SEASONAL STUDIES OF PHYTOPLANKTON PRIMARY PRODUCTION IN RELATION TO LIGHT AND NUTRIENTS IN LAKE AWASA

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TABLE OF CONTENTS

LIST OF TABLES

List of Figures

Abstract

Phytoplankton primary production of Lake Awasa was studied from November, 1983 to March, 1985 by the oxygen light and dark bottle technique. Supporting data include water chemistry, light penetration, thermal characteristics and standing crop of phytoplankton.

The solar radiation falling on the lake surface did not show pronounced variation apart from one low value recorded on a cloudy day. The lake is of fairly high transparency with red and green the most penetrating components.

There has been no indication of deep-seated thermal stratification in Lake Awasa apart from the superficial type of stratification which is generated by solar heating and destroyed by nocturnal cooling or wind-induced vertical mixing.

The chemistry of the lake water is basically similar to other East African lake waters with sodium as the predominant cation and bicarbonate+ carbonate as the predominant anion. The lake was found to have high concentration of silica and low concentration of phosphate and nitrate. Almost all nutrients were found to show some seasonal variations.

The algal crop is fairly high and was found to change seasonally. The vertical distribution of photosynthetic activity per unit water volume was of a typical pattern for phytoplankton with light inhibition on all but the most overcast days. The threshold of inhibition at the lake surface was around 1500μEm^{-2}. Maximum net photosynthesis averaged 214.6 mgO$_2$ (66.95mgC) m^{-3}h^{-1} and integral photosynthesis ranged from 0.3 to 0.73 g O$_2$ (0.094 to 0.226 gC) m^{-2}h^{-1}. The estimated values of daily integral gross photosynthesis were in the range of 3.3 to 7.8 g O$_2$ (1.03 to 2.4 g C) m^{-2}d^{-1}. The correlation between gross photosynthesis and standing crop was poor though there was a general tendency for the maximum photosynthesis to increase with the standing crop.

Though not pronounced, spatial (vertical) and temporal variations of phytoplankton standing crop and primary production were observed. The vertical variations appear to be the result of variation in the underwater radiation which is a function of the lake's transparency and amount of surface radiation. The observed temporal variations in phytoplankton standing crop and primary production seem to be controlled more by nutrient supply than energy supply. The seasonality of rainfall seems, therefore, to play the predominant role in determing the nutrient status and extent of algal growth and primary production.

I. Introduction

The present population explosion constitutes perhaps the most serious problem which mankind has had to face during the course of its history. Man's exploding numbers are outstripping the food supply from land. As a result of increasing human population, it is already clear that there are food shortages particularly of protein.

Most of the world's land suitable for farming has already undergone cultivation. But still we do not have enough food and we will not have enough food in the future.

In the wake of mounting difficulties with producing food from land areas throughout the world, more and more attention is being given to alternative sources of food. Marine and freshwater organic productivity will have to play an increasing part in protein production.

In order to meet the growing food requirements of the world population, great effort is necessary in the development and utilization of the biological wealth of the aquatic environment. The exploitation of this aquatic productivity for human food will involve intensive and extensive research undertakings. Much of the information from such research works is of paramount importance in transforming this sound and promising idea into practical terms.

Studies of the afore-said type have started receiving increased impetus from the need of people to exploit their aquatic resources for sustenance and economic gain. Fish yields from tropical lakes are extremely important sources of protein. Although there is relatively more data available on tropical lakes now, it is clear that there are still very few well-documented aquatic ecosystem studies in the tropics. As a consequence, many of the interpretations of observed phenomena are speculative.

Primary production is the basis of the food chains of all ecosystems and involves the conversion of solar energy into carbohydrates. Primary production is almost unstudied in the Ethiopian rift valley lakes. Lake Awasa is one of the Ethiopian rift valley lakes whose limnological study is still in its infancy. But it is a lake from which, according to the report of National Revolutionary Development Campaign and Central Planning Supreme Council, an annual fish production of 260 to 700 tons is expected.

This paper is the result of the study on the seasonal variation of phytoplankton primary production in Lake Awasa. The paper attempts to throw some light on the seasonal variation of phytoplankton production in relation to light climate and nutrients.

II. Literature Review

1. Standing crop and primary production - Definition and measurement

In discussing any problem, it is advisable to define the terms involved. The definition of terms given in this section is based entirely on the theoretical discussions by Westlake (1965a), Fogg (1975, 1980) Westlake (1980), and Wetzel (1983).

Standing crop (synonymous with biomass when applied to plankton) is the weight of organic material that can be sampled or harvested at any one time from a given area. The term may refer to a part of a plant (e.g. plant tops or above ground portions) or to the entire plant (e.g. net plankton). In this paper the terms are used interchangeably.

Production is the weight of new organic material formed over a period of time including any losses that occurred during that period. Thus primary production is the quantity of new organic matter created by photosynthesis (or chemosynthesis), or the stored energy this material represents.

Productivity is the rate of formation of new organic matter averaged over some defined period of time, such as a day or a year. Gross productivity (sometimes termed real productivity) refers to the observed change in biomass, plus all predatory (grazing by herbivores and carnivores) and non-predatory (respiration, excretion and secretion) losses, divided by the time interval. Net productivity (also termed apparent productivity) is the gross production of new organic matter, or stored energy less losses, divided by the time interval.

Primary productivity of aquatic ecosystems is basically dependent upon the photosynthetic activity of autotrophic organisms (Forti, 1965; Fogg, 1975; Wetzel and Likens, 1979). For this reason, the measurement of primary production of natural waters is based upon the measurement of their photosynthetic activities (Forti, 1965; Cooper, 1975; Fogg, 1980) which is primarily due to algae and macrophytes but also possibly due to photosynthetic bacteria (Fogg, 1975; Hammer, 1981).

Numerous techniques have been used for the estimation of biomass and primary productivity of aquatic ecosystems. The different methods of estimation are discussed in Strickland and Parsons (1960), Vollenweider (1969), Lind, (1979), Wetzel and Likens (1979) and Wetzel (1983). Of all the methods used in primary production determination, the oxygen light and dark bottle technique has received wide application (Wetzel, 1983). In the oxygen method, samples of phytoplankton are incubated at the depths from which they were collected in opaqued (dark) and light bottles. Sometimes, if the water body under study is assumed to be homogenous, surface samples of phytoplankton can be incubated being distributed at different depths in the euphotic zone.

The method involves the measurement of changes in oxygen concentration. The initial concentration of oxygen (C_1) can be expected to decline to a lower value (C_2) by respiration in the opaqued bottles and increase to a higher value (C_3) in the clear bottles. The difference (C_1-C_2) represents the respiratory activity per unit volume of water over the time interval of incubation. The difference (C_3-C_1) is equal to net photosynthetic activity and the sum (C_3-C_1) + (C_1-C_2) which is equal to (C_3-C_2) corresponds to gross photosynthesis.

