TEMPORAL AND SPATIAL VARIATIONS IN BIOMASS AND PHOTOSYNTHETIC PRODUCTION OF PHYTOPLANKTON IN LAKE CHAMO, ETHIOPIA.

A THESIS
PRESENTED TO THE
SCHOOL OF GRADUATE STUDIES
ADDIS ABABA UNIVERSITY

In partial fulfillment of the requirements for the degree of
Master of Science in Biology

BY

EYASU SHUMBULO

JUNE, 2004

TEMPORAL AND SPATIAL VARIATIONS IN BIOMASS AND PHOTOSYNTHETIC PRODUCTION OF PHYTOPLANKTON IN LAKE CHAMO, ETHIOPIA.

A THESIS
PRESENTED TO THE
SCHOOL OF GRADUATE STUDIES
ADDIS ABABA UNIVERSITY

In partial fulfillment of the requirements for the degree of Master of Science in Biology

BY

EYASU SHUMBULO

JUNE, 2004

ACKNOWLEDGMENTS

First and foremost, I would like to express my deep gratitude to my research advisor, Dr. Demeke Kifle, for his wholehearted and consistent guidance and for making available some of the materials required for my field and laboratory work. It is a real pleasure for me to acknowledge my indebtedness to Dr. Seyoum Mengistu, who was always ready to help. I also express my gratitude to Dr. Zenebe Tadesse for his thorough reading and commenting on my thesis.

I am most grateful to my colleagues, Ato Kumlachew Desalegn (AWTI), Ato Yassin Chumburo (KCTE), Ato Yishak Doku (AWTI), my sister Abebech Soka (AWTI), and my brother Ato Markos Shumbulo for their friendship and unreserved support throughout the study period.

I gratefully acknowledge the invaluable cooperation of the Chairman and secretaries of the Department of Biology. I am thankful to the School of Graduate Studies at Addis Ababa University for funding my research project. My sincere thanks also go to the Swedish Agency for Research Cooperation (SAREC) for the financial support I received through my research advisor.

My heartfelt gratitude is due to Arba Minch Water Technology Institute (AWTI) (now Arba Minch University) for sponsoring me to pursue postgraduate studies. I would also like to extend my thanks to all the administrative and technical staff of Arba Mich University without whose cooperation the completion of this research work would have been impossible.

It is my profound pleasure to acknowledge my indebtedness to Arba Minch Zuriya Woreda Agricultural Bureau and Arba Minch Fisheries Cooperation for the provision of boat service. I also wish to thank the National meteorological Agency and Arba Minch Meteorological station for the provision of the solar radiation, rainfall and air temperature data of the study area.

My sincere thanks and heartfelt appreciation goes to my families, who have always been genuinely concerned with my education and professional career. I also acknowledge all my colleagues in Fisheries and Aquatic Sciences Stream.

Finally, I praise God for giving me the strength to withstand all ups and downs.

TO MY MOTHER

KONASIE BUNARIE

WHOM I LOST THIS YEAR

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The temporal and spatial variations in the biomass and photosynthetic production of phytoplankton in relation to some physico-chemical environmental factors were investigated at two (offshore and near-shore) stations in Lake Chamo from August, 2003 to May, 2004. Inorganic nutrients varied temporally, with their low and high concentration levels generally corresponding to the dry and rainy periods respectively. Lake's transparency was always low (Z_{SD} < 40 cm). Because phytoplankton biomass was high throughout the study period, its contribution to the extinction of underwater light is expected to be considerable. Phytoplankton biomass measured as chlorophyll a varied 43 to 95 (mean = 77.2) and 47 to 108 (mean=69.4) mg Chl a m^{-3} at the near-shore and central stations, respectively. The vertical distribution of photosynthetic activity was of a typical pattern for phytoplankton with light-inhibition on all sampling dates. The light-saturated rate of photosynthesis (A_{max}) ranged from 721 to 1789 mg O_2 (≈224.95 to 558.17 mg C) m^{-3} h^{-1} at the central station and from 543 to 1803 mg O_2(≈169. 42 mg C) m^{-3} h^{-1} at the near-shore station. Lack of correspondence between phytoplankton biomass and A_{max} was evident. Biomass-specific rate of photosynthetic production at light-saturation, photosynthetic capacity (Φ_{max}) ranged from 9 to 34 mg O_2 (mg Chl a)$^{-1}$ h^{-1} at the near-shore station and from 10 to 34 mg O_2 (mg Chl a)$^{-1}$ h^{-1} at the central station. An inverse relationship between photosynthetic capacity and phytoplankton biomass was also observed. Hourly integral photosynthesis ranged from 0.36 to 1.72 g O_2 (≈ 0.11 to 0.54 g C) m^{-2} h^{-1} at the central station and from 0.47 to 1.8 g O_2 (≈ 0.15 to 0.56 g C) m^{-2} h^{-1} at the near-shore station. The production rate per unit area seems to have been influenced by the light-saturated rate of photosynthesis as the strong and positive correlation between the two (r = 0.77) suggests. The temporal variations in phytoplankton biomass and primary production in relation to environmental factors are discussed with a view to identify those environmental variables that have regulatory role.

Key words: *Biomass, production, phytoplankton, Lake Chamo, Ethiopia,*

1. INTRODUCTION

Because of the rapid growth of human population, food production has failed to meet demands. Conventional agriculture is no longer capable of providing adequate and high quality food for the ever-increasing human population. Aquatic ecosystems can be of immense importance as actual and potential sources of food for humans. Thus, studies of biological productivity at all levels of the food chains of aquatic ecosystems are imperative. .

Measurement of primary production of phytoplankton and the environmental factors, which limit or regulate this production, forms the basis for the studies on energy fluxes within aquatic ecosystems. Primary production by phytoplankton is also regarded as a better predictor of fish yield in lakes (Melack, 1976a; Oglesby, 1977; Downing *et al.*, 1990).

Studies on the production of tropical phytoplankton started about 70 years ago (Talling and Lemoalle, 1998), although application of the method to assess production rates per unit area had to wait until the early 1950s in Africa (Prowse and Talling, 1958). Nowadays, the literature on the taxonomic composition and primary production of phytoplankton in relation to physicochemical environmental variables in African lakes is enormous.

Ethiopia is endowed with several Rift Valley lakes, whose range of variations in morphometric, physical and chemical features (Wood and Talling, 1988) offers a wide opportunity for superb comparative ecological and taxonomic studies (Elizabeth Kebede, 1996). Despite the vital role, which these inland water bodies may play in ameliorating the effects of protein shortage, the limnology of some of these lakes is unexplored or not synthesized.

Although a large number of studies have been made on the community structure and primary production of phytoplankton in various East African lakes (see review by Talling and Lemoalle, 1998), very little has been done on this aspect in Ethiopian Rift Valley lakes. Most of the studies conducted on phytoplankton of Ethiopian lakes have not been systematic nor sustained. The sporadic information on the dominant or most common species of planktonic algae reported in limnological papers is compiled in Wood and Talling (1988). Of the few systematic studies made on the species composition of phytoplankton in Rift Valley lakes, the only detailed are those of Tsegaye Mihrete-ab (1988), Elizabeth Kebede and Amha Belay (1994), and Elizabeth Kebede and Willen (1998). The only systematic study, which described the species composition of phytoplankton in Lake Chamo is that of Elizabeth Kebede and Willen (1998). Although this published information has given a fairly detailed listing of species of phytoplankton, it was based on a single water sample collected during a short rainy period (March-May, 1991).

Primary production by planktonic algae provides the base upon which the aquatic food chains culminating in natural fish production exploited by man are founded, at the same time generating some 70% of the world's atmospheric oxygen supply (Reynolds, 1984). Primary production of phytoplankton in the Ethiopian Rift Valley lakes, though on a short-term basis, was studied for the first time by Amha Belay and Wood (1984), following the report by Talling *et al.* (1973) on phytoplanktonic primary production in Bishoftu crater lakes, However, the only studies carried out on the temporal and spatial variations of phytoplankton production in relation to some physical and chemical variables over an extended period of time are those of Demeke Kifle (1985), and Demeke Kifle and Amha Belay (1990) on Lake Awassa and Girma Tilahun (1988) on Lake Ziway. A detailed study on the standing stock and primary production of phytoplankton in Ethiopian Rift Valley lakes not only allows us to assess the productive status and ecological health of the lakes but also provides base-line data, which are crucial for their optimum utilization and proper management.

Although there are a number of studies on fisheries aspects (e.g. Zenebe Tadesse, 1998; Elias Dadebo, 2001), published information on the photosynthetic production of phytoplankton in Lake Chamo is non-existent. Moreover, there is a need to update the existent. Moreover, there is a need to update the database on the physico-chemical and biological limnology of Ethiopian Rift Valley lakes including Lake Chamo owing to water quality changes, which emanated largely from the rapid growth of human population coupled with agricultural development and increased industrial operations (Zinabu Gebre-Mariam, 2002).

The purpose of the present study was, therefore, to investigate the temporal and spatial variations in the biomass and photosynthetic production of phytoplankton in relation to some physico-chemical variables in Lake Chamo.

2. DESCRIPTION OF THE STUDY AREA

Lake Chamo, the present study lake (Fig. 1), is a tectonic southernmost lake of the Ethiopian Rift Valley (5° 45' N and 37° 30' E) which is fed by a perennial river, Kulfo, that enters it from the north and a number of small but non-perennial rivers including Rivers Sile and Sego. The lake is characterized by gently sloping shoreline covered by extensive emergent and submergent vegetation; some limnological features of the lake are given in Table 1.

The region around this lake is characterized by moist sub-humid climate with an annual rainfall of about 900mm (Yosef Tekle-Giorgis, 2002). The region experiences alternating dry and wet seasons, with the dry period being between November and February and peak rainfalls occurring during April and May and again during October and November (Yosef Tekle-Giorgis, 2002). The impact of temporal variations in rainfall and water input on the chemical limnology of such a shallow lake as Chamo is expected to be quite high (Wood and Talling 1998).

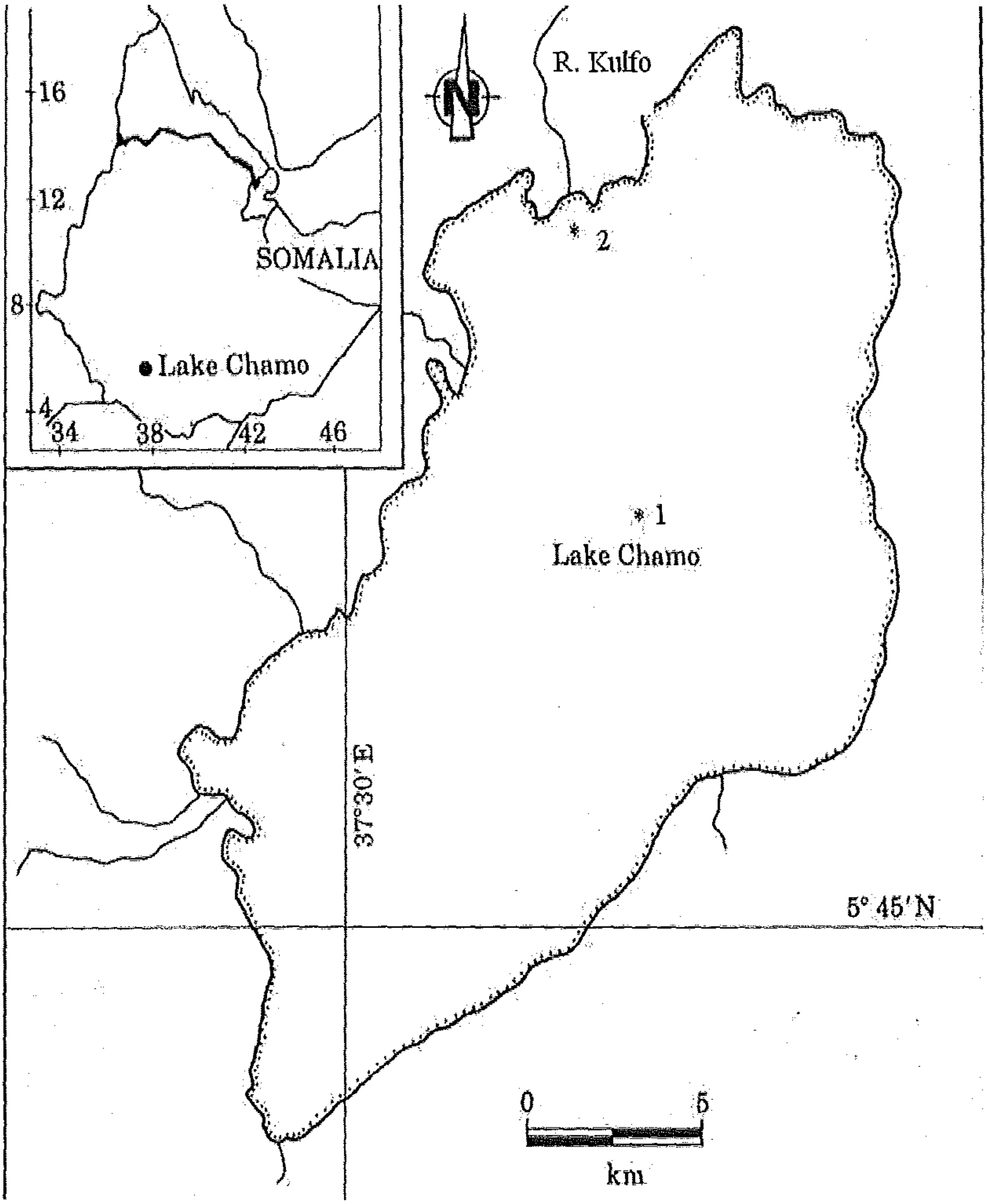

Figure 1 Map of Lake Chamo showing sampling Stations (*). (Inset: Location of Lake Chamo in Ethiopia). 1- Central Station, 2- Near-Shore Station.

Figure-2 (see also Appendix-1) shows the temporal variations in Photosynthetically Active Radiation (PAR), mean maximum and minimum air temperature and monthly rainfall of the region.

Data on the mean daily solar radiation received by a unit surface on the days of production experiments and the mean monthly solar radiation levels in the lake region during the study period were obtained from Arba Minch Meteorology Station. The energy flux of incoming irradiance, which was in **cal cm^{-2} min^{-1}**, was converted to the currently internationally accepted unit, **watts (W) m^{-2}**, using the approximate conversion factor given in Kalff (2002). Photosynthetically Active (Available) Radiation (PAR) was taken as being equal to 46% of the total solar radiation (Talling and Lemoalle, 1998; Kalff, 2002) received by a unit surface. Irradiance (PAR) varied from a low mean value of 113.34 X 10^3 watts m^{-2} in August to the high mean value of 158.61 X 10^3 watts m^{-2} recorded in February, 2004. On days of production measurements, the highest energy flux of irradiance (213.5 X 10^3 watts m^{-2}) was recorded on February 10, 2004, while the lowest (129.72 X 10^3 watts m^{-2}) was measured on 9th and 19th of January, 2004.

The mean minimum air temperature varied between about 16 °C and 19 while the maximum air temperature ranged from 27.5 of August, 2003 to 33.5 °C of March, 2004. The differences between the mean minimum and maximum air temperature ranged from 10.9 °C of August to 16.6 °C of February, corresponding to the wet and dry periods respectively. According to Yosef Tekle-Girogis (2002), the maximum air temperature around lake Chamo was slightly higher (35 °C) with mean annual temperature of 24 °C and with colder months from April to August. The available data seem to suggest that the driest months are also the coldest months.

Monthly rainfall varied from 13.1 mm of March to 164.8 mm of May. The dry period was between November and March. On the basis of the data compiled for the period between 1994 and 1999, Yosef Tekle-Giorgis (2002) has shown the occurrence of peaks in rainfall around Lake Chamo during October-November and April-May.

According to Demeke Admassu (1998), the rainy period was from March to October, with the largest peak (~180 mm) in May and with two smaller peaks (~140 mm), in April and August. Data collected by Demeke Admassu (1998) and Yosef Tekle-Giorgis (2002) have shown that peaks in monthly rainfall have generally been between 180 and 200 mm.

Table 1. Some limnological features of Lake Chamo. Chemical and chlorophyll data from Elizabeth Kebede and Willén (1998). Morphometric data from Grove *et al.* (1975) except in cases where references are cited.

