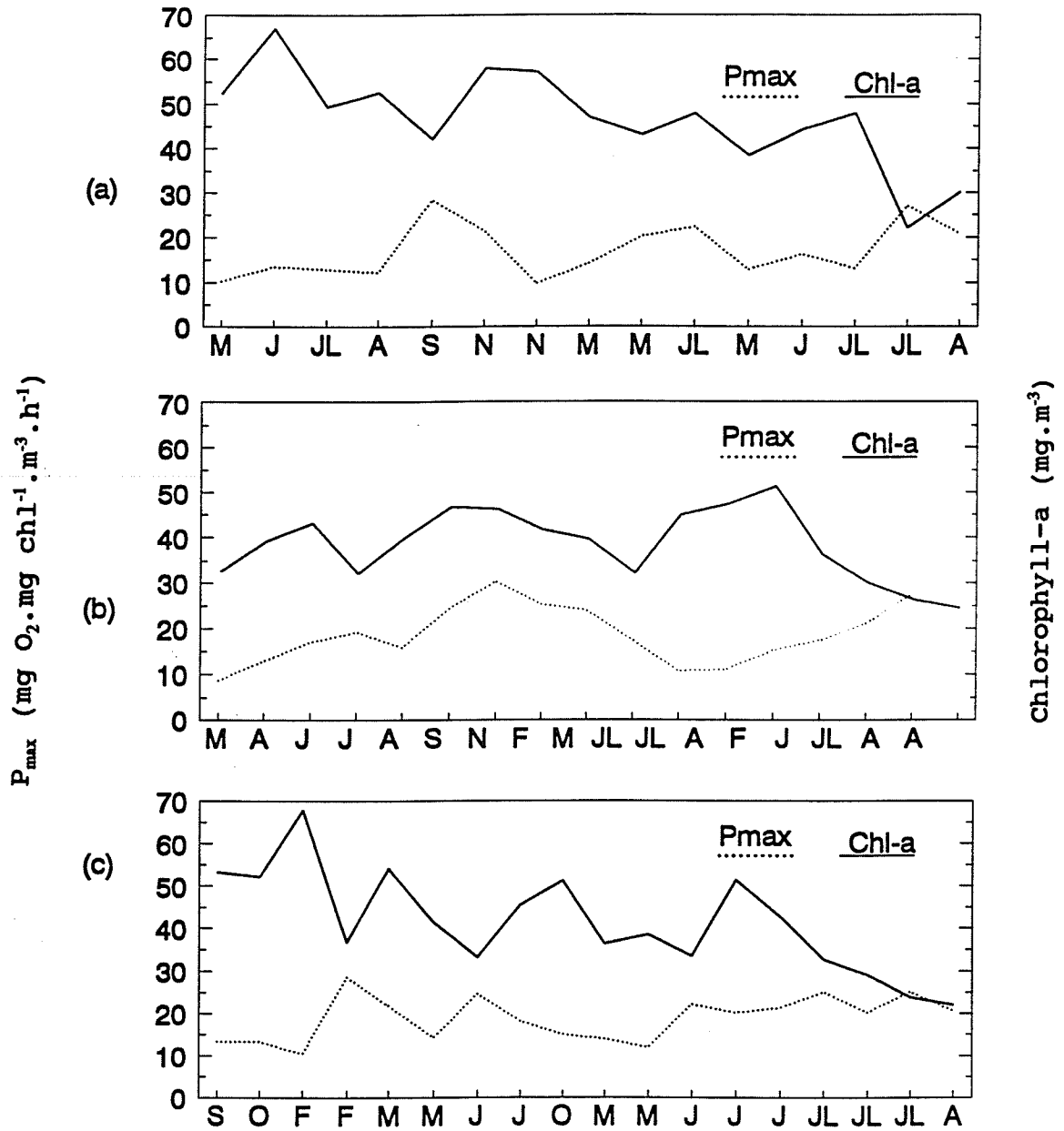


Fig.11. Variation of chlorophyll-a (chl-a) and maximum specific productivity per unit chl-a (P<sub>max</sub>) inshore: (a) Pilkington Bay; (b) Buvuma Channel (c) Napoleon Gulf during 1989-91.

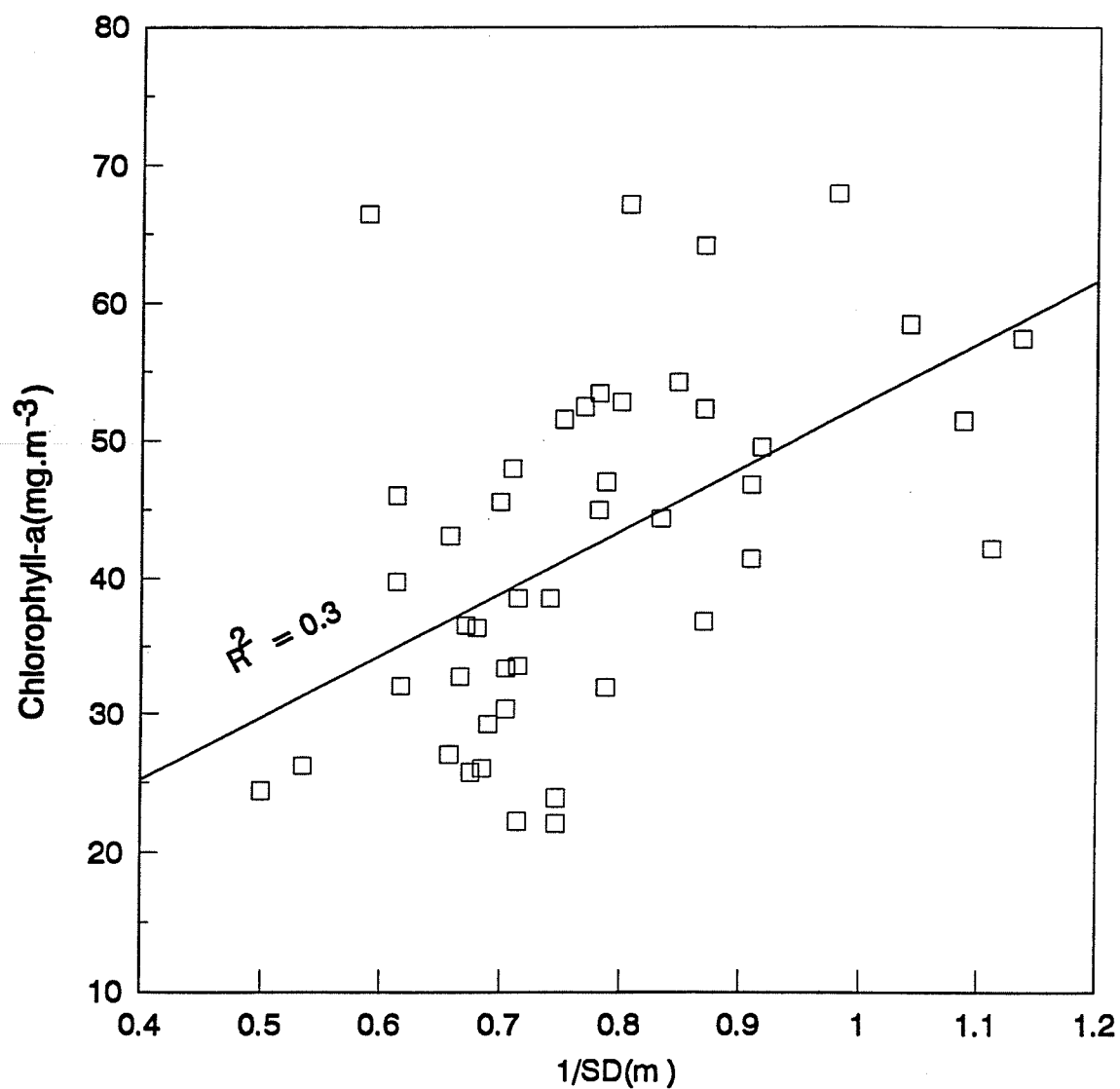


Fig.12. The correlation between chlorophyll-a concentrations and the inverse secchi disc transparency inshore Lake Victoria during 1990-91.

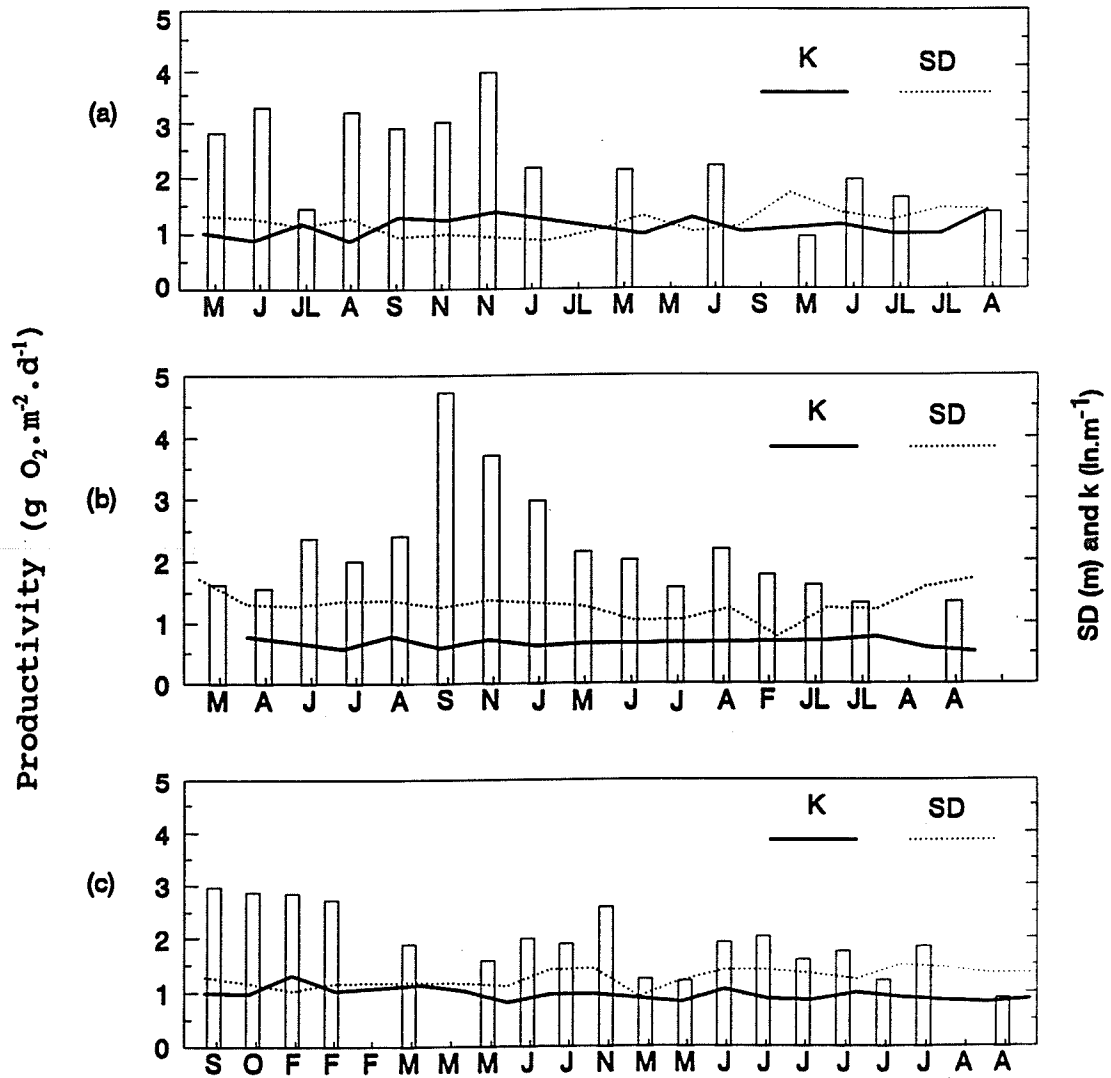


Fig.13. Variation of hourly integral photosynthesis (shown as histograms)