Numerous physiological and methodological problems can affect the measurement of photosynthesis. Examples of these problems include unequal respiratory rates in opaqued and clear bottles (Steemann- Nielsen, 1954; Harris and Lott, 1973; Fogg, 1980), the consumption of oxygen by photooxidation (Mac Allister, 1961; Tolbert, 1971) and the effect of bottles in reducing turbulence, which results in the settling of organisms during the course of the experiment and a consequent reduction in production (Ohle, 1958; Verduin, 1960).

The incorporation of ^{14}C tracers into the organic matter of phytoplankton during photosynthesis has also been reported as an extremely sensitive measure of the rate of primary production (Wetzel and Likens, 1979; Wetzel, 1983). Methodological and physiological problems confront the application of ^{14}C dark and light bottle techniques. The problems include respiratory losses of labelled CO_2 and secretion of labelled organic matter (Wetzel, 1983). The possible limitations of these two methods are given in Talling and Fogg (1969).

For the measurement of biomass, the direct counting of algal cells and the identification of species is generally considered to be time-consuming and laborious. Preference has, therefore, been given to methods by which biomass can be calculated from chemical techniques (Findenegg, 1965b).

The only rapid chemical method known for estimating biomass is the determination of plant pigments (Strickland and Parsons, 1960). The most precise and reproducible methods have involved spectrophotometric measurements of absorbance of extracts of plant pigments, particularly of chlorophylla at one or more wavelengths (Talling and Driver, 1963). Such spectrophotometric methods are discussed in Richards and Thompson (1952), Lund and Talling (1957), and Strickland and Parsons (1960).

According to Talling and Driver (1963) errors in measurements can arise from the presence of phaeophytins in plant extracts, the incomplete extraction of algal cells or possibly from work on pigment mixtures.

In spite of all the problems discussed here and elsewhere, the methods considered here are widely in use.

2. Factors affecting primary production and standing crop.

In order to determine what limits production by phytoplankton in a lake, one needs to consider the factors that are involved. The study and analysis of factors governing primary production and biomass have been made by many workers (Sylvester and Anderson, 1964; Findenegg, 1965a; Dugdale, 1967; Christie, 1968; Moss, 1969a; Schindler and Nighswander, 1970; Talling, 1971; Schindler and Comita, 1972; Brylinsky and Mann, 1973; Schindler and Fee, 1973, 1974; Dillon and Rigler, 1974; Richardson, 1975; Schindler, 1978; Melack et al., 1982 and Setaro and Melack, 1984).

Primary production and biomass of phytoplankton are affected by an array of chemical, physical, and biological factors. The different factors that control primary production and biomass of phytoplanktons will be dealt with in the following sections.

2-1 Primary production, biomass and physical factors.

The physical factors that affect lake productivity (biomass and primary production) include lake morphometry, light and temperature.

2-1-1. Lake morphological features

Certain fundamental conditions of production in an aquatic environment arise directly out of size and form interrelationships (Ohle, 1956; Vinberg, 1963; Kerkes, 1972, 1975; Schindler, 1978; Cole, 1983). Such morphological features as depth, shore-line, slope, volume, and area can affect the productivity of a lake.

There is no doubt that, in general the more frequently a lake is stirred by winds to the bottom, the faster the nutrients are recycled from the mud into the photosynthetic zone where they may accelerate the rate of production. The depth of the water is thus, in principle, negatively correlated with the rate of production (Cole, 1983; Goldman and Horne, 1983; Wetzel, 1983).

An inverse correlation of phytoplankton abundance with depth of a water bain is commonplace in tropical Africa (Lemoalle et al., 1981). Algae of high concentrations are most prevalent in such shallow lakes as lake George, Uganda (Ganf, 1974a), Lakes Abiata and Ziway in Ethiopia (Amha Belay) and Wood, 1984) and in shallow basins within a deeper lake (e.g. Lake Victoria's Winam Gulf) Talling, 1965a).

Lake Shalla in Ethiopia has a gross chemistry remarkably similar to one of the most productive lakes in the Ethiopian rift valley - Lake Abiata, but it is the least productive which is probably due to its depth (Amha Belay and Wood, 1984).

The wind protected situation of a lake may be of similar effect, because the absence of complete circulation leads to meromixis (with part of the water body participating in mixing), and it is clear that meromixis does not favor production. The surrounding topography may be such that the lake is sheltered by hills resulting in little actual wind action on its surface. But, in an exposed lake, wind can sweep uninterrupted the greatest distance across the lake surface. The exposure of a lake to wind has thus a direct effect on water movement, and an indirect effect on the biota within the lake.

The physical dimensions of a lake interact with climatic and edaphic factors to determine the nature of the lake as an environment and thus, its inhabitants (Cole, 1983). The relation of the long axis of the lake to the direction of prevailing winds is of paramount importance to lake productivity.

The shore-line development of a lake may play some role in determining the trophic nature of a lake because shallow water is the most productive (Cole,1983). Moreover, the amount of nutrients arriving at the lake is, to a great extent, a function of shore-line. It is, therefore, tempting to theorize that, of two lakes alike in most features except shore line development, the one with the highest shore-line development would be most productive of phytoplankton (Cole,1983).

The size, slope and geology of a lake's drainage area influence the identity and quantity of minerals dissolved in the lake. The drainage-area size in relation to the surface area is important in many lakes since there is often a higher fertility in lakes with larger drainage area (Goldman and Horne, 1983).

Schindler (1978) has also tried to relate lake volume and catchment area to productivity. He found that catchment area has a direct relationship to lake productivity, because it is proportional to nutrient loading. But lake volume is inversely related to productivity because volume has a dilution effect.

There are many other morphological features which can be equally important to productivity. But the detailed disscussion of the morphological features of a lake is beyond the scope of this thesis.

2-1-2. Light

Light intensity has received the most extensive attention of all the physical factors controlling aquatic production (Stengel and Soeder, 1975). Talling (1970, 1971) gives a clear picture of what is known about the underwater light climate as determined by incident radiation and the optical properties of the medium.

Solar radiation is of fundamental importance to the entire dynamics of aquatic ecosystems. Nearly all the energy that controls the metabolism of lakes comes directly from solar energy (Wetzel, 1983).

2-1-2-1 . Transmission and measurement in water bodies

Solar radiant energy reaching the surface of the earth has a spectral range from about 300 nm (ultraviolet) to about 3000 nm (infrared) (Wetzel and Likens, 1979). About half of the total radiant energy (46 to 48%)(Talling, 1957a; Westlake, 1965b) is the photosynthetically active radiation (Ph.A.R) which is approximately between 390 to 710 nm (Talling, 1957a; Strickland, 1958; Westlake, 1965b).

The underwater photosynthetically active radiation can be measured with a photometer in combination with underwater quantum sensor.