Altitude (m)	1233
Surface Area (Km^2)	551
Shore-Line Development (km)	118*
Catchment Area (Km^2)	2210
Maximum depth (m)	13
Mean depth (m)	6*
SECCHI depth (cm)	65
Conductivity, K_{25} ($\mu S\ cm^{-1}$)	1320
Salinity ($g\ l^{-1}$)	1.0
Alkalinity ($meq\ l^{-1}$)	12
Soluble Reactive Phosphate ($\mu g\ l^{-1}$)	25
Total Phosphate ($\mu g\ l^{-1}$)	135
Dissolved inorganic nitrogen ($\mu g\ l^{-1}$)	30
SiO_2 ($mg\ l^{-1}$)	<1
pH	8.9
Chl a ($\mu g\ l^{-1}$)	44

*Reyntjens (1998)

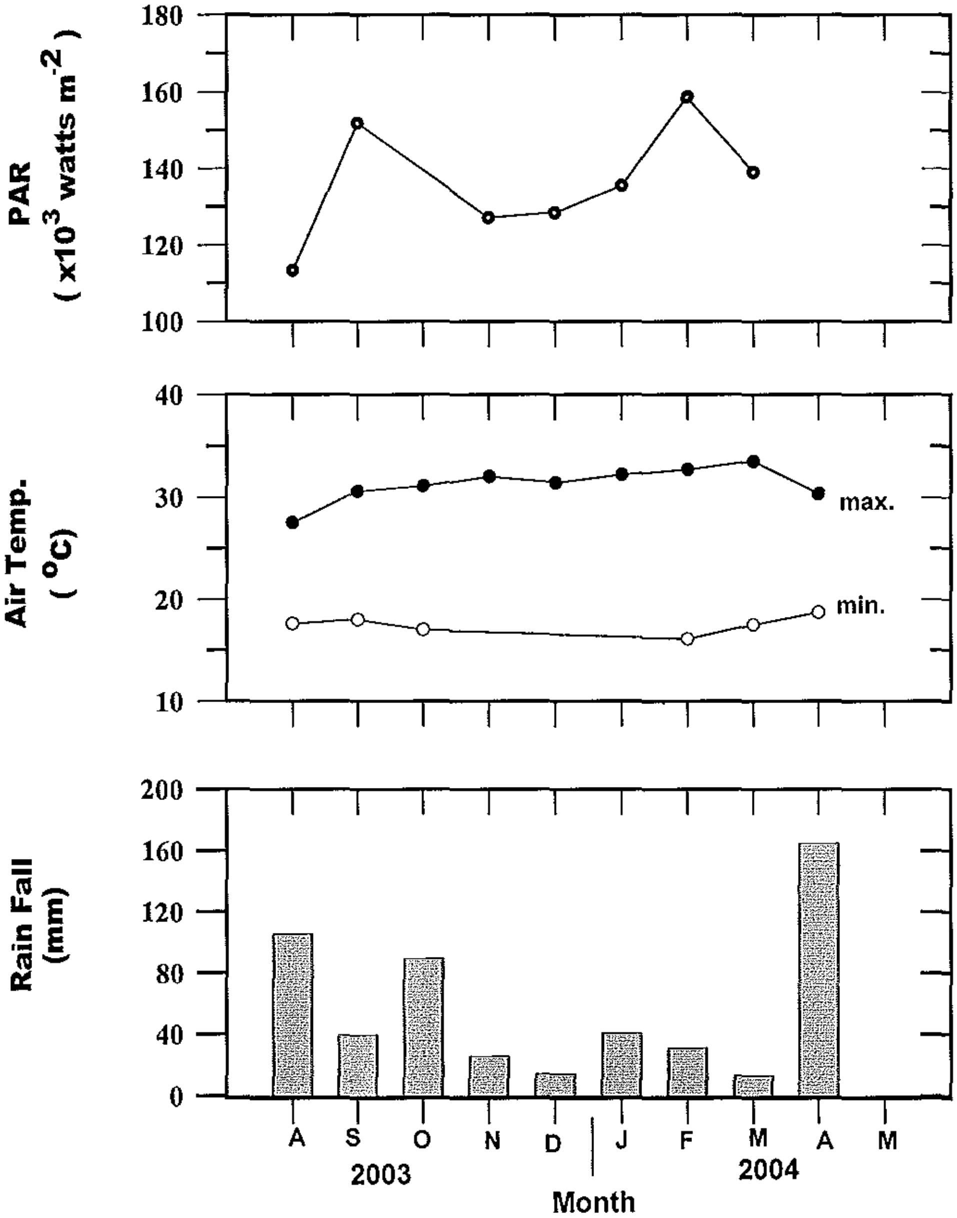

Fig. 2. Meteorological data for Lake Chamo: mean monthly Solar radiation (PAR), monthly rainfall (mm) and mean monthly air Temperature.

Lake Chamo is quite dilute, with salinity ≤ 1 ppt and with sodium (Na^+) and carbonate-bicarbonate (CO_3^{2-} + HCO_3^-) dominating the major ionic composition. The lake has low concentration of soluble reactive phosphate and dissolved inorganic nitrogen (Elizabeth Kebede and Willen, 1998).

The phytoplankton community of L. Chamo, during the short rains in March-May, 1991 was found (Elizabeth Kebede, 1996) to be constituted primarily by blue-greens (species of *Anabaenopsis, Aphanocapsa, Microcystis*),greens (species of *Cosmarium, Pediastrum, Scenedesmus*) and diatoms and these are the main food source for *Oreochromis niloticus* L. (Zenebe Tadesse, 1998). Chrysophytes, euglenoids and dinoflagellates make minor contribution to the planktonic algal flora of the lake (Elizabeth Kebede, 1996).

The Zooplankton community of Lake Chamo is composed mainly of Copepods (*Mesocyclops*) (Defaye, 1988), Cladocerans (*Moina, Ceriodaphnia* and *Daphnia* species) (Seyoum Mengistu, unpublished data) and Rotifers dominated by *Brachinous angularis* (Green and Seyoum Mengestou, 1991), while the benthic fauna is dominated by ostracods (Tudorancea *et al.*, 1989).

Hippopotamus (*Hippopotamus amphibious* L.), Nile monitor lizard (*Varanus niloticus* L) and crocodiles (*Crocodylus niloticus* Laurenti) are abundant in the lake. The crocodiles in particular are found in large numbers, so the name 'crocodile market' was given to the sandy beaches where these animals bask themselves in the sun.

The lake resembles other African lakes and has, with Lake Abaya, a much more diverse pisci-fauna with over 15 species (Reyntjens, 1998) including the piscivorous Nile perch, *Lates niloticus.* The fish species of Lake Chamo represent nine families and 12 genera (Getachew Teffera, 1993; Reyntjens, 1998;). Of these, *Barbus bynni* Forsskal, *Labeo horie* Heckel, *Clarias gariepinus* Burchell, *Lates niloticus* L. and *Oreochromis niloticus* L are the economically important species. Exploitation of the lake seems to be undergoing without for the status of the resource base. A sharp decline in the Nile perch from 190 tones per month (70% of the total landing in1993/94) to less than 20 tones per month (<10% of the total landing in 1995/96) as reported by Reyntjens (1997) clearly indicates the impact of over-fishing.

The lake has experienced cultural eutrophication due to nutrient loading from the nearby, mechanized agricultural lands, particularly from a cotton plantation, which in 1978 resulted in an algal bloom and subsequent massive fish kills and death of wild animals (Amha Belay and Wood, 1982).

3. MATERIALS AND METHODS

3.1. Sampling Protocol

Two sampling stations-one central (9m deep) and another near-shore (2m deep), close to the mouth of the perennial River Kulfo (Fig. 1) were selected for the present study. Samples were collected twice a month from both stations. Water samples were collected with a bottle sampler (Kemmerer) from the near-surface region of the lake. These samples were used for the estimation of the biomass (as chlorophyll a concentration) and photosynthetic production of phytoplankton and for the analyses of inorganic nutrients and Total Solids (TS).

3.2. In-situ measurements

Lake water transparency (= vertical visibility) was estimated using a standard Secchi disc of 20 cm diameter. Electrical conductivity was determined with a field conductivity meter (model: WTW LF 191). Surface water temperature was measured with an ordinary laboratory thermometer while the determination of pH was made with a portable digital pH meter (Model: cd60, WPA, England).

3.3 Estimation of phytoplankton biomass

Phytoplankton biomass was estimated as Chlorophyll a concentration. Appropriate volumes of phytoplankton samples collected with a bottle sampler were filtered onto glass fiber filters (Whatman GF/C) and extracted in 90% acetone. The filters were manually ground with a glass rod in a small volume of 90% acetone to enhance extraction of pigments. The algal material was placed in a parafilm-covered tube and centrifuged at 3000 rpm for 10 minutes. The extract was then decanted into a 10 volumetric flask and made up to the mark with 90% acetone. The absorbance of centrifuged pigment extracts was measured spectrophotometrically at 665 and 750 nm, before and after acidification with 1 N HCl, The absorbance values, which were corrected for both turbidity and absorbance due to phaeopigments, were used to calculate the concentration of chlorophyll a according to the monochromatic method (Lorenz, 1967, as outlined in Wetzel and Likens 2000).

3.4. *In situ* measurements of Primary Production

Primary production was measured by the Light and Dark bottle Technique and the Winkler method of oxygen determination (Mackereth *et al.*, 1978). Water samples were siphoned into 118ml Pyrex light (clear) and dark (covered with dark cloth tape) glass bottles under reduced light conditions. Duplicate clear bottles were attached to a suspension line prepared for this purpose, at each of the five established depths distributed within the euphotic zone (0.00, 0.25, 0.50, 1.00 and 1.50 m). The lower limit of the euphotic zone was approximated as 3 times the Secchi depth. To avoid shading, the arms of the suspension line, intended for the different depths of incubation, were made in such a way that they project out in different directions thereby avoiding overlap of bottles of successive depths of exposure. Dark bottles were also incubated at 0.00 and 1.50 m. The incubation period usually lasted for three hours around mid-day (between 10:00 a.m. _ 2:00 p.m.).

3.5. Species composition of phytoplankton

Species of phytoplankton dominant on each sampling date were identified using samples preserved with Lugol's iodine and Formalin (1%). The phytoplankton samples were examined with an inverted microscope and their identification to genus or species level was made on the basis of various taxonomic literatures available on phytoplankton (Whitford and Schumacher, 1973; Jeeji-Bai, 1977; Durand and Leveque, 1980; Gasse; 1986; Talling, 1987; Rot and Lenzenwger, 1994; Komarek and Komarokova, 2002; John *et al*, 2002)

3.6. Chemical Analyses

For the analyses of the various chemical parameters (except for NH_4^+-N, NO_3-N and NO_2-N) the procedures outlined in APHA et al. (1999) were strictly followed. Samples filtered through glass fiber filters (GF/C) were used for the analyses of various chemical parameters except alkalinity, total phosphate and total solids and the analyses were conducted at water quality laboratory (Arba Minch University). Carbonate-bicarbonate alkalinity was determined within a few hours of sample collection by titration with 0.1N HCl to a pH of 4.5.

The Ascorbic Acid and Molybdosilicate methods were used to estimate phosphate and silicate colorimetrically at 690nm and 410nm, as their respective molybdate complexes respectively. Samples for total phosphorus (TP) analyses were digested with persulfate and the respective phosphate was determined with Ascorbic Acid method. Ammonium-N was estimated by Nesslerization and, subsequent spectrophotometric measurement of absorbance at 400 nm. Nitrate-nitrogen (NO_3-N) and Nitrite-nitrogen (NO_2-N) were determined using a Hach Kit (DR/2000 spectrophotometer). Nitrate was analyzed by the Cadmium Reduction Method, while nitrite was measured by diazotization and subsequent formation of a highly colored azo dye. 'Total solids' was estimated by the evaporation of a well-mixed sample and its subsequent drying in an oven at 105^0C. After drying, the dish cooled in desiccators and then weighed in an analytical balance of

0.0001g precision. The difference in weight of the empty dish and weight after drying was taken as the total solids.

Explanations of the symbols used throughout this thesis are given below:

Z_{sd}	Secchi depth
Z_{eu}	Depth of euphotic zone, in m
EV_{tot}	Total under water light vertical extinction coefficient
B	phytoplankton biomass, in mg Chl a m^{-3}
ΣB	phytoplankton biomass per unit area, within the euphotic zone, mg Chl a m^{-2}
A	Rate of gross photosynthesis per unit water volume, in mg $O_2\,m^{-3}\,h^{-1}$
A_{max}	light-saturated rate of gross photosynthesis, in mg $O_2\,m^{-3}\,h^{-1}$
Φ (=A/B)	Specific rate of gross photosynthesis per unit biomass, mg O_2(mg Chl a)$^{-1}\,h^{-1}$
$\Phi_{max}(A_{max}/B)$	Specific rate of gross photosynthesis per unit biomass at light-saturation, mg O_2 (mg Chl a)$^{-1}\,h^{-1}$
ΣA	Hourly rate of gross photosynthesis per unit area, g $O_2\,m^{-2}\,h^{-1}$
$\Sigma\Sigma A$	Daily rate of gross photosynthesis per unit area, g $O_2\,m^{-2}\,d^{-1}$
PAR	Photosynthetically Active Radiation

4. RESULTS AND DISCUSSION

4.1. Physical parameters.

The physical characteristics of Lake Chamo during the study period are given in Table 2. Surface water temperatures ranged from a minimum of 23^0C at the near-shore station in the second half of December to a maximum of 30^0C at both stations in the first half of the same month, with most recorded values being above 26 ^{0}C. The surface water temperature data collected by Yosef Tekle-Giorgis (2002) show that temperature levels were usually above 26 ^{0}C with drops below 25 °C during June, July August and December.

The surface water temperatures of Lake Chamo are closer to those reported by Ganf and Horne (1975) for the East African lakes, Lake George, Uganda (26-36 ^{0}C) and Lake Turkana (27.5-32.5 ^{0}C). They are, however, slightly higher than those measured in other Ethiopian Rift Valley and crater lakes including Lakes Abijata and Langano (18-27

Lake's transparency (=vertical visibility) varied between 21 and 37.5 cm at the near-shore station and between 25 and 39 cm at the central station (Table-2). The Secchi depths (Z_{SD}) of Lake Chamo are similar to those recorded for Lakes Abaya, Langano, Koka and Ziway (Elizabeth Kebede, 1994) in which attenuation of underwater light is primarily due to silt and clay, which form a stable colloidal suspension in the former two lakes (Wood *et al.*,1978; Amha Belay and Wood, 1984; Elizabeth Kebede, 1996). The observed temporal variations in the transparency of Lake Chamo are attributable to changes in the extent of loading of inorganic particles resulting from wind-driven mixing and to fluctuations in phytoplankton biomass.

While acknowledging the crudity of secchi depth as a tool to evaluate the light climate of aquatic ecosystems, one can compare the optical conditions of a lake at different times of the year. Vertical extinction coefficients for total underwater light (mean vertical extinction coefficient) (EV_{tot}) can be estimated from Secchi depths by the widely used equation which was proposed by Holmes (1970) as a better estimator of the vertical extinction coefficient of total underwater light of turbid waters (see Appendix-2).

Table 2. Surface water temperature, $\mathbf{Z_{SD}}$, $\mathbf{EV_{tot}}$, $\mathbf{Z_{eu}}$ and optical depths ($\mathbf{Z_{op}}$)of the present sampling stations at Lake Chamo.

Sampling Date	Station	Surface water Temp. (°C	Z_{SD} (m)	EV_{tot} (units m^{-1})	Z_{eu} (m)	Optical depth
27/08/ '03	C	27	0.375	3.84	1.20	5
	K	27	0.375	3.84	1.20	
14/09/ '03	C	29	0.280	5.14	0.89	6.7
	K	29	0.260	5.54	0.83	
14/10/ '03	C	30	0.273	5.27	0.87	6.9
	K	30	0.273	5.27	0.87	
8/11/ '03	C	29	0.390	3.69	1.25	4.8
	K	29	0.360	4.00	1.15	
18 /11/ '03	C	27	0.370	3.89	1.18	5.1
	K	27	0.370	3.89	1.18	
5/12/ '03	C	30	0.340	4.24	1.08	5.6
	K	30	0.320	4.50	1.02	
18/12/ '03	C	23.7	0.370	3.89	1.18	5.1
	K	23	0.360	4.00	1.15	
9/01/ '04	C	27	0.380	3.79	1.21	4.96
	K	27	0.370	3.89	1.18	
19/01/ '04	C	28	0.360	4.00	1.15	5.2
	K	28	0.360	4.00	1.15	
10/02/ '04	C	28	0.350	4.11	1.12	5.4
	K	28	0.340	4.24	1.08	
24/02/ '04	C	27	0.290	4.97	0.93	6.5
	K	27	0.275	5.24	0.88	
10/03/ '04	C	29	0.305	4.72	0.97	6.2
	K	29	0.305	4.72	0.97	
25/03/ '04	C	26.5	0.290	4.97	0.93	6.5
	K	25.4	0.290	4.97	0.93	
7/04/ '04	C	26	0.270	5.33	0.86	6.98
	K	26	0.270	5.33	0.86	
25/04/ '04	C	27	0.250	5.76	0.80	7.5
	K	26.5	0.230	6.26	0.73	
13/05/ '04	C	28	0.250	5.76	0.80	7.5
	K	26	0.210	6.86	0.67	
20/05/04	C	26	0.250	5.76	0.80	7.5
	K	26	0.220	6.55	0.70	

$\mathbf{EV_{tot}}$ values of both stations (Table-2), calculated according to Holmes (1970), ranged from 3.69 to 6.86, corresponding to euphotic depths ($\mathbf{Z_{eu}}$) (approximated as being equal to 4.6/ $\mathbf{EV_{tot}}$, Kalff, 2002), of 0.67-1.25 m respectively. The calculation of euphotic depth using the equation given above assumes that light reduction conforms, approximately, to a single 'average' vertical extinction coefficient, Ev_{tot}. Euphotic depths estimated using vertical extinction coefficients calculated from secchi depths seem to indicate that the thickness of the euphotic zone, was often shallower than 1.00 m. However, the true (physiological) compensation depth in Lake Chamo appears to lie well below the computed euphotic depths since appreciable net photosynthetic activity was found to occur down to a depth of at least 1.5 m (see Appendix-6 and Figs. 4 and 5). These observations clearly indicate that the estimation of the euphotic depth (i.e. the depth at which 1% of the surface irradiance is found; Talling, 1957) by multiplying $\mathbf{Z_{SD}}$ by **3,** which has been a common practice of those investigating phytoplankton primary productivity, merits further investigation.

