

A SEASONAL STUDY ON PHYTOPLANKTON
PRIMARY PRODUCTION IN RELATION
TO LIGHT AND NUTRIENTS IN LAKE ZIWAY
(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
/ GIRMA TILAHUN
JUNE, 1988

CONTENTS

	<u>page</u>
ACKNOWLEDGEMENTS	i
LIST OF TABLES	ii
LIST OF FIGURES	ii
ABSTRACT	iv
CHAPTER I INTRODUCTION	1
CHAPTER II STUDY AREA	8
CHAPTER III MATERIALS AND METHODS	13
1. Field procedures	13
2. Laboratory Procedures	15
3. Explanations of Symbols	16
CHAPTER IV: RESULTS	19
1. Temperature/oxygen depth profiles	19
2. Lake water Chemistry	24
3. Under-water light climate	26
4. Phytoplankton biomass and primary production	30
CHAPTER V: DISCUSSION	37
CONCLUSION AND RECOMMENDATIONS	52
REFERENCES	54

ACKNOWLEDGEMENTS

I owe a debt of gratitude to Dr. Amha Belay, my research advisor, for his constant guidance and encouragement.

My sincere thanks go to Prof. G. Hartman for his keen interest in my work and for critically reading the draft manuscript. The invaluable assistance provided by Elizabeth Kebede is greatly appreciated. My thanks are also due to Azeb Mekasha and Tadesse Mehari for helping me with the typewritings.

I am most grateful to the following colleagues who tirelessly and promptly helped me throughout the field work: Semeneh Belay, Tsegaye Miheret-ab and Zenebe Tadesse. I am also thankful for the close cooperation extended from the staff members of the Fish Production and Marketing Corporation of the Ministry of Agriculture at Ziway.

The financial support of the Swedish Agency for Research Cooperation (SAREC) and the material assistance & computer facilities provided by the Freshwater Fisheries and Limnology Project (FFLP) of the Biology Department financed by the Canadian International Development Agency (CIDA) are gratefully acknowledged.

Finally, I wish to record my deep appreciation to my family without whose endless patience everything would have been impossible.

TABLES

1. Principal physical and chemical features of Lake Ziway	12
2. Meteorological information of Lake Ziway region and the thermal regime of the lake on the date of sampling.	23
3. The chemical composition of the surface water of Lake Ziway during the sampling period.	25
4. The underwater light climate of Lake Ziway during the sampling period.	28
5. Algal biomass, photosynthetic rates of phytoplankton and irradiance in Lake Ziway.	32

FIGURES

1. The drainage system of the northern rift valley lakes (A) & the bathymetric map of Lake Ziway (B) (Source: Morandini, 1942) with the sampling station indicated by a star.	11
2. Depth profiles of temperature (0----0) and percentage saturation (0—0) of Lake Ziway on the date and time indicated.	21
3. The mean annual extinction coefficients in Lake Ziway for red, blue and green light (Vertical bars represent standard deviations).	29
4. Depth profiles of gross photosynthesis, Secchi depth (\perp) and respiration (- - -) in Lake Ziway on the sampling date and time (incubation mid-hour) indicated.	33

- 5A-C. Seasonal variation of major algal nutrients (A), algal biomass (B) and photosynthesis in Lake Ziway (Vertical bars represent monthly rainfall in the region, data of Ethiopian National Meteorological services Agency, 1988). 35
- 6A-C Seasonal pattern in photosynthetic production and the ratio of A_{max}/e_{min} (A), underwater light climate (B) and algal biomass in Lake Ziway. 36

Abstract

Primary production by phytoplankton of Lake Ziway, Ethiopia, was studied from February, 1987 to February, 1988 by the oxygen light-dark bottle technique. Supporting information included data on thermal characteristics, water chemistry, light penetration and meteorological conditions.

Isothermal or near isothermal conditions were frequently observed. These were ensured by windy condition prevailing on the large and unsheltered lake surface. Well oxygenated water from top to bottom provided evidence for frequent mixing.

In all the sampling periods sodium clearly dominated the cations and carbonate-bicarbonate dominated the anions. The cationic proportion of the lake followed the order $\text{Na} \gg \text{Ca} > \text{Mg} > \text{K}$ while its anionic proportion followed the order $\text{HCO}_3^- + \text{CO}_3^{2-} \gg \text{Cl} > \text{SO}_4$. The lake was found to have a high concentration of silica and low concentrations of phosphate and nitrate.

The pattern of underwater light penetration was similar in all the sampling periods. The highest penetration occurred in the red, and the lowest in the blue spectral region. Solar irradiance incident on the lake surface did not vary markedly except for the low values recorded on cloudy days.

The maximum photosynthetic rates of bottled phytoplankton varied between 1640 and 4070 $\text{mg O}_2 \cdot \text{m}^{-3} \cdot \text{h}^{-1}$ and areal rates ranged from 288 to 1625 $\text{mg O}_2 \cdot \text{m}^{-2} \cdot \text{h}^{-1}$. A principal reason for high rates of photosynthesis was the combined effect of high chlorophyll *a* content of the euphotic zone (81.1-191.6 $\text{mg Chl a} \cdot \text{m}^{-2}$) and high photosynthetic capacity [$11.0 - 22.5 \text{ mg O}_2 (\text{mgChl a})^{-1} \text{ h}^{-1}$].

Efficiency of utilization of photosynthetically available radiation (Ph.A.R), Q, ranged from 2.4 to 9.6 mmol O₂ per Einstein Ph.A.R. incident on the lake surface. An inverse relation between efficiency and irradiance was observed.

The temporal variation in algal biomass was more pronounced when measured on a per unit area basis (cv = 23.9%), than when measured on a per unit volume basis (cv = 10.1%). This was due to the marked variation in the underwater light climate of the lake. High algal biomass and sustained production seemed to be maintained more by nutrient recycling than by nutrient input as the lake was of low nutrient status through out the year.

Hydrographic (water column structure) factors seemed to play an overriding role in determining the rate of nutrient recycling, the underwater light climate, the extent of algal growth in the lake, and subsequently the spatial (vertical) and temporal pattern of phytoplanktonic photosynthesis.

INTRODUCTION

In a world of ever increasing human population where food production is not meeting demands, study of productivity at all levels of food chain becomes essential. Research on aquatic, as on terrestrial ecosystems, is increasing in intensity. Aquatic ecosystems have received attention as actual and potential sources of food. Such habitats play an important role in ameliorating the effects of draught on food shortage. It is from this point that study of aquatic productivity at the beginning of food chain becomes a logical starting point.

The study of energy transfer in lakes and reservoirs is based on the measurement of primary productivity of phytoplankton and the environmental variables which limit or control this production. The functioning of the phytoplankton community is of practical and theoretical interest. Comparative studies of several sets of variables (Henderson et al., 1973; Melack, 1976b; Oglesby, 1977; Ryder, 1965, 1974) suggested that potential yield may be related to several simple indices of production.

Melack (1976b) and Oglesby (1977) have concluded that primary production is, theoretically and empirically, a better predictor of fish yield in lakes than other suggested variables. Both authors offer linear regression equations relating fish yield and primary production. Other methods of relating fish yield to nutrient concentration and primary production (Henderson et al., 1973; Ryder, 1965, 1974) reinforce the concept of the dependence of potential yield on lake productivity.

Man, for the last sixty years, has been trying to measure primary production of water varying from fresh to saline and from inland to marine. Although a number of detailed studies in this respect have been carried in temperate regions, similar efforts on tropical lakes have gained momentum

recently. As Talling (1986) pointed out, this effort has been longer and more sustained in Africa than in any other tropical or sub-tropical region.

Many investigations have been made on primary production of phytoplankton in East African lakes (Ganf, 1975; Hecky and Fee, 1981; Melack, 1976a, 1979a,b,c; Melack and Kilham, 1974; Milbrink, 1977; Talling, 1965, 1966; Talling et al., 1973; Vareschi, 1982), in lakes situated in the Sahel and Northern Africa (Aleem and Samaan, 1969; Lemoalle, 1973, 1981), and in lakes in Southern Africa (Allanson and Hart, 1975; Robarts, 1986).

The study of phytoplankton photosynthesis in tropical Africa has come up with reports of exceptionally high photosynthetic activity particularly in the soda lakes of East Africa. Melack and Kilham (1974) suggested that in lakes not enriched by human activities, gross photosynthetic rates of $30\text{g O}_2\text{ m}^{-2}\text{ d}^{-1}$ (ca. $11\text{g C m}^{-2}\text{ d}^{-1}$) or greater are seldom encountered. However, these authors have reported gross photosynthesis as high as $36\text{g O}_2\text{ m}^{-2}\text{ d}^{-1}$ (ca. $13\text{g C m}^{-2}\text{ d}^{-1}$) for Lake Nakuru, in Kenya, by the diurnal free-water technique. More recently, Melack (1979a, 1981) reported similar values for the phytoplankton of Lake Simbi (Kenya).

Exceptionally high algal photosynthetic rate in the order of $43\text{-}57\text{g O}_2\text{ m}^{-2}\text{ d}^{-1}$ (Ca. $16\text{-}21\text{g C m}^{-2}\text{ d}^{-1}$) has also been reported by Talling et al. (1973) for Lake Aranguade, an Ethiopian soda lake. These authors attributed the high photosynthetic rate of this cyanophycean (Spirulina platensis) lake to a combination of high algal content in the euphotic zone (ΣB) with high values of photosynthetic capacity (ϕ_{max}). Tropical situations affecting temperature and illumination, high phosphate concentration, and especially considerable reserves of carbondioxide in these soda lakes might have also favoured high photosynthetic productivity.

The shallow well-mixed fresh lakes of equatorial Africa, such as Lake

Chilawa, Zambia, ($\bar{Z} = 3\text{m}$, Howard-William and Henton, 1975), Lake Naivasha, Kenya, ($\bar{Z} = 4\text{m}$, Gaudet, 1977), and Lake George, Uganda, ($\bar{Z} = 2.5\text{m}$, Ganf and viner, 1973) are also known for their high productivity. These lakes contain extensive areas of littoral zone and a large portion of their shoreline falls within the drawdown area, whose inundation during the rainy season results in increased offshore levels of nutrients with a subsequent increase in primary production (Gaudet and Muthuri, 1981a,b; Howard-Williams and Lenton, 1975).

Critical observations by different authors, particularly on shallow tropical lakes, have pointed out the important determinants in algal biomass and photosynthetic activity. Vincent et al. (1986) singled out that flood related changes in nutrient supply and abiotic turbidity are the 'over-riding factors in shallow well-mixed lakes such as Lake Chilwa. Moss and Moss (1969) also believed that these marked hydraulic forces result in a strong seasonal fluctuation of algal biomass and abrupt inter-annual differences in productivity.

Detailed observations from Lake George (Ganf and viner, 1973) illustrated remarkable physical and biological constancy. The constancy of Lake George was caused by the perennial rivers and sufficient internal recycling of nutrients (Melack, 1979b). In this shallow continuously polymictic lake, the largest observed environmental changes took place over the daily mixing cycle.

Vincent et al. (1986) emphasized that the muted seasonal variation of light and temperature in tropical lakes often explains only a small portion of the variation in primary production compared to the temperate counter parts. It is rather, the temporal variability in rain and wind which appear to be the most probable cause of variation in algal biomass and

photosynthetic activities of tropical lakes (Lewis, 1974; Melack 1979b; Pollinger, 1986; Talling, 1966). Winds generate high turbulence which culminates in mixing; as a consequence recirculation of nutrients and resuspension of algae occur. Rains increase the volume of inflows and the supply of nutrients and inorganic turbidity, all of which influence primary production.

The seasonal cycle of phytoplankton standing stock and production in African lakes was reported to vary intimately with fluctuations in water level (Lemoalle, 1975, Melack 1976a). Melack (1976a) found positive correlation between level of primary production and changes in water level. He showed that offshore primary production generally increased with increased rainfall and river discharges. Lemoalle(1975), however, found an inverse relationship between lake water level and algal productivity in his work on polymictic Lake Chad. This relationship may exist because in the shallower water column nutrients are more effectively circulated by wind-induced mixing.

In an attempt to review factors related with temporal variability, Talling (1986) has generalized phytoplankton seasonality in the tropical belt of Africa. This author suggested that seasonality in algal biomass and production is usually dominated either by hydrologic factors (water input-output) or by hydrographic factors (water column structure and circulation). Melack (1979b) proposed that three patterns of temporal changes in abundance and/or photosynthetic rates of phytoplankton occur in tropical African lakes.

The three patterns of algal biomass and production proposed by Melack (1979b) can be summarized as follows:

PATTERN A: A necessary criterion for recognizing this pattern is a

coefficient of variation, cv, (standard deviation/mean) greater than 25%. The reasons for the marked fluctuations include wind-induced mixing, increased river discharge and rainfall and associated changes such as increased turbidity, availability of nutrients, and presumably light. Most African lakes, including Lakes Chad (Lemoalle, 1975), Oloiden and Sonachi (Melack 1979a,b,c), Sibaya (Allanson and Hart, 1975), & McIlwaine (Robarts, 1986) exhibit such pronounced seasonal fluctuations.

PATTERN B: Low cv (i.e., less than 20%) indicating muted seasonality is a distinguishing feature in this pattern. Lakes Naivasha (Melack, 1979a) and Nakuru (Melack and Kilham, 1974) fit this pattern. In such lakes the amplitude of the diel fluctuations often equals or exceeds the monthly changes.

PATTERN C: In contrast to the continuation of regular seasonality (Pattern A) or near constancy (Pattern B) an abrupt switch from one persistent algal assemblage and level of photosynthetic activity to another persistent level characterizes this pattern. Melack (1979b) has observed this situation for lakes Elmenteita and Nakuru.

A serious deficiency in the studies of phytoplankton production in Africa, as in many other parts of the world, is the insufficient attention paid to temporal and spatial variability in algal biomass and photosynthetic activity. There is very little on record about seasonal variation in the photosynthetic activity of tropical African lakes. Published works in this respect include those of Aleem and Samaan (1969), Allanson and Hart (1975), Ganf (1975), Melack (1976a, 1979a, 1981), Robarts (1986) and Talling (1965).

In Ethiopia, research on Limnology has been published for over fifty years. However, this work has not been systematic or sustained and it has

been derived from expedition results or short-term visits of non-residents. Compiled data are generally fragmentary in nature and of varying detail and reliability.

Although there has been increasing attention, particularly in recent years, to the seasonal course of limnological events in Ethiopia (Demeke Kifle, 1985; Elizabeth Kebede, 1987; Kassahun Wodajo, 1982; Prosser et al., 1968; Tilahun Kibret, 1985; Wood et al., 1976, 1984), our knowledge is still far from complete. Even the work published so far on physical, chemical and biological features of Ethiopian lakes needs further review, synthesis and comparison in a wider context. In this respect, it is worth mentioning the contributions of Amha Belay (in press) in preparing a bibliography of Ethiopian Limnology, Talling and Talling (1965), Cerling (1979), and Talling (1986) in overviewing the chemical and biological features of some Ethiopian lakes in a wider African context. Chemical and algal relationships over a wide range of salinities, in Ethiopian inland waters, has also been compiled by Wood and Talling (1988).