The amount and spectral composition of solar radiation falling on a lake are influenced by an array of environmental factors. Direct solar radiation reaching the surface of water bodies varies with the angular height of the sun and therefore with the time of the day, season and latitude (Hutchinson, 1957; Wetzel, 1983). It also varies with the molecular transparency of the atmosphere and the distance light must travel through it. It therefore, varies with altitude and meterological conditions (Edmondson, 1956; Wetzel and Likens, 1979).

Light impinging upon the surface of water does not penetrate completely; a significant portion is reflected or back scattered (Steemann-Nielsen, 1975). Within the water light is rapidly attenuated with depth by absorption and scattering. Absorption is defined as diminution of light energy with increasing depth by transformation to heat (Westlake, 1965b).

In very clear oligotrophic lakes or pure water light attenuation is least in the blue region of the spectrum (Smith _et al._, 1973) and transmission in the red region is almost seventy times less (Lind, 1979). With increasing trophic status or load of dissolved and particulate materials, the least attenuated irradiance may be green, yellow or red (Hutchinson, 1957; Reid and Wood, 1976; Westlake 1980).

Talling (1975) has pointed out the following two causes of light attenuation when discussing the non-linearity of the relationship between high population densities and photosynthetic productivity. Nutrient-rich waters are likely to have a high non-algal (background) attenuation of light which will compete with the photosynthetic pigments for energy capture. Light attenuation also results from algal self-shading.

Heavy concentrations of biomass near the air-water interface are not uncommon (Talling, 1975). In such dense algal covers, the vertical light gradient is determined more by self-shading (self-absorption) than by attenuation from other components in the water column (Talling, 1960a, 1971; Bindloss, 1974; Ganf, 1974 b).

Because of the attenuation of light, the depth of the euphotic zone (i.e, the depth reached by 1% of the light penetrating the water surface) (Talling, 1960 b, 1971) is reduced. In Ethiopia, the depths of the euphotic zone of the most productive lakes, Lake Aranguadi and Kilole, were found to be between 0.15-0.27 and 0.24-0.49 respectively (Talling et al., 1973) due to the abundant phytoplankton population.

In some small ponds in Malawi light was reduced to less than 1% of its surface intensity at a depth of 4mm below the water surface during periods of main rains. This took place in the absence of surface living algae and was due soley to suspended matter (Moss, 1969a). Non-algal attenuators of light either originate from the watershed as in lakes Tahoe (Goldman, 1974; Tilzer et al., 1976) and Chad (Lemoalle, 1973) or are stirred up from the lake bottom by wind action as in lake George (Ganf, 1974b). Such a non-algal attenuation of light is exemplified in Ethiopia by lake Langano in which a stable colloidal suspension of silt is maintained (Wood et al., 1978). In contrast, Lake Shalla, the most transparent of the Ethiopian rift valley lakes has an euphotic depth ranging from 3.7m (Wood et al., 1978) to 4.93m (Amha Belay and Wood, 1984). It has been noted (Amha Belay and Wood, 1982) that Lake Abaya is the most opaque of the Ethiopian rift valley lakes because of light attenuation by background absorption.

The attenuation of the different spectral components of light can be assessed from measurements made with photometers used in conjunction with glass filters (as indicated in material and methods). The data resulting from such measurements are compared in terms of extinction coefficient (the slope of the line obtained by plotting readings on a logarithmic scale against depth) (Lind, 1979).

It was found (Talling et al., 1973) that in the Ethiopian soda lakes, Lakes Aranguadi and Kilole, the extinction of light was highest in the blue and lowest in the red spectral region, a pattern characteristic of very turbid or colored lakes (e.g. Dvihally, 1961). Likewise, the vertical extinction coefficients in Lake George, Uganda (Ganf, 1974b) indicate that red light penetrates the farthest and blue light is very rapidly attenuated.

The extinction coefficients of the different spectral components in Lakes Chammo and Abaya (Amha Belay and Wood, 1982), Lake Awasa (Amha Belay and Wood, unpublished data) and in the four northernmost lakes in the Ethiopian rift valley (Wood _et al._, 1978) indicate that the red and green spectral components are the most penetrating. The transparency of Lake Hayq in Ethiopia is, however, greatest for green light and declines for light of shorter and longer wavelengths (Baxter and Golobitsch, 1970).

The transparency of a lake can be approximated using a standard Secchi disc whose readings are a function of the reflection of light from the disc surface. A secchi disc transparency (=vertical visibility) depends on such factors as the eye-sight of the observer, the contrast between the disc and the surrounding water and the reflectance of the disc (Cole, 1983). But the readings obtained with a Secchi disc (secchi depths in meters), if done by the same person and in the some way, can be used for comparison of the optical conditions of the same lake at different times or different lakes at the same time.

Secchi disc readings as low as 14 cm have been recorded for Hora Orgona, Ethiopia (Loffler, 1978) and 15 cm has been found for Lake Nakuru, Kenya (Melack and Kilham, 1974). Lake Ziway has Secchi disc readings in the range of 10-17cm (Tudorancea, unpublished data). Secchi disc readings as high as 33-41 m were found for lake Tahoe in California-Nevada (Cole, 1983).

Generally the measurement of underwater radiation confronts many problems. Most of the problems encountered during underwater radiation measurement are discussed in Strickland (1958), Westlake (1965b) and Tyler (1973).

2-1-2-2. Light intensity and depth distribution of photosynthesis

The availability of sunlight as a source of energy is an obvious feature of primary production by algae and macrophytes (Fogg, 1975;1980). The productivity by phytoplankton is related to the quantity of radiant energy penetrating the water body, for the intensity of light governs the rate of energy supply for photosynthesis.

On bright days photosynthesis has frequently been found to be lower at the surface than it is at depths below the surface. Thus there is a gradual increase in the oxygen production from the surface to a few meters below the surface, which again declines with increasing depth. Depression of photosynthetic activity at the surface has been reported many times from in situ measurements of primary production (Talling, 1957a; Goldman, 1963; Talling, 1965a, 1966b; Lewis, 1974; Ganf and Horne, 1975). The observed lower photosynthetic activity was attributed to the inhibition of photosynthesis by intense light (Steemann-Nielsen, 1952; Kok, 1956; Ryther, 1956; Steemann-Nielsen, 1962; Goldmann et al., 1963; Jones and Kok, 1966 a,b; Soeder and Stengel, 1974). This phenomenon is associated with photo-oxidative destruction of enzymes (Steemann-Nielsen,1952; Steemann-Nielsen and Jorgensen, 1962) or with the photo-oxidative consumption of oxygen (MacAllister, 1961; Harris and Lott, 1973) or both (Talling, 1966b). The lower surface photosynthetic activity is also attributed to a lower algal biomass of the surface (Talling, 1965a; Ilmavirta, 1974).