4.2. Aggregate Chemical features of Lake Chamo

Aggregate chemical features of Lake Chamo measured over the study period are given in Table 3. Total Solids (TS) varied from 547 mg l^{-1} to 3940 mg l^{-1} at the offshore (central) station and from 538 mg l^{-1} to 4386 mg l^{-1} at the near-shore station with most low values during the relatively dry period. The relatively higher TS values of the near-shore station may be related to the proximity of the sampling point to the mouth of the major feeder river, Kulfo.

Electrical conductivity (K_{25}) varied between 1429 and 1958 µS cm^{-1} at the central station and between 1477 and 1914 µS cm^{-1} at the near-shore station, with most higher values at the former station. The apparent correlation between alternation of dry and wet seasons and conductivity levels reported for Lake Awassa (Elizabeth Kebede and Amha Belay, 1994), Lake Abijata (Kassahun Wedajo and Amha Belay, 1984) and many other African lakes including Lake Nakuru (Vareschi, 1982) is not evident in Lake Chamo, probably due to the small number of the data collected. The present conductivity values are much higher than those reported earlier by Amha Belay and Wood (1982), Elizabeth Kebde *et al.* (1994) and Elizabeth Kebede and Willén (1998). The significant increase in the salinity of this lake over the past several decades, as reflected in the present conductivity values and in the conductivity and salinity measurements compiled in Wood and Talling (1988), is probably attributable to the decrease in the water level (and the consequent increase in the concentration of ions).

The decline in the water level seems to be the result of recurrent drought and diversion of feeder-rivers for irrigation purposes (Talling and Lemoalle, 1998; Zinabu Gebre Mariam *et al.,* 2002), which affect the water input-output relation thereby determining the extent of evaporative concentration of ions (Wood and Talling, 1988). Williams (1999) also considers diversion of inflows as one of the main reasons for the increases in the salinity of many of the world's largest and permanent lakes during the last several decades.

Carbonate-bicarbonate alkalinity (in meq l^{-1}) exhibited marked temporal fluctuations, varying from a low value of 4.75 at both stations in May, 2003 to high values of 15.3 and 15.5 of March at the central and near-shore stations, respectively. The high total alkalinity values are closer to those reported relatively recently for Lake Chamo by Elizabeth Kebede *et al.* (1994) and Zinabu Gebre Mariam *et al.* (2002) than those found in earlier investigations (Amha Belay and Wood, 1982; Wood and Talling, 1988). The pH of the surface water ranged from 8.52 to 9.44 at both stations with lower values in August-September, 2003. The pH values of the present study are similar to those reported in earlier studies (Amha Belay and Wood, 1982; Wood and Talling, 1988; Elizabeth Kebede *et al.*, 1994; Zinabu Gebre Mariam *et al.*, 2002). The high pH values generally coincided with high phytoplankton biomass and/or photosynthetic activity.

Table 3. pH, total alkalinity, Conductivity (K_{25}), and total solids (TS) at the offshore (C) and inshore (K) stations of L. Chamo.

Sampling date	**Station**	**pH**	**Total alkalinity (meq l^{-1})**	**K_{25} ($\mu S\ cm^{-1}$)**	**TS (mg l^{-1})**
27/08/ '03	C	8.52	6.6	-	987
	K	8.52	6.4	-	1115
14/09/ '03	C	8.9	10	1828	1130
	K	8.9	11	1743	1115
14/10/ '03	C	9.16	14.2	1644	1260
	K	9.16	13.3	1681	3158
8/11/ '03	C	9.32	12	1817	1500
	K	9.35	11.1	1812	1499
18 /11/ '03	C	9.2	10.7	1707	1120
	K	9.1	11	1779	1350
5/12/ '03	C	9.0	5.4	-	680
	K	9.0	5.5	-	1104
18/12/ '03	C	9.1	6.1	-	614
	K	9.2	6.3	-	906
9/01/ '04	C	9.0	8.5	1429	1304
	K	9.0	8.8	1541	538
19/01/ '04	C	9.2	8.7	-	1195
	K	9.4	8.9	-	1312
10/02/ '04	C	9.1	12.2	-	3940
	K	9.3	12.3	-	4386
24/02/ '04	C	9.2	10.1	-	627
	K	9.2	11.3	-	4177
10/03/ '04	C	9.18	15.3	-	660
	K	9.18	15.5	-	546
25/03/ '04	C	9.2	9.2	-	700
	K	9.3	8.1	-	539
7/04/ '04	C	9.44	5.25	1958	1045
	K	9.44	5.35	1511	4324
25/04/ '04	C	9.4	6.6	1754	1856
	K	9.4	6.6	1548	2260
13/05/ '04	C	9.41	5.6	1859	1300
	K	9.41	6.6	1477	1043
20/05/ '04	C	9.31	4.75	1935	547
	K	9.3	4.85	1914	547

High rates of primary production allow large daytime CO_2 and HCO_3^- withdrawal (depletion) resulting in a large rise in pH (Maberly, 1996). A pH of between 9.5 and 10.5, which is common in the extremely high alkalinity saline lakes of East Africa (Talling and Talling, 1965; Wood *et al.*, 1984) including the hypertrophic Lake Aranguade in Ethiopia (Talling *et al.*, 1973) is the result of such biological removal of inorganic carbon. The high positive correlation between pH and alkalinity reported for the combined data of Ethiopian lakes (Wood and Talling, 1988) and saline lakes worldwide (Hammer, 1986) was not observed in the present study for Lake Chamo although the correlation was still positive and strong ($r = 0.5$).

Fig.-3. (see also Appendix-3) presents the temporal variations in the concentration of inorganic nutrients in relation to phytoplankton biomass at the central and near-shore stations in Lake Chamo. The variation among the two stations is insignificant as the T-test value indicates. Nitrate-N varied from 10 μg l^{-1} at both stations to 60 and 50 μg l^{-1} at the central and near-shore stations respectively, with low concentrations corresponding to the relatively dry periods. The peaks in concentrations were observed in March, 2004 at the central station and in October, 2003 and February, 2004 at the near-shore station, generally coinciding with high algal biomass. Nitrate levels recorded in this study are much lower than those reported in 1979 (217-445 μg l^{-1}) by Amha Belay and Wood (1982) though they are comparable to those measured during the bloom period of *Microcystis aeruginosa* of 1978 (16-34 μg l^{-1}) (Amha Belay and Wood, 1982). Elizabeth Kebede *et al.* (1994) also reported level of nitrate (18.6 μg l^{-1}) for Chamo, which was closer to the lower boundary of the range of concentrations observed in the present study. In their seasonal study on Lake Awassa, Elizabeth Kebede and Amha Belay (1994) recorded concentrations of nitrate (7-20 μg l^{-1}), which were generally as low as the levels determined for L. Chamo in the present investigation. Nitrate was seldom detectable in the surface waters of Bishoftu crater lakes where the depth distribution of inorganic nitrogen was determined over several years and ammonium-nitrogen was found to be the predominant form of inorganic nitrogen at all depths (Wood *et al.*, 1984). Girma Tilahun (1988) reported concentrations of nitrate ranging from 28 to 166 μg l^{-1} for the shallow frequently mixing productive lake,

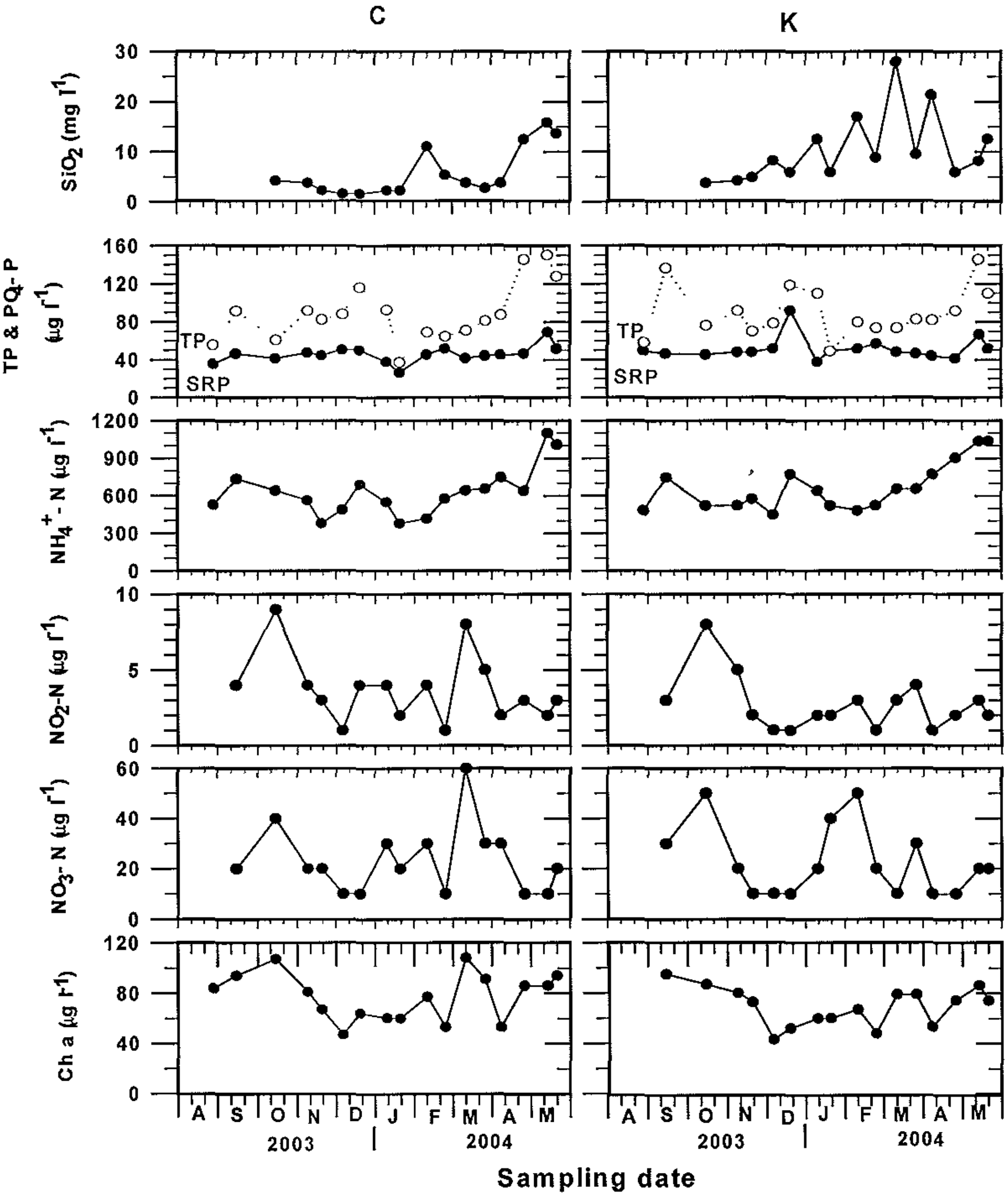

Fig. 3- Concentrations of inorganic nutrients in relation to Phytoplankton biomass at the central (C) and near-shore (k) stations of Lake Chamo.
(TP = Total Phosphorus, SRP= Soluble Reactive Phosphorus)
]

Lake Ziway. Nitrite-nitrogen concentrations were always low (< 10 µg l^{-1}) with peaks in October at both stations and in March at the near-shore station. Similarly low concentrations of nitrite (2 -18 µg l^{-1}) were recorded in 1979, for L. Chammo by Amha Belay and Wood (1982). The concentrations of nitrite-N were always much lower than those of nitrate-N and Ammonium-nitrogen as they usually are in African lakes (Talling and Talling, 1965; Walmsley and Butty, 1980; Girma Tilahun, 1988). Ammonium-nitrogen ranged from about 380 µg l^{-1} in January to 1.1 mg l^{-1} in May, 2004 at the central station and from about 450 µg l^{-1} in December, 2003 to just over 1.0 mg l^{-1} in May, 2004 at the near-shore station, with its seasonal maximum coinciding with a high phytoplankton biomass at both stations. Ammonium-nitrogen, as nitrate, was more often higher at the near-shore station than at the central station. At both stations the seasonal peak in ammonium occurred following a period of fairly high precipitation while the seasonal minimum coincided with a period of relatively low precipitation. The observed concentrations of ammonium-nitrogen are intriguing given that the lake is frequently mixed and well-oxygenated. Though generalizations are difficult to make (Wetzel, 2001), the concentration of ammonium-nitrogen in well-oxygenated waters is usually low relative to those of other nutrients (McCarthy, 1980) due to its prompt oxidation and rapid and preferential uptake by phytoplankton (Eppley *et al.* 1969; Liao and Lean, 1978). Ammonium-nitrogen (NH^{+}_{4}-N) was always found in much higher concentrations than the other two forms of combined nitrogen. Ammonium concentrations in the range of 200 to 400 µg l^{-1} were also reported for surface waters of Lake Chamo (Amha Belay and Wood, 1982) and Lake Hayq (Baxter and Goloistch, 1970). Wood *et al.* (1984) have demonstrated for the crater lakes at Debre Zeit that ammonium are the predominant form of nitrogen at all depths of the water columns. Concentrations of ammonia- and ammonium-nitrogen about five times those of nitrate-nitrogen in the upper 0-5 m of the water column during periods of stratification were also recorded for Lake Awassa by Zinabu Gebre Mariam (1988). Surface concentrations of ammonium-nitrogen in lakes are often temporarily raised following the collapse of algal blooms and during increased circulation (Kalff, 2002). The presence, in Lake Chamo, of unusually high levels of ammonium probably reflects the significance of microbial regeneration and excretion from zooplankton, crocodiles and hippopotamus.

Regeneration of nutrients through faunal excretion in productive lakes like Chamo may make significant contribution to ambient nutrient concentration as has been shown for the shallow tropical lake, Lake George by Ganf and Viner (1973) and Ganf and Blažka (1974). They estimated mean excretion rate of 36 mg NH_4^+-N and 7 mg PO_4-P m^{-2} d^{-1}, which were rather greater than mean annual-based rates of N and P entering the lake from inflows. It is also possible that the high levels of ammonia resulted from the method of analysis used.

The concentration of soluble reactive phosphate (SRP) fluctuated temporally with a seasonal minimum in January, 2004 at both stations. The seasonal peak in the concentration of SRP was observed in May at the central station and in December, 2003 and May, 2004 at the near-shore station. Total phosphate (TP) exhibited a seasonal pattern, which was more or less similar to that of SRP with seasonal minimum and maximum in January and May respectively. The concentrations of both SRP and TP were generally higher at the near-shore station than at the central station, which is probably due to the proximity of the former to the mouth of the feeder river Kulfo.

Concentrations of SRP recorded in this study (26.4 - 91.7 µg l^{-1}) are higher than those reported in the relatively recent investigations on L. Chamo (Elizabeth Kebede *et al.*, 1994; Zinabu Gebre Mariam *et al.*, 2002, See Appendix -4). The remarkably high levels of SRP (200 and 290 µg l^{-1}) reported by Amha Belay and Wood (1982) for the same lake were probably associated with the collapse and subsequent decay of the bloom of *Microcystis aeruginosa,* which was reported to have occurred before the investigation was made. The high TP value of the present study (37 -150.2 µg l^{-1}) is comparable to that measured in a relatively recent survey made by Elizabeth *et al.* (1998) (See Appendix-4) but is about one-third of the concentration (490 µg l^{-1}) reported in the 1980s (Amha Belay and Wood, 1982).

Molybdate reactive silica varied from 1.6 to 15.9 mg l^{-1} at the central station and from 3.8 to 27.9 mg l^{-1} at the near-shore station. The temporal variations in silica concentration had no apparent relation to changes in the amount of precipitation although the seasonal peaks at both stations coincided with periods of high rainfall. As is the case with the other algal nutrients, silica concentration was generally higher at the near-shore station than at the central station. As is the case with many African shallow waters (Talling, 1992), silica concentration was generally in excess of those levels (< ~ 0.03 mg or 0.5- µmol Si l^{-1}) (Reynolds, 1984) at which a possibility of growth limitation might be suspected. Owing to the greater mobility of Si in most tropical soils, the importance of groundwater inputs for many lakes and the enhanced dissolution of solid silicates in saline waters of high alkalinity and pH, concentrations over 10 mg SiO_2 l^{-1} are common in African lakes (Talling and Talling, 1965; Talling, 1992) including the Ethiopian freshwater lakes, Lakes Ziway (Girma Tilahun, 1988) and Awassa (Demeke Kifle, 1985; Elizabeth Kebede *et al.*, 1994; Zinabu Gebre Mariam *et al.*, 2002).