with extinction coefficient ( $k$ ) and Secchi depth (SD) at inshore stations:

(a) Pilkington bay (b) Buvuma channel and (c) Napoleon gulf.

Buvuma channel. The estimated average hourly and daily integral productivity per unit area was about 60-80 % higher than offshore despite fact that the euphotic zone was half as deep as offshore (Table 1 & 2).

#### Variation of light characteristics of Lake Victoria

Offshore the Secchi visibility showed a two fold range with a mean of 2 m (Table 2). The vertical light extinction coefficient ( $k$ ) declined from  $0.62 \text{ ln.m}^{-1}$  in May to  $0.16 \text{ ln.m}^{-1}$  in July 1991 offshore. Inshore, the mean  $k$  values were twice as high and Secchi disc visibility was lower than offshore; The higher light absorption inshore is undoubtedly caused by higher phytobiomass (Table 1 & 2). Offshore, the euphotic depth ( $Z_{eu}$ ) showed a four fold range and was deepest in July-August, the mixing period. The light intensity at the onset of light saturation of photosynthesis expressed as the quantity ( $I_k$ ) varied little throughout the period of study at all stations. The average value was between 10 to 11  $\text{mEin.m}^{-2}.\text{min}^{-1}$  (Table 2). The average  $I_{24}$  offshore was 2  $\text{mEin.m}^{-2}.\text{min}^{-1}$ , which was about 25% lower than inshore. The  $I_{24}$  may actually have been higher in the shallow inshore bays because it was calculated using the maximum depth in the sampling area, as the mean depth was unknown. Because these inshore areas shoal to zero depth at nearby shorelines, use of the maximum depth overestimates mean depth of the mixing in the vicinity of the station. All inshore sites mix daily to the

maximum depth. The ( $I_k$ ) values for phytoplankton of Lake Victoria were consistently much higher than the corresponding values of the mean light intensity in the water column integrated for 24 hours ( $I_{24}$ ).

#### Photosynthesis and biomass in Lakes Kyoga and Albert.

Table 3 shows the mean photosynthetic and light parameters of Lakes Kyoga and Albert. Phytoplankton photosynthesis in Lake Kyoga was 30% lower than rates observed in offshore Victoria. Daily integral production per unit area ranged from 6-16 g  $O_2 \cdot m^2 \cdot d^{-1}$ , with an average of 10 g  $O_2 \cdot m^2 \cdot d^{-1}$ . The euphotic zone was compressed (mean depth of 4 m; Table 3). High average photosynthetic activity per unit volume (mean 650 mg  $O_2 \cdot m^3 \cdot h^{-1}$ ) corresponding to average chlorophyll-a concentrations of 41 mg  $\cdot m^{-3}$  were observed during 1989-91. Mean Secchi transparency was low (0.9 m), while the average light extinction coefficient was 1.7  $ln \cdot m^{-1}$  (occasionally  $> 3.0 ln \cdot m^{-1}$ ) probably due to high turbidity and sometimes coloured waters. The mean  $I_k$  was 10.0 mEin  $\cdot m^{-2} \cdot min^{-1}$  (range 7-14 mEin  $\cdot m^{-2} \cdot min^{-1}$ ) for Lake Kyoga and was close to those of Lake Victoria (Tables 2 and 3). However, the  $I_{24}$  values in Lake Kyoga (mean 7.0 mEin  $\cdot m^{-2} \cdot min^{-1}$ , range 4-12 mEin  $\cdot m^{-2} \cdot min^{-1}$ ) are about 30-50% higher than those of Lake Victoria. The  $I_{24}/I_k$  ratio was usually close to 1, and occasionally greater than 1, indicating moderate or no light limitation. There are no earlier phytoplankton productivity and light data

Table 3. Average photosynthetic and light parameters of Lakes Kyoga and Albert during 1989-91. Chl, chlorophyll ( $\text{mg.m}^{-3}$ ); IPD, daily integral production ( $\text{g O}_2.\text{m}^{-2}.\text{d}^{-1}$ ); Zeu, euphotic depth (m); SD, Secchi depth (m); k, light extinction coefficient ( $\text{ln.m}^{-1}$ );  $I_k$ , irradiance at the onset of light saturated photosynthesis ( $\text{mEin.m}^{-2}.\text{min}^{-1}$ );  $I_{24}$ , mean light intensity in the water column integrated over 24 hours ( $\text{mEin.m}^{-2}.\text{m}^{-1}$ );  $I_{24}/I_k$ , the ratio of  $I_{24}$  to  $I_k$ .

	Kyoga		Albert
		Inshore	Offshore
Chl	41.0	16.0	9.0
IPD	10.0	13.0	8.0
Zeu	4.0	9.0	11.0
SD	0.9	2.0	3.5
k	1.7	1.0	0.5
$I_k$	10.0	15.0	16.0
$I_{24}$	7.0	6.0	1.4
$I_{24}/I_k$	0.8	0.4	0.1
$Z_m$	4.0	15.0	60.0



for Lake Kyoga with which to compare these results. However, qualitative consideration of the present phytoplankton community showed similar phytoplankton species composition as Lake Victoria in the 1960s with the diatom Melosira appearing regularly in the plankton.

The inshore integral production in Lake Albert approached levels of offshore Lake Victoria waters, while offshore Albert values were lower. The estimated mean daily integral production in Lake Albert was  $8 \text{ g O}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  offshore and  $13 \text{ g O}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  inshore (Table 3). Albert's photosynthetic rates are integrated over a deeper photosynthetic zone (9 m inshore and 11 m offshore). Chlorophyll concentrations were 3-20  $\text{mg} \cdot \text{m}^{-3}$  offshore and 6-29  $\text{mg} \cdot \text{m}^{-3}$  inshore, with mean values of 9 and 16  $\text{mg} \cdot \text{m}^{-3}$  respectively. Albert's mean chlorophyll concentrations are less than those of Lake Victoria (Table 1 & 3). Albert had higher mean Secchi disc transparency offshore (3.5 m) than inshore (2.0 m), with the latter equal to values observed offshore in Lake Victoria. Albert's mean vertical light extinction coefficient ( $k$ ) inshore and offshore were  $1.0 \text{ ln} \cdot \text{m}^{-1}$  and  $0.5 \text{ ln} \cdot \text{m}^{-1}$  respectively. These values are similar to those of the corresponding regions in Lake Victoria. The mean  $I_k$  of Lake Albert was about 30 % higher than lakes Victoria and Kyoga. The inshore regions of Lake Albert had a 4 fold higher mean  $I_{24}$  ( $6.0 \text{ mEin} \cdot \text{m}^{-2} \cdot \text{min}^{-1}$ ) than offshore ( $1.4 \text{ mEin} \cdot \text{m}^{-2} \cdot \text{min}^{-1}$ ) (Table 3). The inshore and offshore regions of Lake Albert yielded a ratio  $I_{24}/I_k$  always

below 1. The  $I_{24}$  values at the inshore areas of Lake Albert (mean  $6.0 \text{ mEin.m}^{-2}.\text{min}^{-1}$ , range  $3-11 \text{ mEin.m}^{-2}.\text{min}^{-1}$ ) was similar to that of Lake Kyoga (mean  $7.0 \text{ mEin.m}^{-2}.\text{min}^{-1}$ , range  $3-12 \text{ mEin.m}^{-2}.\text{min}^{-1}$ ), but 2-3 times higher than that in Lake Victoria (Tables 2 & 3).

The daily integral production in offshore Lake Albert has not apparently changed over the last 30 years. In the 1960s production ranged from 2-12 with a mean of  $7 \text{ g O}_2.\text{m}^{-2}.\text{d}^{-1}$  for three observations (Talling 1965) and in the 1990s it ranged from 2-10  $\text{g O}_2.\text{m}^{-2}.\text{d}^{-1}$  with a mean of  $8 \text{ g O}_2.\text{m}^{-2}.\text{d}^{-1}$  for 6 observations. Similarly, light penetration offshore Lake Albert is of the same range in the 1990s ( $0.4-1.0 \text{ ln.m}^{-1}$ ) as in the 1960,s ( $0.5-1.0 \text{ ln.m}^{-1}$ ). The euphotic zone was measured as 6-11 m deep (Talling 1963) which is close to that seen in the 1990s (4-14 m). The algal composition in Lake Albert was dominated by Cyclostephanos and Nitzschia species during the mixing period (July-August, 1990). Anabaena species were very abundant during June 1990 and May 1991 inshore. These species composed the main part of the phytoplankton in the 1960s and 1970s (Talling 1963; Hecky and Kling 1987).

## DISCUSSION

Seasonality in biomass (as chlorophyll-a) and productivity offshore Lake Victoria during the study were similar to that observed by Talling (1965 & 1966), except for the trends in  $P_{\max}$ . Historically, there was an annual biomass maximum offshore in August to November dominated by Melosira; blue green algae were of secondary importance (Fish 1957; Talling 1965; Talling 1987). The major chlorophyll maximum now occurs in September-November and is dominated by the diatom Nitzschia acicularis (H. Kling and R. Mugidde, unpublished). In the 1960-61 seasonality in primary productivity in Lake Victoria was less pronounced than it currently is but highest rates still occurred in October-November.