In spite of the vast inland water resources (>7000Km²) contained in Ethiopia, satisfactory limnological investigations have been carried out on only a few of the numerous Ethiopian lakes. No adequate study has, for example, been made on any of the shallow well-mixed Ethiopian lakes which are supposed to be productive and economically important. Lake Ziway is one such lake which has not received attention in spite of its economic importance as one of the major inland fisheries of the country.

Previous investigations on Lake Ziway include short-term studies of basic morphometry (Cannicci and Almagia, 1947), geology and hydrology (Di Paola, 1972; Gasse and Street, 1978; Makin et al., 1975), thermal characteristics (Baxter et al., 1965), water chemistry (Makin et al., 1975;

Talling and Talling, 1965; Von Damm and Edmond, 1984), optical characteristics (Wood et al., 1978), fishery (Getachew Teferra, 1987; Schroder, 1984; Wolde-Michael Getaneh and Maria Getaneh, 1979) and primary productivity (Amha Belay and Wood, 1984).

The present work on Lake Ziway attempts to fulfill the following objectives:

1. Provide an estimate of primary production by phytoplankton in this lake.
2. Attempt to identify the factors controlling primary production.
3. Assess the seasonal trend of other limnological events.
4. Provide base-line data of value for proper management and sustainable utilization of this shallow water body.
5. Provide limnological report of comparative value and, to a certain extent, fills the gap of information about Ethiopian lakes.

STUDY AREA

Lake Ziway, the study area, is the most northerly of the Ethiopian Rift Valley lakes. It is an open lake within the closed Ziway-Shalla basin. The lake lies near the highest part (1636m a.s.l) of the main Ethiopian rift floor 140kms due south of Addis Ababa (Fig. 1). The principal physical and chemical features of the lake are given in Table 1.

Lake Ziway is of tectonic origin (Di Paola, 1972). From this point of view, the lake lies within a down-faulted basin (Gasse & Street, 1978) which appears to be one of the least active sectors of the Ethiopian rift systems. Hence its morphology is relatively simple.

A high portion of the lake bed and the swampy lake margins are comprised of coarse pumice (Makin et al., 1975). The shores are sandy or rocky (Schröder, 1984) with the shoreline determined by the Wonji fault belt (Mohr, 1960). The lake is separated from Lake Langano by the extensive and complex volcanic massif of Alutu, a dormant volcano manifesting strong fumarolic activity (Mohr, 1966).

The weather of the Lake Ziway region is arid for most of the year. It is frequently windy and stormy. It is reported (Gasse and Street, 1978; Makin et al., 1975) that the mean annual rainfall is generally less than 600mm and there are no months in which average rainfall exceeds potential evaporation. These authors also estimated an annual open water evaporation of the order of 2000mm.

Lake Ziway is primarily dependent on rainfall from distant uplands because the local precipitation is inadequate to maintain lake level. The lake is principally fed by the Katar and Meki rivers, which drain a catchment area of 3400km² and 2300km², respectively (Von Damm and Edmond,

1984). These authors estimated that the Meki River discharges about $420 \times 10^6 \text{ m}^3$ per annum and the Katar river discharges in the order of $437 \times 10^6 \text{ m}^3$ annually. Makin et al. (1975) have estimated a total influx of $1150 \times 10^6 \text{ m}^3$ of water per annum from the Meki and Katar rivers plus the rainfall on the lake surface.

Lake Ziway has a surface outlet from its west corner into the Bulbula River which enters Lake Abijata. The Bulbula River discharges about $210 \times 10^6 \text{ m}^3$ of water per annum (Makin et al., 1975; Von Damm and Edmond, 1984).

Pronounced fluctuations in rainfall in the Ziway basin cause the lake level to fluctuate on both a monthly and yearly basis. The main rainy season occurs between mid-June and mid-September, which causes a rise in the water level and flooding of the shores. The dry season lasts from October to February decreasing the water level. The "small" rainy season occurs in the months of March and April (Shröder, 1984).

The shoreline of Lake Ziway is fringed with reed and papyrus and dotted with big Ficus sycamora trees. The lake contains extensive areas of littoral vegetation. A large portion of its littoral zone falls within the draw-down area which is dried out during the dry season and inundated during the rainy season. The lake has five main islands of volcanic origin.

Over half the land surrounding Lake Ziway is subject to cultivation. There is increasing practice of water diversion for the purpose of irrigation and this causes more lake level fluctuation and further disrupts the balance between water input and output.

The phytoplankton community of Lake Ziway is dominated by species of blue-green, green algae and diatoms. The most important phytoplankter

species as determined by cell counts are Microcystis spp., Lyngbya spp., Navicula spp. and Staurastrum spp. (Tsegaye Miheretab, Pers. Comm.). The zooplankton community is dominated by Mesocyclops spp., Microcyclops sp., Diaphanosoma sp., Brachionus angularis and Keratella tropica (Semeneh Belay, pers. Comm.). The fish population consists of Oreochromis niloticus, Barbus sp. and Tilapia zilli (Zenebe Tadesse, pers. comm.). Hippopotamus amphibius is the common grazer in the littoral macrophyte belt of Lake Ziway.

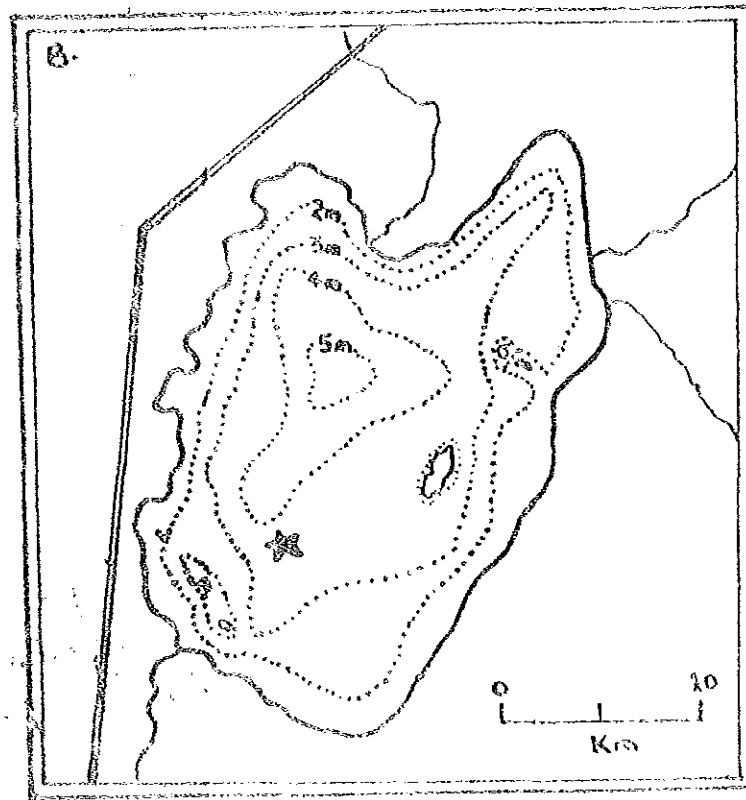
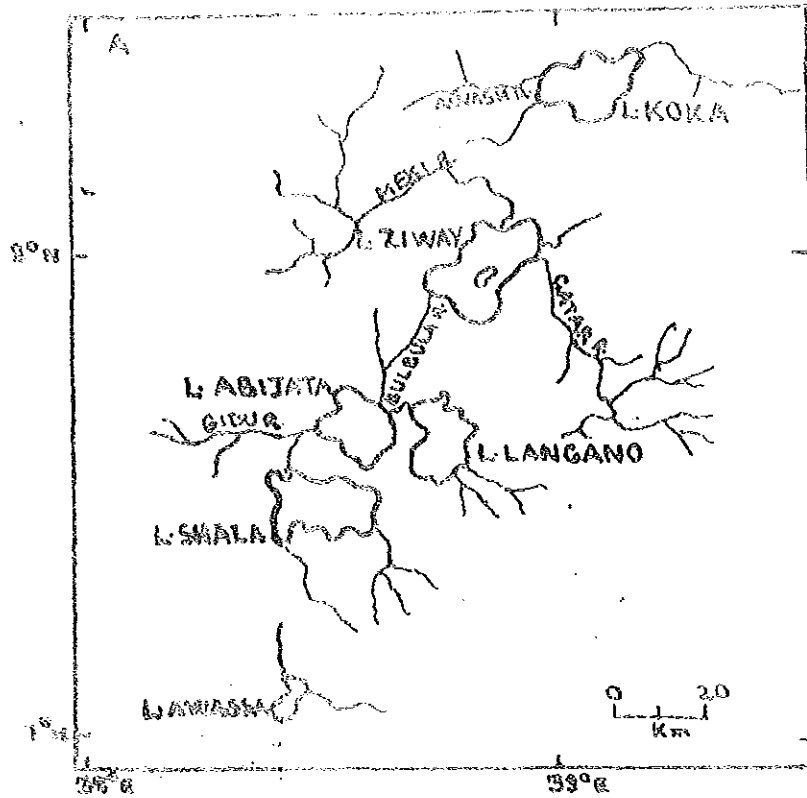


Fig. 1 The drainage system of the northern rift valley lakes [A] and bathymetric map of Lake Ziway [B] (Source: Morandini, 1911) with sampling station indicated by star.

TABLE 1. Principal physical and chemical features of Lake Ziway

Topography & Morphology	Water Chemistry	Climate & Hydrology
Latitude 7°52'1"-8°08'1"N	TDS 0.349 g l ⁻¹ (c)	Annual rainfall < 600mm (d)
Longitude 38° 40'1"-38°56'1"E	K ₂₅ 359 μ-S cm ⁻¹ (c)	Annual open water evap. 2000mm(d)
Altitude 1636m a.s.l.	pH 8.9 (C)	Mean Air-temp.
Surface area 434km ² (a)	Σ cat. 3.72meq.l ⁻¹ (c)	Max. 26.9°C (d)
Shoreline Length 102km (a)	Σ an. 3.80meq. l ⁻¹ (c)	Min. 11.7°C (d)
	Na ⁺ 2.11 meq.l. ⁻¹ (c)	Surface inflow
		Meki River 420x10 ⁶ m ³ (b)
Max length 32km (a)	K ⁺ 0.30 meq.l ⁻¹	Katar River 437x10 ⁶ m ³ (b)
Max width 20km (a)	Ca ²⁺ 0.70 meq.l ⁻¹ (c)	Surface outflow
	Mg ²⁺ 0.62 meq.l ⁻¹ (c)	Bulbula River 210 x 10 ⁶ m ³ (b)
Mean depth 2.4m (a)	HCO ₃ ⁻ +CO ₃ ⁼ 3.34meq.l ⁻¹ (c)	
Volume 1.1x10 ⁹ m ³ (a)	Cl ⁻ 0.24 meq.l ⁻¹ (c)	
Catchment area 7025km ² (a)	SO ₄ ²⁻ 0.22 meq.l ⁻¹ (c)	
	SiO ₂ 45mg l ⁻¹ (c)	

a = Cannicci and Almagia (1947), b= Von Damm and Edmond (1984), C = Wood and Talling (1988), d = Makin *et al.* (1975)

MATERIALS AND METHODS

1. Field Procedures

1.1. Sampling

A single open water station (Fig. 1) was used throughout the sampling period (February, 1987 - February, 1988). Sampling was done at fortnightly or monthly intervals. Integrated water samples over the euphotic depth were collected using a Kemmerer sampler of 2 liter capacity. These samples were used for photosynthetic measurements and for pigment and chemical analyses.

1.2. In-situ Measurements

Lake water temperature and dissolved oxygen concentrations were measured with an oxygen probe, incorporating a thermistor thermometer, connected with oxygen meter (YSI-model 57). Percentage saturation of oxygen was calculated as in Wetzel and Likens (1979). Measurements were done from the surface down to 3.5m in the months of high water level (February, 1987 - October, 1987) and to 3m in the months of low water level (November, 1987-February, 1988).

Conductivity was measured with combined conductivity-salinity and thermistor thermometer probe (YSI-model 33 S-C-T meter). Temperature corrections were made to 25°C as in Wetzel and Likens (1979).

pH measurements of lake surface water were made with a portable digital pH meter (Camlab, model 607) readable to 0.05 pH units.

Lake transparency (= vertical visibility) was determined with

a standard Secchi disk.

Under-water light penetration was measured with a selenium rectifier photocell equipped with diffusing opal and interchangeable glass color filters (Mainz, W. Germany) of types BG12, VGg and RG630. Optical mid-points of the cell filters used were estimated to be 460, 540, and 630nm respectively. Results were used to calculate the spectral variation of light extinction, expressed by vertical extinction coefficients, K_d , (\ln units m^{-1}).

Under-water photosynthetically active radiation (Ph.A.R.) was measured in $\mu\text{Em}^{-2}\text{s}^{-1}$ with a LI-COR quantum sensor (LI-192SB) which was connected to LI-185B quantum photometer.

Surface incident radiation near the lake shore was measured at 30 minute intervals from dawn to dusk using LI-S10B integrator. The readings were converted to absolute units, $\text{Em}^{-2}\text{h}^{-1}$, following the manual for the instrument.

1.3. In-situ Photosynthesis

Gross photosynthesis was measured by the Winkler method (Mackereth et al., 1978) from in-situ changes in oxygen concentration in light and dark bottles suspended in the euphotic zone.

Integrated water samples were siphoned into 120 ml pyrex transparent and opaque (covered with dark cloth) glass bottles. Duplicates of the transparent bottles were suspended at depths 0.00, 0.05, 0.10, 0.15, 0.30, and 0.50m. To avoid shading effects, the bottles were suspended at intervals of 10cm or more, down the water column in two sets about 30cm apart along a horizontal metal bar suspended by means of floats.

To assess respiration, duplicates of opaque bottles were also incubated at depths 0.00 and 0.60 m. Exposures of incubation bottles usually lasted for one hour near mid-day (11:30 - 12:30 hours).

2. Laboratory Procedures

2.1. Chemical Analysis

Methods for chemical analyses, unless stated, are the same as those given in APHA et al. (1981). All further analyses, with the exception of alkalinity, were carried on water samples passed through Whatman GF/C glass fibre filters.

Alkalinity due to carbonate and bicarbonate was determined by titration with 0.1NHCl to pH 4.5 with mixed indicator.

Nitrate-nitrogen was estimated as nitrite after reduction in a cadmium - copper column. Nitrate-nitrogen was determined spectrophotometrically by diazotization of sulfanilamide and coupling with N-(1-naphthyl) - ethylenediamine di-HCl. Ammonia/ammonium nitrogen was estimated as blue indophenol using visible spectrophotometer as in Mackereth et al. (1978).

Orthophosphate (without extraction) and molybdate reactive silica (without digestion) were colorimetrically estimated as their respective molybdate complexes. Sulphate was determined by precipitation as barium salt and spectrophotometric estimation of turbidity.