According to Elizabeth Kebede *et al.* (1994) and Zinabu Gebre Mariam *et al.* (2002), there has generally been a consistent decline in silicate concentrations in the Ethiopian Rift Valley lakes over the last two decades or so, which was pronounced in Lake Chammo with concentrations in some samples dropping to below 1.0 mg SiO_2 l^{-1}. Although the reason for the decline was not obvious, a decline in silica level can be related to its removal from solution in diatom-dominated lakes like Shalla (Elizabeth Kebede and Willén, 1998) or its slower rate of regeneration resulting from accumulation of organic matter as was shown for alkaline lakes in Africa (Hecky and Kilham, 1973). A relation between decreasing silica concentrations and larger diatom growth was also reported for many freshwater bodies of the tropical region including Lake Chamo (Amha Belay and Wood, 1982), Lake Chad (Lemoalle, 1978) and Lake Victoria (Talling, 1966; Hecky and Bugenyi, 1992) and for lakes (Reynolds, 1973; Gibson, 1981) and rivers (Swale, 1969) of the temperate region. There is also evidence for a long-term depletion of silica over the last two decades accompanying increased phytoplankton production in Lake Victoria (Hecky, 1993; Lehman and Branstrator, 1994). The present results are not consistent with the observations of Elizabeth Kebede *et al.* (1994) and Zinabu Gebre Mariam *et al.* (2002). The predominance of blue-greens over greens and diatoms throughout the study period in Lake Chamo, however, seems to corroborate the observed high levels of silica even at times of high phytoplankton biomass.

Table. 4. pH, conductivity, alkalinity and concentration of inorganic nutrients in Lake Chamo and its feeder river-Kulfo. Results are based on samples collected on 13 May, 2004 (this study) and on September 7, 1978 (Amha Belay and Wood, 1982). Units are µg l^{-1} unless otherwise indicated.

Chemical parameter / Water body	**pH**	**Cond. (K_{25}) (µS cm^{-1})**	**Alkalinity (meq l^{-1})**	**NO_2-N**	**NO_3-N**	**NH_4^+-N**	**PO_4-P**	**TP**	**SiO_2 mg l^{-1}**	**Source**
River Kulfo	---	---	5.6	3	43	290	120	350	21.9	**Amha Belay & Wood (1982)**
Lake Chamo	---	---	10.0	3	20	290	200	290	17.5	
River Kulfo	7.45	203	5.9	2	300	600	37	91	1.6	**This study**
Lake Chamo										
Near-shore station	9.41	1477	6.6	3	20	1035	67	146	8.2	**This study**
Central station	9.41	1859	5.6	2	10	1101	69	150	15.9	**This study**

The concentrations of inorganic nutrients and levels of aggregate chemical parameters in the perennial feeder river-River Kulfo-and the lake water measured on 13th May, 2004 are given in Table-4. Data generated through an earlier investigation (Amha Belay and wood, 1982) are also included in the same table for comparison. The concentrations of all inorganic nutrients except nitrate-nitrogen and nitrite-nitrogen measured in the present study were much higher in the lake water than they were in the river water.

The present observations are not consistent with those of Amha Belay and Wood (1982) in which total phosphate and silica were found to be higher in the river water while nitrite- and ammonium-nitrogen had the same concentrations in the river and lake waters.

4.3. Biological features of the lake

4.3.1. Composition of major species of phytoplankton

Table- 5 presents a list of the most commonly encountered species of phytoplankton in lake Chamo. Blue-green algae, green algae and diatoms were the most important groups in terms of species richness and biomass (as can be judged by their abundance). *Microcystis aeruginosa (*Kütz.) Kütz. was the most abundant and persistent of the phytoplankton in Lake Chamo. Diatoms were represented primarily by *Melosira granulata* Ralfs, which persisted as an important component of the phytoplankton throughout the study period. Among the green algae, *Scenedesmus* and *Pediastrum* were each represented by several species.

It is interesting to note that *Microcystis aeruginosa* and *Melosira granulata* persistently dominated the phytoplankton community of Lake Chamo over the entire study period with peaks of abundance in November and May.Lake Chamo is a frequently mixing lake in which light may penetrate only to shallow depths. Buoyancy regulation in *Microcystis aeruginosa* would offset light-limitation to some extent and give it a competitive advantage over other algal groups in turbid environments. Furthermore, the high levels of ammonium-nitrogen must have favored *Microcystis aeruginosa* since ammonium-N pools are known to support expansion of non-nitrogen fixing cyanobacteria (Blomqvist *et al.*, 1994)

Melosira granulata Ralfs (also known as *Aulacoseira granulata*) is, however, a rapidly sinking planktonic diatom (Reynolds, 1994). But, the frequently turbulent water conditions of the lake and its adaptation to low light conditions (Reynolds (1994) favor its persistence and abundance in shallow eutrophic lakes like Lake Chamo. It is known for its wide distribution (Gasse *et al.,* 1983) and is the most common diatom species in shallow mixing lakes and in deeper lakes during high turbulence (Kilham and kilham, 1975; Hecky and Kling, 1987).

Table 4. List of the most dominant/most common species of phytoplankton in Lake Chamo. (+ refers to less common, +++ - common and +++++ - very common)

Blue-green algae	
*Microcystis aeruginosa (*Kütz.) Kütz	+++++
Anabaenopsis tanganyikae (G.S. West) Miller (1923)	+
Anabaena cf. spiroides KLEB.	+
Merismopedia sp.	+
Diatoms	
Melosira granulata Ralfs (= *Aulacoseira granulata*)	+++
Synedra dorsiventralis O. Müller	+
Surirella sp.	+
Green algae	
Cosmarium constractum KIRCHN. *var. minutum* (DELP.) West et West	+
Pediastrum boryanum (Turp.) Meneghini	+
Pediastrum duplex var. ??????	+
Pediastrum biradiatum Meyen	+
Scenedesmus quadricauda (Turp.) Brebisson	+
Scenedesmus apoliensis P. Richter	+
Cryptomonads	
Cryptomonas sp.	+

There is opportunity for long-term persistence of similar levels of total biomass and component species of phytoplankton in lakes where the amplitude of phytoplankton changes within a year is small (Talling, 1986). Such a condition seems to prevail in Lake Chamo. That is probably why a persistent species assemblage consisting of *Microcystis aeruginosa* and *Melosira granulata* occurred In lake Chamo. One has the complementary occurrence of not only major algal groups (i.e. blue-greens and diatoms) but also of the species *Microcystis aeruginosa* and *Melosira granulata.*

4.3.2. Phytoplankton biomass

Phytoplankton biomass estimated as chlorophyll a concentration exhibited temporal changes (see Fig.-3 and Appendix-7) with seasonal minima corresponding to low ambient concentration of nutrients. Phytoplankton biomass varied from 47 to 108 (mean=77.2) mg m^{-3} at the central station and from 43 to 95 (mean=69.4) mg m^{-3} at the near-shore station. Biomass values recorded for Lake Chamo in this study are comparable to those reported for lakes Abaya and Chamo (Amha Belay and Wood, 1982), Lake Abijata (Wood *et al.*, 1978) and Lake Ziway (Amha Belay and Wood, 1984). Similarly high levels of phytoplankton biomass were also reported for the two crater lakes in Ethiopia, Bishoftu (Zinabu Gebre-Mariam, 1994) and Kilole (Prosser *et al.*, 1968). Much higher values of phytoplankton biomass measured as chlorophyll a (125-900 mg m^{-3}) are, however, known from many shallow African lakes including Lakes Elmenteita (Kalff, 1983), George (Ganf and Horne, 1975), Kilole (Talling *et al.*, 1973) and Nakuru (Melack, 1976).

At both stations, peaks in phytoplankton biomass were associated with increased concentration of nitrite- and nitrate-nitrogen although the relation with other nutrients was not very obvious. Seasonal chlorophyll minima were, however, generally associated with low levels of inorganic nutrients. Phytoplankton biomass, of both stations combined, was positively, but modestly correlated (r = 0.4) with both nitrate-nitrogen and total inorganic nitrogen while its correlation with nitrite-nitrogen, was positive, and stronger ($r = 0.7$). A positive but poor correlation was, however, found between phosphorus ($r = 0.2$) and PAR ($r = 0.26$) and biomass of phytoplankton. The observed greater correlation of phytoplankton biomass with inorganic nitrogen, and not phosphorus, is consistent with the observations made in such tropical water bodies as Lake Victoria (Talling, 1966), Lake Lano (Lewis, 1974) and some reservoirs of the Nile River (Talling and Rzoska, 1967), in which reduced algal productivity was associated with nitrate depletion. Talling and Talling (1965) also gave nitrogen the role of a limiting nutrient in tropical African lakes since nitrate levels were often very low, whereas phosphate levels were relatively high.

Considering the differences in biomass values observed between the two sampling stations, a t-test was conducted to determine if the spatial variation was significant. The t-test conducted at $p = 0.05$ gave a value of 0.21, which was less than the tabulated (see Appendix 2, p.236 of Fowler *et al.*, 1998) indicating that the spatial variation of phytoplankton biomass was not significant. This appears to be related to the generally similar levels of nutrients and underwater light and temperature conditions, which presumably resulted from the frequent horizontal mixing of the water body. Furthermore, the macrophytes found at the mouth of the feeder river-Kulfo-may act as a nutrient filter thereby moderating the seasonal input of nutrients into the lake.

Euphotic zone chlorophyll a content ($\sum B$, mg Chl a m^{-2}) (Appendix 7) was calculated as a product of the depth of euphotic zone and phytoplankton biomass per unit volume of water (B; mg Chl a m^{-3}). The phytoplankton biomass of the euphotic zone varied from 45.58 to 104.76 mg Chl a m^{-2} at the central station and from 42.24 to 86.14 mg Chl a m^{-2} at the near-shore station. The euphotic zone chlorophyll content of Lake Chamo was generally much lower than that of Lake Ziway (Girma Tilahun, 1988) but still comparable to that of Lake Awassa (Demeke Kifle and Amha Belay, 1990).

4.3.3. Photosynthetic production

4.3.3.1. Depth profiles of photosynthesis

In situ experimental measurements of rates of gross photosynthesis per unit water volume (A, mg O_2 m^{-3} h^{-1}) are shown in Figs. 4 and 5 (see also Appendix 6). Because near-surface water samples were used for all incubations, the observed depth-profiles were not expressions of varying photosynthetic biomass, but were rather differing responses of presumably uniform algal biomass to different irradiance. The depth distribution of gross photosynthesis was of a typical pattern for phytoplankton, with profiles including three main regions: near-surface light-inhibition, light-saturation and a lower region of light-limitation. On all days of measurement, the depth-profiles of gross photosynthesis exhibited a sub-surface peak, with maximum photosynthetic production occurring at a depth of 0.25 m.

Depression of production rates at a lake's surface is a common feature of profiles of photosynthesis in tropical waters as it is of temperate (Talling and Lemoalle, 1998). Profiles with reduced photosynthetic activity at the surface have been reported from many African lakes including those in Ethiopia (Talling *et al.*, 1973; Girma Tilahun, 1988; Amha Belay and Wood, 1984; Demeke Kifle and Amha Belay, 1990), Chad (Lemoalle, 1983), Kenya (Talling, 1965; Melack, 1979, 1981; Vareschi, 1982) and Tanzania (Melack and Kilham, 1974). Lower photosynthetic rates of phytoplankton at a lake's surface are linked to photoinhibition, which occurs when light exceeds physiological saturation and results in excess of photons that are not dissipated by photosynthetic carbon fixation (Long *et al*, 1994; Falkowski and Raven, 1997). The decrease in photosynthetic rates is associated with photo-oxidative disruption of pigment systems (Amha Belay and Fogg, 1978; Falkowski and Raven, 1997), inactivation of photosynthetic enzymes (Steemann-Nielsen, 1962; Steemann-Nielsen and Jørgensen, 1962) and increased photorespiration (Harris and Lott, 1973; Osmond, 1981).

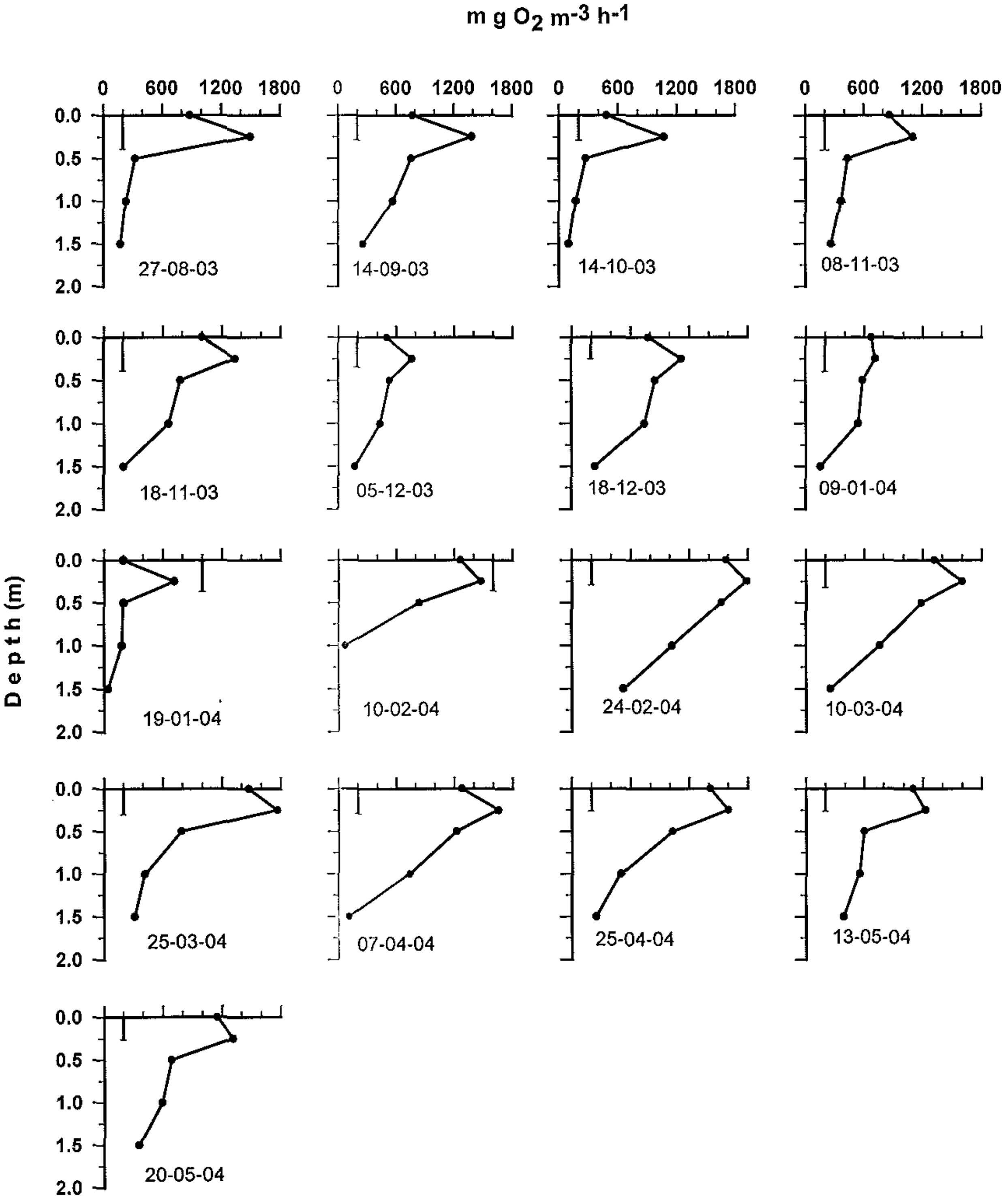

Figure 4- Depth profiles of gross photosynthesis (•) and Secchi depth (⊥) at the Central Station (C).