The fact that seasonal patterns of areal productivity and chlorophyll-biomass are now similar to those observed in the 1960s suggests that these are driven by annual mixing regime, which has not changed from that reported in the 1950s and 1960s (Talling 1965, 1966; Bugenyi, F.W.B, unpublished data on temperature and oxygen). The major chlorophyll maxima and maximum areal productivity occurred when stratification was moderate (October-December 1990) while the minor peaks coincided with breakdown of thermal stratification (May 1991). Higher phytoplankton productivity and biomass during September-November may be a consequence of increased light

availability to the algae due to relatively shallower mixed depth as thermal stratification is re-established (Talling 1966). At this time the algal cells offshore are exposed to low unsaturating irradiances for a shorter time than during the near isothermal conditions in July-August when the lake is deeply mixing or from January-April when the thermocline is deep. Nutrients previously added to the mixed layer during the mixing period are also available at that time.

Low production and biomass in July-August is probably caused by extreme light limitation; mean light intensities in the water column at that time are at a seasonal minima because of the deep mixed depth (Fig. 7). Lack of obvious seasonal trends inshore is because these bays are shallow (10-20m); these stations have no marked thermal or chemical stratification (Bugenyi, unpublished) and probably experience regular diurnal mixing. The higher productivity and biomass inshore than offshore may be because light is more available due to a shallower mixed depth for most of the year. Consequently, higher biomass is produced before self-shading limits further increases.

The seasonal changes in the specific productivity per unit chlorophyll ( $P_{\max}$ ) offshore Lake Victoria were different than Talling (1965) observations in 1960-61.  $P_{\max}$  was highest when the lake was destratified (July-August), and heterocystous cyanobacteria were less abundant. Heterocystous cyanobacteria are thought to dominate at other times because

of their ability to fix nitrogen (Hecky 1993). It has been suggested that the energetic costs of N-fixation, which competes with C-fixation for reducing power, might systematically lower  $P_{\max}$  at times of peak N fixation in Lake Victoria (J. Lehman, pers. com.). Alternatively, extreme light limitation during deep mixing may increase chlorophyll content per cell (Hecky and Guildford 1984) and thereby result in lower  $P_{\max}$  values.

Phytoplankton photosynthesis in Lake Albert and Kyoga is frequently light limited ( $I_{24}/I_k \ll 1$ ). Light extinction,  $k$ , and therefore,  $I_{24}$  seem to be controlled by different factors in the three lakes. Thermal data suggest deep mixing offshore Lake Albert during 1989-91, which was in agreement with Talling (1963) findings of a weak or non-existent thermal stratification. Lake Albert still mixes deeply throughout the year with a strong diurnal heating in surface waters. This greater mixed depth (60 m) coupled with the suspended high sediment load and the high total dissolved solids (Talling 1963) reduce light penetration. This apparently controls  $k$  in Lake Albert, which is almost certainly controlled by chlorophyll concentrations in lakes Victoria and Kyoga.

The mean  $I_{24}$  was higher in Lake Kyoga than inshore Lake Victoria despite the higher  $k$  values in Kyoga and the almost similar mean chlorophyll concentrations.  $I_{24}$  is a function of depth and  $k$ , and the shallower mean mixed depth (4.0 m) in Lake Kyoga compensates for higher values of  $k$  and causes

higher mean  $I_{24}$ . Algal cells in Lake Kyoga on average are thus exposed to saturating irradiances for a longer time than in Lake Victoria. Therefore, higher phytoplankton photosynthesis than in Victoria is expected since light limitation is moderate, as evidenced by the mean  $I_{24}/I_k$  ratio (0.8) being close to 1.0. However, integral production is lower in Lake Kyoga than in Lake Victoria (where light limitation is more severe), suggesting that light is not the only factor controlling phytoplankton production in Lake Kyoga.

In Lake Albert the four fold higher mean  $I_{24}/I_k$  values inshore than offshore suggests that severe light limitation is relieved inshore. That is, low light causes phytoplankton production offshore to be low. This conclusion is supported by the fact that offshore  $I_{24}/I_k$  ratios in Lake Albert were 50% lower than in offshore Victoria and daily integral production was about 40 % lower in Lake Albert than in Victoria. It seems certain that there have been no significant changes in light extinction coefficients, biomass and integral production in offshore Lake Albert since the 1960s. Since the current  $k$  values in Lake Albert equal those of the corresponding regions in Lake Victoria which is now light limited these data infer that algal growth in Albert was light limited in the 1960s. Because of this, substantially higher integral production would not be expected in Lake Albert even if nutrient enrichment had occurred.

## CHAPTER II

THE INCREASES IN PHYTOPLANKTON PRIMARY PRODUCTIVITY AND BIOMASS IN LAKE VICTORIA (UGANDA): A COMPARISON OF HISTORIC AND MODERN PHOTOSYNTHETIC PARAMETERS.

## ABSTRACT

The daily integral phytoplankton productivity per unit area was two times higher both inshore and offshore in the 1990s than in the 1960s. Phytoplankton photosynthesis has not increased in proportion to chlorophyll-a concentrations, which are about 2 to 10 times (offshore) and 5 to 10 times (inshore) higher than 30 years ago. Production in Lake Victoria is offset by the decreased efficiency of the photosynthetic system at low light intensities, and there is evidence suggesting that photosynthesis in Lake Victoria is now light limited.

## INTRODUCTION

Initial studies on the phytoplankton photosynthesis on Lake Victoria near Jinja, Uganda were done by Talling (1965). He reported rates of primary productivity of the range 5-11 g  $O_2 \cdot m_2 \cdot d^{-1}$  at inshore stations. The phytoplankton and nutrient regimes of the Ugandan waters of Lake Victoria were also examined in the 1950s and 1960s by Fish (1952,57), Talling (1957a,b), Evans (1961,1962), Talling and Talling (1965),

Talling (1966). Recently algal blooms are thought to have become more common and intense in Lake Victoria and have been observed in the Kenyan (Ochumba and Kibaara 1989) as well as Tanzanian and Ugandan waters. Since earlier limnological surveys, various changes have taken place in Lake Victoria and its catchment area. Land use has intensified as population increased, especially along the lakeshore and islands of Lake Victoria. The food web of the lake also has been radically altered partly due to over exploitation of the fisheries and introduction of the piscivorous Nile perch and herbivorous Nile Tilapia (Ogutu-Ohwayo 1990a, b). Benthic invertebrates especially Chironomids, Chaoborus and Caridina, are reported to have increased in abundance following the decline of the haplochromines (L. Ndawula, unpublished; G. Mhahizireki, unpublished; Witte et al. 1992). There is also evidence that nutrient chemistry of Lake Victoria has changed (Hecky and Bugenyi 1992; Bootsma and Hecky, submitted).

From many studies it is evident that changes in the nutrient loading and/or alterations in the food-web structure can change phytoplankton productivity through either the "bottom up" or "top down" effects (Shapiro 1980, Carpenter et al. 1985). For example, abundance of benthic feeding fishes and invertebrates have been observed to release nutrients from bottom sediments and stimulate algal production (Lammens, 1988). Changes in the grazing pressure will primarily affect phytoplankton production and biomass and may consequently



affect the abiotic properties of the water.

The objective of this study was to determine the present phytoplankton photosynthesis and biomass in Lake Victoria in the same areas previously studied by Talling and others in the 1950s and 1960s. The work described here was carried out during 1989-91.

### Materials and methods

#### Study areas

Lake Victoria (69000 km<sup>2</sup>, mean depth 40 m; maximum 90 m; Beadle 1981) has an extensive open water region that experiences seasonal stratification and shallow, protected regions which mix daily (Talling, 1963). The phytoplankton measurements were done in the northern, Ugandan portion of Lake Victoria due to the availability of historical limnological data for Pilkington bay and a 65 m depth offshore station (Bugaa) near Talling's (1965) offshore station.

#### Sample collection, treatment and analysis

The methods of Talling (1965) were used to estimate integral hourly and daily phytoplankton production and the maximum specific productivity per unit of chlorophyll-a at optimal irradiance for photosynthesis ( $P_{\max}$ ).

Light attenuation, Secchi transparency and temperature profiles were measured directly at sampling stations using Li Cor 1000 quantum sensor and meter, resistance thermometer

and/or Hydrolab and Secchi disc. Underwater irradiance was used to calculate the total vertical light extinction coefficient ( $k$ ) (Hutchinson 1957) and mean water column light intensity for 24 hours ( $I_{24}$ ) (Hecky and Guildford 1984). The  $I_{24}$  was calculated using simulated cloudless solar irradiance based on global models (Fee 1990). The light intensity which measures the onset of light saturation of photosynthesis ( $I_k$ ) was calculated using a computer programme (Fee 1990). The ratio of the global-radiation integrated over the whole day to the sum of the radiation during the incubation period was used to estimate daily gross production as detailed in Talling (1965).

Phytoplankton chlorophyll was determined by filtration of 100mls of sample on to a GF/C filter. The filter was immersed in 10 mls of 95% methanol for approximately 20 hours at 4°C in the dark, and the extract analysed on a Turner fluorometer (Stainton et al. 1977).