Chloride was estimated by titration with silver nitrate using chromate indicator. Calcium and magnesium were quantified by atomic absorption spectrophotometry while potassium and sodium were measured by a flame photometer.

2.2. Biomass Estimation

Estimation of phytoplankton biomass was made using chlorophyll a as an index. Algae were concentrated on glass fibre filters (Whatman GF/C, 4.7 cm diameter) by filtering aliquots of 20ml lake water. Pigment was extracted in warm 90% methanol, centrifuged and absorbancy was read with a visible spectrophotometer (Pye Unicam SP-350, Path length 1cm), at 665 and 750nm. Correction for possible turbidity was made by subtracting readings at 750nm from the corresponding readings at 665nm.

Chlorophyll a was estimated from the corrected absorbance at 665nm, using the abbreviated formula of Talling and Driver (1963). No correction was made for degradation products.

2.3. Gross Photosynthesis estimation

Concentrations of dissolved oxygen in the light and dark bottles incubated in-situ were estimated by potentiometric titration (Talling, 1973) using N/400 thiosulphate to titrate 100ml aliquots of the iodine solution. Duplicate samples were always titrated from each of the paired bottles at each depth. The results were used to calculate the increase in oxygen concentration in the light bottles over the concentration in the dark bottles, i.e., gross photosynthesis.

3. Explanations of Symbols

Symbols used for biological and related parameters are as described in Ganf and Horne (1975), Melack (1979c), Roberts (1986) and Talling et al. (1973). These are listed and defined below:

B = biomass as mg chlorophyll a m⁻³

ΣB = biomass per unit area, within the euphotic zone, in mg chlorophyll a m^{-2}

ρ = gross photosynthetic rate per unit water volume, in $mg\ O_2\ m^{-3}h^{-1}$

ΣA = hourly rate of gross photosynthesis per unit area, in $mgO_2\ m^{-2}h^{-1}$

$\Sigma\Sigma A$ = daily rate of gross photosynthesis per unit area, in $gO_2\ m^{-2}d^{-1}$

A_{max} = light saturated photosynthetic rate per unit water volume, in $mg\ O_2\ m^{-3}h^{-1}$

$\phi (A/B)$ = Specific rate of gross photosynthesis per unit biomass, in $mg\ O_2/mg\ Chl-a\ h^{-1}$

ϕ_{max} = value of ϕ , at light saturation, in $mg\ O_2/mg.Chl-a.h^{-1}$ (measure of photosynthetic capacity).

Ph.A.R. = Photosynthetically available irradiance (400-700nm), in $\mu\ Em^{-2}s^{-1}$

I_0 = irradiance on the water surface, in $Em^{-2}h^{-1}$ or $Em^{-2}d^{-1}$

I_k = irradiance indicating onset of light-saturation of photosynthesis, in $\mu\ Em^{-2}s^{-1}$

I_0 at Z_{Amax} = irradiance at the depth of maximum photosynthesis, in $Em^{-2}s^{-1}$

ϵ = vertical extinction coefficient, in \ln units m^{-1}

ϵ_{min} = the vertical extinction coefficient of the most penetrating light.

ϵ_{total} = the vertical extinction coefficient determined from 30% blue + 35% green + 35% red (Wood et al., 1978).

SD_{det} = Secchi depth, in m, determined from Secchi disk reading.

SD_{cal} = Secchi depth calculated from the relation

$$SD = 1.7 / \epsilon_{total} \text{ (Poole \& Atkins, 1929)}$$

Z_{eu} = depth of the euphotic zone, in m.

$Z_{eu_{det}}$ = euphotic depth determined as depth of 1% surface irradiance, in m.

$Z_{eu_{cal}}$ = euphotic depth, in m, calculated from the relation

$$Z_{eu} = 3.7 / \epsilon_{min} \text{ (Talling, 1965).}$$

Z_{mix} = mixed depth, in m, determined from the temperature depth profile of the lake under study.

Q = efficiency of light utilization by phytoplanktonic photosynthesis, $\text{mmoles } O_2 \text{ per Einstein of Ph.A.R.}$

RESULTS

1. Temperature/Oxygen Depth Profiles

The seasonal variations in the vertical distribution of temperature and oxygen are shown by a family of depth profiles in Fig. 2. Meteorological data including air temperature & wind speed are also indicated in Table 2.

The immediate sub-surface temperature of Lake Ziway varied from 18.5^oc to 27.5^oc, a 9^oc range, and the bottom temperature varied from 17.5^oc to 24.0^oc, a 6.5^oc range. The maximum surface temperature (27.5^oc) occurred in May, 1987 and the minimum (18.5^oc) occurred in December, 1987. The majority of thermal data were taken during the morning. Afternoon temperature measurements could thus give higher maximum temperatures and wider daily ranges.

The average surface and bottom water temperatures of Lake Ziway were 23.1^oc and 21.2^oc respectively. The difference between surface and bottom water temperature averaged 2^oc with a maximum difference of 7.6^oc and a minimum of 0^oc (isothermal).

As can be seen in Fig. 2, isothermal or near isothermal conditions occurred frequently during the study period. However, during calm periods of intense solar heating a sharp thermal gradient occurred in the superficial layer of the lake (Table 2). Under such conditions a temperature difference greater than 5^oc was recorded within the top 50cm of the water column as in November, 1987 and February, 1988. (Fig.2).

Figure 2 also reveals that the water column of Lake Ziway was well oxygenated at all times during the study. All depth profiles indicate oxygen maxima in the upper 50 cm of the water column. The maximum

difference in oxygen content between surface and bottom water, was 6.6 mg l⁻¹ and the average difference was 2.5 mg l⁻¹. Percentage saturations of dissolved oxygen close to the bottom of the lake ranged from 37-166% (Ca. 2.7 - 12.2 mg O₂ l⁻¹). Saturations at the surface, in the same period, were between 91- 179% (Ca.6.4-12.8 mg O₂ l⁻¹)

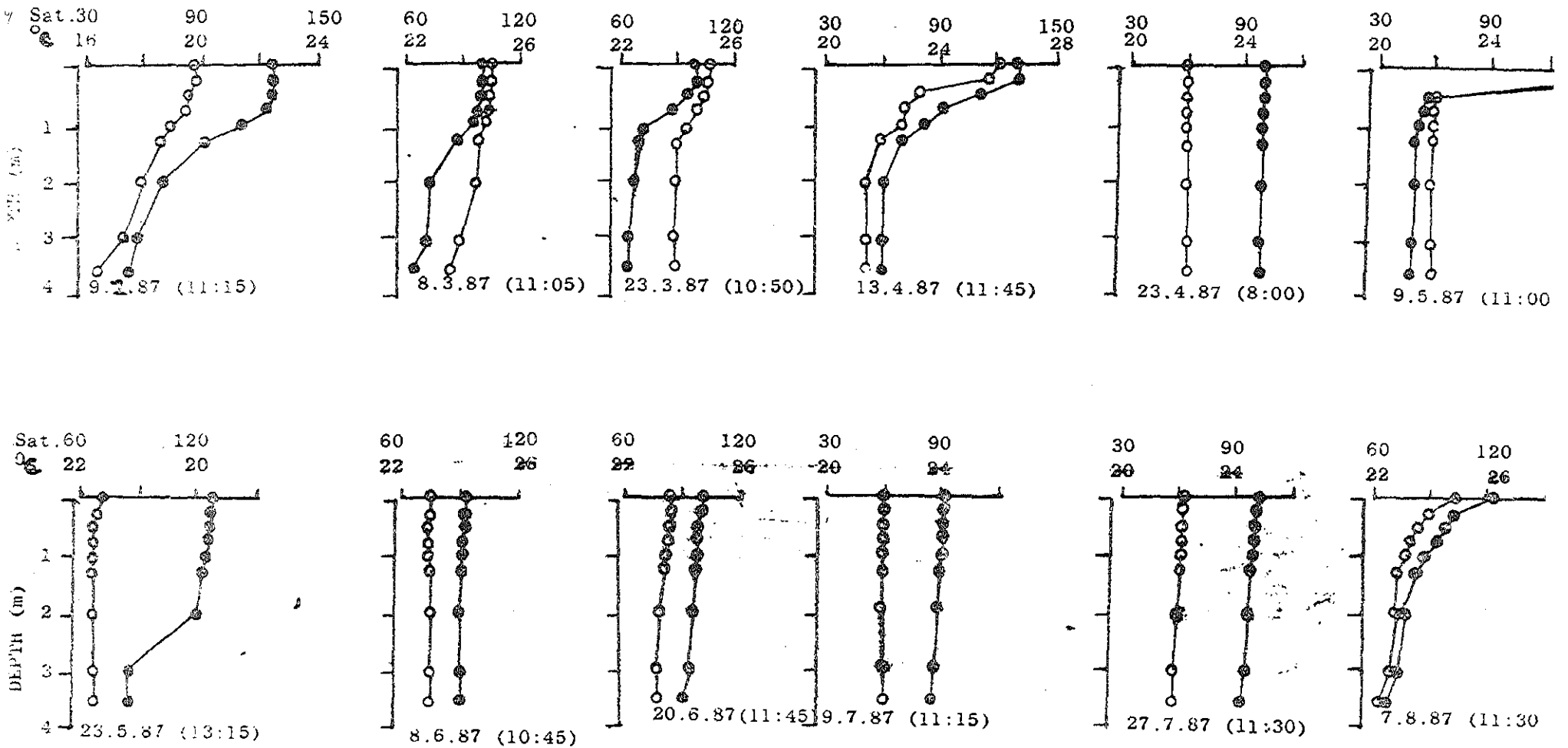


Fig. 1. Depth profiles of temperature (○—○) and percentage oxygen saturation (●—●) in Lake Uwa on the date and time indicated.

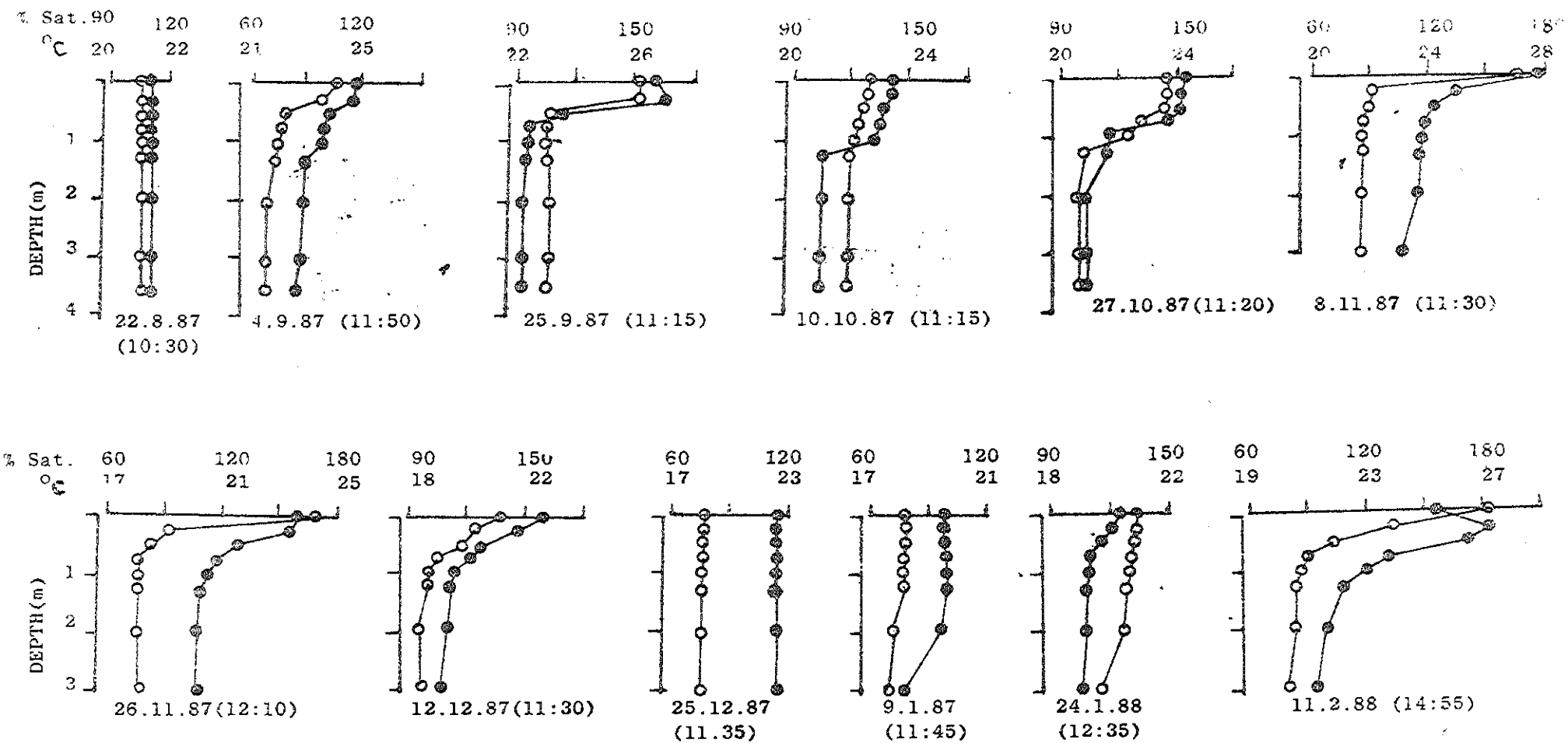


Fig. 2. Continued

Table 2: Meteorological Information of Lake Ziway region and the thermal regime of the lake on the date of sampling.

Sampling dates	Irradiance E_m-2d^{-1}	Air temperature at 0.5m, °C			Wind Speed, ms^{-1}				Near mid-day thermal structure of the Lake
		max	min	max-min	0600 0900hrs	0900 1200hrs	1200 1500hrs	1500 1800hrs	
9.2.87	43.2	31.3(29.4)*	7.1(12.2)*	24.2(17.2)*	0.56	1.36	2.19	2.11	W
8.3.87	42.3	28.8(28.4)	15.1(15.6)	13.7(12.8)	0.56	1.70	2.99	2.90	W
13.4.87	39.7	28.5(29.6)	15.8(14.1)	12.7(15.5)	2.02	2.64	2.79	4.76	S
9.5.87	42.2	27.0(28.1)	16.2(15.2)	10.8(12.9)	1.66	1.43	2.53	2.89	S
8.6.87	47.6	26.8(28.0)	16.0(14.4)	10.8(13.6)	2.21	5.34	3.72	3.11	I
9.7.87	46.9	28.0(27.2)	15.4(14.2)	12.6(13.0)	3.25	4.69	2.77	2.24	I
7.8.87	45.2	30.4(27.8)	13.7(14.4)	16.7(13.4)	1.56	3.97	4.74	2.78	W
4.9.87	46.1	28.5(29.6)	14.5(13.7)	14.0(15.9)	1.11	2.52	1.74	1.27	W
10.10.87	30.1	26.2(29.6)	16.0(13.3)	10.2(16.3)	1.47	1.70	1.23	2.72	W
8.11.87	39.7	-	9.0(10.5)	-	1.06	3.09	4.63	3.69	S
12.12.87	44.3	28.6(28.5)	8.2(10.8)	20.4(17.7)	1.29	2.30	2.08	2.27	W
9.1.88	17.3	27.2(27.8)	12.2(12.2)	15.0(16.6)	1.32	2.94	3.04	2.28	I
11.2.88	41.8	29.5(29.2)	13.3(14.3)	16.2(15.9)	1.93	2.49	2.45	1.94	S

△ Data of National Meteorological Services Agency, Ethiopia, (1988).