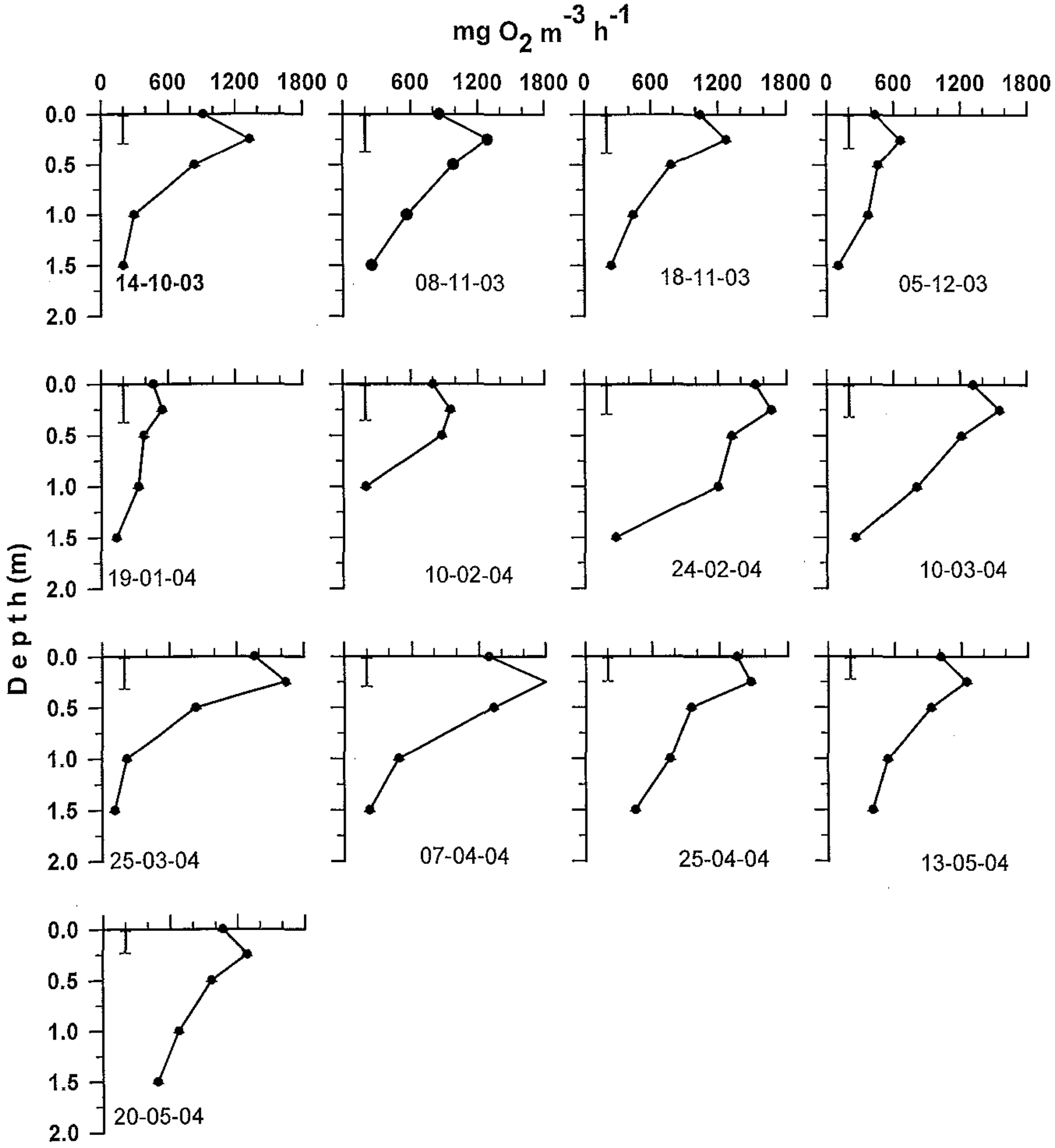

Figure 5- Depth profiles of gross photosynthesis (•) and Secchi depth (⊥) at the **Near-shore Station (K)**

The extent of photoinhibition was estimated by calculating the difference between the photosynthetic rate at the surface and A_{max} as a fraction (percentage) of the latter. The reduction in photosynthetic rates due to inhibition varied from 7.6 % to 74.5 %, corresponding to losses of 18.375 to 193.5 mg C m^{-3} h^{-1} (49 to 516 mg O_2 m^{-3} h^{-1}) assuming a photosynthetic quotient of 1.2 for the conversion of the amount of oxygen evolved to carbon fixed (Laws, 1991). The significance of inhibition of photosynthesis at a lake's surface for water column production can be considerable; although Talling and Lemoalle (1998) think that it is controversial because of its dependence on previous light history and hence possible overrepresentation in experimental exposures maintained at fixed depths.

As a function of irradiance, the extent of inhibition of photosynthetic production was variable. Hence, an irradiance of (PAR) of 167.6 x 10^3 watts m^{-2} on August 27, 2003 produced a 40.7 % reduction from the light-saturated rate (A_{max}), while irradiance of 129.7 x 10^3 watts m^{-2} on January 9, 2004 caused only a 7% reduction from A_{max}. The same irradiance (129.7 x 10^3 watts m^{-2}) on the 9th and 19th of January, however, produced 7% and 72% reduction of A_{max} respectively. Similar results were reported from other water bodies of the tropical (Demeke Kifle and Amha Belay, 1990) and temperate (Jones, 1978; Demeke Kifle, 1992) regions. It, therefore, seems that the extent of surface depression of photosynthetic rates is not a function of only the intensity of incident irradiance. Experimental studies have shown that the extent of photoinhibition varies with photoacclimation state (previous light history, Kok, 1956) and species-specific differences in photoacclimation strategies (Jorgensen, 1964; Behrenfeld *et al.*, 1998). The difference in the extent of photoinhibition between different days of incubation in Lake Chamo may be related to differences in the relative importance of different species of phytoplankton at different times of the study period since nearly the same species were found consistently in the samples examined.

Below the depth of light-saturated photosynthetic rate (A_{max}), a nearly exponential decline in photosynthetic rates with increasing depth was observed on some sampling dates (e.g. on 08-11-03 and 10-03-4 at the near-shore station and on 24-02-04 and 10-03-04 at the central stations), probably reflecting a corresponding exponential decline in underwater irradiance with an increase in depth. The compensation depth (where community respiration equals photosynthetic production) was not clearly located for most of the depth profiles owing to, presumably, the inadequate spacing of the depths of exposure of incubation bottles.

Net photosynthetic rates showed a depth-distribution pattern (see Appendix 6), which was similar to that of gross photosynthesis with maximum volumetric rates at a depth of 0.25 m.

The minimum net photosynthetic rates at light-saturation occurred at both stations in January, corresponding to a photosynthetic biomass of ≈ 60 mg Chl a m^{-3}, while the maximum net photosynthetic rates were observed in March (central station) and in April (near-shore station) coinciding with photosynthetic biomass of 91 and 53 Chl a m^{-3} respectively. The minimum net photosynthetic rates at light-saturation also coincided with a period of relatively low rainfall (≈40 mm) at both stations. Correspondence between a period of high precipitation and high net photosynthetic activity at light-saturation was also evident for the near-shore station. The corresponding levels of inorganic nutrients support the association of net photosynthetic rates with the amount of precipitation received by the study area. Strong seasonal changes in nutrient levels have also been found to follow marked seasonal rainfall in many tropical regions (Talling and Lemoalle, 1998). Thus, the minimum net photosynthetic activity at light-saturation occurred when all inorganic nutrients were at relatively low concentration at the central station and, when all except nitrate levels were low at the near-shore station. The maximum net photosynthetic rates coincided with relatively high levels of nitrate and ammonium-nitrogen at the central station and with elevated concentrations of ammonium-nitrogen and silicate (SiO_2) at the near-shore station. The minimum net photosynthetic rates were also associated with low levels of photosynthetically active radiation.

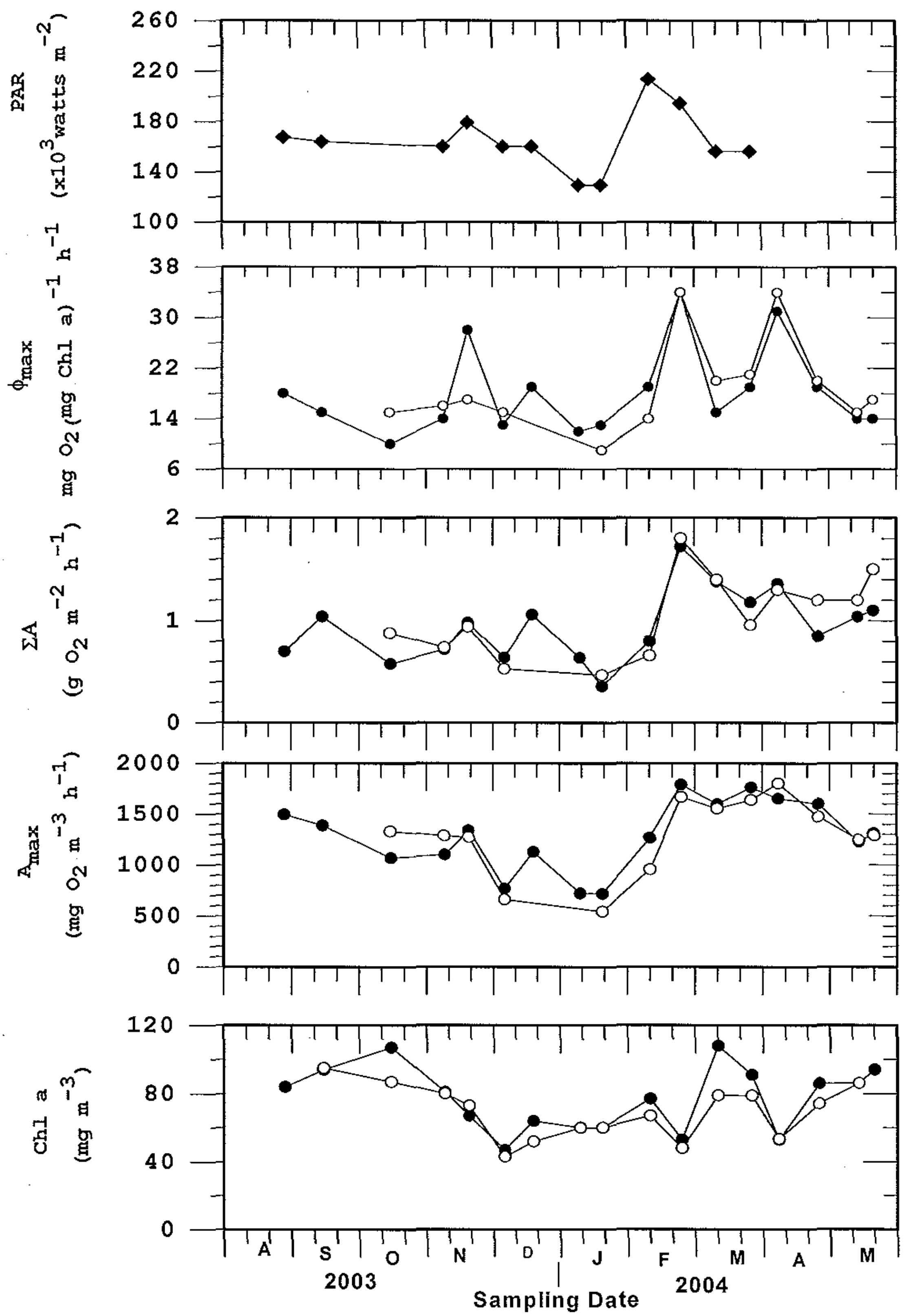

Fig. 6 Seasonal variations in factors controlling primary production and photosynthetic characteristics at the offshore (closed circle) and near-shore (open circle stations of Lake Chamo

Respiration, which reflects the use of fixed carbon by both photosynthetic and heterotrophic components of the system or oxygen consumption in dark exposures, varied from 23 mg O_2 (≈7.2 mg C) m^{-3} h^{-1} to 394 mg O_2 (≈122.93 mg C) m^{-3} h^{-1} at the central station and from about 33 mg O_2 (10.3 mg C) m^{-3} h^{-1} at the near-shore station. The minimum and maximum respiratory losses occurred at both stations in January and May respectively.

4.3.3.2. Photosynthetic characteristics

Fig. 6 shows the seasonal variations in light-saturated rate of photosynthesis (A_{max}), specific rates of gross photosynthesis at light-saturation [Φ, mg O_2 (mg Chl a)$^{-1}$ h^{-1}], and hourly rates of integral photosynthesis (∑A, g O_2 m^{-2} h^{-1}) in relation to phytoplankton biomass (B) and photosynthetically active radiation (PAR).

Better analysis of photosynthetic depth-profiles should involve characterization of the rate of photosynthesis (A or Φ) versus light flux (I) relationship, which is described by parameters representing absolute and biomass-specific rates at light-saturation (A_{max} and Φ_{max}), the onset of light-saturation (I_k), and initial gradient (slope, α) at low light of the A (or Φ)-I relationship. The estimation of I_k and α was not possible in this study due to lack of data on irradiance reaching the different depths of incubation.

Light-saturated rates of photosynthesis (A_{max}) varied over the study period from 716 to 1789 mg O_2 (~223.4 to 558.2 mg C) m^{-3} h^{-1} at the central station and from 543 to 1803 mg O_2 (~169.4 to 562.5 mg C) m^{-3} h^{-1} at the near-shore station (see also Appendix-7). A t-test conducted for the means of A_{max} values of the two stations showed the absence of significant spatial variation in A_{max}. Most of the absolute rates of gross photosynthesis at light-saturation are considerably lower than those reported (in mg O_2 m^{-3} h^{-1}) for Lake Ziway (1640 - 4670; Girma Tilahun, 1988) and Lake George, Uganda (1 900 - 6 000; Ganf, 1975) although they are still higher than those recorded for Lake Abijata (0.96; Amha Belay and Wood, 1984), Lake Awassa (217- 425; Demeke Kifle and Amha Belay, 1990), Sonachi, Kenya (130- 850; Melack, 1976) and several perennial irrigation reservoirs in Sri Lanka (110 to 640; Silva *et al.,* 2002). A_{max} values of much higher magnitude are also known from several tropical lakes including Lakes Arangaude (10 000-30 000; Talling *et al.*, 1973) and Kilole (4 000--10 000; Talling *et al.*, 1973) in Ethiopia and Lake Simbi (950-12 900; Melack, 1979) in Kenya.

The wide range of the saturation parameter per unit water volume, A_{max}, is known to be a function of primarily variable biomass concentration, B and photosynthetic capacity [the light-saturated specific rate per unit biomass, Φ_{max}, mg O_2 (mg chl a) h^{-1} (Talling and Lemoalle, 1998). The correlation between A_{max} and phytoplankton biomass for Lake Chamo was positive but weak (r = 0.3). Similarly low correlation was found for phytoplankton in Lake Ziway (r= 0.36; Girma Tilahun, 1988) although much higher correlations are not uncommon (see, for example, Pentecost and Happey-Wood, 1978; Silva *et al.*, 2002).

The highest phytoplankton biomass (95 mg Chl a m^{-3}) at the near-shore station of Lake Chamo was associated with an A_{max} value of 1387 mg O_2 $m^{-3}h^{-1}$ while a relatively low biomass (48 mg Chl a m^{-3}) at the same sampling station yielded the highest A_{max} (1789 mg O_2 m^{-3} h^{-1}).

Lack of correspondence between biomass and A_{max} was also reported for phytoplankton of several reservoirs in Sri Lanka (Silva *et al.*, 2002) and Lakes Aranguade (Talling *et al.*, 1973) and Awassa (Demeke Kifle and Amha Belay, 1990) in Ethiopia. According to Talling (1965) and Hammer (1981), high maximum rates associated with low algal biomass are the result of high specific activity [Φ_{max}, mg O_2 (mg chl a)$^{-1}$ h^{-1}]. The strong correlation between A_{max} and Φ_{max} (r = 0.71) found in this study may provide an explanation for the association of high light-saturated rates with low algal biomass observed for Lake Chamo. A strong and positive correlation (r = 0.54) was also found between A_{max} and the photosynthetically active radiation (PAR) falling on a horizontal surface in the lake's area.

It is common practice to consider the magnitude of the light-saturated rate of photosynthesis per unit of chlorophyll a [Φ_{max}, mg O_2 (mg chl a)$^{-1}$ h^{-1}] when comparing the photosynthetic capacity of phytoplankton communities. Depth-distributions of biomass-specific rates of photosynthesis were similar to the depth-profiles of absolute volumetric rates of gross photosynthesis (see Appendix- 6). The specific rates were always low at the surface due to inhibiting irradiance levels. Biomass-specific rates at light-saturation ranged from ≈10 to 34 mg O_2 (mg chl a)$^{-1}$ h^{-1} at the central station and from ≈ 9 to 34 mg O_2 (mg chl a)$^{-1}$ h^{-1} at the near-shore station, with most values above 15 at both stations. Φ_{max} values of similar magnitude were reported for Lake Kilole (16.3 - 33.7; Talling *et al.*, 1973) and an offshore station in Lake Victoria, Uganda (14 - 35; Talling, 1965). The upper values of the range of Φ_{max} for Lake Chamo are considerably higher than those reported for Lake Ziway (9.6 - 22.5; Amha Belay and Wood, 1984; Girma Tilahun, 1988), Lake Awassa (4-19; Demeke Kifle and Amha Belay, 1990), Lake Abijata (14.8; Amha Belay and Wood, 1984) and Lake Aranguade (11-18; Talling *et al.*; 1973), all in Ethiopia and Lakes Simbi and Sonachi, Kenya (15-17 and 8-14; Mealck, 1981). In lakes of temperate regions, values rarely exceed 20 mg O_2 (mg chl a)$^{-1}$ h^{-1} (Bindloss, 1974).

The highest photosynthetic capacity was associated with low phytoplankton biomass at both stations in Lake Chamo. An inverse correlation between photosynthetic capacity and phytoplankton biomass is often encountered worldwide and the trend is represented in the tropics as in Lake George, Uganda (Ganf, 1972), and Lake MacIlwaine, Rhodesia (Robarts, 1979).

It has been demonstrated that temperature (Eppley, 1972), light (Beardall and Morris, 1976; Falkowski, 1981), nutrient regimes (Falkowski and Stone, 1975) and cell size (Malone, 1971) directly affect photosynthetic capacity. As temperature and light are uniformly high in the tropics, algal type including cell size, nutrients and CO_2 supply may be considered to be of greater importance in determining the magnitude of photosynthetic capacity of phytoplankton. It is interesting to note that the minimum and maximum values of Φ_{max} corresponded to the lowest and highest mean daily photosynthetically active radiation respectively. There, however, appears to be negative correlation between levels of nutrients and photosynthetic capacity as highest values of Φ_{max} of phytoplankton in Lake Chamo occurred when ambient concentrations of inorganic nutrients (e.g. nitrite-, nitrate- and ammonium-nitrogen) were low at both stations, while the lowest values of Φ_{max} coincided with high levels of nitrite-, nitrate- and ammonium-nitrogen at the central station.