## Results and Discussion

### Comparison of inshore and offshore stations

Seasonality in phytoplankton productivity and biomass was well defined offshore (Fig. 14a). The biomass maxima and especially the July-August minima, were synchronous in offshore and inshore waters, but the yearly average chlorophyll-a concentrations were about twice as high inshore than offshore (Table 4). Variance analysis of  $P_{\max}$  indicated

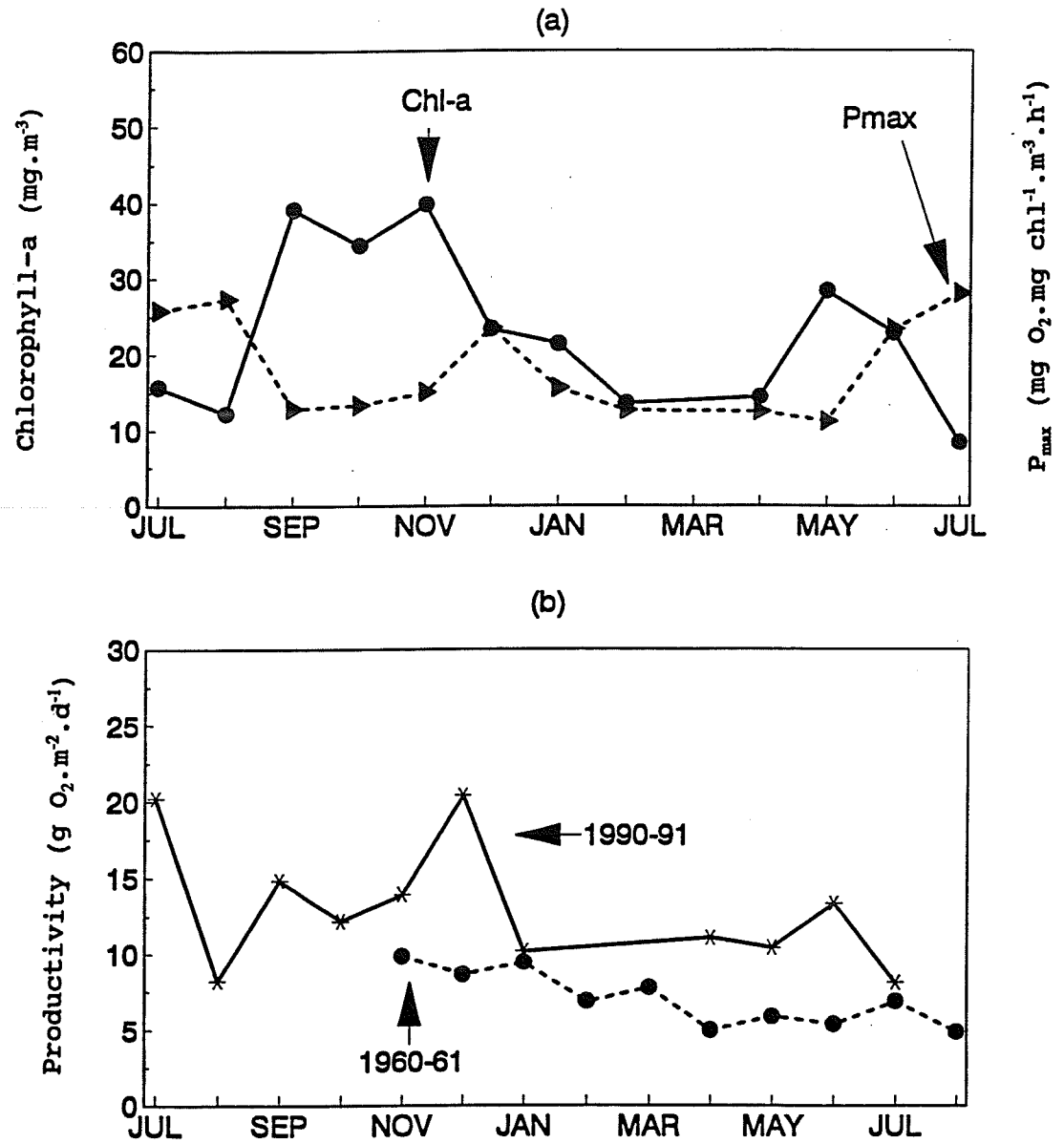


Fig. 14. Seasonal variation in 1990-91 of (a) Chlorophyll-a (Chl-a) and maximum specific productivity (Pmax) at Bugaia; (b) seasonality of the present and past daily productivity

Table 4. The present (1989-91) and past (1960-61) photosynthetic characteristics of Lake Victoria. Chl, chlorophyll-a ( $\text{mg.m}^{-1}$ );  $P_{\text{max}}$ , maximum productivity per unit chlorophyll at optimal irradiance ( $\text{mg O}_2.\text{mg chl}^{-1}.\text{h}^{-1}$ ); IPD, daily integral production per unit area ( $\text{g O}_2.\text{m}^{-2}.\text{d}^{-1}$ ); Zeu, euphotic depth (m); k, vertical light extinction coefficient ( $\text{ln.m}^{-1}$ ); SD, Secchi depth (m).

	Present				Past			
	Low	mean	High	n	Low	mean	High	n
Offshore (Bugala)								
Chl-a	8.4	24.5	40.0	15	1.2		5.5	14
$P_{\text{max}}$	11.2	19.0	28.0	15	19.0	25.0	31.0	14
IPD	8.2	13.0	20.4	15	4.9	7.4	11.4	14
Zeu	7.8	13.5	29.2	4	15.0		20.0	14
k	0.2	0.5	0.6	4	0.2		0.3	4
SD	1.3	2.0	3.0	15	6.4		8.4	
Inshore (Pilkington bay)								
Chl	22.2	46.7	67.1	15	10.0	12.5	15.0	2
$P_{\text{max}}$	10.5	17.1	28.5	15				
IPD	8.9	22.3	36.2	14	10.2	10.6	11.0	2

no significant statistical difference between inshore and offshore regions ( $P=0.09$ ). This could be due to similarity in phytoplankton species composition (H. Kling and R. Mugidde, unpublished). The trends in  $P_{\max}$  were not associated with the trends in chlorophyll-a concentrations offshore. Modern phytoplankton photosynthesis was higher than in the 1960s (Table 5) and underwent great seasonality offshore (Fig. 14b). Some of the variations in photosynthesis per unit volume at optimal light ( $P_{\text{opt}}$ ; the notation of Fee 1990) offshore can be explained by variations of chlorophyll-a ( $R^2=0.51$ ), but there was poor correlation ( $R^2<0.2$ ) at the inshore stations (not significant at  $p<0.05$ ). Regression analysis of integral productivity per unit area per hour and chlorophyll-a per unit volume yielded poor correlations ( $R^2<0.2$ ; not significant). Estimates of integral photosynthesis per unit area regressed as a function of the ratio  $P_{\text{opt}}/k$  yielded a positive correlation ( $R^2=0.45$ ) that was significant. Gross production was about 62% higher inshore than offshore (Table 5) despite the shallower euphotic zone (about half as deep as offshore).

Inshore and offshore phytoplankton communities had similar  $I_k$  values (Table 5). The  $I_k$  values for the phytoplankton of Lake Victoria were consistently higher than the corresponding  $I_{24}$ , thus the ratio  $I_{24}/I_k$  was always below 1, suggesting light availability may limit on photosynthesis in Lake Victoria.

Table 5. Summary of the light and photosynthetic characteristics of Lake Victoria during 1989-91. SD, Secchi depth (m);  $k$ , light extinction coefficient ( $\ln.m^{-1}$ );  $Z_{eu}$ , euphotic depth (m);  $P_{opt}/k$ , the ratio of optimal photosynthesis per unit volume ( $P_{opt}$ ) to  $k$ ;  $I_k$ , irradiance at the onset of light saturated photosynthesis ( $mEin.m^{-2}.min^{-1}$ );  $I_{24}$ , mean light intensity in the water column integrated over 24 hours ( $mEin.m^{-2}.min^{-1}$ );  $I_{24}/I_k$ , the ratio of  $I_{24}$  to  $I_k$ .

STA	SD	$k$	$Z_{eu}$	$P_{opt}/k$	$I_k$	$I_{24}$	$I_{24}/I_k$
Bugaia (offshore)							
max	3.0	0.6	29.2	1468.8	13.1	2.1	0.2
mean	2.0	0.4	13.5	889.1	10.8	1.8	0.2
min	1.3	0.1	7.8	511.8	9.4	1.3	0.1
n	15	4	4	4	4	4	4
Pilkington bay (inshore)							
max	1.7	1.3	6.7	1102.0	14.4	3.8	0.4
mean	1.2	1.0	5.0	740.0	9.6	2.8	0.3
min	0.8	0.8	3.7	450.5	7.7	2.0	0.1
n	15	11	11	15	11	11	11

### Present and Past

Fig. 14b depicts the seasonal fluctuations of phytoplankton production per day based on the present and past observations. Seasonality in the phytoplankton production and biomass at the offshore station is similar to that described by Talling 30 years ago. The most striking feature of the comparison between the present and past is the higher biomass both inshore and offshore than 30 years ago. Chlorophyll-a increased from 1.2-5.5  $\text{mg.m}^3$  to a range of 8.38-40  $\text{mg.m}^3$  offshore and from 10-15 to 22.2-67.1  $\text{mg.m}^3$  in Pilkington bay (Table 5). These higher biomasses have caused the euphotic to move upwards, and photosynthesis is now confined to shallower depths than in the 1960s. This has been accompanied by reduced Secchi transparency of the lake: from values of 7-8 m (Worthington, 1930) to 1.5-3 m offshore. Similarly, light attenuation is more rapid as depicted by the increased  $k$  values (Table 5).

Daily integral productivity per unit area at the offshore station increased from an average of 7.0  $\text{g O}_2.\text{m}^2.\text{d}^{-1}$  to 13.9  $\text{g O}_2.\text{m}^2.\text{d}^{-1}$  offshore. Inshore (Pilkington Bay) it increased from an average of 10-11  $\text{g O}_2.\text{m}^2.\text{d}^{-1}$  to 22.2  $\text{g O}_2.\text{m}^2.\text{d}^{-1}$ . However, the maximum specific productivity per unit chlorophyll-a ( $P_{\text{max}}$ ) decreased from a mean of 25 to 19  $\text{mg O}_2.\text{m}_3.\text{h}^{-1}$  (Table 5).

## Discussion

The present measurements of phytoplankton photosynthesis in Lake Victoria suggest that higher productivity is maintained throughout the year than that reported by Talling (1965). Phytoplankton photosynthesis has not increased in proportion to chlorophyll-a concentrations. This may be due to the negative effect of higher chlorophyll concentrations on the underwater light observed in this study. The maximum population density observed in the euphotic zone (370 mg chl. m<sup>-2</sup>) exceeds Talling's predicted maximum (185 mg chl.m<sup>-2</sup>. The ratio  $P_{opt}/k$  ratio is now 1960, which exceed the maximum theoretical value of 1250 (Talling 1965), also indicating light limitation. Light limitation of photosynthesis in Lake Victoria is further indicated by values of  $I_{24}/I_k$  (below 1.0) (Hecky and Guildford, 1984; Guildford et al. 1987). The maximum rates of photosynthesis at light saturation per unit chlorophyll-a ( $P_{max}$ ) are about 22% lower than 30 years ago, indicative of a less efficient photosynthetic system. Further increases in integral photosynthesis are unlikely because of self shading effects.