Both in situ (Amha Belay, 1981) and Laboratory (Amha Belay and Fogg, 1978) experiments have shown that inhibition increases with both irradiance and exposure time. The same experiments have also shown that inhibition becomes greater at high temperature and oxygen concentrations and when the cells are nutrient deficient.

Many studies have shown (Vollenweider and Nauwerck, 1961; Rodhe, 1965; Talling, 1970; Steemann-Nielsen, 1975) that the effect of light on photosynthesis can be described by a curve which is generally hyperbolic. As a general rule, active production by phytoplankton will extend to the depth at which the incident light (measured just below the surface) is attenuated to about 1% (Talling, 1960b; Fogg, 1980). This usually corresponds to the compensation depth (The depth at which oxygen production in photosynthesis and oxygen consumption in respiration are equal).

2-1-2-3. Diurnal and seasonal changes of biomass and photosynthesis in relation to light intensity.

Biomass and photosynthetic rates of phytoplankton in an aquatic environment change not only with depth, but also with the time of the day and seasons of the year. Diurnal phytoplankton migrations normally decrease photosynthesis close to the surface around noon in addition to inhibitory effects, and at the same time lead to enhanced photosynthesis in deeper water (Tilzer, 1973; Ganf, 1974C). Photosynthesis is lower in the afternoon than in the morning at similar irradiances, which can be due to depletion of nutrients (Ohle, 1958; Ganf, 1975), accumulation of inhibiting substance and increasing respiration (Doty and Oguri, 1957; Lorenzen, 1963; Ganf, 1974c), bleaching of pigments (Yentsch and Scagel, 1958;

Goldman et al., 1963) and grazing by diurnally migrating zooplankton (MacAllister, 1963). As a result of great variation in incident irradiance, the position of the most productive layer shows a diurnal change (Vollenweider and Nauwerck,1961).

Phytoplankton growth and primary production show characteristic seasonal variations (Fogg, 1975; Golterman, 1975). Variation in light inputs seems to be the major reason for seasonal changes of primary production (Fogg, 1980; Westlake, 1980).

Seasonality of phytoplankton abundances and photosynthesis are familiar features of African lakes. Descriptions of seasonal changes in species composition and abundance of phytoplankton in the white Nile (Prowse and Talling, 1958), in Lake Victoria (Talling, 1966a) in Lake George, Uganda (Ganf. 1974a), in Lakes Oloidien (Melack, 1979 a,b) and Sonachi in Kenya (Melack, 1976) and in Lake Chad (Lemoalle, 1973) are available.

Seasonal changes of the total concentration of phytoplankton and primary production reflect many factors, among which the seasonal aspect of climate is of great importance (Talling, 1965b). According to Talling (1965b), the winter minimum of incident solar radiation was the most critical environmental feature responsible for the seasonal fluctuations observed in Lake Windemere, England. As a result of this minimum solar radiation, the phytoplankton crop was brought to low levels as shown by chlorophylla (Talling, 1965b) and cell counts (Lund, 1964). In Lake Victoria (a tropical lake) this factor is substituted by seasonal loss of heat with resulting vertical mixing dependent upon wind regime, as a critical cycle-generating event (Talling, 1965b).

In temperate lakes, phytoplankton number and biomass increase during spring when light conditions are improved, and build up to a spring maximum (Wetzel, 1983). Also primary production follows the annual cycle of solar radiation.

In keeping with the relatively constant environmental conditions, the seasonal variations in tropical waters are much lower, often as little as five fold (Fogg, 1965) as compared to the thousand fold variations of temperate lakes (Wetzel, 1983). Most tropical lakes exhibit pronounced seasonal variation that usually correspond with differences caused by rains, rivers, or vertical mixing (Melack,1979b).

2-1-3. Temperature and related phenomena

Solar radiation has a critical role, both as a direct supply of energy for photosynthesis and as a more indirect determinant of water temperature, thermal stratification, and associated chemical variations in inland water bodies (Talling, 1965b). Since most of the incident light energy is transformed into heat, temperature conditions are usually dependent upon the light regime (Hutchinson, 1957). The temperature of equatorial lakes of the world show very little variation, though diel changes very near the surface could be great (Beadle, 1981).

The surface temperature of Lake Awasa was found to be in the range of 21-25°C (Gasse et al., 1983). It has also been reported (Baxter and Golobitsch, 1970) that the surface temperature of Lake Awasa was between 24 and 27°C. The surface temperature of other Ethiopian Lakes is not very much different from that of Lake Awasa except for the very low temperature (11-11.2°C) of Garba Guratch, a Bale mountain Lake in Ethiopia (Loffler, 1978).

The Ethiopian highland lakes can experience high diel fluctuations of surface temperatures because of their relatively high altitudes as well as great seasonal fluctuations in rainfall, humidity, and cloud cover (Wood et al., 1976).

Temperature exerts many fundamental effects on limnological phenomena such as lake stability, gas solubility, and metabolism of organisms (Boney, 1975; Lind, 1979). With rise in temperature, there is decreased solubility of oxygen (Ruttner, 1963; Cole, 1983). Moreover, as a result of temperature differences with the resulting density gradient thermal stratification ensues.

During periods of stratification and a stable thermocline, exchange of materials between epilimnion and hypolimnion is reduced. Therefore, the supply of nutrients from deeper layers is reduced (Findenegg, 1965a; Talling, 1969). It appears (Wood et al., 1978) that circulation in the Ethiopian rift valley lakes is frequent for there has been no indication of strongly developed thermal stratification, although slight gradients of temperature were observed for Lake Shalla (Baxter et al.,1965).

Studies on the thermal characteristics of the Bishoftu crater lakes in Ethiopia were made by Baxter and Wood (1965), Baxter et al. (1965), Wood et al. (1969) and Wood et al. (1976). The two deepest and most sheltered lakes, Lake Bishoftu (87m) and Lake Pawlo (65m), showed the most stable thermal stratification and an anoxic lower layer.

The observations over a long period by Wood et al. (1969) suggest that Lake Pawlo is annually mixed towards the end of the year. This is attributed to the breakdown of thermal stability through cooling at the surface due both to increased evaporation during the day and to a greater loss of heat at night. The shallowest lake, Kilole (6.5m) is almost continually stirred to the bottom. Lake Aranguadi (35m) is markedly stratified but its high algal productivity is suggestive of frequent stirring into atleast the upper part of the anoxic layer.

The effect of temperature is not confined to physical stratification. This physical stratification can also result in the subsequent chemical and biological stratifications. In lake Windemere (England) stratification in summer resulted in the epilimnion being stripped of silica below the critical level of 0.5 mg m^{-3} (Talling, 1965b).