* = average monthly temperature

I = Isothermal, S = Sharp thermal gradient, W = weak thermal gradient

23

2. Lake Water Chemistry

The seasonal fluctuation in the chemical composition of the surface water of Lake Ziway during the study period is summarized in Table 3.

The pH of the surface water of Lake Ziway varied between 8.15 and 8.75. The maximum conductivity (K_{25}) of the lake ($400 \mu\text{S cm}^{-1}$) occurred in January, 1988 while the minimum value ($347 \mu\text{S cm}^{-1}$) was recorded in May 1987.

The sum total of major cations in Lake Ziway varied between 3.46 meq l^{-1} and 5.22 meq l^{-1} while the sum total of the major anions ranged between 3.94 and 4.99 meq l^{-1} . The anionic proportion of the lake followed the order $\text{HCO}_3^- + \text{CO}_3^{2-} \gg \text{Cl} > \text{SO}_4$ and the cationic proportion followed the order $\text{Na} \gg \text{Ca} > \text{Mg} > \text{K}$.

Among the major algal nutrients molybdate reactive silicate varied from 18.6 to 49.7 mg l^{-1} and soluble phosphate ($\text{PO}_4\text{-P}$) ranged from 5.5 to 16.2 $\mu\text{g l}^{-1}$. Concentrations of $\text{NO}_3\text{-N}$ in Lake Ziway were usually higher than those of $\text{PO}_4\text{-P}$. They ranged from 28 to 136.6 $\mu\text{g l}^{-1}$. Maximum values occurred during the rainy period while minimum values coincided with dry period.

$\text{NO}_2\text{-N}$, ranging from 0.4 to 10.1 $\mu\text{g l}^{-1}$, contributed less to the total inorganic nitrogen ($\text{TIN} = \text{NO}_3\text{-N} + \text{NO}_2\text{-N} + \text{NH}_3/\text{NH}_4^+\text{-N}$) of the lake than the other form. An unusually high fraction of $\text{NH}_3/\text{NH}_4^+\text{-N}$, 1-46 $\mu\text{g l}^{-1}$ out of 40 - 209.7 $\mu\text{g l}^{-1}$ of TIN, was recorded in Lake Ziway in this study.

Table 3: The chemical composition of the surface water of Lake Ziway during the sampling Period

SAMPLING DATES	CONDUCTIVITY (K ₂₅) μScm ⁻¹	IONIC CONCENTRATION (meq.l ⁻¹)										INORGANIC NITROGEN μg l ⁻¹				PH	Na+K Ca+mg	
		ΣCat.	Σan	Na ⁺	K ⁺	Ca ²⁺	Mg ²⁺	HCO ₃ ⁻ + CO ₃ ⁼	Cl ⁻	SO ₄ ⁼	SiO ₂ mg l ⁻¹	PO ₄ -P μg l ⁻¹	NH ₃	NO ₂ -N	NO ₃ -N			TIN
9.2.87	356	4.28	4.26	2.17	0.32	0.90	0.89	3.8	0.39	0.07	20.5	12.5	46.1	8.3	136.6	191.1	8.15	2.0
8.3.87	360	4.41	4.28	2.35	0.45	0.88	0.73	3.8	0.41	0.07	18.6	16.2	40.2	10.1	122.3	172.6	8.45	2.1
30.3.87	365	4.88	4.18	2.78	0.33	0.96	0.81	3.7	0.41	0.07	22.1	6.1	39.9	3.8	166.0	209.7	8.60	1.8
13.4.87	348	3.95	4.39	2.17	0.33	0.80	0.65	4.0	0.41	0.08	22.3	8.0	53.0	3.6	128.8	185.4	8.50	1.7
9.5.87	347	5.22	4.99	3.13	0.40	0.89	0.80	3.9	0.39	0.07	25.3	8.9	34.6	2.0	132.1	168.7	8.45	2.1
23.5.87	395	4.84	4.33	2.96	0.38	0.83	0.67	3.8	0.39	0.14	24.8	8.0	25.8	2.6	135.6	164.0	8.55	2.2
8.6.87	374	4.32	4.24	2.52	0.33	0.80	0.67	3.7	0.42	0.12	27.4	11.6	4.5	5.1	136.5	146.1	8.50	1.9
9.7.87	360	4.47	4.15	2.61	0.36	0.83	0.67	3.7	0.42	0.03	21.5	8.0	4.5	5.0	43.9	53.4	8.50	2.0
7.8.87	390	4.40	4.30	2.52	0.36	0.85	0.67	3.8	0.42	0.08	20.0	8.4	6.8	3.4	50.1	60.3	8.35	1.9
4.9.87	377	4.46	4.20	2.61	0.33	0.85	0.67	3.7	0.42	0.08	22.8	6.4	10.0	2.0	28.0	40.0	8.45	1.9
25.9.87	360	4.23	4.11	2.52	0.34	0.80	0.57	3.6	0.42	0.09	26.6	10.7	2.0	1.8	47.2	51.0	8.55	2.1
10.10.87	385	4.33	3.94	2.52	0.36	0.78	0.67	3.5	0.42	0.02	26.8	8.8	1.0	0.4	44.1	45.5	8.60	2.0
27.10.87	377	3.46	4.05	2.12	0.33	0.55	0.46	3.6	0.42	0.03	24.8	9.7	2.0	0.8	48.2	51.0	8.55	2.4
8.11.87	388	4.32	4.36	2.61	0.36	0.68	0.67	3.9	0.43	0.03	28.6	13.5	10.0	1.6	33.8	45.4	8.50	2.2
26.11.87	357	4.17	4.18	2.57	0.31	0.83	0.46	3.7	0.43	0.05	30.7	8.8	34.6	1.0	47.4	82.9	8.60	2.2
12.12.87	378	4.63	4.53	2.78	0.38	0.80	0.67	4.0	0.45	0.08	49.7	10.7	34.6	1.6	47.3	83.5	8.55	2.1
9.1.88	396	4.67	4.61	2.96	0.38	0.85	0.50	4.1	0.46	0.05	38.3	9.7	15.0	2.5	33.0	50.5	8.70	2.5
11.2.88	400	4.96	4.90	3.04	0.83	0.71	0.71	4.4	0.45	0.05	36.6	5.5	20.3	1.3	33.9	54.2	8.75	2.2

3. The Under Water Light Climate

The over-all seasonal variation in the under water light climate in Lake Ziway during the study period is given in Table 4.

The extinction values for the different spectral regions in \ln units m^{-1} varied as follows: Blue (ϵ_{460}) from 7.5 - 15.3, Green (ϵ_{540}) from 3.9 - 11.2, Red (ϵ_{630}) from 3.7 - 9.3 and total radiation ($\epsilon_{400-700}$) from 4.6 - 10.4.

The mean annual vertical extinction coefficients at the mid-points of the filters used, at the time of primary productivity measurements, are shown in Fig. 3. These mean extinction values, in \ln units m^{-1} , showed that the highest value (12.2) was for blue, the lowest (5.7) was for red, and the intermediate value (7.5) was for green.

The minimum extinction coefficient, i.e. the extinction coefficient of the light that penetrates furthest, showed some seasonal variation and the highest values occurred from February, 1987 to October, 1987 while the lowest values were recorded from November, 1987 to March 1988 (Table 4).

The percentage of light extinction by algal biomass was calculated using an extinction value, E_S , which has been determined to be between 0.01 - 0.02 \ln units per mg Chl a. m^{-2} for a wide range of natural population (Talling, 1965). Here it has been estimated from a fractional value of 0.015 and the calculated values varied between 32 and 78% ($\bar{X} = 52.7$).

The transparency of Lake Ziway, as measured by Secchi disk, had values between 13 and 27cm ($\bar{X} = 19$ cm). Two distinct phases of lake water transparency were evident during the study period. Secchi disk

readings were generally 16cm or less from February, 1987 to September, 1987. They increased abruptly to 21cm and more from September 1987 to March, 1988 (Table 4). The Secchi depth calculated using the Poole-Atkins equation ($SD_{cal} = 1.7/\epsilon_{total}$) was always greater than the measured one.

The euphotic depth in Lake Ziway was approximated from the relationship: $z_{eu} = 3.7/\epsilon_{min}$ (Talling, 1965; Talling *et al.*, 1973). As indicated in Table 4 the calculated z_{eu} varied seasonally with a minimum value of 0.40m on July 9, 1987 and with a maximum value of 1.10m on February 11, 1988 ($\bar{X} = 0.72m$).

The euphotic depth of Lake Ziway was also determined from total light extinction as described in the methods. This varied between 0.38m and 0.98m ($\bar{X} = 0.68$). The calculated euphotic depth was always greater than the measured euphotic depth.

During the study period the optical depth, the ratio of the freely mixed depth (Z_{mix}), determined from the temperature depth profile, to the euphotic depth ($Z_{eu_{cal}}$), in Lake Ziway varied between 2.3 and 8.8 ($\bar{X} = 4.6$).

Table 4 The underwater light climate of Lake Ziway during the sampling period

Sampling Date	Extinction Coefficient in m^{-1}				Zeu (m)		SD(m)		Optical Depth	% light extinction due to algae
	K_{460}	K_{540}	K_{630}	K_{total}	Det	Cal	Det	Cal		
9.2.87	12.0	9.2	5.8	7.4	0.60	0.64	0.16	0.23	3.9	51
8.3.87	11.8	10.3	7.3	9.6	0.48	0.51	0.13	0.18	6.9	39
13.4.87	13.5	10.9	7.5	9.6	0.47	0.49	0.14	0.18	5.7	41
9.5.87	10.3	8.1	7.4	9.5	0.47	0.50	0.17	0.18	6.0	42
8.6.87	12.2	9.2	8.3	10.4	0.43	0.45	0.16	0.16	7.8	38
20.6.87	14.9	9.3	7.0	8.9	0.50	0.53	0.16	0.19	6.6	42
9.7.87	15.3	11.2	9.3	9.5	0.38	0.40	0.15	0.18	8.8	34
7.8.87	14.8	10.2	5.8	9.1	0.60	0.64	0.16	0.19	4.7	49
4.9.87	14.9	10.4	8.4	9.7	0.41	0.44	0.16	0.18	6.8	32
25.9.87	12.9	7.1	4.6	6.0	0.77	0.88	0.23	0.28	3.7	60
10.10.87	7.5	4.9	3.9	4.6	0.94	0.99	0.24	0.37	2.3	68
27.10.87	11.4	6.9	4.2	7.4	0.74	0.88	0.21	0.23	2.6	61
26.11.87	9.9	4.8	4.1	4.9	0.89	0.90	0.24	0.38	3.1	55
12.12.87	11.6	4.1	3.9	5.3	0.88	0.95	0.24	0.32	2.4	63
9.1.88	10.4	4.9	3.8	5.3	0.91	0.97	0.23	0.32	3.1	67
24.1.88	11.9	4.7	3.7	7.3	0.94	1.00	0.22	0.23	3.0	65
11.2.88	11.9	3.9	3.7	4.8	0.98	1.06	0.27	0.35	2.4	79
26.2.88	11.6	5.1	4.9	6.1	0.75	0.76	0.21	0.28	3.3	65

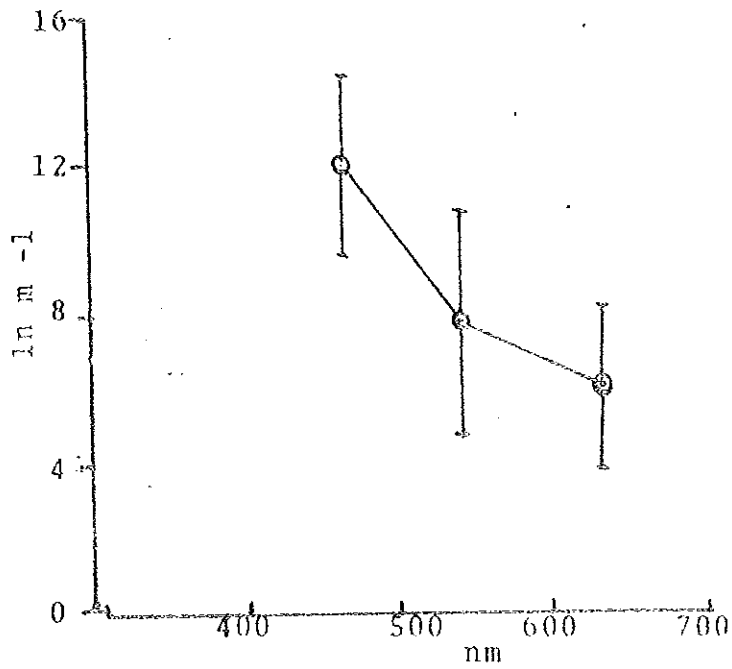


Fig. 5. The mean annual extinction coefficients in Lake Ziway for red, blue and green light (Vertical bars represent standard deviations)

4. Algal Biomass & Primary Production

The algal biomass of Lake Ziway as determined by chl a, as an index of biomass, over the study period ranged from 149.5 to 212.0 mg chl a m⁻³ (\bar{X} = 186.9), (Table 5). The maximum value was recorded in July, 1987 and February, 1988 while the minimum value occurred in November, 1988. The algal biomass in the euphotic zone of the lake varied from 81 to 191.6 mg Chl a m⁻² (\bar{X} = 127.8).

The depth profiles of photosynthetic activity recorded for Lake Ziway (Fig. 4) reveal depressed rate of photosynthesis at the surface throughout the study period. The figure also reveals temporal and spatial variations in both the maximum rates (A_{max}) attained and the depth range occupied within the euphotic zone.

The maximum rates of phytoplanktonic photosynthesis in Lake Ziway ranged from 1.64 to 4.07 g O₂ m⁻³ h⁻¹ (Table 5). The maximum volumetric rates of photosynthesis occurred at a depth of 5cm from February, 1987 to August, 1987 and was displaced to 10cm from September, 1987 to March, 1988 (Fig. 4). The euphotic zone of the lake was shallow usually less than 80 cm.

Maximal values of the photosynthetic capacity, P_{max} , in Lake Ziway varied between 11.0 and 22.5 mgO₂ (mg Chl a)⁻¹. h⁻¹. The photosynthetically available irradiance of the maximal photosynthetic rates, I_0 at $Z_{A_{max}}$, usually ranged from 450 - 950 μ E m⁻² s⁻¹ (\bar{X} = 620) apart from exceptionally two low values in overcast sky and one high value at full sunlight. Surface irradiance integrated over the incubation period ranged from 2.7 to 7.7 Em⁻²h⁻¹ (Table 5).