## GENERAL DISCUSSION

The recent significant increases in phytoplankton productivity and biomass in Lake Victoria likely involve the role of one or more critical nutrients, either by altered input or altered circulation and /or reduction in herbivory. Lake Victoria is clearly more eutrophic than it was 30 years ago (Ochumba and Kibaara 1989; Hecky and Bugenyi 1992; Hecky et.al 1993; Hecky 1993; Mugidde 1993). Two theories are available to explain the increase in phytoplankton productivity and biomass.

"Bottom up" theories emphasize the importance of nutrient loading or physical effects upon species composition, biomass and production. In contrast "top down" theories emphasize the role of the top predator and selective grazing controlling these variables (Shapiro, 1980; Carpenter et al. 1987).

There is a great deal of evidence linking phytoplankton productivity, biomass, and species composition to changed nutrient loading (Schelske 1975; Schindler 1977, 1978; Kilham et al. 1986; Hecky and Kilham 1988). Nutrients, especially P and N, enter the mixed layer of the lake from precipitation, runoff from the catchment area, and from internal recycling. Nutrient inputs to Victoria through precipitation and runoff have undoubtedly increased because of diverse natural and anthropogenic activities in the catchment area of Lake Victoria (Hecky and Bugenyi 1992; Hecky 1993; Bootsma and Hecky, submitted). The effect of these nutrients should be

more dramatic inshore where dilution by offshore waters is poorest. However, profound increases in phytobiomass and productivity have occurred lake-wide, suggesting that increased nutrients are widespread.

Most of the water input (80%) of Lake Victoria comes from direct rainfall (Hecky and Bugenyi 1992) which suggests that atmospheric sources of nutrients are important. Phosphorus, nitrogen and sulphur input into the lake through precipitation may have increased (Hecky and Bugenyi 1992; Bootsma and Hecky, submitted). It has also been suggested that acidity of the rain in Africa caused by S and N compounds has increased because of the increased frequency savanna and woodland burning (Simons 1989). Phosphorus has been observed to exceed algal demand in some tropical lakes (Talling and Talling 1965; Melack et al. 1982), but total phosphorus concentrations have not changed significantly since the 1960s in Lake Victoria (Talling 1966; Hecky and Bugenyi 1992), suggesting that P may not be the nutrient directly responsible for the increases in phytobiomass and productivity. Nitrogen is known to limit algal production in many tropical lakes (Melack et al. 1982; Hecky and Kling 1987). Talling and Talling (1965) and Talling (1966) suggested nitrogen limitation in Lake Victoria. Past evidence of N deficiency was from algal bio-assays of phytoplankton samples from Lake Victoria (Evans 1961). The concentration of dissolved inorganic fixed nitrogen in Lake Victoria is still very low

(Hecky and Bugenyi 1992) and can limit phytoplankton growth (Lehman and Branstrator 1993) of some phytoplankton species which cannot fix nitrogen. Any increase in the direct input of N or N-fixation may therefore stimulate algal growth and hence increase productivity and biomass as seen in Lake Victoria. Heterocystous nitrogen fixing cyanobacteria now dominate the phytoplankton of Lake Victoria throughout the year and nitrogen fixation may dominate N input to the lake.

The alternative theory that has been advanced to explain increases in algal biomass and productivity in Lake Victoria is based on the changes in fish fauna. According to this theory, the abundance of a piscivore, Nile perch (Ogutuhwayo 1990 a, b), and the disappearance of many of the native fish species, especially the haplochromines (Witte et al. 1992), reduced herbivory, resulting in increases of algal biomass and productivity. It has been shown elsewhere that alteration in the food-web structure is associated with changes in the abundance and composition of herbivore populations, and algal responses (Shapiro 1980; Carpenter et al. 1985, 1987). For example, in Lake Michigan a trophic cascade resulting in water clarity was proposed (Scavia et al. 1986). Turner (1982) showed that as zooplanktivore abundance increased, herbivorous zooplankton were reduced, phytoplankton increased and water clarity decreased. It is therefore possible that the increases in phytoplankton productivity and biomass reflect consequences of the introduction of the Nile perch into Lake

Victoria.

Studies of the variability and magnitude of phytoplankton photosynthesis and biomass have been investigated in other tropical African lakes (Talling 1965; Burgis et al. 1973; Melack and Kilham 1974; Melack 1979a, b; Hecky and Fee 1981). Moderate to high phytoplankton productivity and biomass have been measured in Lakes George, Edward, and occasionally Albert and inshore Victoria (production in the range  $10-16 \text{ g O}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ , Talling 1965). Chlorophyll concentrations in Lake George (Uganda) ranged from  $150-350 \text{ mg} \cdot \text{m}^{-3}$  (Burgis et al. 1973) while Lake Aranguadi, in Ethiopia had even higher levels ( $917-2170 \text{ mg} \cdot \text{m}^{-3}$ , Talling et al. 1973). The trophic efficiency and water quality of the East African great Lakes are in part a product of the distinctive fish faunas (Hecky 1981).

The lower phytoplankton productivity in Lake Albert, where diversity and endemism of the fish species is still preserved, suggest that the increases in primary productivity and biomass observed in Lake Victoria are not happening in all lakes of this region. Moreover, the relatively lower productivity in shallow Lake Kyoga compared to stations of similar depth in Lake Victoria suggests that the changes in Lake Victoria are not solely a result of alterations in the food-web structure. The Lake Kyoga fish community underwent a simplification similar to that of Lake Victoria, with the Nile perch, Nile Tilapia and Rastrineobola argentea now dominant in Kyoga (Wandera 1988; Ogutu-Ohwayo 1990a, b), yet

the productivity of Kyoga is 50% less than inshore areas of Victoria. These differences strongly suggest that altered nutrient inputs in Lake Victoria, which remain to be quantitatively determined are the primary cause of its more eutrophic state compared to the 1960s and to lake Kyoga.

Based on the  $I_{24}/I_k$  ratio, phytoplankton photosynthesis in lakes Victoria, Albert and frequently Kyoga are light limited to varying degrees. It seems possible that the phytoplankton community in Lake Albert has limited ability to respond to nutrient enrichment because of extreme light limitation. On the other hand phytoplankton production would likely increase in Lake Kyoga if more nutrients were input into it because it is less light limited. Lake Victoria's light environment has changed dramatically from what it was in the 1960s and it exhibits many symptoms of extreme eutrophication. It is probable that phytoplankton photosynthesis in Lake Victoria is now light limited much of the time due to self-shading, therefore, it is unlikely that substantially higher integral production can be achieved.

## CONCLUSIONS

Lake Victoria exhibits 2x higher phytoplankton photosynthesis and chlorophyll concentrations about 3-5x higher than the mean values of the 1960s. Photosynthesis has not increased proportionally to chlorophyll. These lower specific productivity rates per unit chlorophyll-a ( $P_{max}$ ) suggest a general decrease in phytoplankton growth rates since the 1960s. The high mean phytobiomass and more frequent algal blooms in Lake Victoria result in greater light absorption in the water column, and photosynthesis has become light limited, especially in the offshore waters. Photosynthesis is now operating near the theoretical maximum much of the year and further increases in integral production are not likely because of self shading effects.

The increases in productivity and biomass have been accompanied by qualitative changes in phytoplankton composition, with greater representation of blue-greens especially the filamentous nitrogen fixing Cylindrospermopsis (H. Kling and R. Mugidde, unpublished). Changes in diatom dominance from Melosira to Nitzschia have coincided with increased depletion of soluble-reactive silicon, which is about 10 fold lower than recorded in the 1960's (Hecky and Mungoma 1990; Hecky and Bugenyi 1992; Hecky 1993). The decrease in the lake's transparency because of higher chlorophyll concentrations has resulted in a shallower euphotic depth which causes loss of the photosynthetic zone.

Higher biomass accompanied by the more frequent algal blooms, can result in high oxygen demand during decomposition which can result in fish kills (Ochumba and Kibaara 1989) and increasing deoxygenation of the hypolimnion (Hecky et al. in review). Overall there has been a reduction in the volume of the oxygenated habitable waters. These changes are cause for concern as the remaining fish fauna is threatened by habitat degradation from eutrophication, putting in doubt the sustainability of the present high fish catches (Ogutu-Ohwayo 1990). The possible contributing factors to the dramatic changes in the Lake Victoria ecosystem in the 1990s are the large and increasing human population and land use activity in the catchment area (Bootsma and Hecky, in review), and fish introductions in the late 1950 and early 1960s, with subsequent reduction in faunal diversity. Although the causes of eutrophication are yet to be determined fully, the fact of higher primary production and phytobiomass are definitively established by this study.

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Appendix 1. The in situ phytoplankton parameters of Lake Victoria during 1989-91. Chl, chlorophyll-a ( $\text{mg.m}^{-3}$ );  $\text{nP}_{\text{max}}$ , maximum productivity rate per unit volume ( $\text{mg O}_2.\text{m}^{-2}.\text{h}^{-1}$ );  $\text{P}_{\text{max}}$ , maximum productivity rate per unit chlorophyll ( $\text{mg O}_2.\text{mg chl}^{-1}.\text{h}^{-1}$ );  $\text{nP}_{\text{max}}/\text{k}$ , the ratio  $\text{nP}_{\text{max}}$  to  $\text{k}$ , the vertical light extinction coefficient ( $\text{ln.m}^{-1}$ ); IPH, hourly integral productivity per unit area ( $\text{g O}_2.\text{m}^{-2}.\text{h}^{-1}$ ); d/f, day hour factor (h); IPD, the daily rate of integral productivity ( $\text{g O}_2.\text{m}^{-2}.\text{d}^{-1}$ ).