Various explanations have been given to the relatively high values of the photosynthetic capacity, $\Phi_{max,}$ obtained from tropical water bodies. Comparison of mean photosynthetic production in the trophogenic zone of tropical and temperate lakes led Lemoalle (1981) to the conclusion that higher tropical rates originate from high photosynthetic capacity, which is probably the result of the usually higher tropical temperature. This view is supported by the results of the studies made on lakes Macllwaine, Rhodesia (Robarts, 1979) and Chad (Lemoalle, 1983), which showed a drop in photosynthetic capacity during the markedly cooler season. As it has been shown by Talling *et al.* (1973) for Lake Aranguade, Melack (1979) for Lake Simbi, Kenya and Lemoalle (1973) for Lake Chad in Chad, tropical soda lakes can show a combination of high phytoplankton standing crop and above-average biomass-specific rates, partly due to the large reserve of CO_2 for localized photosynthetic activity in condensed photosynthetic zones (Talling *et al.*, 1973).

4.3.3.3. Production Rates per unit area

The area enclosed by each depth-profile is a measure of the integral rate of photosynthesis per unit area of Lake Surface ($\sum A$, g O_2 m^{-2} h^{-1}). Values obtained by the Grid Enumeration Analysis (Olson, 1960) are listed in Appendix 7 (and their temporal variation shown in Fig.-6). Hourly integral photosynthesis ranged from 0.36 to 1.72 g O_2 (~0.11 to 0.54 g C) m^{-2} h^{-1} at the central station and from 0.47 to 1.8 g O_2 (~0.15 to 0.56 g C) m^{-2} h^{-1} at the near-shore station, with higher values generally at the latter. The seasonal peaks of hourly integrals coincided with seasonal peaks in $A_{max,}$ which were observed when phytoplankton biomass was relatively low. The production rates per unit area seem to be influenced by the light-saturated rate of gross photosynthesis as the maximum depth of the photosynthetic zone was the same for all depth-profiles except one. The positive and strong correlation ($r = 0.77$) between A_{max} and $\sum A$ seems to corroborate the conclusion that gross photosynthesis per unit area is influenced by the light-saturated rate of photosynthesis. Although the correlation between phytoplankton biomass and hourly integral photosynthesis is negative and poor ($r = -0.2$), gross photosynthesis per unit area ($\sum A$) seems to depend on the biomass-specific rate (Φ) as Talling *et al.* (1973) have shown for the Ethiopian lakes, Aranguade and Kilole.

Hourly integral rates of more or less similar magnitude were measured in Lake Ziway, Ethiopia (0.3 - 1.6 g O2 m^{-2} h^{-1}, Girma Tilahun, 1988) and Lake Elmenteita, Kenya (0.11-1.74; Melack, 1979). Higher integral rates (in g O_2 m^{-2} h^{-1}) were also reported for lakes with larger photosynthetic biomass including Lake Simbi (0.62 - 5.22; 120-970 mg Chl a m^{-3}), Lake Aranguade (1.43 - 2.56; 917-2170 mg Chl a m^{-3}) and Lake Bogoria, Kenya (0.28 - 3.00; 150-800 mg Chl a m^{-3}) by Melack (1979), Talling *et al.* (1973) and Melack (1976) respectively.

The present measurements of phytoplankton photosynthesis in Lake Chamo suggest that high primary productivity is maintained in the lake throughout the year. Phytoplankton photosynthetic production did not, however, increase consistently in proportion to chlorophyll a concentration. This could be due to the contribution, to some extent, of phytoplankton biomass to the extinction of underwater light. Temporal variations in the photosynthetic production of phytoplankton were observed. It is generally assumed that there is a trend towards limited variability at the equator (Talling and Lemoalle, 1998) although the degree and patterns of temporal variability of biological parameters have not generally been documented. In order to determine the extent of monthly variability in the rates of phytoplankton production per unit area in Lake Chamo, the coefficient of variation (CV= standard deviation/mean: Melack, 1979a; Ashton, 1985) was used as an index. The estimated CV (37%) of production rates, which partly reflect biomass concentration, places Lake Chamo under Pattern A of Melack (1979a), the necessary criterion of which is a CV greater than 25%. Pattern A group includes the Kenyan lakes Naivasha Crater lake and Oloiden lake, in which production rates varied in approximate correlation with rainy and dry seasons (Melack, 1979b). The pronounced variation implied by the high CV calculated for production rates was not reflected in the phytoplankton biomass measured as chlorophyll a concentration (CV=23%). According to the CV of phytoplankton biomass, Lake Chammo comes under Pattern B of Melack (1979a), which includes the Kenyan lake, Naivasha, characterized by near-constancy in phytoplankton biomass and primary production and their little coupling to the seasonality of weather conditions. The extensive littoral vegetation of Lake Chamo and the Papyrus swamp that fringes Lake Naivasha may act as nutrient filter thereby buffering the impacts of seasonal rain on nutrient supply to the lakes. Furthermore, the persistence of the same phytoplankton assemblage throughout the study period corroborates the muted variability implied for Lake Chamo by the low CV of chlorophyll concentration.

Daily production rates per unit area ($\sum\sum A$, g O_2 m^{-2} d^{-1}), which are used as descriptive characteristics of a water body (Talling and Lemoalle, 1998), were also estimated from the hourly integral rates. With a view to make the data comparable to those of many African lakes, the hourly rates were converted to daily rates by a factor used by Talling (1965) for other east African lakes. The calculation assumes that the specific activity of phytoplankton does not show strong diurnal variation. The empirically derived factor of 0.9 was multiplied by the number of hours of sunlight and the product multiplied by the hourly rate per unit area. Values of daily integral photosynthetic rates estimated accordingly are given in Appendix-7. The calculated values ranged from 3.8 to 18.58 g O_2 (~1.1 to 5.8 g C) m^{-2} d^{-1} at the central station and from 5 to 19 g O_2 (~1.56 to 5.93 g C) m^{-2} d^{-1} at the near-shore station, exhibiting patterns of seasonal and spatial variations, which were more or less similar to those of the hourly integrals. Girma Tilahun (1988) reported daily integral production values of similar magnitude (3.1 - 17.6 g O_2 m^{-2} d^{-1}) for the shallow productive lake Ziway. Most of the daily integral production rates of Lake Chamo are much higher than those reported (in g O_2 m^{-2} d^{-1}) for many tropical African lakes including Baringo, Kenya (3.8; Patterson and Wilson, 1995), Lake Muzahi, Uganda (6 to 9.5; Mukankomeje *et al.*, 1993) and Lake Awassa, Ethiopia (3.3 to 7.8; Demeke Kifle and Amha Belay, 1990). In lakes not enriched by human activities, gross photosynthetic rates of 30 g O_2 (~9.36 g C) m^{-2} d^{-1} or greater are seldom encountered (Melack and Kilham, 1974; Talling and Lemoalle, 1998). Although the data may not be fully comparable, exceptionally high values of daily production rates (43 and 57 g O_2 m^{-2} d^{-1}) were reported for Lake Aranguade in Ethiopia based on diurnal changes in dissolved oxygen *in situ*. Other examples for exceptionally high daily integrals include those determined from oxygen evolution and ^{14}C uptake by bottled phytoplankton in Amaravathy Reservoir, India (56.9 g O_2 or ~17.75 g C m^{-2} d^{-1}; Sreenivasan, 1965) and Red Rock Tarn, Australia (17.5 g C or ~56.1 g O_2 m^{-2} d^{-1}; Hammer, 1981).

5. ENVIRONMENTAL REGULATION OF PHYTOPLANKTON BIOMASS AND PRODUCTION IN LAKE CHAMO.

Lake Chamo is a productive lake as the measured phytoplankton biomass and production rates seem to suggest. There is abundant food available (Getachew Teffera, 1993), obviously emanating from phytoplankton production, for a herbivorous fish like Tilapia (*Oreochromis niloticus* L.). Although not marked, temporal and spatial variations in phytoplankton biomass and photosynthetic production rates were observed in Lake Chamo. The temporal and spatial changes in such biological parameters of lakes are related to input-output relationships of energy (light) and materials-nutrients and gases (Talling, 1992), which are dictated by hydrographic (water-column structure and circulation) and/or hydrological (water input-output) factors (Talling, 1986).

Shallow lakes like Chamo may show nutrient concentration changes in time, which are induced by periods of greater evaporative concentration alternating with those of greater water income as has been shown for the saline lakes Elementeita (Melack, 1988) and

Nakuru (Vareschi, 1982) in the Rift Valley of East Africa. The general correspondence between elevated concentrations of inorganic nutrients, amount of precipitation and phytoplankton biomass and/or production in Lake Chamo is in support of this view.

Water-level fluctuations are quite important in nutrient-regeneration from mud. The mud in the shallow waters of Lake Chamo may have a large reserve of nutrients, which are released to the overlying water during high water levels. Lake Chamo has extensive littoral vegetation, which is fringed by terrestrial vegetation on which wild (like the hippos) and domestic animals graze. During the dry season, the soil at the edge of the lake is exposed resulting in dried, cracked and aerated soil. This soil is enriched with dung deposited by wild and domestic animals that graze in the immediate proximity of the lakeshore. When the water level rises and this zone is inundated, the previously submerged flora, cattle dung and the previously oxidized aerated soils will release large quantities of nutrients into the open water.

The concentrations of inorganic nutrients, particularly those of phosphate and silicate were consistently high in Lake Chamo, as it has been shown for most African lakes (Talling and Talling, 1965; Walmsley and Butty, 1980). The data on nutrient concentrations in this lake show the frequent occurrence of relatively high values for PO_4-P and Si (as SiO_2) but low values for NO_3-N. Ignoring ammonium-nitrogen whose concentration levels are unusual for frequently mixing and oxygenated lakes like Chamo, one may be tempted to assign a limiting role to nitrogen considering the relative concentrations of nitrate, phosphate and silicate. Based on the data they generated on African and Ethiopian lakes respectively, Talling and Talling (1965) and Elizabeth Kebede and Willén (1998) also suggested that nitrogen-limitation rather than phosphorus-limitation might be prevalent in some East African lakes including those in Ethiopia. Historically, the Refield Ratio (Redfield, 1958) has been proposed as one approach to the question of assigning a limiting role to major phytoplankton nutrients-nitrogen and phosphorus. It is based upon the observation that the atomic ratio of nitrogen and phosphorus (N:P) in both phytoplankton and nutrient-rich water originating from below the thermocline is approximately 15:1. The N:P (TN:TP) ratios of ambient concentrations calculated for Lake Chamo were generally low (see Appendix-5) probably suggesting that nitrogen-limitation is more likely than phosphorus-limitation. The fact that the concentrations of nitrate- and nitrite-nitrogen in this lake were more closely associated with phytoplankton biomass than the concentrations of all the other inorganic nutrients measured also supports this view. Nitrogen-limitation appears to be very common in tropical lakes, as the reviews by Lewis (1996) and Talling and Lemoalle (1998) seem to show although Kalff (1983) has presented data for Kenyan lakes, which suggest to the contrary.

Studies on production ecology of phytoplankton are based on measurements of bottled phytoplankton samples suspended at a nearly static sequence of depths. Possible effects of mixing and increasing oxygen tension are not, however, reflected by such an experimental setup. In the alkaline soda lakes of tropical Africa like Aranguade, Ethiopia and Lake Simbi, kenya, vertical movements of only 5-20 cm can result in a marked change in light intensity and spectral composition (Talling *et al.*, 1973). Phytoplankton cells in Lake Chamo are obviously subjected to different light conditions for varying lengths of time as wind-driven turbulence seems to be frequent in this lake. The sustainability of growth or the maintenance of phytoplankton biomass in a lake depends on whether or not photosynthesis exceeds or equals respiratory losses through the whole mixed water column. Thus, a quantitative expression for the afore-mentioned condition is deemed appropriate. The absolute depth of the euphotic zone is of less ecological significance than the ratio of the freely mixed depth (Z_{mix}) to the euphotic depth (Z_{eu}). This ratio (Z_{mix}/ Z_{eu}) is the optical depth, which may be a limiting factor in phytoplankton production (Talling, 1971). Light limitation is expected to prevail in a body of water if the critical value of 4 to 5 (Strickland, 1965; Wood *et al.*, 1978) is exceeded. The question of the total depth to which mixing occurs in Lake Chamo is not so easily answered with the present data as no measurements of depth-profiles of temperature and oxygen were made. However, because Lake Chamo is considered a frequently mixing (polymictic) lake (Elizabeth Kebede and Willén, 1994), it is reasonable to take its mixed depth as being equal to its mean depth ($\check{z}$) (Wood *et al.*, 1978). The optical depths of Lake Chamo were calculated accordingly. Euphotic depths estimated using

EV_{tot} values calculated according to Holmes (1970) were employed. Many of the calculated optical depth values of Lake Chamo (see Table-2, p.12) were considerably higher than the critical value of 4 to 5, suggesting that phytoplankton production in Lake Chamo may be light-limited at least during periods of heavy precipitation since the high optical depth values are associated with periods of rainfall. Moreover, the high algal biomass combined with suspension of sediment resulting from wind-driven mixing particularly in the shallow waters should be expected to result in reduced light penetration in Lake Chamo.

6. CONCLUSIONS AND RECOMMENDATIONS

Lake Chamo is a productive lake in which biomass and photosynthetic production of phytoplankton show small temporal and spatial (horizontal) variations. The long-term occurrence of the two species as the dominant member of the phytoplankton community is a clear indication of the fact that there is no marked seasonality in the physico-chemical conditions of the lake and hence in the biomass and photosynthetic production of phytoplankton. The extensive macrophyte vegetation in this lake might have contributed to the observed small temporal variation in the physico-chemical as well as biological parameters by acting as a nutrient filter. From N:P ratio it seems that nitrogen is limiting nutrient in Lake Chamo.

In order to have a better picture of the functioning of the aquatic system, future investigations need to have a closer look at the hydrology and nutrient flux (vertical nutrient transfer). The significance of nutrient-regeneration through zooplankton, hippopotamus and crocodile excretion and microbial transformation needs to be researched.

Human activities (over-fishing, shore-line modification etc) in and around the lake are increasing with an alarming rate. If they go on unchecked for some time, they will represent a serious threat to the future of the lake. Management strategies should, therefore, be developed at the earliest possible time with a view to avoid the occurrence of irreversible changes.

7. LIST OF CITED REFERENCES

APHA, AWWA and WEF (1999). *Standard methods for the examination of water and waste water.* 20th edn. American Public Health Association, New York.

Amha Belay and Fogg, G.E. (1978). Photoinhibition of photosynthesis in *Asterionella formosa (Bacillariophyceae).J. Phycol, 14:*341-347

Amha Belay. and Wood, R.B. (1982). Limnological aspect of algal bloom on lake Chamo in Gemu Gofa Adminstrative region of Ethiopia in 1978. *SINET: Ethiop. J. Sci.,* **5**: 1-19

Amha Belay and Wood, R.B. (1984). Primary productivity of five Ethiopian Rift Valley lakes. *Verh. Internat. Verein. Limnol.* **22**: 1187 - 1192

Ashton, P.J. (1985). Seasonality in Southern Hemisphere phytoplankton assemblages . *Hydrobiologia,* **125**: 179-190

Baxter,R.M. and Golobistch, D.L.(1970).A note on the limnology of Lake Hayq, Ethiopia. *Limnol. Oceanogr.,***15**:144-149.

Beardall, J. and Morris, I. (1976). The concept of light intensity adaptation in marine phytoplankton : Some experiments with *Phaeodactylum tricornutum. Mar. Biol., 37:377-387.*

Behrenfeld, M.J., Prasil, O., Kolber, Z.S., Babin, M., and Falkowski, P.G. (1998). Compensatory changes in PSII electron turnover rates protect photosynthesis from photoinhibition. *Photosynthesis Research*, **56**:259-68.

Bindloss, M.E. (1974). Primary productivity of phytoplankton in Loch Leven, Kinross. *Proceedings of the Royal Society of Edinburgh*, **B, 74**:157-181

Blomqvist,P., Petterson, A. and Hynestrand, P. (1994). Ammonium-nitrogen: A key regulatory factor causing dominance of non-nitrogen-fixing cyanobacteria in aquatic systems. *Arch. Hydrobiol.,* **132(2)**:141-164.

Day, J.A. (1993). The major ion chemistry of some southern African saline systems. *Hydrobiologia*, **267**:37-59.

Demeke Admassu (1998). Age and growth determination of tilapia, *Oreochromis niloticus* L. (Pisces: Cichlidae) in some lakes in Ethiopia. PhD Thesis, Addis Ababa University, Addis Ababa.

Demeke Kifle (1985). Variation in phytoplankton primary production in relation to light and nutrients in Lake Awassa. M. Sc. Thesis, Addis Ababa University, Addis Ababa: 108 pp.

Demeke Kifle (1992). Seasonal and spatial variations in species composition, abundance, biomass and primary production of phytoplankton in Southampton Water, U...K. PhD Thesis, University of Southampton, England.

Demeke Kifle and Amha Belay (1990). Seasonal variation in phytoplankton primary production in relation to light and nutrients in Lake Awassa, Ethiopia. *Hydrobiologia,* **196** : 217 - 227.

Defaye, D. (1988). Contribution à la connaissance des Crustacés Copépodes d'Ethiopie. *Hydrobiologia*, **164**:103-147.

Downing, J.A. , Plante, C. and Lalonde, S. (1990). Fish production correlated with primary productivity, not the morphoedaphic index. *Can. J. Fish. Aqquat. Sci.*,**47**:1929-1936.

Durand, J.R. and Leveque, C. (1980). Flore et Faune aquatiques de L'Afrique sahelo-Soudanienne, O.R.S.T.M., Paris.