Photosynthetic rates on a per unit area basis, determine by

planimetry of the depth profiles, ranged from 288 to 1625 mg O₂ m⁻²h⁻¹.

The daily rates of photosynthesis of Lake Ziway were also determined from the hourly rates multiplied by a factor of 0.9 used by Talling (1965) for the other East African lakes. These products were then multiplied by the number of hours of sunlight during the days of the experiments. The calculated values ranged from 3.1 to 17.6g O₂ m⁻²d⁻¹. Maximum productivity per unit area coincided with periods of increased rainfall, high nutrient input (particularly NO₃-N) & high algal biomass (Fig. 5A-C).

The onset of light saturation of photosynthesis, I_k, was extrapolated from the initial linear region of a curve which relates photosynthetic rate and light intensity. Except for two high and two low values, the calculated values of I_k in Lake Ziway lie between 170- 370 μEm⁻² s⁻¹ (\bar{X} = 269.4) (Table 5).

It has been shown (Talling, 1965) that if photosynthesizing algal populations are evenly distributed and not markedly differentiated with depth, the ratio A_{max}/A_{min} is a principal determinant of the integral photosynthetic productivity per unit area (ΣA). The general correspondence between the seasonal variation in these two quantities is illustrated in Fig. 6A-C.

The efficiency of utilization of photosynthetically available irradiance (Ph.A.R.) by photosynthesis, Q, was calculated on molar basis, i.e. moles of oxygen evolved per moles of photons of Ph.A.R. incident on the lake surface (Melack, 1979C). The calculated values ranged from 2.4 - 9.6 mmol O₂ E⁻¹ (\bar{X} = 4.7). Lower efficiencies tended to occur during incubation with greater irradiance (See Table 5).

Table 5 Algal Biomass, Photosynthetic rates of phytoplankton and irradiance in Lake Ziway

Sampling Date	B mgChlam ³	ΣB mgchl _a m ⁻²	A _{max} mgO ₂ m ⁻³ h ⁻¹	φ _{max} mgO ₂ (mgchl _a) ⁻¹ h ⁻¹	Σ A mgO ₂ m ⁻² h ⁻¹	ΣΣA gO ₂ m ⁻² d ⁻¹	I ₀ Em ⁻² h ⁻¹	I _K μEm ⁻² S ⁻¹	I ₀ at I _A μEm ⁻² S ⁻¹	Q mmolO ₂ E ⁻¹
9.2.87	197.4	125.9	2290	11.6	425	4.6	4.7	280	690	2.8
8.3.87	191.7	97.2	2380	12.4	288	3.1	3.8	330	570	2.4
13.4.87	205.9	101.5	3630	17.6	753	8.1	7.3	470	900	3.2
9.5.87	206.6	103.2	4670	22.5	1625	17.6	5.3	90	650	9.6
8.6.87	208.5	110.3	3750	18.0	1005	10.9	6.9	150	900	4.6
9.7.87	212.0	84.4	4030	19.0	913	9.9	6.7	270	990	4.3
7.8.87	187.7	119.8	3780	20.7	735	7.9	7.1	450	1000	3.2
4.9.87	184.2	81.1	3010	16.8	800	8.6	6.5	360	700	3.8
25.9.87	184.2	148.1	3040	16.5	1025	10.6	6.6	180	600	4.9
10.10.87	177.2	166.6	2190	12.4	570	5.8	2.7	80	110	6.6
27.10.87	170.2	125.9	2140	12.6	555	5.7	4.5	150	200	3.9
26.11.87	149.5	133.1	1640	11.0	525	5.4	5.9	290	700	2.9
12.12.87	163.3	143.7	2110	12.9	656	7.4	6.6	310	500	3.1
9.1.88	170.3	154.9	3210	18.9	1036	10.4	3.8	330	600	8.7
24.1.88	159.5	150.3	2980	18.6	900	8.9	5.8	270	600	4.8
11.02.88	194.6	151.2	2210	14.5	651	6.9	2.7	270	360	7.5
26.02.88	212.0	159.0	2750	13.0	938	10.1	7.7	270	360	3.8

22

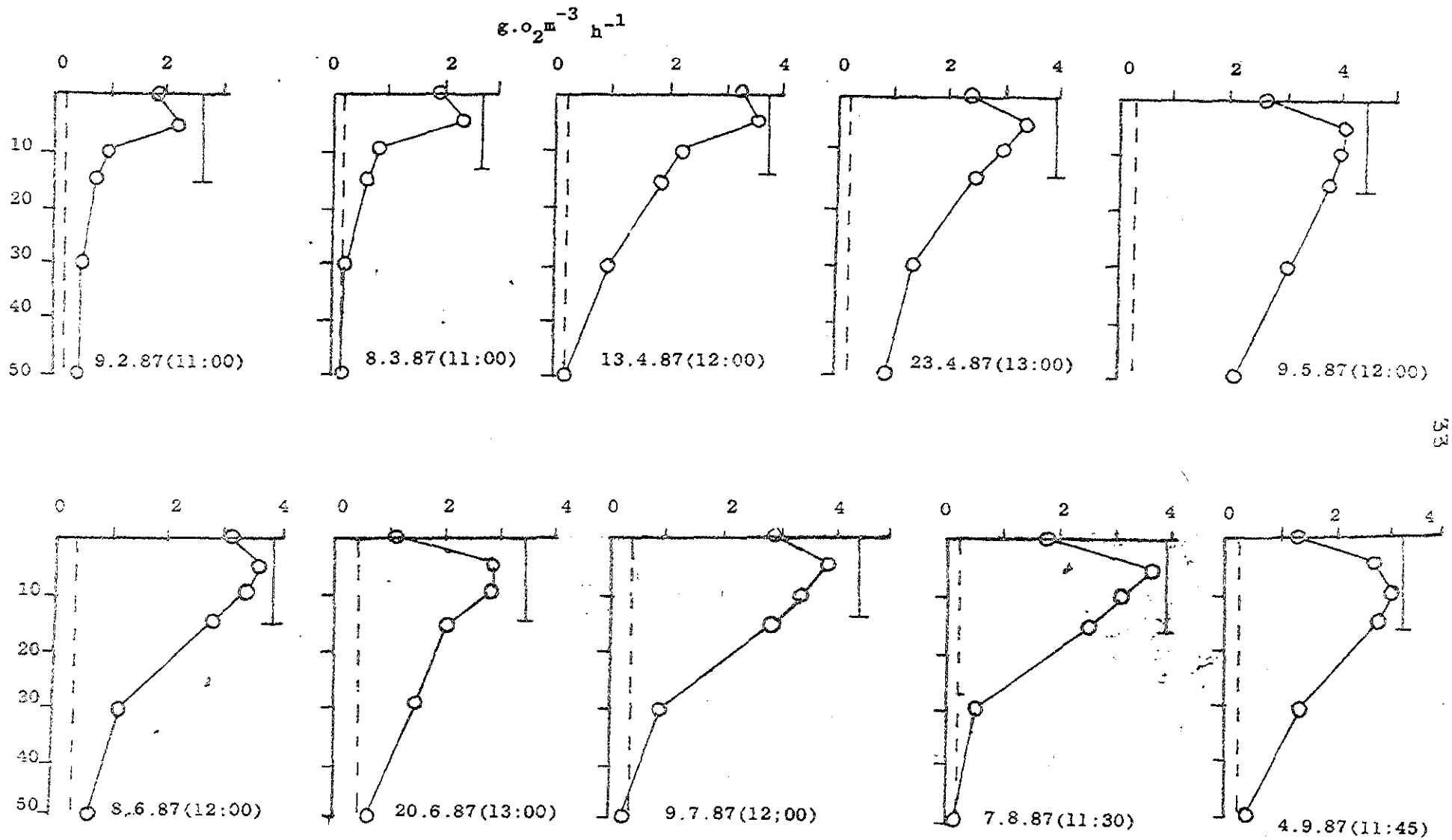


Fig. 4. Depth profiles of gross photosynthesis, Secchi depth (↓) and respiration(----) in Lake Ziway on the sampling date and time (incubation mid hour) indicated.

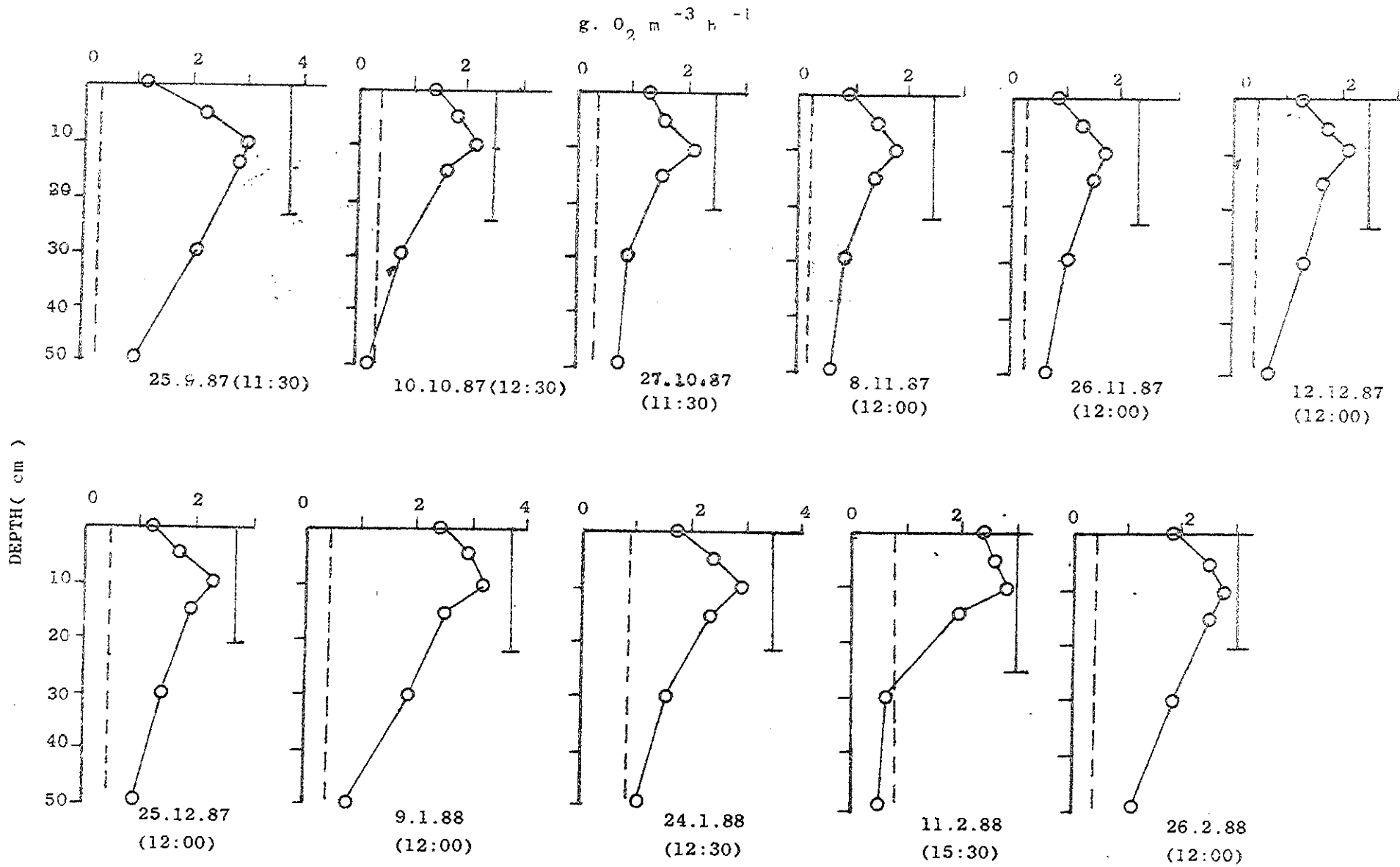


Fig. 4. Continued

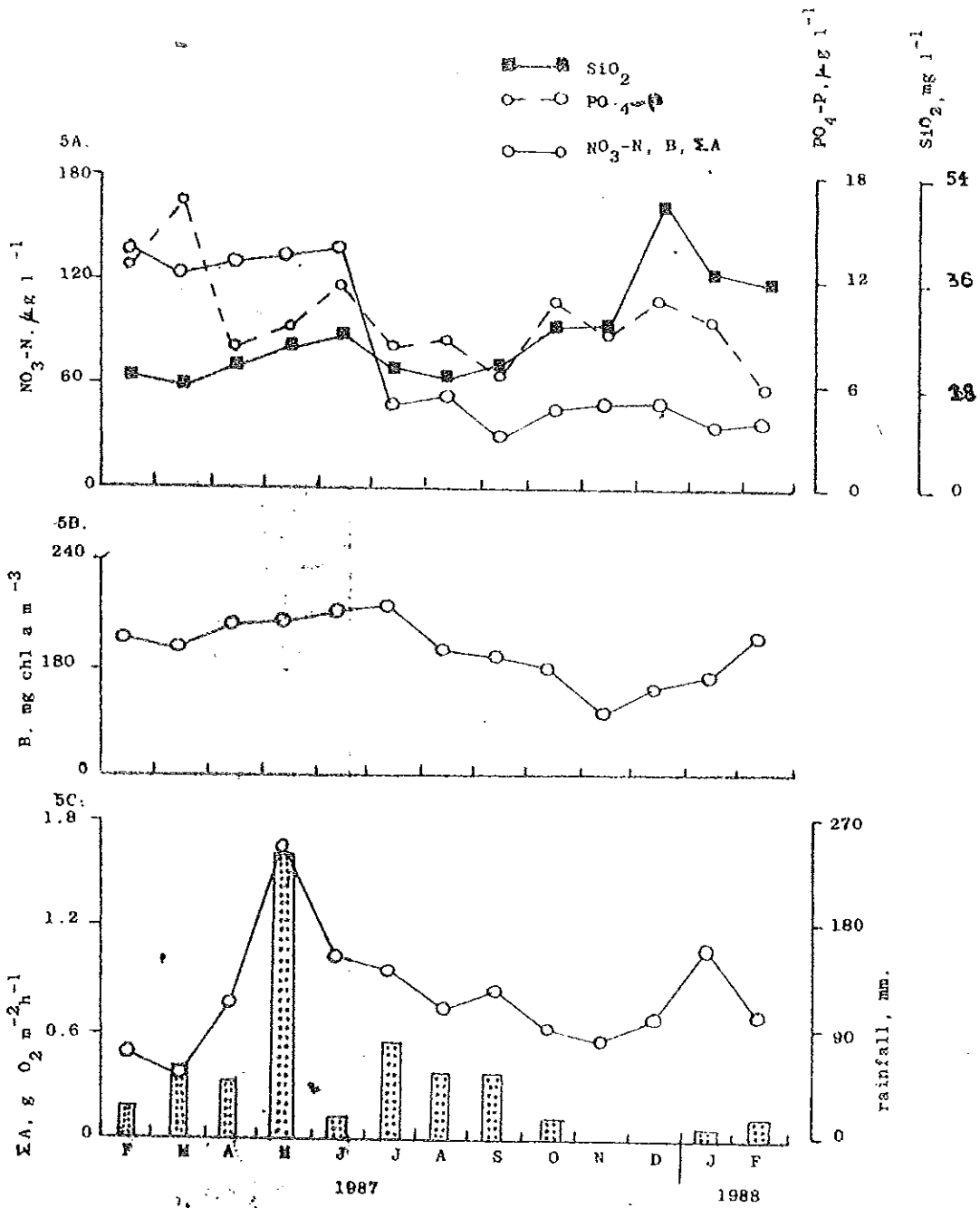


Fig. 5A-C Seasonal variation of major algal nutrients (A) algal biomass (B) and photosynthesis (C) in Lake Ziway (Vertical bars represent monthly rainfall in the region, data of Ethiopian National Meteorological Service Agency, 1988)