STA	Date	Chl	$\text{nP}_{\text{max}}$	$\text{P}_{\text{max}}$	$\text{nP}_{\text{max}}/\text{k}$	IPH	d/f	IPD
BUG	15-Mar-90	39.5						
	20-Jul-90	15.7	405	25.8	653.2	1.6	12.5	20.2
	01-Aug-90	12.3	335	27.3		1.9	8.8	17.1
	24-Aug-90					0.9	9	8.3
	25-Sep-90	18.5	325	17.6		1.7	9	14.9
	30-Oct-90	39.1	505	12.9		1.4	8.5	12.2
	27-Nov-90	34.4	460	13.4		1.5	9.3	13.9
	18-Dec-90	39.8	600	15.1		2.1	9.9	20.4
	29-Jan-91	23.4	550	23.5		1.2	8.8	10.2
	26-Feb-91	21.4	365	15.6			9.4	
	23-Apr-91	14.4	180	12.5		1.3	8.5	11.1
	29-May-91	28.3	317.3	11.2	511.8	1.1	9.4	10.4
	25-Jun-91	22.9	535	23.4	922.4	1.4	9.6	13.4
	30-Jul-91	8.4	235	28.0	1468.8	0.9	9	8.2
	mean	24	401	19	889	1	9	13
PLK	10-May-89	52.4	540	10.3	566.7	2.8	9.4	26.5
	01-Jun-89	67.1	914.5	13.6	1088.7	3.3	9.6	31.4
	19-Jul-89	49.5	644	13.0	560.0	1.4	9	13.0
	22-Aug-89	52.8	650	12.3	806.5	3.2	9	28.7
	22-Sep-89	42.2	1200	28.5	952.4	2.9	9	26.1

## Appendix 1. (continued)

STA	Date	Chl	nP <sub>max</sub>	P <sub>max</sub>	nP <sub>max</sub> /k	IPH	d/f	IPH
	02-Nov-89	58.1	1250	21.5	1024.6	3.0	9.3	28.0
	23-Nov-89	57.4	564	9.8	414.7	3.9	9.3	36.2
	17-Jan-90					2.2	8.8	19.1
	22-Mar-90	47.0	668.3	14.2	718.6	2.1	9.1	19.5
	24-May-90	43.1	875	20.3	711.4			
	13-Jul-90	48.0	1080	22.5	1102.0	2.2	9	19.7
	13-May-91	38.5	500	13.0	450.5	0.9	9.4	8.7
	21-Jun-91	44.3	730	16.5	776.6	3.0	9.6	28.3
	16-Jul-91	48.0	630	13.1	670.2	1.6	9	14.6
	30-Jul-91	22.2	600	27.0	705.9			
	22-Aug-91	30.3	635	21.0	616.5	1.4	9	12.3
	mean	47	765	17	744	2	9	22
BUV	03-Mar-89	32.4	282	8.70		1.62	9.1	14.7
	26-Apr-89	39.0	500	12.8	505	1.6	8.5	13.3
	09-Jun-89	43.0	730	17.0		2.4	9.6	22.8
	22-Jun-89	32.0	615	19.2	809	2.0	9.6	19.3
	09-Aug-89	39.7	630	15.9	630	2.4	9.0	21.6
	22-Sep-89	46.5	1135	24.4	1455	4.7	9.0	42.6
	14-Nov-89	46.0	1400	30.4	1505	3.7	9.3	34.5
	07-Feb-90	41.5	1055	25.4	1302	3.0	9.4	28.0
	09-Mar-90	39.4	950	24.1	1092	2.2	9.1	19.6
	13-Jul-90	31.9				2.0	9.0	18.2
	23-Jul-90	44.9	485	10.8		1.6	9.0	14.1
	30-Aug-90	47.1	520	11.0		2.2	9.0	19.7
	20-Feb-91	51.0	781	15.3		1.8	9.4	16.7
	07-Jun-91	36.3	630	17.4	685	1.6	9.0	14.5
	12-Jul-91	29.8	630	21.1	643	1.3	9.0	11.9
	02-Aug-91	26.2	720	27.5	923			
	22-Aug-91	24.3				1.34	9	12.0
	mean	38	738	19	955	2	9	20

## Appendix 1. (continued)

STA	Date	Chl	nP <sub>max</sub>	P <sub>max</sub>	nP <sub>max</sub>	IPH	d/f	IPD
NAP	25-Sep-89	53.4	720	13.5	720.0	3.0	9.0	26.8
	28-Oct-89	52.2	700	13.4	721.6	2.9	8.5	24.6
	02-Feb-90	67.9	710	10.5	542.0	2.9	9.4	26.9
	09-Feb-90	36.8	1055	28.7	1034.3	2.7	9.4	25.8
	07-Mar-90	54.2	1192	22.0	1045.6	1.9	9.1	17.5
	02-May-90	41.4	592.5	14.3	731.5	1.6	9.4	15.0
	04-Jun-90	33.3	820	24.6	854.2	2.0	9.6	19.3
	29-Jun-90	45.5	830	18.2	864.6	1.9	9.6	18.5
	11-Oct-90	51.4	770	15.0		2.6	8.5	22.1
	09-May-91	36.3	510	14.0	629.6	1.3	9.4	11.8
	28-May-91	38.5	465	12.1	447.1	1.2	9.4	11.5
	14-Jun-91	33.5	745	22.2	856.3	1.9	9.6	18.6
	19-Jun-91	51.5	1050	20.4	1250.0	2.0	9.6	19.7
	26-Jun-91	42.9	915	21.3	915.0	1.6	9.6	15.6
	04-Jul-91	32.7	820	25.1	911.1	1.8	9.0	15.9
	11-Jul-91	29.2	590	20.2	702.4	1.2	9.0	11.0
	30-Jul-91	23.9	600	25.1	740.7	1.9	9.0	16.8
	28-Aug-91	22.1	455	20.6	583.3	0.9	9.0	8.2
	mean	41	752	19	797	2	9	18

Appendix 2. The light and photosynthetic data of Lake Victoria during 1989-91.  $\alpha^B$ , the slope of the irradiance curve per unit chlorophyll ( $\text{mg O}_2 \cdot \text{mg chl}^{-1} \cdot \text{mEin}^{-1} \cdot \text{m}^{-2}$ ); PBM, the rate of photosynthesis per unit chlorophyll at optimal PAR ( $\text{mg O}_2 \cdot \text{mg chl}^{-1} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ );  $I_k$ , irradiance at the onset of light saturated photosynthesis ( $\text{mEin} \cdot \text{m}^{-2} \cdot \text{min}^{-1}$ );  $I_{24}$ , mean light intensity in the water column integrated over 24 hours ( $\text{mEin} \cdot \text{m}^{-2} \cdot \text{min}^{-1}$ );  $I_{24}/I_k$ , the ratio  $I_{24}$  to  $I_k$ .

STA	Date	$\alpha^B$	PBM	$I_k$	$I_{24}$	$I_{24}/I_k$
BUG	15-Dec-89					
	15-Mar-90					
	04-Jul-90					
	20-Jul-90	44.0	24.8	9.4	1.8	0.20
	01-Aug-90					
	24-Aug-90					
	30-Oct-91					
	27-Nov-91					
	18-Dec-91					
	29-Jan-91					
	26-Feb-91					
	23-Apr-91					
	29-May-91	13.5	10.6	13.0	2.1	0.16
	25-Jun-91	20.4	12.4	10.2	1.3	0.12
	30-Jul-91	49.7	31.3	10.5	2.1	0.20
	mean	32	20	11	2	0.2
PLK	10-May-89	26.9	15.7	9.7	2.0	0.21
	01-Jun-89	23.2	13.1	9.4	3.6	0.38
	19-Jul-89	31.0	14.4	7.7	2.7	0.34
	22-Aug-89	22.8	19.7	14.4	3.8	0.26
	22-Sep-89	45.7	32.8	12.0	2.8	0.24
	02-Nov-89	25.5	19.9	13.0	2.6	0.20

## Appendix 2. (continued)

STA	Date	$\alpha^B$	PBM	$I_k$	$I_{24}$	$I_{24}/I_k$
	23-Nov-89					
	17-Jan-90					
	07-Feb-90					
	22-Mar-90	25.7	12.6	8.2	3.2	0.39
	24-May-90	42.9	20.7	8.0	2.3	0.28
	13-Jul-90	25.2	13.8	9.1	2.4	0.27
	21-Sep-90					
	13-May-91	25.2	13.8	9.1	2.8	0.30
	21-Jun-91	24.7	14.3	9.7	3.1	0.32
	16-Jul-91	26.1	13.1	8.4	2.8	0.33
	31-Jul-91	49.6	24.8	8.3	2.9	0.35
	22-Aug-91	38.1	18.1	8.1	2.5	0.31
	mean	31	18	10	3	0.3
BUV	03-Mar-89	24.4	15.6	10.7	2.7	0.25
	26-Apr-89	22.5	12.0	8.9		
	09-Jun-89	17.8	16.7	15.7	2.4	0.15
	22-Jun-89	36.1	16.1	7.4	1.9	0.25
	09-Aug-89	23.8	14.9	10.4	1.6	0.15
	22-Sep-89	31.6	21.7	11.5	2.4	0.21
	14-Nov-89	45.3	24.5	9.0	1.8	0.20
	09-Mar-90	32.3	22.0	11.4	2.3	0.20
	13-Jul-90				1.8	
	23-Jul-90	18.9	10.3	9.1	2.2	0.24
	07-Jun-91	18.8	16.8	14.9	2.1	0.14
	12-Jul-91	32.4	21.0	10.8	1.8	0.17
	02-Aug-91					
	22-Aug-91	39.8	26.7	11.2	2.5	0.22
	mean	29	18	11	2	0.2

## Appendix 2.(continued)

STA	Date	$\alpha^B$	PBM	$I_k$	$I_{24}$	$I_{24/I}k$
NAP	25-Sep-89	27.8	13.0	7.8	2.9	0.37
	28-Oct-89	20.7	12.8	10.3	4.7	0.46
	02-Feb-90	31.3	18.2	9.8	2.9	0.29
	09-Feb-90	40.6	26.4	10.8	3.8	0.35
	07-Mar-90	22.0	18.1	13.7	2.1	0.15
	02-May-90	15.3	12.3	13.5	2.5	0.18
	04-Jun-90	23.8	18.5	13.0	2.4	0.18
	29-Jun-90	21.3	17.0	13.3	2.3	0.17
	11-Oct-90					
	09-May-91	24.7	12.7	8.6	2.1	0.25
	28-May-91	27.2	11.7	7.2	2.0	0.28
	14-Jun-91	29.8	21.8	12.2	2.2	0.18
	19-Jun-91	44.6	24.5	9.2	1.5	0.16
	26-Jun-91	19.6	16.2	13.8	1.9	0.14
	04-Jul-91	28.0	19.5	11.6	2.4	0.20
	11-Jul-91	36.3	19.2	8.8	1.9	0.22
	31-Jul-91	28.5	23.1	13.5	1.9	0.14
	28-Aug-91	33.8	23.8	11.7	2.9	0.25
	mean	28	18	11	2	0.2

Appendix 3. The SD, Secchi depths (m); k, vertical light extinction coefficient ( $\ln.m^{-1}$ ); Zeu, euphotic depth (m); and  $P_{opt}$ , photosynthesis per unit volume at optimal (PAR) photosynthetically active radiation ( $mg\ O_2.m^{-3}.h^{-1}$ ) of Lake Victoria during 1989-91.