Elias Dadebe (2001). Reproductive biology and feeding habit of some fish species in Lake Chamo, Ethiopia. Ph.D. Thesis, Addis Ababa University, A.A. pp. 105

Elizabeth Kebede (1996). Phytoplankton in an alkalinity-salinity series of lakes in the Ethiopian Rift Valley. PhD Thesis, Uppsala Universiity, Uppsala, Sweden.

Elizabeth Kebede and Amha Belay (1994). Species composition and phytoplankton biomass in a tropical African lake(Lake Awassa, Ethiopia) *Hydrobiologia,* **288** :3 - 32

Elizabeth Kebede, Zinabu Gebre-Mariam and Ahlgreen, A. (1994). The Ethiopian rift valley lakes. Chemical characterstics along a salinity- alkalinity series. *Hydrobiologia,* **288** : 1 - 12

Elizabeth Kebede and Willen, E. (1998), Phytoplankton in a salinity -alkalinity series of lakes in the Ethiopian Rift Valley, *Arch. Hydrobiol.Suppl. 4/Algological studies* **89:** 63-96.

Eppley, R.W., Rogers, J.N. and McCarthy, J.J. (1969). Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton. *Limnol. Ocanogr.*, **14**:912-920.

Eppley, R.W. (1972). Temperature and phytoplankton growth in the sea. *Fisheries*

Bulletin, **70**; 1063-1085

Falkowski, P.G. (1981). Light-shade adaptation and assimilation numbers. J. *Plankt. Res.,* **3**:203-216.

Falkowski, P.G. and Raven, J.A. (1997). *Aquatic photosynthesis.* Blackwell Sciences, Oxford, 375 pp.

Falkowski, P.G. and Stone, D.P. ((1983). Nitrate uptake in marine phytoplankton: energy sources and the interaction with carbon fixation, *Mar. Biol.*,**32:**77-84

Fowler, J., Cohen, L. and Jarvis, P. (1998). Practical statistics for field biology. 2nd edition. John Wiley and Sons, N.Y.259pp.

Ganf,G.G. (1972). The regulation of net primary productivity in Lake George, Uganda, East Africa. In: *Productivity problems of freshwaters* , Z. Kajak and A. Hilbricht-Ilkowska (eds.), pp. 693-708, Krakow, Polish Scientific Publishers.

Ganf,G.G. (1975). Photosynthetic production and irradiance photosynthesis relationships of phytoplankton from a shallow equatorial lake (Lake George, Uganda). *Oecologia,* **18**: 165 - 183

Ganf, G.G. and Blazka, P. (1974). Oxygen uptake, ammonia, and phosphate excretion by zooplankton of a shallow equatorial lake (Lake George, Uganda).*Limnol. Oceanogr.*,**19**;313-326

Ganf, G.G. and Horne, A.J. (1975). Diurnal stratification, photosynthesis and nitrogen-fixation in a shallow equatorial lake (Lake George, Uganda). *Oecologia,* **18:** 165-183.

Ganf, G.G. and Viner, A.B. (1973). Ecological stability in a shallow equatorial lake(Lake George, Uganda) .*Proc.Roy.Soc.*(B), **184**:321-346.

Gasse, F. (1986). *East African diatoms: Taxonomy and ecological distribution.* Gebruder Burntraeger, Berlin.

Gasse, F., Talling, J.F. and Kilham, P. (1983). Diatom assemblage in East Africa: classification, distribution and ecology. *Rev. Hydrobiol. Trop.*, **16**;3-14.

Getachew Teffera (1993). The composition and nutritional status of the diet of *Oreochromis niloticus* L. (Pisces:Cichlidae) In Lake Chammo, Ethiopia. *J. Fish. biol.*, **42**:865-874.

Gibson, C.E. (1981). Silica budgets and the ecology of planktonic diatoms in an unstratified lake (Lough Neagh, N. Ireland). *Internat. Res. ges. Hydrobiol.*, **66**: 641-

664.

Girma, Tilahun (1988). *A seasonal study on primary production in relation to light and nutrients in Lake Ziway, Ethiopia*. M.Sc. Thesis, Addis Ababa University, Addis Ababa, 62 pp.

Green, J. and Seyoum Mengistou (1991). Specific diversity and community structure of Rotifera in a salinity series of Ethiopian inland water bodies. *Hydrobiologia* **209**: 95-106.

Grove, A.T. and Alayne-Street, F. and Goudie, A.S. (1975).Former lake levels and climatic change in the Rift Valley of Southern Ethiopia. *Geography Journal*, **141**:177-202.

Hammer, U.T. (1981). Primary production in saline lakes. *Hydrobiologia,* **18**:47-57.

Hammer, U.T. (1986).Saline Lake Ecosystems of the World. *Monographiae Biologicae,* Vol. 59, Dordrecht: W-Junk Publ.

Harris, G.P. and Lott, J.N.A. (1973). Light intensity and photosynthetic rates in phytoplankton . *J. Fish. Res. Bd. Can.*, **20**;1771-1778.

Hecky, R.E. (1993).The eutrophication of lake Victoria. *Verh. Int. Verein.Limnol.*,**25:**39-48.

Hecky, R.E. and Bugenyi, F.W.B. (1992). Hydrology and chemistry of African Great lakes and water quality issues: Problems and solutions. *Mitt. Verein. nternat.Limnol., **23**:45-54*

Hecky, R.E and Kilham, P. (1973), Diatoms in alkaline-saline lakes: Ecology and Geolchemical implications. *Limnol. Oceanogr.* **18**:53-71.

Hecky, R.E. and Kling, H.J. (1987). Phytoplankton ecology of the great lakes in the rift valleys of Central Africa. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* **25**:197-228.

Holmes, R.W. (1970). The Secchi disc in turbid coastal waters. *Limnol. Oceanogr.*,**15**: 688-694.

Jeeji-Bai, N., Hegewald, E. and Soeder, C. J. (1977). Revision and taxonomic analysis of the genus *Anabaenopsis. Arch. Hydrobiol.* **51**:3-24

Jones, R.I. (1978). Adaptations to fluctuating irradiance by phytoplankton communities. *Limnol. Oceanogr.*,**23**:920-926.

John, D.M.,Whitton, B.A., Brook, A.J. and (eds.) (2002).The freshwater algal flora of the

British Isles: An identification guide to freshwater and terrestrial algae. The British Physiological Society, Cambridge.

Jorgensen, E.G. (1964). Adaptations to light intensities in the diatom *Cyclotella meneghiniana* Kütz. *Physiol. Plant.* **17**; 136-145.

Kalff, J. (1983).Phosphorus limitation in some tropical African lakes. *Hydrobiologia,* **100:**101-112.

Kalff, J. (2002). *Limnology: Inland water Ecosystems.* Prentice-Hall, Inc, NJ 592pp.

Kassahun Wedajo (1982). *Comparative limnology of Lake Abijata and.Lake Langano in elation to primary and Seconday production. M. Sc. Thesis.* Addis Ababa University.

Kassahun Wedajo and Amha Belay (1984). Species composition and seasonal abundance of zooplankton in two Ethiopian Rift Valley lakes -Lakes Abiata and Langano. *Hydrobiologia,* **113:**129-136.

Kilham, P. and Kilham, S.S. (1975), *Melosira granulata* (Ehr.) Ralfs:morphology and ecology of a cosmopolitan freshwater diatom. *Verh. int. Verein. Limnol.*, **19**: 2716-2721.

Kilham, P. and Kilham, S.S. (1989), Endless Summer:internal loading processes dominate nutrient cycling in the tropical lakes. *Freshwat. Biol.***23**:379-389.

Kok, B. (1956). On the inhibition of photosynthesis by intense light. *Biochim. Biophys. Acta,* **21**: 234-244.

Komarek, J. and Komarokova, J. (2002). Review of th European *Microcystis*-morphospecies (cyanoprokaryotes) from nature. *Czech phycology, Olomouc,* **2**:1-24.

Laws, E.A. (1991). Photosynthetic quotients : new production and net community production in the open ocean. *Deep Sea Research,* **38**:143-167.

Lehman, J.T. and Branstrator, D.K. (1994). Nutrient dynamics and turnover rates of phosphate and sulfate in Lake Victoria, East Africa. *Limnol. Oceanogr.,* **39(2):**227-233.

Lemoalle, J. (1978). Relations silice-diatomees dans le Lac TChad. *Cah. ORSTO ser. Hydrobiol.,* **12**:137-141.

Lemoalle, J. (1981). Photosynthetic production and phytoplankton in the euphotic zone of some African and temperate lakes. *Rev. Hydrobiol. trop.*, **11:** 31-37

Lemoalle, J. (1983). Phytoplankton production. In:*Lake Chad: Ecology and productivity of a shallow tropical ecosystem.*, J.P.Carmouze, J.R.Durandand C. Leveque(eds.), pp. 357-384, Monogr. Biologicae **53,** The Hague, Junk.

Lewis, W.M. (1974). Primary production in the plankton community of a tropical lake. *Ecological Monographs, **44:** 377-409.*

Lewis, W.M. (1996). Tropical lakes: How latitude makes a difference. In: Schiemer, F. .and Boland, K.T.(eds).,*Perspectives in Tropical Ecology*, 43-64. SPB Academic Publishers. Amesterdam.

Liao, C.F.H. and Lean, D. R.S. (1978). Nitrogen transformations within the trophogenic zone of lakes. *J. Fish. Res. Board Can.*, **35**:1102-1108.

Long, S.P., Humphries, S. and Falkowski, P.G. (1994). Photoinhibition of photosynthesis in nature. *Ann. Rev. Plant Physiol. Plant. Mol. Biol.*, **45**:633-662.

Lorenzen, C.J. (1967). Determination of chlorophyll and phaeopigments : some spectrophotometric equations. **3:** 343-346.

Maberly, S.C. (1996). Diel, episodic and seasonal changes in pH and concentrations of inorganic carbon in a productive lake. *Freshwat. Biol.*, **35**: 579-598.

MacCarthy, J.J. (1980). Nitrogen. In: *The physiological ecology of phytoplankton*, Morris, I. (ed.), pp. 191-234, Studies in Ecology , Vol.7.Blackwell.

Mackereth, F.G.H, Heron, J. and Talling, J..F.(1978). Water Analysis: Some revised methods for limnologists. FBA, Scientific Publication No, 36, 120pp.

Malone, T.C.(1971). The relative importance of nanoplankton and netplankton as primary producers in the California Current System. *Fish. Bull.*, U.S., **69**:779-820.

Melack, J.M. (1976a). Primary productivity and fish yields in tropical lakes. *Trans. Am. Fish. Soc.,* **105**:575-580.

Melack, J.M. (1976b). *Limnology and dynamics of phytoplankton in Equatorial African lakes* . PhD. Thesis. Duke University Durham, N.C, 453 pp

Melack, J.M. (1979a). Photosynthetic rates of four tropical African freshwaters. *Freshwat. Biol.,* **9**: 555 - 571

Melack, J.M. (1979b). Temporal variability of phytoplankton in tropical lakes. *Oecologia,* **44**: 1 - 7

Melack, J.M. (1979c). Photosynthesis and growth of *Spirulina platensis* (Cyanophyta) in an equatorial lake (Lake Simbi, Kenya). *Limnol. Oceanogr.*, **24**: 753 - 760

Melack, J.M. (1981). Photosynthetic activity of phytoplankton in tropical African soda lakes. *Hydrobiologia,* **81**: 71 - 85

Melack, J.M. (1988). Primary producer dynamics associated with evaporative concentration in a shallow equatorial soda lake (Lake Elmenteita, Kenya). *Hydrobiologia,* **158**:1-14.

Melack, J.M. and Kilham, P. (1974). Photosynthetic rates of phytoplankton in East African alkaline saline lakes. *Limnol. Oceanogr.*, **19**: 743-745.

Mukankomeje, R., Plisner, P.D. Descy, J.P and Massaut, L. (1993). Lake Muzahi, Ruwanda: Limnological features and phytoplankton production. *Hydrobiologia,* **257**:107-120.

Oglesby, R.T. (1977). Relationship of fish yield to phytoplankton standing crop, production and morphoedaphic factors. J. *Fish. Res. Bd, Can., **34**:2271-2279.*.,

Olson, F.C.W. (1960). A system of morphometry. *Int. Hydrogr. Rev.* **37**:147-155

Osmond, C. B. (1981). Photorespiration and photosynthesis: some implications for the energetics of photosynthesis. *Biochim. Biophys. Acta*, **639**: 77-98.

Patterson, G. and Wilson, K..K. (1995). The influence of the diel climatic cycle on the depth-time distribution of phytoplankton and photosynthesis in a shallow equatorial l lake .(Lake Baringo,Kenya). *Hydrobiologia*, **304:** 1-8

Pentecost, C. and Happey-Wood, C.M. (1978). Primary production studies in two linked but contrasting Welsh lakes. *Freshwat. Biol.* **8**:9-23.

Prosser, M.V., Wood, R.B., and Baxter, R.M. (1968). The Bishoftu crater lakes: a bathymetric and chemcial study. *Arch. fur Hydrobiol.,* **65**:309-324.

Prowse, G.A. and Talling, J.F. (1958). The seasonal growth and succession of planktonic algae in the White Nile. *Limnol. Oceanogr.,* **3**; *223-238.*

Redfield, A.C. (1958). The biological control of chemical factors in the environment. *Amer. Sci.,* **46;**205-221.

Reynolds, C.S. (1973). The seasonal periodicity of planktonic diatoms in a shallow eutrophic lake. *Freshwat. Biol.*, **3**:89-110.

Reynolds, C.S. (1984). *The Ecology of Freshwater phytoplankton.* Cambridge University Press, Cambridge.

Reynolds, C.S. (1994). The long, the short and the stalled: on the attributes of phytoplankton selected by physical mixing in lakes and rivers. *Hydrobiologia*, **289:**9-21.

Reyntjens, D. (1997). *Lake Fishery Development Project – Working paper,* No.26: Statistical Bulletin No.5, Ministry of Agriculture, Addis Ababa.

Reyntjens, D. (1998). *Lake Fishery Development Project, Phase II - Final report* , Ministry of Agriculture, Addis Ababa.

Robarts, R.D. (1979). Underwater light penetration, chlorophyll a and primary production in a tropical African lake, Lake McIlwaine, Rhodesia. *Arch. Hydrobiol.*, **86**:423-444.

Robarts, R.D. (1986). Underwater light penetration, Chlorophyll a and Primary production in a tropical African lake (Lake McIlwaine, Rhodesia). *Arch. Hydrobiol.* **86**: 423 -444

Rot, E. and Lenzenwger, R. (1994). Some rare and interesting plankton algae from Sri Lankan reservoirs. *Biologia*. **49** (4) 479-500.

Silva, E.L.L., Amarasinghe, U.S., De Silva, S.S,, Nissanka, C. and Schiemer,F. (2002). Some aspects of photosynthetic characteristics in a set of perennial irrigation reservoirs located in the river basins in Sri Lanka. *Hydrobiologia*, **485:**19-33.

Serrenivasan, A. (1965). An instance of unusual oxygen production in a tropical impoundment. *J. Mar. Biol.Assoc.* (India),**7**:469-471.

Steemann-Nielsen, E. (1962). Inactivation of the photochemcial mechanism in photosynthesis as a means to protect the cells against too high light intensities. *Physiol. Plant.* **15**:161-171.

Steemann-Nielsen, E. and Jorgensen, E.G. (1962). The physiological background for using chlorophyll measurements in hydrobiology and a theory explaining daily variations in chlorophyll concentration. *Arch. Hydrobiol.*, **58**:349-357.

Strickland, J.D.H. (1965). Phytoplankton and marine production. *Ann. Rev.Microbiol.*, **19:**127-162.

Swale, E. M. F. (1969). Phytoplankton in two English rivers. *J. Ecol.*, **57**:1-23.

Talling, J.F. (1957). The phytoplankton population as a compound photosynthetic system. *New Phytol.*, **56**:133-149.

Talling, J.F. (1965). The photosynthetic activity of phytoplankton in East African lakes. *Int. Rev. ges. Hydrobiol.*, **50**:1-32

Talling, J.F.(1966). The annual cycle of stratification and phytoplankton growth in lake Victoria(East Africa).*Int. Rev. ges. Hydrobiol.*,**51**:545-621.

Talling, J.F.(1971). The underwater light climate as a controlling factor in the production ecology of freshwater phytoplankton. Mitt. *Internat.Verein.Limnol.*,**19**:214-243.

Talling, J.F. (1986). The seasonality of phytoplankton in African lakes. *Hydrobiologia,* **138**:139 -160.

Talling, J.F. (1987). The phytoplankton of Lake Victoria (East Africa). *Arch. Hydrobi Beih.* **25**:229-256

Talling, J.F. (1992). Environmental regulation in African shallowlakes and wetlands.Rev. Hydrobiol. Trop., **25(2):** 87-144

Talling, J.F. and Lemoalle, J. (1998). *Ecological dynamics of tropical inland waters.* Cambridge University Press,Cambridge.

Talling , J.F. and Rzozka, J. (1967).The development of a plankton in relation to hydrological regime in the Blue Nile. *J. Ecol.*, **55**:637-662.

Talling, J.F. and Talling, I.B. (1965) The chemical composition of African lake waters. Int. Rev. ges. Hydrobiol., **50**:421-463.