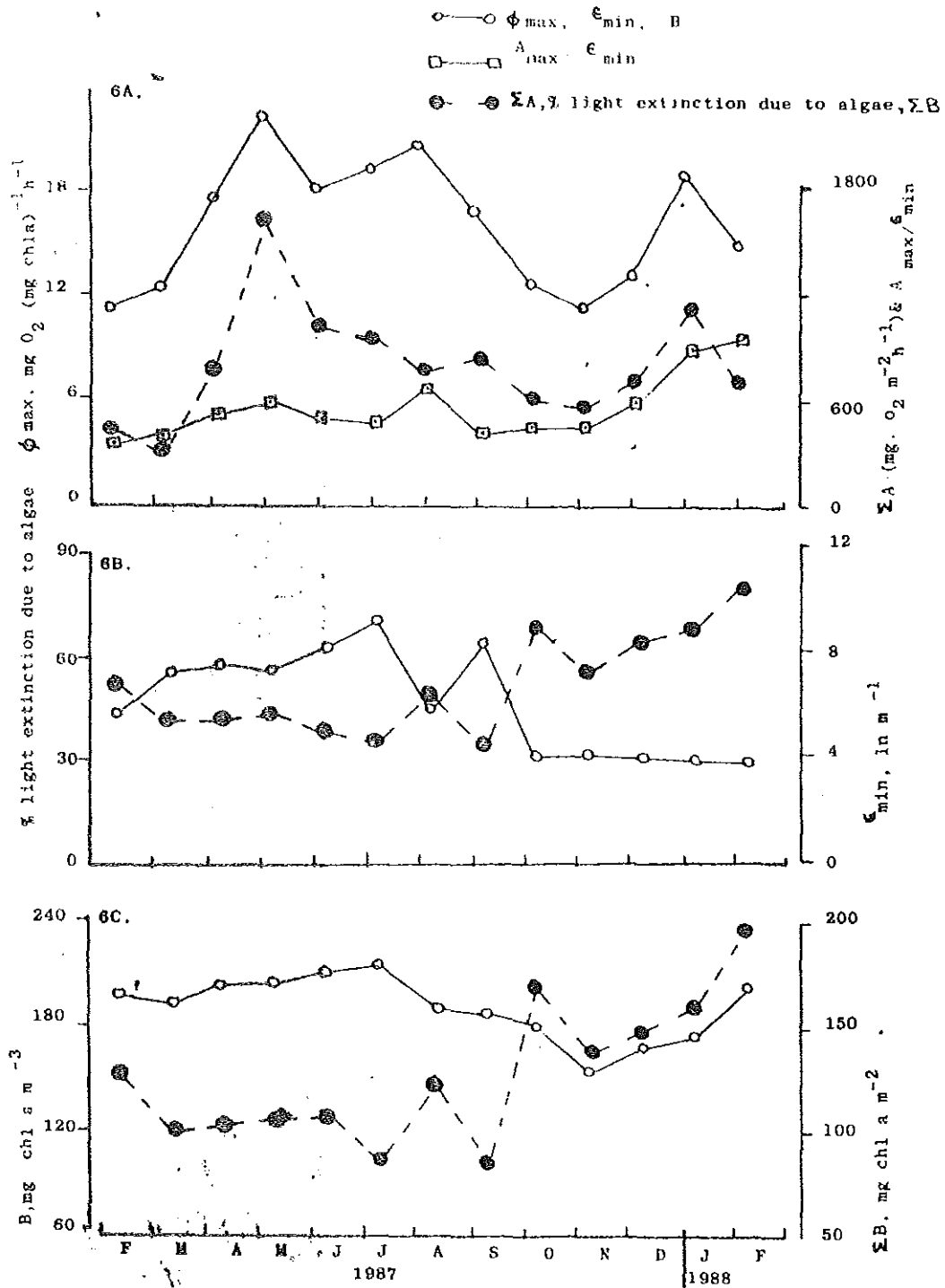


Fig. 6A - C. Seasonal pattern in photosynthetic production and ratio of A_{max}/ϵ_{min} (A), underwater light climate (B) and algal biomass (C) in Lake Ziway.

DISCUSSION

The temperatures of the equatorial lakes of the world do not show pronounced seasonal variation, though diel changes very near the surface may be great (Beadle, 1981). Observations on the thermal characteristics of Lake Ziway are consistent with this generalization. The lake did not show marked variation in its surface water temperature ($cv = 9.8\%$) over the whole sampling period. The seasonal variation of the bottom temperature of the lake ($cv = 6.8$) was even lower than that of the surface. This is to be expected because daily heating and cooling are less pronounced in the deeper water than in the superficial layer.

Maximum and minimum air temperatures, with daily differences ranging from 10.2 to 24.2°C (Table 2), are good indicators for the marked diel changes in the surface temperature of Lake Ziway. Intense solar radiation ranging from 17.63 to 47.6 $E\ m^{-2}\ d^{-1}$ ($\bar{X} = 40.5$) ensured a daily maximum air temperature between 26.0 and 32.0°C (Table 2). Nocturnal cooling, on the other hand, would be expected to cause a significant drop in air temperature. These two conditions combined would also induce a wide daily range of surface water temperature.

The surface temperature of Lake Ziway (18.5 - 27.5°C) is very similar to that of the surface temperatures of other Ethiopian lakes. Demeke Kifle (1985) reported surface temperature of 20.5-28.4°C for Lake Awassa. Kassahun Wodajo (1982) gave surface temperatures of 18-27°C for both lakes Abijata and Langanjo. Wood et al. (1976) also reported surface temperatures of 18.8-22.5°C and 19.7 - 27°C for lakes Kilotes and Aranguadi, respectively. The exception to these is Garba Guratch, a high mountain

lake, with very low surface temperatures (11-11.5°C) (Baxter and Golobitsch, 1982; Loffler, 1978).

Comparison with the other shallow East African lakes reveals that the surface temperature of Lake Ziway is similar to that of Lake Nakuru, Kenya, 21-27°C, (Melack, 1976a) but much lower than that of Lake George, Uganda and Lake Turkana, Kenya, 26-36°C and 27.5 - 32.5°C respectively, (Ganf and Horne, 1975).

Frequent mixing is common in the shallow East African Lakes. Shallow and exposed lakes such as Lake George, Uganda (Ganf and Horne, 1975) and Kilotes, Ethiopia (Wood et al., 1976) are frequently mixed except in rare periods of calm weather. Similarly, vertical mixing associated with reduced insolation and high turbulence (Table 2) was observed in Lake Ziway.

Well oxygenated water from top to bottom in Lake Ziway (Fig. 2) provides evidence for frequent mixing. The temperatures of the water below the superficial layer, during morning measurements, were also good indicators for the development of isothermal condition of the lake during the previous night. The pronounced diurnal fluctuations in air temperature suggest that the lake probably mixes almost every night.

As can be seen in Table 2, the mornings at Lake Ziway are calm while the afternoons tend to be windy. This, coupled with the progressive increase in solar heating, would induce superficial stratification that could persist for few hours in the morning till it is broken by wind induced mixing in the afternoon.

In accordance with the revised classification of lakes by Lewis (1983) Lake Ziway may be categorized as a continuously warm polymictic type. Such a lake is characterized by daily mixing followed by stratification, at most

for a few hours at a time. This pattern occurs in response to variation in wind or daily heating and cooling.

Temporal fluctuation in the vertical distribution of temperature and dissolved oxygen were observed in Lake Ziway in association with local meteorological conditions. For instance, intense radiation at the surface ($> 39 \text{ Em}^{-2}\text{d}^{-1}$, Table 2) raised the temperature of the superficial layer and was responsible for the short-lived thermal gradient developed within a few centimeters of the surface as in May 9, 1987 and February 11, 1988 (Fig. 2). Under such conditions lower concentrations of dissolved oxygen, associated with low solubility of oxygen at higher temperatures, were observed in the immediate sub-surface water.

Windy conditions, (see Table 2) which culminated in mixing of the vertical column of the lake, resulted in an increase in bottom temperature and commonly led to high oxygen concentration value. Under well mixed conditions, concentrations of oxygen of the order of $6-8 \text{ mg O}_2 \text{ l}^{-1}$ were observed.

population and/or its under-estimation by the analytical method used in this study. Higher phosphate concentrations ($5-45 \mu\text{g l}^{-1}$) were recorded in Lake Awassa (Demeke Kifle, 1985; Elizabeth Kebede, 1987). Soluble $\text{PO}_4\text{-P}$ concentration as high as $290 \mu\text{g l}^{-1}$ has also been reported for the moderately saline lakes Abaya and Chamo (Amha Belay and Wood, 1982).

Concentrations of available $\text{NO}_3\text{-N}$ in Lake Ziway were usually higher than those of soluble $\text{PO}_4\text{-P}$. They ranged from 28 to $136.6 \mu\text{g l}^{-1}$. Maximum values of $\text{NO}_3\text{-N}$ ($> 120 \mu\text{g l}^{-1}$) coincided with the rainy period from February, 1987 to May, 1987 (Fig. 5A-C). This could be the result of higher nitrate input from the catchment area as well as from the extensive inundated draw down area of the littoral zone.

$\text{NO}_2\text{-N}$ was present in only minimal concentrations in Lake Ziway, especially in comparison with $\text{NO}_3\text{-N}$ and $\text{NH}_3/\text{NH}_4^+ \text{- N}$; nitrate was the dominant form of inorganic nitrogen. This is a typical feature of most African lakes (Talling and Talling, 1965; Thornton 1986).

An unusually high fraction ($1-46 \mu\text{g l}^{-1}$) of $\text{NH}_3/\text{NH}_4^+\text{-N}$ was recorded in Lake Ziway in this study. Although $\text{NH}_4^+\text{-N}$ was reported (Wood *et al.*, 1984) as the predominant form of inorganic nitrogen in three of the four Bishoftu crater lakes, Ethiopia, no ammonium was ever detected by these authors in the neighboring shallow and well-mixed Lake Kilotes. In view of this, the presence of large fraction of the reduced form of inorganic nitrogen in polymictic Lake Ziway indicates the importance of microbial process and excretion by zooplankton.

The concentrations of dissolved silicate ($18.6 - 49.7 \text{ mg l}^{-1}$) in Lake Ziway were higher than the other major algal nutrients ($\text{NO}_3\text{-N}$ and $\text{PO}_4\text{-P}$). However, these values are much lower than those reported for Lake Awassa ($50-97 \text{ mg l}^{-1}$, Demeke Kifle, 1985). This may result in part from the

uptake of silica by diatoms which make up a higher proportion of the phytoplankton of Lake Ziway (Tsegaye Miheret-Ab, pers.comm.).

Unusually high silica concentrations were reported (Wood and Talling, 1988) in the more saline and alkaline lakes of the most northerly part of Ethiopian Rift Valley. In these lakes, measured concentrations of silica exceeding 100mg l^{-1} were frequently encountered and values as high as 320mg l^{-1} were recorded for Lake Chitu. In contrast, very low concentrations of silica, as low as 2mg l^{-1} , were recorded for Lake Hayq (Baxter and Golobitsch, 1970).

In Lake Ziway, sodium clearly dominated the cations while bicarbonate and carbonate dominated the anions. This pattern of ionic dominance is characteristic of many African lakes (Talling and Talling, 1965; Wood and Talling, 1988). The orders of both the anionic proportion ($\text{HCO}_3^- + \text{CO}_3^{2-} \gg \text{Cl} > \text{SO}_4$) and the cationic proportion ($\text{Na} \gg \text{Ca} > \text{Mg} > \text{K}$) are basically similar to those in other Ethiopian lakes such as lakes Abaya and Chamo (Amha Belay and Wood, 1982), Lake Awasa (Demeke Kifle, 1985), lakes Abijata and Langano (Kassahun Wodajo, 1982) and Lake Tana (Talling & Talling, 1965).

Cationic proportions different from those of Lake Ziway have been reported for Lake Hayq (Baxter and Golobitsch, 1970), for the Bale mountain lakes (Baxter and Golobitsch, 1982; Loffler, 1978), and the Bishoftu crater lakes (Baxter *et al.*, 1965; Prosser *et al.*, 1968). These Ethiopian lakes are characterized by a marked predominance of magnesium or calcium over the remaining three cations.

According to the classification of lakes on the basis of conductivity (Talling & Talling, 1965), Lake Ziway falls in class I. The mean conductivity ($372\ \mu\text{S cm}^{-1}$) per unit ionic content in the lake gives

quotients of 86 & 84 $\mu\text{S cm}^{-1}$ per meq.l^{-1} of total mean anions and cations respectively. These values are very close to the mean value of 85 that Talling and Talling (1965) calculated for 67 African lakes.

The correlation between alkalinity and pH ($r = +0.151$) in Lake Ziway was poor. Although maximum pH values coincided with relatively high alkalinities (January and February, 1988), high alkalinity values also coincided with low pH (February and March, 1987). On the other hand, low alkalinity values overlapped with high pH values as in October, 1987 (Table 3). These may be attributable to the accumulation of dissolved carbondioxide from respiration and decomposition which tend to reduce the pH. It may also be due to the removal of carbondioxide by photosynthesizing algae which tends to raise the pH without significant change in alkalinity.

It is well known that a lake, under natural conditions, is characterized by a particular spectral pattern of light extinction which is attributed to differences in dissolved colours and suspended particles. The spectral pattern of Lake Ziway was similar on all the sampling dates. The highest penetration occurred in the red, and the lowest in the blue spectral region. A similar pattern has been reported for other Ethiopian lakes (Demeke Kifle, 1985; Elizabeth Kebede, 1987; Kassahun Wodajo, 1982; Talling *et al.*, 1973; Wood *et al.*, 1978). Such patterns of spectral light extinction have been found typical of lakes with dense standing crop of phytoplankton or in waters which are very turbid due to non-algal materials (Bowling *et al.*, 1986; Ganf, 1975; Melack and Kilham, 1974; Talling *et al.*, 1973).