Station	Date	SD	k	Zeu	$P_{opt}$
BUG	15-Dec-89	1.7			
	15-Mar-90	2.2			
	04-Jul-90	1.9			
	20-Jul-90	1.9	0.5	8.6	389
	01-Aug-90	2.5			
	24-Aug-90	2.3			
	30-Oct-91	1.3			
	27-Nov-91	1.4			
	18-Dec-91	1.9			
	29-Jan-91	2.0			
	26-Feb-91	1.8			
	23-Apr-91	2.0			
	29-May-91	1.7	0.6	7.8	300
	25-Jun-91	2.0	0.6	8.3	294
	30-Jul-91	3.0	0.2	29.2	200
	mean	2	0.5	13	296
PLK	10-May-89	1.3	1.0	5.2	457
	01-Jun-89	1.1	0.8	6.7	846
	19-Jul-89	1.1	1.2	4.4	332
	22-Aug-89	1.3	0.8	6.6	527
	22-Sep-89	0.9	1.3	3.7	697
	02-Nov-89	1.0	1.2	4.0	694
	23-Nov-89	0.9			
	17-Jan-90	0.8			
	07-Feb-90	1.0			

## Appendix 3. (continued)

Station	Date	SD	K	Zeus	P <sub>opt</sub>
	22-Mar-90	1.3	0.9	5.4	603
	24-May-90	1.0	1.2	4.1	987
	13-Jul-90	1.1	1.0	4.7	990
	21-Sep-90	1.7			
	13-May-91	1.4	1.1	4.6	529
	21-Jun-91	1.2	0.9	5.4	638
	16-Jul-91	1.4	0.9	5.5	629
	31-Jul-91	1.4	0.9	5.7	549
	22-Aug-91	1.4	1.0	4.6	559
	mean	1	1	5	646
BUV	03-Mar-89	2.0			507
	26-Apr-89	1.6	0.7	6.2	469
	09-Jun-89	1.5			720
	22-Jun-89	1.6	0.8	6.3	514
	09-Aug-89	1.6	1.0	4.7	590
	22-Sep-89	1.7	0.8	7.3	1010
	14-Nov-89	1.6	0.9	5.2	1126
	09-Mar-90	1.5	0.9	5.6	869
	13-Jul-90	1.3	0.9	5.5	
	23-Jul-90	1.3			461
	07-Jun-91	1.5	0.9	5.5	610
	12-Jul-91	1.5	1.0	4.9	546
	02-Aug-91	1.9	0.7	6.2	
	22-Aug-91	2.0	0.7	6.7	431
	mean	2	1	6	654
NAP	25-Sep-89	1.3	1.0	5.1	692
	28-Oct-89	1.2	1.0	6.2	666



## Appendix 3. (continued)

Station	Date	SD	k	Zeü	P <sub>opt</sub>
	02-Feb-90	1.0	1.3	4.1	688
	09-Feb-90	1.2	1.0	5.3	970
	07-Mar-90	1.2	1.1	4.3	900
	02-May-90	1.1	0.8	5.8	510
	04-Jun-90	1.4	1.0	4.6	383
	29-Jun-90	1.4	1.0	5.2	822
	11-Oct-90	0.9			
	09-May-91	1.2	0.8	5.6	490
	28-May-91	1.4	1.0	4.8	452
	14-Jun-91	1.4	0.9	5.4	618
	19-Jun-91	1.3	0.8	4.7	897
	26-Jun-91	1.2	1.0	5.6	696
	04-Jul-91	1.5	0.9	5.4	701
	11-Jul-91	1.5	0.8	5.5	461
	31-Jul-91	1.3	0.8	5.8	552
	28-Aug-91	1.4	0.8	6.1	439
	mean	1	1	5	643

Appendix 4. The integral production and photosynthetic data of Lake Kyoga during 1989-91. Chl, chlorophyll-a ( $\text{mg} \cdot \text{m}^{-3}$ );  $nP_{\text{max}}$ , maximum productivity per unit volume ( $\text{mg O}_2 \cdot \text{m}^{-3} \cdot \text{h}^{-1}$ );  $P_{\text{max}}$ , maximum productivity per unit chlorophyll ( $\text{mg O}_2 \cdot \text{O}_2 \cdot \text{h}^{-1}$ );  $nP_{\text{max}}/k$  the ratio  $nP_{\text{max}}$  to  $k$ , light extinction coefficient ( $\ln \cdot \text{m}^{-1}$ ); IPH, hourly integral productivity per unit metre area ( $\text{g O}_2 \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ ); d/f, day day hour factor (h); IPD, daily integral per unit area ( $\text{g O}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ )

STA	Date	Chl	$nP_{\text{max}}$	$P_{\text{max}}$	$nP_{\text{max}}/k$	IPH	d/f	IPD
Bba	14-Apr-89	31.0	720	23.2	809	1.8	8.5	15.2
	08-Dec-89	52.0	746	14.3	228	1.4	9.9	14.1
	29-Jun-91	29.5	405	13.7	296	0.9	9.6	8.2
	11-Aug-91	28.2	677	24.0	517	1.3	9	11.9
	mean	35	637	19	462	1	9	12
MTA	13-Apr-89	28.5	386	13.5	382	0.7	8.5	5.8
	08-Dec-89	43.5			0		9.9	
	13-Feb-90	42.1	650	15.5	546	1.7	9.4	15.8
	30-Jul-90	32.9					9	
	12-Nov-90	48.4	900	18.6		1.5	9.3	13.7
	19-Apr-91	51.3	800	15.6		1.0	8.5	8.9
	01-Jun-91	39.6					9.6	
	01-Jul-91	53.8	550	10.2		1.0	9	9.2
	12-Aug-91	46.9					9	
	mean	43	657	15	309	1	9	11
MTB	13-Apr-89						8.5	
	13-Feb-90					0.9	9.4	8.6
	19-Apr-91					1.0	8.5	8.9
	01-Jun-91	32.2						
	01-Jul-91	57.3	1220	21.3	758	1.3	9	12.1

## Appendix 4. (continued)

STA	Date	Chl	nP <sub>max</sub>	P <sub>max</sub>	nP <sub>max</sub> /k	IPH	d/f	IPD
	12-Aug-91						9	7.9
	mean	45	1220	21	758	1	9	9
Mus	01-Apr-89	21.3	200	9.4	290	0.8	8.5	7.0
	07-Dec-89	51.5					9.9	
	30-Jul-90	42.1	585	13.9		0.6	9	5.5
	10-Nov-90	37.1	590	15.9		0.8	9.3	7.6
	19-Apr-91	51.3	605	11.8		1.0	9.3	9.7
	31-May-91	30.5	620	20.3	279	0.9	9.4	8.4
	30-Jun-91	27.0	620	23.0	339	1.0	9.6	9.6
	10-Aug-91	31.7	583	18.4	353	0.9	9	7.7
	mean	34	543	16	315	1	9	8
Kiw	12-Apr-89	48.2	808	16.8	646	1.4	8.5	12.3
	07-Dec-89	40.1	909	22.7	659	1.2	9.9	11.8
	30-Jul-90	42.1					9	
	10-Nov-90	37.1					9.3	
	01-Jun-91	32.0	600	18.8			9.6	
	30-Jun-91	26.0	519	20.0	167	0.8	9.6	8.2
	12-Aug-91	21.7					9	
	mean	35	709	20	491	1	9	11
Kaw	11-Nov-90	45.8	915	20.0		1.5	9.3	13.6
	20-Apr-91		690			0.9	8.5	7.9
	31-May-91	37.2	850	22.9	697	1.4	9.4	13.0
	11-Aug-91	53.9	1010	25.3	962	1.8	9	16.0
	mean	46	866	23	829	1.4	9	10

Appendix 5. The light and photosynthetic data of of Lake Kyoga during 1989-91.  $\alpha^B$ , slope of the irradiance curve per unit chlorophyll ( $\text{mg O}_2 \cdot \text{mg chl}^{-1} \cdot \text{mEin}^{-1} \cdot \text{m}^{-2}$ ); PBM, the rate of photosynthesis per unit chlorophyll at optimal PAR ( $\text{mg O}_2 \cdot \text{mg chl}^{-1} \cdot \text{h}^{-1}$ );  $I_k$ , the irradiance at the onset of light saturated photosynthesis ( $\text{mEin} \cdot \text{m}^{-2} \cdot \text{min}^{-1}$ );  $I_{24}$ , mean light intensity in the water column integrated over 24 hours ( $\text{mEin} \cdot \text{m}^{-2} \cdot \text{min}^{-1}$ );  $I_{24}/I_k$ , the ratio  $I_{24}$  to  $I_k$ .

STA	Date	$\alpha^B$	PBM	$I_k$	$I_{24}$	$I_{24}/I_k$
Bba	14-Apr-89	22.7	13.0	9.5	11.2	1.18
	08-Dec-89	33.2	14.1	7.1	8.8	1.23
	29-Jun-91	26.2	12.4	7.9	7.5	0.95
	11-Aug-91	39.4	23.5	10.0	8.3	0.83
	mean	30	16	9	9	1.0
MTA	13-Apr-89	25.9	11.7	7.5	11.8	1.58
	08-Dec-89				5.0	
	13-Feb-90	26.3	14.9	9.4	10.2	0.92
	30-Jul-90					
	12-Nov-90					
	19-Apr-91					
	01-Jun-91	29.4	16.9	9.6	5.6	0.58
	01-Jul-91	23.3	12.3	8.8	5.8	0.66
	12-Aug-91	28.9	19.5	11.3	4.8	0.42
	mean	27	15	9	7	0.83
MTB	13-Apr-89					
	13-Feb-90					
	19-Apr-91					
	01-Jun-91	27.06	19.04	11.7	6.7	0.57

## Appendix 5. (continued)

STA	Date	$\alpha^B$	PBM	$I_k$	$I_{24}$	$I_{24}/I_k$
	01-Jul-91	26.83	17.34	10.8	4.7	0.44
	12-Aug-91				3.5	
	mean	27	18	11	5.0	0.50
Mus	01-Apr-89	28.9	14.2	8.2	8.9	1.09
	07-Dec-89					
	30-Jul-90					
	10-Nov-90					
	19-Apr-91					
	31-May-91	33.8	15.2	7.5	4.7	0.63
	30-Jun-91	38.8	18.6	8.0	3.6	0.45
	10-Aug-91	42.7	20.4	8.0	5.6	0.70
	mean	36	17	8	5.7	0.71
Kiw	12-Apr-89	25.3	13.5	8.9	7.3	0.82
	07-Dec-89	27.2	13.7	8.4	7.0	0.83
	30-Jul-90					
	10-Nov-90					
	01-Jun-91				6.4	
	30-Jun-91	38.7	19.4	8.3	8.8	1.06
	12-Aug-91	39.9	22.4	9.3	2.8	0.30
	mean	33	17	9	6.5	0.75
Kaw	11-Nov-90					
	20-Apr-91					
	31-May-91	35.0	21.5	10.2	7.4	0.73
	11-Aug-91	30.1	26.0	14.4	8.3	0.58
	mean	33	24	12	8.9	0.65

Appendix 6. The SD, Secchi transparency (m); k, light extinction coefficient ( $\ln.m^{-1}$ ); Zeu, euphotic depth (m) of Lake Kyoga during 1989-91.