In lakes Bunyoni and Mutanda in Uganda, an oxygen free lower layer was created as a result of sharp thermal discontinuities (Baxter *et al.*, 1965). Lake Mutanda is sufficiently deep (44m) and sheltered to be stratified and deoxygenated for a long time. The most stratified of all known African lakes, Lake Kivu (480m deep) in the western rift has very high salinity in the lower water (below 70m) and an accumulation of very high concentrations of nitrate and phosphorus in the saline lower water (Degens *et al.*, 1971)

When thermal stratification occurred in Lake Waldsea in Australia, a difference in the metalimnion and hypolimnion from a PH of 6.9 to 8.2 and redox potential of +390 to -185 mv was observed (Cohen et al., 1977).

During periods of thermal stratification, there is a concomitant stratification of phytoplankton (Westlake, 1980). The stratification may be stable over quite long periods (Moss, 1969b) but may also be altered daily by vertical movements of photosynthetic flagellates (Happey and Moss, 1967; Tilzer, 1973).

There is another interrelationship between temperature and the concentration of many essential nutrients since the remineralization rate due to bacterial degradation is temperature-dependent (Stengel and Soeder, 1975).

Finally, the increasing sensitivity of algae to high light intensities at supraoptimal and suboptimal temperatures may be of ecological significance (Sorokin and Krauss, 1962). Moreover, temperature inhibition of photosynthesis may take place through the inhibition of the temperature dependent dark reactions of photosynthesis and respiration (Bauer et al., 1975). Extreme temperatures may not only inhibit CO_2 uptake, but may also have aftereffects which inhibit subsequent photosynthesis at optimal temperatures (Edmondson, 1956; Bauer et al., 1975). According to Talling

(1965a) the phtosynthetic activity of phytoplankton in the east African lakes was always high compared to temperate lakes probably, due to a high and rather uniform value of the photosynthetic capacity (ϕ) which may be influenced by temperature.

2-2. Primary production, biomass and chemical factors.

At a given depth, the upper threshod of productivity per unit biomass is clearly set by the under water light climate (Stengel and Soeder, 1975). That rates of actual production in natural waters are far below the production potential offered by the radiant energy input, is due to the limitation by factors other than light.

In addition to light energy, plants are dependent upon an adequate supply of nutrients (Stewart, 1974; Fogg, 1975). It has been indicated (Hutchinson, 1957) that critically low levels of certain inorganic nutrients are believed to limit primary productivity at certain times of the year in many temperate lakes. But detailed knowledge of nutrient limitation in tropical lakes is scarce (Talling and Talling, 1965; Moss, 1969a; Schindler, 1978) in spite of the many works done on factors controlling primary production.

In tropical lakes light and temperature are probably not as frequently limiting as they are in temperate lakes (Lund, 1964) and nutrient availability probably plays a major role in controlling the seasonal pattern of algal growth (Moss, 1969a).

Latitude was found (Brylinsky and Mann, 1973)to provide much more predictive information about the productivity of lake than nutrient concentrations. However, Schindler and Fee (1973,1974) found a good correlation between annual phytoplankton production and phosphorus input. Moreover, the importance of nutrient supply to the productivity and abundance of phytoplankton has been shown by enrichment experiments on natural populations (eg. Melack et al., 1982; Setaro and Melack, 1984).

In many tropical lakes surrounded by extensive nutrient buffering wetlands and receiving perrenial inflows, total phytoplankton biomass and productivity are larger and more constant seasonally than those found in temperate lakes (Beadle, 1981). This phenomenon is attributable to nutrient loading as a result of wind-induced vertical mixing and marked seasonality of rainfall (Talling, 1969; Lewis, 1974; Melack, 1979b).

It is because of the abundant supply of nutrients that primary production and biomass are exceedingly high in Lake Aranguadi, Ethiopia (11-22g $Cm^{-2}d^{-1}$ and 221-325 mg chla.m^{-2}) (Talling et al., 1973), in Lake Simbi, Kenya (200 mg chla m^{-2}) (Melack,1979c) and in Lake George, Uganda (400 mg chla m^{-2}) (Ganf, 1974a). Most of the photosynthetic activity of phytoplankton is carried out in the surface layers and it is here where nutrient limitation is likely to have a great effect on the total primary production of a water body (Moss, 1969a). Algal communities may respond to a decreased supply of a limiting nutrient either by decreasing the optimum photosynthetic rate of production or by producing less efficiently at suboptimal irradiances (Schindler and Fee, 1975).

Studies on plant nutrients emphasize the importance of nitrogen and phosphorus (Boney, 1975). There is a rapidly growing body of evidence (Schindler, 1974; Schindler and Fee, 1974) that control of phosphorus alone is sufficient to halt or even reverse the course of eutrophication in many cases.

According to Talling and Talling (1965) and Melack and Kilham (1974) high concentrations of phosphate are not typical of African lakes, especially of the Soda Lakes including those in Kenya (Lake Nakuru and Magadi). Very high concentrations of phosphate were found in Lake Chammo and Abaya (Amha Belay and Wood, 1982) and in the two Ethiopian *Spirulina* lakes--Lake;Aranguadi and Chitu, (Wood, 1968). Phosphate may be limiting in Lake Mariut, Egypt (Aleem and Samaan, 1969) during periods of high photosynthetic activity.

The comprehensive studies in the rivers of the Nile (Talling and Rzoska, 1967) and in Lake Victoria, Uganda (Talling, 1966b) suggest that nitrogen may limit algal growth in East African lakes because nitrate concentrations in the water bodies surveyed were often very low (Talling and Talling, 1965; Hammer, 1981).

A clear case of correspondence between depletion of nitrate and reduced algal growth and productivity was reported for Lake Victoria (Talling, 1966b), Lake Lano, phillipines (Lewis, 1974) and in the reservoirs along the Nile river in the Sudan (Prowse and Talling, 1958). Nitrate is generally low in saline lakes (Hammer, 1981). Exceptions include Lake Humboldt in Canada (Haynes and Hammer, 1978) and Lake Werowrap in Australia (Walker, 1973). In the former drainage and sewage are the responsible agents whereas in the latter gull populations make a large contribution.

Distinct relationships between silica and diatom periodicity have been found in Lake Windemere, England (Lund, 1964). Very high concentrations of silica were found in Lake Nakuru, Kenya (Melack and Kilham, 1974), Kilole and Aranguadi (Prosser _et al._, 1968).

Most African lake waters studied so far show a marked predominance of $HCO_3^- + CO_3^=$ among the anions (Talling and Talling, 1965; Prosser _et al._, 1968; Wood, 1968; Melack and Kilham, 1974). Unlike other African lakes in which sodium bicarbonate and carbonate dominate, the dominance of sulphate and chloride in Lake Mahega, Uganda is very unusual (Melack and Kiham, 1972).

The proportional concentration of major cations and the ratios of monovalent to divalent cations (M:D) are also known to influence the metabolism of certain algae as much as absolute concentrations can (Wetzel, 1983). According to Wetzel (1983) the three major genera of diatoms common to oligotrophic lakes - _Fragillaria_, _Asterionella_ and _Tabellaria_- are stimulated by high levels of calcium. With decreasing M:D ratios, decreased rates of photosynthesis were also observed. This is exemplified by the apparent relationship noted between low levels of algal productivity and unfavorable M:D ratios (Wetzel, 1965).