In Lake Ziway extinction coefficients for the different spectral regions varied temporally. Maximum extinction coefficients occurred during periods

of high water inflow (February 1987 - March 1987) and/or episodes of mixing. For instance, extinction coefficients ranging from 8.3 to 15.3 \ln units m^{-1} have been recorded in June, August and September 1987 (Table 4). These high values coincided with episodes of complete mixing (Fig. 2). This is to be expected, as both water discharge and mixing lead to high light absorption or rapid attenuation of light by suspended materials, particularly at the blue end of the spectral region. Correspondingly, a pronounced decline in extinction coefficients of the different spectral regions occurred under calm conditions of particularly dry periods (October 1987 to February 1988, See Fig. 2 and Table 4). This, in turn, may be attributed to a decrease in the amount of suspended matter in the superficial layer, for the lake was thermally stable.

Although the minimum vertical extinction coefficients in Lake Ziway are high in comparison with most natural waters, such values are typical of lakes with dense algal crops or with suspended silts, and produce very shallow euphotic zone (Melack and Kilham, 1974; Talling *et al.*, 1973). Comparable ϵ_{\min} have been reported for Lake George, Uganda, (4.1 - 7.7 \ln units m^{-1} , Ganf and Horne, 1975) and for lakes Nakuru and Elmenteita, Kenya, (10 and 7 \ln units m^{-1} respectively, Melack and Kilham, 1974). Exceptionally high ϵ_{\min} values have been reported from the very productive Ethiopian soda lakes, Aranguade and Kilotes (13.7 - 24.7 and 7.6 - 15.4 \ln units m^{-1} respectively, Talling *et al.*, 1973). In all of these lakes the extinction coefficient of the least penetrating light (blue) reaches a value which is twice that of the most penetrating light component (red).

The high ϵ_{\min} values which persisted in Lake Ziway over most of the study period resulted in a very shallow euphotic depth, usually less than 0.80 m (Table 4). Such a shallow euphotic depth has also been reported for

Lake George, Uganda (0.48 - 0.91m, Ganf and Horne, 1975). Compared to Lake Ziway, lakes Aranguade and Kilotes, Ethiopia, have even lower euphotic depths. They range from 0.15 to 0.27m in Lake Aranguade and from 0.24m to 0.49m in Lake Kilote (Talling et al., 1973). In contrast, Lake Shalla, the most transparent of the Ethiopian Rift Valley lakes, has an euphotic depth ranging from 3.7 to 4.9m (Amha Belay and Wood, 1984; Wood et al., 1978).

The turbidity of Lake Ziway resulted from a combination of high algal density and high suspended silt. The shallowness of its euphotic depth, therefore, was attributed to both algal and non-algal attenuation of light (Table 4). Attenuation by non-algal materials overrode attenuation due to algae during periods of high water discharge from inflowing rivers (February, 1987 to September, 1988). Episodes of mixing would also increase attenuation of light by non-algal materials in this shallow lake ($\bar{Z} = 2.4m$) by introducing sediment resuspension. Conversely, light attenuation by algal materials dominated over that caused by non-algal material when the lake was calm and thermally stable (see Tables 2 and 4).

The mean percentage of light extinction due to algal biomass (= 52.7%) in Lake Ziway is lower than that which was recorded for Lake Awassa (= 57%, Demeke Kifle, 1985). The percentage algal light extinction value found in this study was much higher than was reported earlier for the lake (Wood et al., 1978). A recent measurement of chlorophyll *a* in the lake by Amha Belay and Wood (1984), however, suggests a higher percentage of light extinction due to algal biomass than was previously reported.

The determination of a quotient or a factor relating secchi depth, euphotic depth and extinction coefficient to one another is of practical value (Poole & Atkins, 1929; Talling, 1965). In the approximation of the euphotic depth from Secchi depth, the ratio of the mean euphotic depth

(0.68m) and the mean Secchi depth (0.19m) in Lake Ziway gave a quotient 3.58 which is higher than 3. Hence, taking 3.58 as a factor and multiplying with Secchi disk reading gives a better approximation of euphotic depth in Lake Ziway.

The approximation of a constant value by multiplying the mean κ_{\min} value (5.7 \ln units m^{-1}) by the mean euphotic depth (0.68m) in Lake Ziway gave a value 3.88 which is very close to 3.7 determined by Talling (1965) for a number of East African lakes. Similarly, the approximation of a constant by multiplying mean κ_{total} (7.2 \ln units m^{-1}) by the mean Secchi depth (0.19m) gave a value 1.37. Though this value is lower than 1.70 approximated by Poole & Atkins (1929), it is very close to 1.45 approximated by Walker (1980).

The optical depth, the ratio of the mixed depth to euphotic depth, is reported to be a limiting factor in primary production when it exceeds the critical value 4-5 (Talling et al., 1971; Wood et al., 1978). This ratio of the mixed depth determined from the temperature depth profiles, to the euphotic depth in Lake Ziway, gave a mean value of 4.6. This value falls in the boarder line of the critical value of 4-5 suggested by the above authors.

As can be seen in Table 4, phytoplankton production would be light limited in episodes of mixing and windy conditions which frequently occur in Lake Ziway leading to the oscillation of both the mixing depth and euphotic zone. For instance, complete mixing could extend the mixed depth to more than 3.5 m and at the same time diminishing the euphotic depth of the lake to less than 50cm as in June and July 1987. Under such conditions an optical depth greater than 7 would be encountered. Hence, the optical

depth of Lake Ziway is highly affected by hydrographic factors (water column structure - mixing and stratification).

Observations of phytoplankton biomass from 1947 until present indicate a progressive increase toward eutrophy in Lake Ziway. Cannicci and Almagia (1947) described the lake as having 'clear water' which indicated a low chlorophyll content. Wood et. al. (1978) recorded chlorophyll a values in the order of 7 mg m^{-3} . However, recent measurements of chlorophyll a by Amha Belay & Wood (1984) were much higher ($91 \text{ mg chl a m}^{-3}$). The mean annual chlorophyll a concentration (186.9 mg m^{-3}) from the series of measurements in the present study represents the highest value and suggests that the lake is in the process of eutrophication.

Extremely high phytoplankton density is characteristic of the very shallow East African lakes, such as Lake George, Lake Elmenteita, Lake Kilotes, and Lake Nakuru. Chlorophyll a concentrations, in mg m^{-3} , range from 125 - 345 in Lake George (Ganf & Horne, 1975), 273-367 in Lake Elmenteita (Kalff, 1983), 205-412 in Lake Kilotes (Talling et al., 1973) and 200-900 in Lake Nakuru (Melack, 1976). The chlorophyll a concentrations of Lake Ziway ($149.5 - 212 \text{ mg m}^{-3}$) are similar to those in Lake George, but they are lower than those reported for lakes Elmenteita, Kilotes and Nakuru.

The amount of chlorophyll a in the euphotic zone of Lake Ziway is also comparable with that of most African lakes listed by Melack (1979b, 1981). The temporal variation in algal biomass was more pronounced on a per unit area ($\text{cv} = 23.9\%$) than on a per unit volume ($\text{cv} = 10.1\%$) basis. This is mainly due to background light extinction which alters the quantity of algae present in the euphotic zone at any given population density. In line with this, low level background light extinction could permit high

euphotic zone content of chlorophyll to be achieved at relatively low population density. Similarly, a high level of background light extinction could inturn result in low chlorophyll a content at relatively high population density (Fig. 6A-C).

An increase in algal density in Lake Ziway was generally followed by increase in light extinction, expressed by the minimum vertical extinction coefficient, and decrease in the depth of euphotic zone. Algal biomass per unit area had a highly significant inverse relationship ($r = 0.92$, $P < 0.001$, $n = 18$) with euphotic depth. It also had a highly significant positive relationship ($r = 0.91$, $P < 0.001$, $n = 18$) with minimum extinction coefficient.

The algal biomass within the euphotic zone of Lake Ziway was nearly uniform due to frequent mixing over the study period. Thus, the vertical changes in algal photosynthesis were mainly due to the vertical changes in the intensity and spectral composition of light. The depth-profiles of photosynthetic activity per unit water volume in Lake Ziway were typical of the pattern for phytoplankton. They showed a depressed rate of photosynthesis at the surface, a maximum rate in the subsurface water and a regular decline in the lower portion of the euphotic zone throughout the study period (Fig. 4).

The possible depressed photosynthetic activity at the lake surface could include photoinhibition of the photosynthetic reactions and structures (Steeman Nielsen, 1962), increased photorespiration (Harris & Lott, 1973) and sinking of phytoplankton (Talling, 1965). The persistence of subsurface maxima during both superficial stratification and complete mixing in Lake Ziway suggests, however, that reduced photosynthesis, not phytoplankton sedimentation, was the major cause for depression near the

surface. It also suggests that the intensity of light at the surface, even on partly overcast days, exceeds the compensation abilities of the phytoplankton. The cause for consistent surface depression, however, could further be complicated by the interaction between the ability of plankton cells to adapt to a light level and the circulation of cells through a light gradient (Lewis, 1974; Melack, 1979a).

The relation between photosynthetic rates and population density in Lake Ziway can be expressed by the photosynthetic capacity (ϕ_{\max}), the photosynthetic rate at light saturation per unit chlorophyll a (Table 5). A photosynthetic capacity of about $20 \text{ mg O}_2 (\text{mg Chl a})^{-1} \text{ h}^{-1}$ may well be considered as representative for many African lakes (Robarts, 1986; Talling 1965; Talling *et al.*, 1973). The ϕ_{\max} in Lake Ziway which ranged from 11.0 to $22.5 \text{ mg O}_2 (\text{mg Chl a})^{-1} \text{ h}^{-1}$ is comparable to the given value.

There was a positive but low correlation between the maximum volumetric rates (A_{\max}) and algal biomass (B) ($r = 0.36$) in Lake Ziway. The A_{\max} in Lake Ziway ($1640\text{-}4070 \text{ mg O}_2 \text{ m}^{-3}\text{h}^{-1}$) was significantly higher than those of Naivasha and Oloiden, Kenyan lakes ($147\text{-}240$ and $272\text{-}748 \text{ mg O}_2 \text{ m}^{-3}\text{h}^{-1}$ respectively, Melack 1979 c), and that of Lake Awassa, Ethiopia ($217\text{-}408 \text{ mg O}_2 \text{ m}^{-3}\text{h}^{-1}$, Demeke Kifle, 1985). The range is comparable with that of Lake George, Uganda ($1900\text{-}6000 \text{ mg O}_2 \text{ m}^{-3} \text{ h}^{-1}$, Ganf 1975) although it is significantly lower than was reported for lakes Aranguade and Kilotes, Ethiopia ($10\text{-}30$ and $4 - 10 \text{ g O}_2 \text{ m}^{-3} \text{ h}^{-1}$ respectively, Talling *et al.*, 1973).

The photosynthetic rate per unit area of Lake Ziway ($0.3 - 1.6 \text{ g O}_2 \text{ m}^{-2} \text{ h}^{-1}$) remained within the range of other African lakes ($0.1 - 3 \text{ g O}_2 \text{ m}^{-2} \text{ h}^{-1}$, Vareschi, 1982). The most favourable situation for higher yields per unit area ($0.7\text{-}1.6 \text{ g O}_2 \text{ m}^{-2} \text{ h}^{-1}$) was provided by the lake when it contained denser population ($184\text{-}212 \text{ mg Chl a m}^{-3}$) of high photosynthetic capacity

[16.5 - 22.5 mg O₂ (mgChl_a)⁻¹h⁻¹] (See Table 5). This situation coincided with the rainy periods during which high nutrient input by high water discharges led to higher algal biomass and primary production. The correlation between rainfall and photosynthetic rate per unit area is highly significant ($P < 0.009, n = 13$) but not particularly strong ($r = +0.67$).

High water discharges in the rainy periods reduced the euphotic zone of Lake Ziway to below 50cm (Table 4) by introducing suspended materials, however, they were followed by higher values of photosynthetic rate per unit water volume. This marked increase in photosynthetic capacity during the rainy periods may reflect the stimulation of photosynthetic rate by essential algal nutrients, which is probably NO₃-N. The marked increase in nitrate concentration during the rainy season (see Fig. 5A-C) would stimulate high algal growth leading to high primary production. The correlation, r , between biomass and NO₃-N is significant ($P < 0.05, n = 13$) but not particularly strong ($r = +0.57$). This suggests that about 32% of the variation in biomass between sampling dates can be accounted for by variation in NO₃-N. The relationship between PO₄-P and biomass, however, is very weak ($r = +0.05$).

The relationship between NO₃-N and integral productivity (\bar{A}) in Lake Ziway was very weak ($r = 0.12$). This might be a reflection of the weak relationship between biomass and integral productivity ($r = +0.35$). Bindloss (1974) noted that low correlation value between integral productivity and biomass was due to population density influencing the photosynthetic depth profiles by self-shading. In addition to this, high suspended silt will remove or screen out light that would otherwise be used by photosynthesizing pigment. These factors, therefore, could affect both components of the ratio $A_{\max} / \bar{A}_{\min}$ which were shown to be determinants of

the areal productivity (Talling, 1965). Moreover, no correlation was found between ΣA ($\text{mg O}_2 \text{ m}^{-2} \text{ h}^{-1}$) and ΣB (mg Chl a m^{-2}) in Lake Ziway. Bindloss (1974) and Robarts (1986) also found no correlation between these two parameters.

With photosynthetic rates $0.3-1.6 \text{ g O}_2 \text{ m}^{-2} \text{ h}^{-1}$ or $3.1 - 17.6 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, Lake Ziway would be among the most productive lakes in Eastern Africa. Melack and Kilham (1974) found rates of $0.3 \text{ g O}_2 \text{ m}^{-2} \text{ h}^{-1}$ or 3.2 to $20.6 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ for a number of East African soda lakes. Perhaps the most productive lakes in Africa is Lake Aranguade, an Ethiopian soda lake, for which Talling et al. (1973) reported a productivity rate of $43 - 57 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$.

High photosynthetic efficiency appears to be characteristic of high production associated with heavy phytoplankton concentration (Hammer, 1981). The efficiency of light utilization (Q , $\text{mmoles O}_2 / \text{Einsteins of Ph.A.R}$) by phytoplanktonic photosynthesis in Lake Ziway ($2.4 - 9.6 \text{ mmoles O}_2 \text{ E}^{-1}$) is comparable with most productive East African lakes. The range is significantly higher than those of four Kenyan lakes reported by Melack (1979c) which were usually $2-4 \text{ mmol O}_2 \text{ E}^{-1}$. Talling's (1965) data from ten African freshwater bodies converted to efficiencies in molar units by Melack (1979c) varied from 1.8 to $10.2 \text{ mmol O}_2 \text{ E}^{-1}$.

Lower photosynthetic efficiencies in Lake Ziway tended to occur during incubation with greater irradiance (Table 5). There is inverse ($r = 0.48$) but not significant relationship between photosynthetic efficiency and irradiance incident on the lake surface. The correlation between areal productivity and irradiance ($r = + 0.31$) is very weak - suggesting that the variation in both photosynthetic efficiency and integral productivity in Lake Ziway can be minimally accounted by variation in irradiance.