STA	Date	SD	k	Zeu
Bba	14-Apr-89	1.5	0.9	5.9
	08-Dec-89	0.6	3.3	1.8
	29-Jun-91	0.8	1.4	3.9
	11-Aug-91	1.0	1.3	4.1
	mean	1	2	4
MTA	13-Apr-89	1.2	1.0	5.2
	08-Dec-89	0.6	1.4	4.1
	13-Feb-90	0.6	1.2	4.4
	30-Jul-90	1.0		
	12-Nov-90	0.7		
	19-Apr-91	0.6		
	01-Jun-91			
	01-Jul-91			
	12-Aug-91	0.6	2.7	2.5
	mean	0.8	2	4
MTB	13-Apr-89	0.7		
	13-Feb-90	0.8		
	19-Apr-91	0.6		
	01-Jun-91	0.7	1.6	3.4
	01-Jul-91			
	12-Aug-91		2.7	2.5
	mean	0.7	2	3

## Appendix 6 (continued)

STA	Date	SD	k	Ze
Mus	01-Apr-89	1.6	0.7	
	07-Dec-89	0.6		
	30-Jul-90	0.6		
	10-Nov-90	0.6		
	19-Apr-91	0.5		
	31-May-91		2.2	2.5
	30-Jun-91	0.6	1.8	2.9
	10-Aug-91	0.7	1.7	3.2
	mean	0.7	2	3
Kiw	12-Apr-89	1.0	1.3	4.4
	07-Dec-89	0.8	1.4	3.9
	30-Jul-90	1.5		
	10-Nov-90	0.6		
	01-Jun-91		1.1	
	30-Jun-91	0.6	3.1	2.2
	12-Aug-91	0.6	3.0	
	mean	0.8	2	4
Kaw	11-Nov-90	1.3		
	20-Apr-91	1.6		
	31-May-91	1.2	1.2	4.2
	11-Aug-91	1.4	1.1	4.9
	mean	1.3	1	5

Appendix 7. The photosynthetic parameters and integral production of Lake Albert during 1989-91. Chl, chlorophyll-a(mg.m<sup>-1</sup>); nP<sub>max</sub>, maximum productivity per unit volume(mg O<sub>2</sub>.m<sup>-2</sup>.h<sup>-1</sup>; P<sub>max</sub>, maximum productivity per unit chlorophyll(mg O<sub>2</sub>.mg chl<sup>-1</sup>.h<sup>-1</sup>); nP<sub>max</sub>/k, the ratio nP<sub>max</sub> to k, the vertical light extinction coefficient (ln.m<sup>-1</sup>); IPH, hourly integral productivity rate(g O<sub>2</sub>.m<sup>-2</sup>.h<sup>-1</sup>); d/f day hour factor(h); IPD, daily integral production (g O<sub>2</sub>.m<sup>-2</sup>.d<sup>-1</sup>).

STA	Date	Chl	nP <sub>max</sub>	P <sub>max</sub>	nP <sub>max</sub> /k	IPH	d/f	IPD
B1	30-9-89	20.1	480	24	686	0.9	9	7.8
	17-6-90	5.4	160	29	400	0.8	9.6	7.5
	26-7-90	3.2	92	29	153	0.2	9	2.0
	12-8-90	9.3	270	29	675	1.1	9	10.2
	21-5-91	7.1	230	32	575	1.1	9.4	10.0
	24-7-91	6.0	190	31	475	1.1	9	9.8
	mean	9	237	29	494	1	9	8
B2	1-10-89	23.4	590	25		1.8	8.5	14.9
	17-6-90	11.8	310	26	775	1.4	9.6	13.0
	19-6-90	15.1	460	30	920	1.7	9.6	16.7
	21-6-90	5.9	175	30	350	0.6	9.6	6.0
	27-7-90	6.4	190	30	380	0.5	9	4.9
	11-8-90	10.3	275	27	687.5	1.1	9	9.8
	23-5-91	18.5	450	24	1125	2.0	9.4	18.7
	26-7-91	11.1	280	25		1.0	9	8.7
	mean	13	341	27	706	1	9	12
B3	02-10-89						8.5	
	03-10-89	22.4	550	24.6	917	2.5	8.5	21.3
	20-5-91	10.8	320	29.8	640	1.4	9.4	12.9
	mean	17	435	27	778	2	9	17



## Appendix 7. (continued)

STA	Date	Chl	$nP_{\max}$	$P_{\max}$	$nP_{\max}/k$	IPH	d/f	IPD
Bg	18-6-90	29.0	678	23	848	2.1	9.6	20.1
	20-6-90						9.6	
	22-5-91	15.6	475	31	950	1.8	9.4	17.1
	25-7-91	18.7	675	36	1350	2.1	9.6	19.9
	mean	21	609	30	1049	2	10	19
Wa	20-6-90	18.3	521	28	744	1.3	9.6	12.2
	21-7-91	10.4	335	32	419	0.8	9	7.5
	mean	14	428	30	582	1	9	10
Pa	22-7-91	29.2	940	32	22	1	9	11

Appendix 8. The light and photosynthetic data of Lake Albert during 1989-91.  $\alpha^B$ , the slope of the irradiance curve per unit chlorophyll ( $\text{mg O}_2 \cdot \text{mg chl}^{-1} \cdot \text{mEin}^{-1} \cdot \text{m}^{-2}$ ); PBM, the rate of photosynthesis per unit chlorophyll at optimal PAR ( $\text{mg O}_2 \cdot \text{mg chl}^{-1} \cdot \text{h}^{-1}$ );  $I_k$ , the irradiance at the onset of light saturated photosynthesis ( $\text{mEin} \cdot \text{m}^{-2} \cdot \text{min}^{-1}$ );  $I_{24}$ , mean light intensity in the water column integrated over 24 hours ( $\text{mEin} \cdot \text{m}^{-2} \cdot \text{min}^{-1}$ );  $I_{24}/I_k$ , the ratio  $I_{24}/I_k$ .

STA	Date	$\alpha^B$	PBM	$I_k$	$I_{24}$	$I_{24}/I_k$
B1	30-Sep-89	20.9	16.5	13.2	1.3	0.1
	17-Jun-90	23.6	26.9	19.0	1.6	0.08
	26-Jul-90	30.7	26.4	14.3	1.3	0.09
	12-Aug-90	29.3	25.4	14.5	1.3	0.09
	21-May-91	36.0	35.6	16.5	1.4	0.08
	24-Jul-91	25.6	28.0	18.3	1.5	0.08
	mean	28	26	16	1.4	0.09
B2	01-Oct-89	22.7	18.2	13.4	7.9	0.59
	17-Jun-90	17.5	22.5	21.4	5.9	0.28
	19-Jun-90	28.5	25.3	14.8	5.4	0.36
	21-Jun-90	40.8	27.6	11.3	4.7	0.42
	27-Jul-90	26.4	23.6	14.9	4.8	0.32
	11-Aug-90	23.1	25.2	18.2	6.4	0.35
	23-May-91	18.8	21.9	19.5	7.2	0.37
	26-Jul-91	27.2	15.9	9.7	5.4	0.56
	mean	26.0	23.0	15.0	6.0	0.4
B3	02-Oct-89					
	03-Oct-89	23.8	21.7	15.2	11.2	0.74

## Appendix 8. (continued)

STA	Date	$\alpha B$	PBM	$I_k$	$I_{24}$	$I_{24/Ik}$
	20-May-91	36.4	28.4	13.0	8.7	0.67
	mean	30.0	25.0	14.0	10.0	0.7
Bg	18-Jun-90	33.8	20.9	10.3	4.3	0.42
	20-Jun-90					
	22-May-91	24.9	27.6	18.5	6.5	0.35
	25-Jul-91	29.0	29.0	16.7	6.1	0.38
	mean	29	26	15.2	5.6	0.4
Wa	20-Jun-90	33.2	27.3	13.7	4.3	0.31
	21-Jul-91	48.5	30.6	10.5	3.9	0.37
	mean	41.0	29.0	12.0	4.0	0.3
Pa	22-Jul-91	38.7	29.5	12.7	2.5	0.2

Appendix 9. The SD, Secchi transparency (m); k, the vertical light extinction coefficient ( $\ln.m^{-1}$ ); Zeu, euphotic depth (m) of Lake Albert during 1989-91.

STA	Date	SD	k	Zeu
B1	30-Sep-89	2.1	0.7	6.6
	17-Jun-90		0.4	12.7
	26-Jul-90	2.2	0.6	7.9
	12-Aug-90	4.4	0.4	11.0
	21-May-91	4.5	0.4	13.6
	24-Jul-91	4.2	0.4	11.5
	mean	3	0.5	11
B2	01-Oct-89	2.4	0.5	10.8
	17-Jun-90		0.4	12.7
	19-Jun-90	3.8	0.5	10.5
	21-Jun-90		0.5	9.9
	27-Jul-90	2.4	0.5	10.2
	11-Aug-90	2.5	0.4	12.2
	23-May-91	3.3	0.4	12.0
	26-Jul-91	2.3		
	mean	3	0.4	11
B3	03-Oct-89	2.2	0.4	11.7
	20-May-91	2.3	0.5	9.1
	mean	2.0	0.5	11.0

## Appendix 9. (continued)

STA	Date	SD	k	Ze
	18-Jun-90			
	18-Jun-90	1.8	0.8	6.2
	20-Jun-90	2.3	0.7	6.6
	22-May-91	3.4	0.5	9.4
	25-Jul-91	2.4	0.5	9.3
	mean	2	1	8
Wa	20-Jun-90	2.3	0.7	6.5
	21-Jul-91	2.3	0.8	6.3
	mean	2	1	6
Pa	22-Jul-91	0.9	1.4	3.6