Talling, J.F., Wood, R.B., Prosser, M.V. and Baxter, R.M. (1973). The upper limit of photosynthetic productivity by phytoplankton : evidence from Ethiopian soda lakes. *Freshwat. Biol.,* **3**: 53 -76

Tsegaye Mihrete-Ab (1988). *A seasonal study on the species composition and phytoplankton biomass in Lake Ziway, Ethiopia.* M .Sc Thesis, Addis Ababa University, Addis Ababa, 72 pp.

Tudorancea, C.; Baxter, R.M. and Fernando, C.H. (1989). A comparative limnological study of Zoobenthic associations in lakes of the Ethiopian Rift Valley. *Arch. Hydrobiol. Suppl.*, **83** 121 -174

Vanden Bossche, J.P and Bernacsek, G.M.(1991). *Sourcebook for Inland Fishery Resources in Africa.* Vol.3 Technical paper 18/3 FAO,Rome, 219 pp.

Vareschi, E. (1982). The Ecology of Lake Nakuru. III. Abiotic factors and primary production. *Oecologia,* **55**:81-101.

Walmsley, R.D. and Butty, M. (1980). *Guidelines for the control of eutrophication in South Africa.* Water Research Commission. National Institute for Water Research collaborative report, Pretoria. 36 pp.

Wetzel, R.G. (1983). *Limnology.* 2nd edition, Academic Press, London

Wetzel R.G. (2001). *Limnology:* Lake and River Ecosystems. 3rd edition. Academic Press. N.Y.1006 pp.

Wetzel, R.G. and Likens, G.E. (2000). *Limnological analyses.* Third edition. Verlag, New York, Inc. N.Y.

Whitford, L.A. and Schumacher, G.J. (1973). A manual of freshwater algae. Sparks Press Raleigh, N.C.

Williams, W.D. (1999). Salinization: a major threat to water resources in the arid and semi-arid regions of the world. *Lakes and Reservoirs: Research and management,* **4**: 85-91.

Wood, R.B., Baxter, R.M. and Prosser, V. (1984). Seasonal and comparative aspects of chemical stratification in some tropical crater lakes, Ethiopia. *Freshwat. Biol.*, **14**:551-573.

Wood, R.B., Prosser, M,V. and Baxter, R.M. (1978). Optical characteristics of the Rift Valley lakes. Ethiopia. *SINET: Ethiopian Journal of Science*, **1**:73-85.

Wood, R.B. and Talling, J.F (1988). Chemical and algal relationships in a salinity series of Ethiopian inland waters. *Hydrobiologia* **15**: 29 - 67.

Yosef Tekle-Giorgis (2000). Comparative age and growth assessment of the African catfish, *Clarias gariepinus Burchell (Clariidae)* and Nile Perch , *Lates niloticus Linn. (Centropomidae)* in the three southern Rift Valley lakes of Ethiopia , Lakes Awassa, Abaya and Chammo. Ph.D. Thesis, Addis Ababa University, Addis Ababa.

Zenebe Tadesse (1998). Food and Feeding ecology of Tilapia, *Oreochromis niloticus* L. and effects of diet on the lipid quality of fish in some lakes in Ethiopia. Ph.D. Thesis, Addis Ababa University, A.A., 138pp.

Zinabu Gebre-Mariam (1988). *Dynamics of heterotrophic bacterioplankton in an Ethiopian Rift Valley lake (Awassa).* Ph.D. Thesis, University of Waterloo, Waterloo, Canada. 110 pp.

Zinabu Gebre-Mariam (2002). The Ethiopian Rift Valley lakes: Major threats and strategies for conservation. In: *Ethiopian Rift Valley lakes*, Tudorancea, C. and Taylor, D.W. (eds.), p. 259-271, Backhuys Publishers, Leiden, The Netherlands.

Zinabu Gebre Mariam, Elizabeth Kebede-Westhead and Zerihun Desta (2002). Long term changes in chemical features of waters of seven Ethiopian rift valley lakes. *Hydrobiologia,* **477**:81-91.

8. APPENDICES

Appendix 1. Meteorological Data of Lake Chamo: Total Monthly rainfall, mean monthly Solar Radiation (PAR), mean maximum and minimum air temperature. (Source: Arba Minch meteorological Station, through National Meteorological Agency)

Month	Mean Maximum air Temperature (^{0}C)	Mean Minimum air Temperature (^{0}C)	Total Monthly Rainfall (mm)	PAR ($X10^3$ watts m^2)
Aug.	27.5	17.6	105.5	113.3412
Sept.	30.6	18	39.6	151.8708
Oct.	31.1	17	89.4	-
Nov.	32	-	25.8	127.1477
Dec.	31.4	-	14.2	128.4320
Jan.	32.2	-	40.8	135.4958
Feb.	32.7	16.1	31.2	158.6135
March	33.5	17.5	13.1	139.0276
April	30.3	18.7	164.8	-
May	-	-	-	-

Appendix 2. Equations used to estimate Mean Vertical Extinction Coefficients (EV_{tot}) and Euphotic depths (Z_{eu}).

According to Holmes (1970)

$$EV_{tot} = \frac{1.44}{Z_{SD}}$$

where Z_{SD} is Secchi depth (m)

According to Kalff (2002)

$$Z_{eu} = \frac{4.6}{EV_{tot}}$$

Appendix 3. Ambient concentration of inorganic nutrients at the Central and Near shore stations of Lake Chamo.

Sampling Date	NO_2–N (μg/L)		NO_3N (μg/L)		NH_3-N (μg/L)		PO_4-P (μg/L)		TP (μg/L)		SiO_2 (mg/L)	
	C	K	C	K	C	K	C	K	C	K	C	K
27/08/03	_	_	_	_	526	482	35	50	55	58	_	_
14/09/03	4	3	20	30	733	745	46	46	91	137	_	_
14/10/03	9	8	40	50	641	521	41	45	61	76	4.0	3.8
8/11/'03	4	5	20	20	562	521	47	48	91	91	3.8	4.2
18/11/03	3	2	20	10	377	574	44	48	82	70	2.2	4.9
5/12/'03	1	1	10	10	487	447	51	52	88	78	1.6	8.2
18/12/03	4	1	10	10	690	771	50	92	116	119	1.6	6.0
9/01/'04	4	2	30	20	549	640	38	38	92	110	2.2	13
19/01/04	2	2	20	40	378	522	26	49	37	49	2.2	6.0
10/02/'04	4	3	30	50	417	482	45	52	69	80	11.0	17
24/02/04	1	1	10	20	575	522	51	57	94	73	5.3	8.8
10/3/2004	8	3	60	10	641	653	41	48	71	73	3.8	27.9
25/03/'04	5	4	30	30	654	653	44	46	81	82	2.7	9.5
7/04/'04	2	1	30	10	746	771	45	44	87	82	3.8	21.3
25/04/04	3	2	10	10	641	903	46	41	146	91	12.6	6.0
13/05/04	2	3	10	20	1101	1035	69	67	150	146	15.9	8.2
20/05/04	3	2	20	20	1010	1035	52	52	127	110	13.7	12.6
Mean	3.03		21.67		648.1		48.6		89.1		8.19	
T-test ($p=0.05$)	0.17		0.89		0.63		0.12		0.63		0.04	

Appendix 4. Measurements of chemical and biological parameters on Lake Chamo as reported by various authors.

Parameter	Date of sampling	Depth sample was collected (m)	Concentration	References
Conductivity (K_{25}) (µS cm^{-1})	July-66	0	1120*	Amha Belay and Wood (1982)
	Feb.-64	0	1232*	Wood and Talling (1988)
	March-May, 1991	0	1320	Elizabeth Kebede et al. (1994
	1999-2000	0	1260-2310	Zinabu Gebre-Mariam et. al (2002)
Soluble Reactive P (µg l^{-1})	July-66	0	290	Amha Belay and Wood (1982)
	March-May, 1991		25.5	Elizabeth Kebede et al. (1994)
	1999-2000		6.4-82	Zinabu Gebre-Mariam et. al (2002)
Total Phosphate (µg l^{-1})	Sep., 1978	0	490	Amha Belay and Wood (1982)
	March-May, 1991	0	135	Elizabeth Kebede et al. (1994)
Nitrate-N (µg l^{-1})	Sep., 1978	0-2	2-32	Amha Belay and Wood (1982)
	May, 1979	0	217-445	Amha Belay and Wood (1982)
	March-May, 1991	0	18.6	Elizabeth Kebede et al. (1994)
Ammonium-N (µg l^{-1})	Sep., 1978	0	290-400	Amha Belay and Wood (1982)
Silica (mg l^{-1})	July-66	0	38	Amha Belay and Wood (1982)
	Sep., 1978	0	15	Amha Belay and Wood (1982
	Feb.-64	0	28	Wood and Talling (1988)
	March-May, 1991	0	< 1	Elizabeth Kebede et al. (1998)
	1999-2000		0-4	Zinabu Gebre-Mariam et. al (2002
Chlorophyll a (µg l^{-1})	July, 66 /May, 1979	0	89/73	Amha Belay and Wood (1982)
	March-May, 1991	0	44	Elizabeth Kebede et al. (1994)
	March, 1998	0	108	Ahlgren and Ahlgren, cited in Demeke Admassu (1998)

* -converted to K_{25} by multiplying the reported K_{20} by 1.12 (Wood and Talling, 1988).

Appendix 5. Atomic ratios of total nitrogen and total phosphorus (N:P) estimated from their ambient concentration at the Central (C) and near-shore (K) Stations of the lake.

Date	Central Station (C)	Near-Shore Station (K)
27/08/03	-	-
14/9/03	6.5:1	6.6:1
14/10/03	8.6:1	4.4:1
8/11/'03	5:1	5.6:1
18/11/03	3.7:1	4.6:1
5/12/'03	4.5:1	6.6:1
18/12/03	4.8:1	4.6:1
9/1/'04	4.9:1	5.2:1
19/01/04	8:1	4.7:1
10/2/'04	5:1	8.7:1
24/02/04	5:1	5.0:1
10/3/'04	7:1	5.8:1
25/03/04	6.6:1	6.5:1
7/4/'04	6.9:1	7.6:1
25/04/04	3.5:1	8.0:1
13/05/04	5.8:1	5.7:1
20/05/04	6.4:1	7.6:1

Appendix 6. Depth distribution of gross photosynthesis, A (mg O_2 m^{-3} h^{-}), net photosynthesis, Net P (mg O_2 m^{-3} h^{-}) and specific rate of photosynthesis, ∅ [mg O_2 (mg Chl a $)^{-1}$ h^{-1}] at the Central (C) and near-shore (K) stations of Lake Chamo.

Sampling Date	Depth (m)	Central Station (C)			Near-Shore Station (K)		
		A	Net P	∅	A	Net P	∅
27/08/03	0.00	886	815	11	_	–	_
	0.25	1439	1368	18	_	–	_
	0.50	326	255	4	_	–	_
	1.00	229	157	3	_	–	_
	1.50	176	105	2	_	–	_
14/09/ 03	0.00	774	629	8	_	–	_
	0.25	1387	1242	15	_	–	_
	0.50	758	613	8	_	–	_
	1.00	565	419	6	_	–	_
	1.50	258	112	3	_	–	_
14/10/ 03	0.00	483	417	5	914	771	11
	0.25	1067	1000	10	1329	1185	15
	0.50	267	200	2	843	700	10
	1.00	167	100	1.5	300	157	3
	1.50	100	33	1	200	57	2
08/11/03	0.00	867	766	11	857	628	10
	0.25	1100	1000	14	1000	771	16
	0.50	433	333	5	971	742	12
	1.00	367	266	1.5	571	342	7
	1.50	267	166	3	257	29	3
18/11/ 03	0.00	1000	923	15	1043	971	14
	0.25	1338	1261	28	1271	1200	17
	0.50	785	708	12	786	714	11
	1.00	662	584	11	443	371	6
	1.50	200	123	3	243	171	3

5/12/03	0.00	500	416	8	435	375	10
	0.25	767	683	13	661	600	15
	0.50	533	450	9	465	405	11
	1.00	433	350	6	375	315	9
	1.50	167	83	3	105	45	2
18/12/03	0.00	782	581	13	–	–	–
	0.25	1127	927	19	–	–	–
	0.50	855	654	11	–	–	–
	1.00	745	545	14	–	–	–
	1.50	236	36	2	–	–	–
09/01/04	0.00	672	590	11	–	–	–
	0.25	721	639	12	–	–	–
	0.50	590	508	11	–	–	–
	1.00	541	459	5	–	–	–
	1.50	148	66	2	–	–	–
19 /01/04	0.00	200	177	3	467	433	8
	0.25	716	693	13	543	510	9
	0.50	200	177	2	383	350	6
	1.00	184	161	2	333	300	5.5
	1.50	39	16	1	133	100	2
10/02/04	0.00	1264	1180	16	800	677	12
	0.25	1347	1263	19	954	830	14
	0.50	917	833	11	877	753	13
	1.00	153	69	2	200	77	3
	1.50	–	–	–	–	–	–
24/02/ 04	0.00	1579	1289	30	1528	1333	32
	0.25	1789	1500	34	1667	1472	34
	0.50	1526	1236	29	1458	1264	27
	1.00	1078	189	19	1194	1000	25
	1.50	526	236	10	278	83	6
10/03/04	0.00	1319	1083	12	1316	1171	17
	0.25	1597	1361	15	1553	1407	20
	0.50	1181	944	11	1211	1065	15
	1.00	764	527	7	803	657	10
	1.50	250	14	2	250	105	3

25/03/ 04	0.00	1474	1394	16	1361	1305	17
	0.25	1763	1684	19	1639	1583	21
	0.50	789	710	7	833	777	11
	1.00	421	342	4	222	166	3
	1.50	131	52	3	111	55	1
07/04/ 04	0.00	1278	1180	24	1289	1197	24
	0.25	1653	1555	31	1803	1710	34
	0.50	1222	1125	23	1329	1236	25
	1.00	736	638	14	487	394	9
	1.50	194	97	4	224	131	4
25/04/ 04	0.00	1414	1328	16	1355	1302	18
	0.25	1314	1228	19	1474	1421	20
	0.50	1029	943	12	947	894	13
	1.00	500	428	6	763	710	10
	1.50	250	171	3	447	394	6
13/05/ 04	0.00	1097	774	13	1169	861	12
	0.25	1226	903	14	1246	938	15
	0.50	597	274	7	923	615	11
	1.00	548	225	6	538	230	6
	1.50	387	64	4	400	92	5
20/05/04	0.00	1148	754	12	1065	806	14
	0.25	1311	918	14	1290	1032	17
	0.50	689	295	7	968	710	13
	1.00	590	196	6	677	419	9
	1.50	361	33	4	484	225	7

Appendix 7. Measurements of biomass and photosynthetic production rates of phytoplankton at Central (C) and Near-Shore (K) Stations with test statistics.

Sampling Date	B - mg Chl a m^{-3} (Σ B - mg Chl a m^{-2})		A_{max} ($mgO_2\ m^{-3}\ h^{-1}$)		% reduction of A_{max} due to photo inhibition		$\varnothing_{max}$ mgO_2 (mg Chl a)$^{-1}$ h^{-1}		ΣA ($g\ O_2\ m^{-2} h^{-1}$)		$\Sigma\Sigma A$ ($g\ O_2\ m^{-2}\ d^{-1}$)	
	C	K	C	K	C	K	C	K	C	K	C	K
27/08/03	84(100.8)	_	1495	_	40.7	_	18	_	0.7	_	7.56	_
14/09/03	94(83.66)	95(78.85)	1387	_	44	_	15	_	1.04	_	11.23	_
14/10/03	107(93.1)	87(75.69)	1067	1329	55	31	10	15	0.58	0.88	6.26	9.5
8/11/'03	81(101.3)	80(92)	1100	1286	22	34	14	16	0.72	0.74	4.5	8
18/11/03	67(79.1)	73(86.14)	1338	1271	25	18	28	17	0.98	0.94	10.6	10
5/12/'03	47(50.8)	43(43.86)	767	661	35	34	13	15	0.64	0.53	6.9	5.7
18/12/03	64(75.5)	52(59.8)	1127	_	31	_	19	_	1.06	_	11.5	_
9/01/'04	60.1(72.7)	60(70.8)	721	_	7	_	12	_	0.64	_	6.9	_
19/01/04	60(69)	60.1(69.1)	716	543	72	14	13	9	0.36	0.47	3.8	5
10/02/'04	77(86.2)	67(72.36)	1264	954	14	16	19	14	0.8	0.66	8.6	7
24/02/04	53(49.3)	48(42.24)	1789	1667	12	8	34	34	1.72	1.8	18.58	19
10/3/2004	108(104.76)	79(76.63)	1597	1553	17	15	15	20	1.38	1.4	14.9	15
25/03/'04	91(84.63)	78.9(73.38)	1763	1639	16	17	19	21	1.18	0.96	12.7	10
7/04/'04	53(45.58)	53.5(46.01)	1653	1803	23	29	31	34	1.36	1.3	14.7	14
25/04/04	86(68.8)	74.2(54.12)	1600	1474	11	8	19	20	0.85	1.2	9.2	13
13/05/04	86.2(68.96)	86.2(57.75)	1226	1246	10.5	19	14	15	1.04	1.2	11.2	13
20/05/04	94(75.2)	74(51.8)	1311	1290	12	17	14	17	1.1	1.5	11.9	16
Mean	73.1		1313.9		27.3		18.4		0.96		10.2	
T-test (P=0.05)	0.2		0.8		0.4		0.9		0.7		0.6	