Talling and Talling (1965) have found the predominant cation to be sodium in the very saline lakes of Africa including those in Ethiopia: Lake Shalla, Abiata, and Metahara. On the other hand, in the more dilute waters of Africa, such as Lake Victoria in Uganda and Lakes Tana and Ziway in Ethiopia, calcium or less frequently magnesium is present in high proportions by equivalents. The excess of magnesium over calcium has also been reported for Lake Hayq, Ethiopia (Baxter and Golobitsch, 1970), Bale mountain lakes in Ethiopia (Loffler, 1978) and Bishoftu crater lakes (Prosser _et al_., 1968). In lakes Chammo and Abaya calcium was found to be in excess of magnesium (Amha Belay and Wood, 1982).

A very strong correlation has been found between the species composition of algal community and the inorganic carbon system (PH, CO_2, Alkalinity and others) (Lund, 1964; Moss, 1973). The high alkalinity of the East African lakes including lake Aranguadi (Wood, 1968; Talling _et al_., 1973) and Chitu (Wood, 1968) in Ethiopia and Lake Simbi in Kenya (Melack, 1979c) is believed (Melack and Kilham, 1974) to influence the species composition of algal communities. This has been indicated by the association of the blooms of _Spirulina platensis_ with high alkalinity (Iltis, 1968).

Limitation of production by pH is probably more frequently important at low than at high hydrogen concentrations (Stengel and Soeder, 1975). Some algae like _Chlorella_ vulgaris (Osterlind, 1950) are unable to use bicarbonate as a carbon source and are restricted to waters with pH values very near or slightly above 7 since they become carbon limited if pH approaches 8. A further ecologically important action of pH concerns the solubility and hence the availability of polyvalent cations such as iron (Wetzel, 1965). Reducing and acid conditions promote the solubility of iron, whereas iron precipitates in alkaline and oxidizing conditions (Cole, 1983. Iron is found in acid to neutral waters which are very low in oxygen and with redox potentials between 0.3 and o.2 v.

The most productive saline lakes, including Red Rock Tarn in Australia (Hammer, 1981), Mariut in Egypt (Aleem and Samaan, 1969) and Aranguadi in Ethiopia (Talling et al., 1973), tend to have pH values between 9.0 and 10.5. These high alkalinity lakes are so well buffered that pH tends to be stable at high levels.

In the Ethiopian rift valley, pH values for surface water were found to be 8.7-8.8 for Lake Awasa, 7.6 for Moki river, 8.0 for Black river (Tikur Wiha), 8.6 for Lake Chammo and 7.4 for Lake Ziway(Makin et al., 1975).

Carbon dioxide limitation of photosynthesis is most likely to occur in waters of low alkalinity (Schindler and Fee, 1975) where the liberation of CO_2 by degradation of sewage-borne organic substrates may result in an escalation of eutrophication (Lange, 1971).

Salinity becomes the limiting factor in production only under extreme conditions, i.e. in hypersaline waters (Stengel and Soeder, 1975). Extremely dense algal populations with very high rates of photosynthesis are found in hypersaline lakes of very high alkalinity and $_pH$ (eg. Aranguadi) or with relatively low alkalinity and near neutral $_pH$, as in Lake Mariut in Egypt (Beadle, 1981).

The most saline Lake, Lake pink in Australia has very low production (Hammer, 1981). Another lake, Waldesa in Canada (Hammer, 1978; Hammer and Haynes, 1978; Hammer et al., 1978) is similar in productivity to Lake Pink but has low salinity. The most productive lakes tend to encompass a broad spectrum of salinity from 3 to 10 m S cm^{-1}, although most of the highly productive lakes fit into the 3 to 50 m S cm^{-1} range (Hammer, 1981).

In the Ethiopian rift valley salinity tends to increase from Ziway (Makin et al., 1975) to Lake Shalla (Baumann et al., 1975). Hora Orgona, a high mountain lake in Bale (Ethiopia) is known to have considerably elevated salt content due to the contribution of alkaline Trachyte of the surrounding rocks (Loffler, 1978). Lake Awasa has very low salinity which, according to Beadle (1981), is attributable to probable seepage as subterranean outflow through the bed of the lake.

It is known (Elster, 1965; Stern, 1975) that within certain limits, there is no general correlation between the trophic level of a lake and the photosynthetic activity of its phytoplankton at a given time. At similar environmental conditions, relative photosynthetic activities may differ by more than one order of magnitude (Elster, 1965). These discrepancies point to the importance of physiological status of algae (Fogg, 1980; Westlake, 1980).

Given an optimum temperature, with unlimited nutrients and CO_2, the theoretical limit to the rate of photosynthesis would be set mainly by the numbers of algal cells that can be exposed to the most light below the inhibiting light intensity for the longest time (Talling, 1970). Doubtless, the productivity of phytoplankton depends on a complicated and multidimensional network of extrinsic and intrinsic factors besides the availability of nutrients, inorganic carbon, light and temperature conditions.

III. Description of the Study Area.

Lake Awasa (Fig.1), the study area is a lake of fairly high altitude found between the four northernmost lakes (Shalla Abiata, Langano, Ziway) and the two southernmost lakes (Chammo and Abaya) of the main Ethiopian Rift Valley. The lake basin is totally enclosed by faulting, a feature which renders it unique (Mohr, 1962). Some of the physical and chemical characteristics of the lake as described on previous works are given in table 1.

The lake has no discernible outlet, and its comparatively low salinity is, according to Beadle (1981), probably due to subterranean out flow by seepage through the bed of the lake. It is fed by the Tikur Wiha river, which enters from north-east draining an extensive swamp, which is a remnant of a drying lake, lake Shallo. The main runoff entering the lake is derived from slopes to the south and east of basin. The catchment to the north and west appears to contribute little surface runoff possibly due to permeable volcanic soils (Makin et al., 1975).

The lake is oval in shape. The drainage basin is of varied relief, predominantly agricultural and is underlain by quartz and pumice (Mohr,1960). The geology of the lake is documented in Mohr (1960,1962).