Melack (1979b) statistically analysed the magnitude of monthly variability in photosynthetic rates in tropical lakes. Among the 26 tropical lakes analysed, the coefficient of variation (cv, standard deviation/mean) ranged from 15% to 86%. The cv for Lake Ziway (36.8%) is of intermediate value. The calculated cv puts the lake under pattern A. Such a pattern of pronounced seasonal fluctuations result from wind induced mixing, increased river discharge and rainfall and the associated changes such as increased turbidity and presumably the availability of nutrients and light.

CONCLUSION & RECOMMENDATIONS

The seasonal amplitude of variation in phytoplankton photosynthesis in Lake Ziway was dependent on the coupled effect of hydrologic (Water input-output) and hydrographic (water column structure) factors. However, frequent mixing due to strong wind and intense nocturnal cooling would cause the hydrographic factor to be paramount in determining the productivity status of the lake. Mixing ensures recirculation of nutrients and resuspension of algae. It also increases turbidity and decrease light penetration all of which influence primary production.

The characteristics of Lake Ziway are explained interms of high amounts of suspended matter with high light extinction, shallow euphotic depth, high production per unit standing crop, low nutrient status and frequent mixing. The paradox of high sustained production on low nutrient base is explained by rapid enrichment of the euphotic zone as a result of frequent mixing.

Zooplanktonic regeneration and bacterial transformation of nutrients have not been studied in any detail in African lakes. In view of this, the presence of large fraction of $\text{NH}_3/\text{NH}_4^+$ -N in a well oxygenated Lake Ziway lends special interest for future investigations.

Time series of chlorophyll a data, as an index of algal biomass, are signs of progressive increase toward eutrophy in Lake Ziway. However, the lake is presently endangered by the increasing human activities in and around it. There is pressing need for proper management of the lake inorder to avoid a marked reduction in the trophic activity and consequent impacts on an important protein source. Overzealous use of Lake Ziway will

endanger not only the fisheries resources but also the very supply of irrigation water sought. Hence, serious attention must be given to the maintenance of the lake water budget and the balance of essential ecological processes for the sustainable utilization of this life supporting water body.

REFERENCES

- Aleem, A.A. and Samaan, A.A. (1969). Productivity of Lake Maruit. Egypt Part II. Primary Productivity. Int. Revue ges. Hydrobiol. 54: 473-490.
- Allanson, B.R. and Hart, R.C. (1975). The primary production of Lake Sibya, Kwa Zulu, South Africa. Verh. Internat. Verein. Limnol. 19: 1426 - 1433.
- American Public Health Association, American Water Works Association, and Water Pollution Control Federation (1981). Standard methods for the examination of water and waste water. 15th ed. New York. 1134pp.
- Amha Belay and Wood, R.B. (1982). Limnological aspects of an algal bloom on Lake Chamo, Gamo Gofa Administrative 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.
- Baxter, R.M., Prosser, M.V., Talling, J.F. and Wood, R.B. (1965). Stratification at moderate altitudes (1500 to 2000m) Limnol. Oceanogr. 10: 510-520
- Baxter, R.M. and Golobitsch, D.L. (1970). A note on the limnology of Lake Hayq, Ethiopia, Limnol. Oceanogr. 15: 144-149.
- Baxter, R.M. and Golobitsch, D.L. (1982). Observations on Garba Guratch, an Ethiopian mountain lake. Sinet: Ethiop. J. Sci. 4: 63-68.
- Beadle, L.C. (1981). The Inland Waters of Tropical Africa. An

- introduction to Tropical Limnology. 2nd. ed. Longmans, London.
- Bindloss, M.E. (1974). Primary productivity of phytoplankton in Loch Leven, Kinross. Proc. R. Soc. B. **74** : 157 - 181.
- Bowling, L.C., Steane, M.S. and Tyler, P.A. (1986). The spectral distribution and attenuation of underwater irradiance in Tasmanian inland waters. Freshwater Biol. **16**: 313-335.
- Cannicci, G. and Almagia, F. (1947). Notizie Sulla "facies" Planctonica di alcuni laghi della Fossa Galla. Boll. Pesca, Piscic. Idrobiol. **23**:54-77.
- Cerling, T.E. (1979). Paleochemistry of Plio-Pleistocene Lake Turkana, Kenya. Palaeogr. Palaeoclim. Plaeoecol. **27**: 247-285.
- Demeke ~~Kite~~ (1985). Seasonal studies of phytoplankton primary production in relation to light and nutrient in Lake Awassa, Ethiopia. M.Sc. dissertation, Addis Ababa: Addis Ababa University, 116pp.
- Di Paola, G.M. (1972). The Ethiopian Rift Valley (between 7° 00' and 8° 40' latitude North). Bull. Volcanol. **36**: 517-560.
- Elizabeth Kebede (1987). A seasonal study on the species composition and phytoplankton biomass in Lake Awassa, Ethiopia. M.Sc. dissertation. Addis Ababa: Addis Ababa University, 70pp.
- Ganf, G.G. (1975). Photosynthetic production and irradiance photosynthesis relationships of the phytoplankton from a shallow equatorial lake (Lake George, Uganda). Oecologia **18**: 165-183.
- Ganf, G.G. and Horne, A.J. (1975). Diurnal stratification, photosynthesis and nitrogen-fixation in a shallow equatorial lake (Lake George, Uganda). Freshwat. Biol. **5**: 13-39.
- Ganf, G.G. and Viner, A.B. (1973). Ecological stability in a shallow equatorial lake (Lake George, Uganda). Proc. R.Soc. B. **184**: 321-

346.

- Gasse, F. and Street, F.A. (1978). Late quaternary lake level fluctuations and environments of the Northern Rift Valley and Afar region (Ethiopian and Djibouti). Palaeogr. Palaeoclim. Palaeoecol. 24: 279-325.
- Gaudet, J.J. (1977). Uptake, accumulation, and loss of nutrients by papyrus in tropical swamps. Ecology 58: 415-422.
- Gaudet, J.J. and Muthuri, F.M. (1981a). Nutrient relationships in shallow water in an African Lake, Lake Naivasha (Kenya). Oecologia 49: 109-118.
- Gaudet, J.J. and Muthuri, F.M. (1981b). Nutrient regeneration in a shallow tropical lake water. Verh. Internat. Verein. Limnol. 21: 725-729.
- Getachew Teferra (1987). A study on an herbivorous fish, Oreochromis niloticus L., diet and its quality in two Ethiopian Rift Valley lakes, Awassa and Zwai. J. Fish Biol. 30: 439-449.
- Hammer, U.T. (1981). Primary Production in saline lakes. A review Hydrobiol. 81: 47-57.
- Harris, G.P. & Lott, J.N.A. (1973) Light intensity and photosynthetic rates in phytoplankton. J. Fish. Res. Bd. Can. 30: 1771-1778.
- Hecky, R.E. and Fee, E.J. (1981). Primary production and rates of algal growth in Lake Tanganyika. Limnol. Oceanogr. 26: 532-547.
- Henderson, H.F., Ryder, R.A. and Hudhongania, A.W. (1973). Assessing fishery potentials of lakes and reservoirs. J. Fish. Res. Board. Can. 30: 2000-2009.
- Howard-Williams, C. and Lenton, G. (1975). The role of littoral zone in the functioning of a shallow tropical lake ecosystem. Freshwat. Biol. 5: 445-459.

- Kalff, J. (1983). Phosphorous limitation in some Tropical African lakes. Hydrobiol. 100: 101-112.
- Kassahun Wodajo (1982). Comparative limnology of Lake Abijata and Lake Langano in relation to primary and secondary production. M.Sc. dissertation. Addis Ababa: Addis Ababa University, 112pp.
- Lemoalle, J. (1973). L'energie lumineuse et l'activite photosynthetique du phytoplancton dans lac Tchad. Cahiers ORSTOM, Serie Hydrobiologie 7: 95-116.
- Lemoalle, J. (1975). L'activite photosynthetique du phytoplancton en relation avec le niveau des eaux du lac Tchad (Afrique). Verh. Internat. Verein. Limnol. 19: 1398-1403.
- Lemoalle, J. (1981). Photosynthetic production and phytoplankton in the euphotic zone of some African and Temperate lakes. Rev. Hydrobiol. trop. 14: 31-37.
- Lewis, W.M., Jr. (1974). Primary production in a plankton community of a tropical lake. Ecol. Monogr. 44: 377-409.
- Lewis, W.M., Jr. (1983). A revised classification of lakes based on mixing. Can. J. Fish Aquat. Sci. 40: 1779-1787.
- Loffler, M. (1978). Limnological and paleolimnological data on the Bale mountain lakes, Ethiopia, Verh. Internat. Verein. Limnol. 20: 1131-1138.
- Mackereth, F.J.H., Heron, J. and Talling, J.F. (1978). Water analysis: Some revised methods for limnologists. FBA. Scientific publication No. 36. 120pp.
- Makin, M.J., Kingham, T.J., Waddam, A.E., Birchall, C.J. and Tamene Teffera (1975). Development projects in the southern rift valley of

- Ethiopia. Land Resources. Study 21. Land Resources Division. Ministry of overseas Development, England.
- Melack, J.M. (1976a). Limnology and dynamics of phytoplankton in equatorial African lakes. Ph.D. Thesis. Duke University, Durham, N.C. 453pp.
- Melack, J.M. (1976b). Primary productivity and fish yields in tropical lakes, Trans. Am. Fish. Soc. **105**: 575-580.
- 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. Hydrobiol. **81**: 71-85.
- Melack, J.M. and Kilham, P. (1974). Photosynthetic rates of phytoplankton in East African alkaline-saline lakes. Limnol. Oceanogr. **19**: 743-755.
- Milbrink, G. (1977). On the limnology of two alkaline lakes (Nakuru and Naivasha) in the East Rift Valley system in Kenya. Int. Rev. ges. Hydrobiol. **62**: 1-17.
- Mohr, P.A. (1960). Report on a geological excursion through Southern Ethiopia. Bull. Geophys. obs. **2**: 9-20.
- Mohr, P.A. (1966). Geological report on Lake Langano and adjacent plateau regions Bull. Geophys. obs. **9**: 59-75.
- Morandini, G. (1942). Recenti studi limnologici nell'Africa orientale

Italiana Memorie 1: 255-266.

- Moss, B. and Moss, J. (1969). Aspects of the limnology of an endorheic African lake (Lake Chilawa, Malawi). Ecology, 50: 109-118.
- Oglesby, R.T. (1977). Relationships of fish yield to lake phytoplankton standing crop, production, and morphoedaphic factors. J. Fish. Res. Bd. Can. 34: 2271-2279.
- Pollinger, U. (1986). Phytoplankton periodicity in a sub-tropical lake (Lake Kinneret, Israel). Hydrobiol. 138 : 127-138.
- Poole, H.H. and Atkins, W.R.G. (1929). Photoelectric measurement of submarine illumination throughout the year. J. Mar. Biol. Assoc. 16: 297-324.
- Prosser, M.V., Wood, R.B. and Baxter, R.M. (1968). The Bishoftu Crater lakes: a bathymetric and chemical study. Arch. Hydrobiol. 65: 309-324.
- Robarts, R.D. (1986). Underwater light penetration, chlorophyll a and primary production in a tropical African lake (Lake Mcllwaine, Rhodesia). Arch. Hydrobiol. 86: 423-44.
- Ryder, R.A. (1965). A method for estimating the potential fish production of north-temperate lakes. Trans. Am. Fish. Soc. 94: 214-218.
- Ryder, R.A., Kerr, S.R., Loftus, K.H. and Reioger, H.A. (1974). The morphoedaphic index, a fish yield estimator - review and evaluation. J. Fish. Res. Board can. 31: 663-688.
- Schröder, R. (1984). An attempt to estimate the fish stock and the sustainable yield of Lake Ziway and Lake Abaya, Ethiopian Rift Valley. Arch. Hydrobiol. 3: 411-441.
- Steeman-Nielson, E. (1962). Inactivation of the photochemical mechanism in photosynthesis as a means to protect the cells against too high

- light intensities. Physiologia Plantarum 15: 161-171.
- Talling, J.F. (1965). The photosynthetic activity of phytoplankton in East African Lakes. Int. revue ges. Hydrobiol. 50: 1-32.
- Talling, J.F. (1966). The annual cycle of stratification and phytoplankton growth in Lake Victoria (East Africa). Int. Revue ges. Hydrobiol. 51: 545-621.
- Talling, J.F. (1973). The application of some electrochemical methods to the measurement of photosynthesis and respiration in fresh waters, Freshwat. Biol. 3: 335-362.
- Talling, J.F. (1986). The seasonality of phytoplankton in African lakes. Hydrobiologia. 138: 139-160.
- Talling, J.F. and Driver, D. (1963). Some Problems in the estimation of chlorophyll a in phytoplankton. Proc. conf. on primary productivity measurement, marine and freshwater U.S. Atomic Energy Comm. TID-7633, pp142-146.
- Talling, J.F. and Talling, I.B. (1965). The chemical composition of African lake waters, Int. Revue 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.
- Thornton, J.A. (1986). Nutrients in African lake ecosystems: Do we know all? J. Limnol. Soc. sth. Afr. 12: 6-21.
- Tilahun Kibret (1985). The benthos study of Lake Awassa. M.Sc. dissertation. Addis Ababa: Addis Ababa University, 216pp.
- Vareschi, E. (1982). The ecology of Lake Nakuru (Kenya). III. Abiotic factors and primary production. Oecologia 55: 81-101.
- Vincent, W.F., Wurtsbaugh, W., Neale, P.J. and Richerson, P.J. (1986).

- Polymixis and algal production in a tropical lake: latitudinal effects on the seasonality of photosynthesis. Freshwat. Biol. **16**: 781-803.
- Von Damm, K.L. and Edmond, J.M. (1984). Reverse weathering in the closed basin lakes of the Ethiopian Rift. American J. Sci. **284**: 835-862.
- Walker, A.T. (1980). Correction to the Poole & Atkins Secchi disc /light attenuation formula. J. Mar. Biol. Assoc. **60**: 769-771.
- Wetzel, R.G., and Likens, G.E. (1979). Limnological Analysis, W.B. Saunders Co. Philadelphia and London. 357pp.
- Wolde Michael Getaneh and Maria Getaneh (1979). Breeding period and fecundity of Tilapia nilotica in Lake Zwai Ethiop. J. Agric. Sc. **1**: 13-21.
- Wood, R.B., Baxter, R.M. and Prosser, M.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. (1976). The seasonal pattern of thermal characteristics of four of the Bishoftu crater lakes, Ethiopia. Freshwat. Biol. **6**: 519-530.
- Wood, R.B., Prosser, M.V. and Baxter, R.M. (1978). Optical characteristics of the Rift Valley Lakes, Ethiopia. Sinet: Ethiop. J. Sci. **1**: 73-85.
- Wood, R.B. and Talling, J.F. (1988). Chemical and algal relationships in salinity series of Ethiopian inland waters. Hydrobiol. **158**: 29-67.