The lake experiences a pronounced fluctuation of water

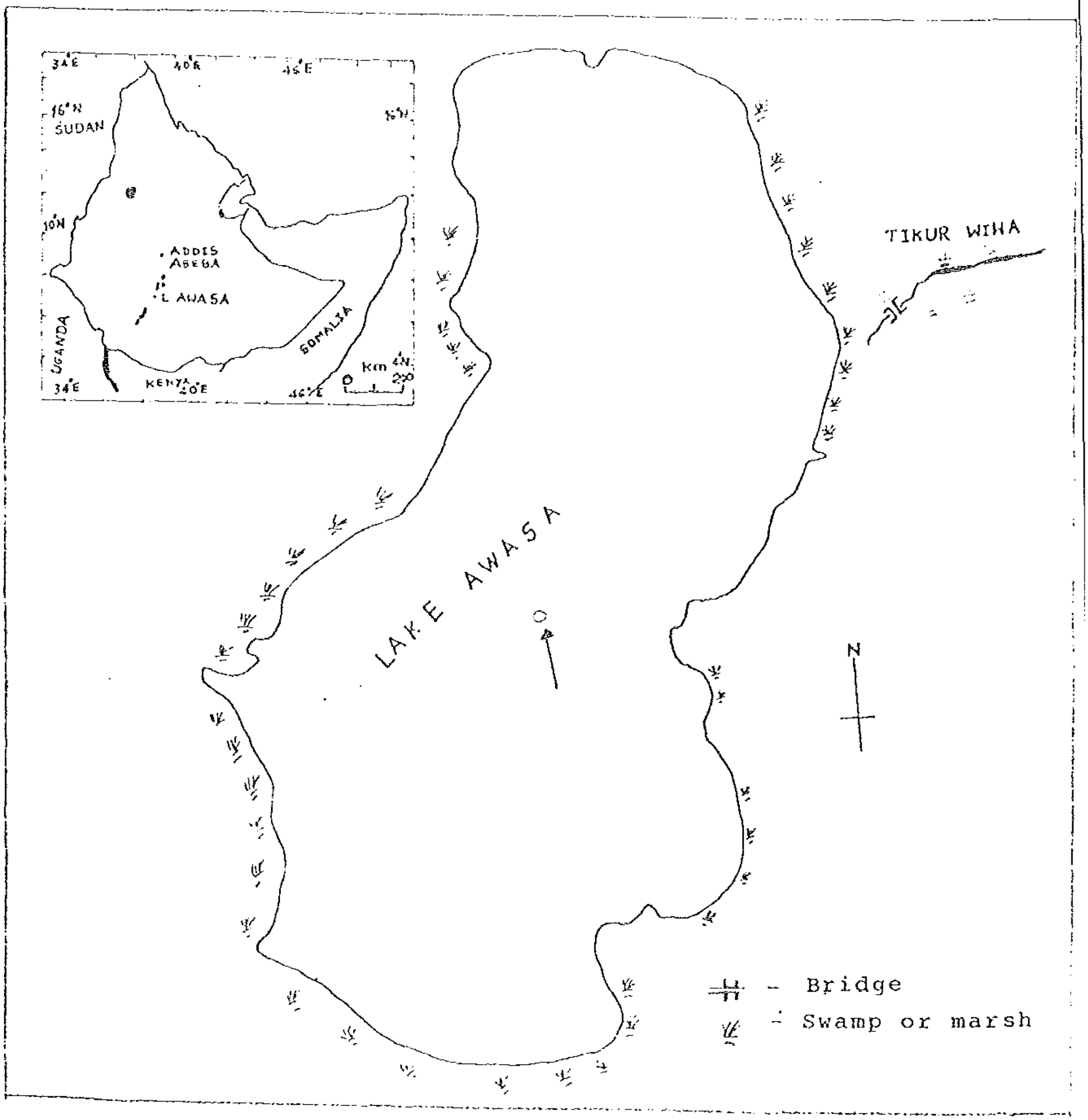

Fig. 1. Map of Lake Awasa with the sampling station indicated by an arrow.

level with alternating dry and wet seasons. There are indications that it may well have stood some meters above its present level in the relatively recent past (Grove and Goudie, 1972). The annual rainfall over the area is between a monthly average total rainfall of 26.7 mm for the driest months (November-December-January) and 133 mm for the wettest months (July, August and September)(Tilahun Kibret, 1985)

The lake has an extensive littoral emergent and submergent macrophyte vegetation with *Potamogeton schweinfurthi*, *Pospallidium germinatum*, *Typha latifolia* and *T. angustifolia* as the dominant species. Among the plankton, the diatom assemblages include some species of the genera *Melosira*, *Nitzschia*, *Cyclotella* and *Navicula* (Gasse *et al*., 1983). Baxter *et al*. (1965) reported the prevalence of phytoplankton of mixed myxophyceae. According to Getachew Teffera (unpublished data) the lake plankton includes Cyanophyta (*Chroococcus*, *Gleocystis*, *Microcystis*, *Gleocapsa*, *Arthrospira*, *Oscillatoria*, *Gleotheca*, *Merismopedia*), Chlorophyta (*Botryococcus*, *Scendesmus*, *Ankistrodermis*) and *Bacillariophyta* (*Pinularia*, *Cymbella Navicula*).

There is a flourishing commercial fishery which is based almost entirely on *Oreochromis niloticus*. The species of fish encountered in the lake are *Oreochromis niloticus*, *Barbus gregorii* and *Clarias* sp. (Getachew Teffera, pers.

Table 1. Some characteristics of the lake

Characteristic	
Latitude *	$6^{\circ}33' - 7^{\circ}33'$ N
Longitude*	$38^{\circ}22' - 38^{\circ}29'$ E
Altitude*	1680 m
Area***	88 km^2
Volume*	$1.3 \times 10^9 m^3$
Depth-maximum*	22 m
-mean*	11 m
Maximum length*	17 km
Maximum width*	11 km
Shore- line length *	52 km
Catchment area*	1250 km^2
Conductivity (K_{20})**	1050 μmho cm^{-1}
Total dissolved solids ** (TDS)***	650.4 mg/l
Na**	235 mg l^{-1}
K **	45 mg l^{-1}
Ca**	4.4 mg l^{-1}
Mg **	4.7 mg l^{-1}
$HCO_3 + CO_3$**	10.5 mg l^{-1}
CL**	34 mg l^{-1}
SO_4**	2 mg l^{-1}
Total P	98 μg l^{-1}
SiO_2	72 mg l^{-1}

* from Welcome (1972)

** from Talling and Talling (1965)

*** from Herrmann (unpublished data)

comm.; Shibru Tedla, 1973). Close to the lake, th
life is rich and varied. Limnological studies mad
lake are limited and of short-duration. Previous
include those of Baxter *et al*. (1965), Talling and
Gasse *et al*. (1983) and Amha Belay and Wood (1984)

IV. Materials and Methods

The following parameters were measured durin study period (November, 1983- March, 1985).

1. Biological parameters

1-1. Phytoplankton photosynthesis

For the first four months of the study pe integrated samples were collected. Thereafter, samples were collected with a Van Dorn sampler 5 litre capacity. The collected materials were into 120 ml pyrex clear and dark (covered with glass bottles which were attached at intervals and suspended at depths distributed over the eu zone. The dark bottles (one pair) were incubat the bottom of the series of bottles. Samples w for four hours (10:00 a.m-2:00p.m).

A buoy was used which consisted of two fl connected by a rigid metal tube from which line bottles could be hung without shading. Duplica were always used from which the mean values wer

Photosynthesis and respiration were measu change in oxygen concentration in dark and ligh Oxygen concentration was determined by the Wink (Mackereth *et al.*, 1978).

1-2. Phytoplankton standing crop (=Biomass)

Pigment extracts were used to estimate

standing crop. The phytoplankton samples were off from 0.25 to 1.0 litre of lake water with W GF/C glass fiber filters and extracted using wa methanol as the solvent. The absorbance of cen pigment extracts was measured at 665 nm (the r maximum) spectrophotometrically and corrected f possible turbidity by subtracting the correspon reading at 750 nm. The corrected value was use calculate the optically equivalent concentratio chlorophylla using the approximate relations of and **Driver**(1963). No determinations of chlorop degradation products were made.

2. Physical parameters.

During the incubation, the photosyntheticall radiation (Ph.A.R) for the incident radiation falli horizontal surface was measured at 30-minute interv using IL-COR quantum sensor (LI-190)SB) connected t integrator. The values obtained for the different periods were calculated and compared. The readings converted to cal cm^{-2} h^{-1} after caliberation with a instrument that records in g cal cm^{-2} min^{-1}.

Light penetration was measured using a selen cell in a waterproof housing with diffusing opal an color filters which were of the types VG9, BG12, RG RG610, RG695, BG7 and VG14 of Schotts, Mainz, West

Germany. The operational mid-points of the cell-fi combinations were approximately 540, 460, 630, 610, 530 (Ganf, 1974 b; Ganf and Horne, 1975; Wood *et al* The optical characteristics of the lake at differen of the year were compared in terms of extinction coeffic Extinction coefficients (ε, In units m^{-1}) were calcu using the following relation

$$\varepsilon = \frac{1}{Z} \ln \frac{I_o}{I_Z}$$

Where I_o is the intensity just below the surface an the intensity at depth Z in m (Wetzel and Likens, 1 Euphotic depth (Z_{eu}) was determined by ascribing 30 35% of the Ph.A.R. to the blue, green and red spect respectively (Talling, 1957). Z_{eu} was also calcula using the relation which was found to give the best fit for optically wide range of East African lakes (1965 a; Ganf, 1974 b).

$$Zeu = \frac{3.7}{\varepsilon\ min}$$

where ε_{min} is the extinction coefficient of t penetrating component of light.

Underwater photosynthetically active radiatio measured in $\mu E m^{-2} S^{-1}$ with LI-COR quantum sensor (LI which was connected to LI-185 B quantum photometer.

Lake transparency (= vertical visibility)
using a standard secchi disc.

Depth distribution of temperature and oxygen
followed by readings taken on a dissolved oxygen mo
using a dissolved oxygen probe with builtin thermis
(YSI Model 57) thermometer. Percentage saturation
oxygen was calculated as in wetzel and Likens (1979

3. Chemical parameters

In situ conductivity (in μmho cm^{-1}) and sal
were measured with a combined conductivity and sali
meter probe, and a thermistor temperature sensor (Y
33 S-C-T meter). Temperature corrections to 25°C w
made as in Wetzel and Likens (1979) for *in situ* con
measurements.

In situ pH measurements of lake surface wat
made with a portable digital pH meter (Model 607).

Water samples collected in polythylene bottl
the lake surface or from various depths and filtere
Whatman GF/C glass fiber filters were used for seve
analyses. Alkalinity due to carbonate and bicarbon
determined by titration with HCl to pH 4.5 with met

as end-point indicator. These results were used wi p^H of the samples to approximate total free CO_2 as Lind (1979). Chloride was estimated by titration wi nitrate using chromate indicator (APHA *et al.*, 198 phosphate (without extraction) and silica (after di with $NaHCO_3$) were determined colorimetrically as th molybdate complexes. Nitrite was measured colorim diazotization with sulphanilamide and by azo compou with N-(1-naphthyle ethylene diamine di-HCl) (Golte Nitrate was measured as nitrite after reduction wi Society for Microbiology, 1981). Sulphate was det pitation as barium salt and by spectrophotometric turbidity (APHA *et al.*, 1980). Sodium and potassi by flame photometry and calcium and magnesium by

Explanation of the symbols used throughout are listed below. The symbols are those used by T *et al.* (1973) and Ganf and Horne (1975).

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

ε_{min} - minimum extinction coefficient over the s

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

$Z_{eu_{cal}}$ - euphotic depth calculated from the relati

$Z_{eu_{det}}$ - euphotic depth determined as depth of 1% irradiance

$Z_{eu}(max)$ - euphotic depth at zero chlorophyll concen

B - population density or standing crop, in
ΣB - population density per unit area (populat
in the euphotic zone), in mg chla m^{-2}
A - gross photosynthesis per unit water volum
mg $O_2 m^{-3} h^{-1}$
A_{max} - light-saturated rate of photosynthesis pe
water volume in mg O_2 $m^{-3} h^{-1}$
ΣA - hourly rate of gross photosynthesis per u
in g $O_2 m^{-2} h^{-1}$
$\Sigma\Sigma A$ - daily integral gross photosynthesis, in g
ϕ (=A/B) - specific rate of gross photosynthesis per
biomass (standing crop), in mg O_2 (mg chl
ϕ_{max} - light-saturated rate of gross photosynthes
of chlorophyll a, in mg O_2 (mg chl a)$^{-1}$ h
Ph.A.R.- photosynthetically-active radiation in cal
or $\mu E m^{-2} s^{-1}$
S_D- secchi depth, in m.
I_o- Irradiance immediately below the surface
(400-700 nm)
I_K - irradiance measuring onset of light-satura
of photosynthesis, in % of the irradiance
below the surface.
Optical depth - $\frac{Z_{mix}}{Z_{eu}}$ where Z_{mix} is the freely mixed
Z_{eu} is euphotic depth determined as
1% level of irradiance.

V. Results and Discussion

1. The thermal characteristics of Lake Awasa

The seasonal patterns of depth distribution and oxygen are given in Fig 2.

The temperature of the surface water of Lake averaged 23.8°C with a maximum of 28.4°C in May and minimum of 20.5°C in February, 1984. The temperatu the deeper layers did not show very pronounced vari and averaged 21.0°C with a maximum of 23.2°C in May a minimum of 20°C in February, April, 1984 and Janu

The temperature of the upper 1 m stratum was higher than that of the underlying layers. The max recorded temperature difference between surface and deepest depth of measurement (15m) was 5.2°C (May,1 and the minimum was only 0.5°C (February, 1984). O sampling dates, from about 5 meters downwards the t was nearly uniform.

The vertical temperature profiles measured d study period usually lacked pronounced stratificati thermal gradient extended from the surface to an al isothermal region below the depth of superficial he

Although gentle thermal gradients prevailed the upper part of the water column, there has been

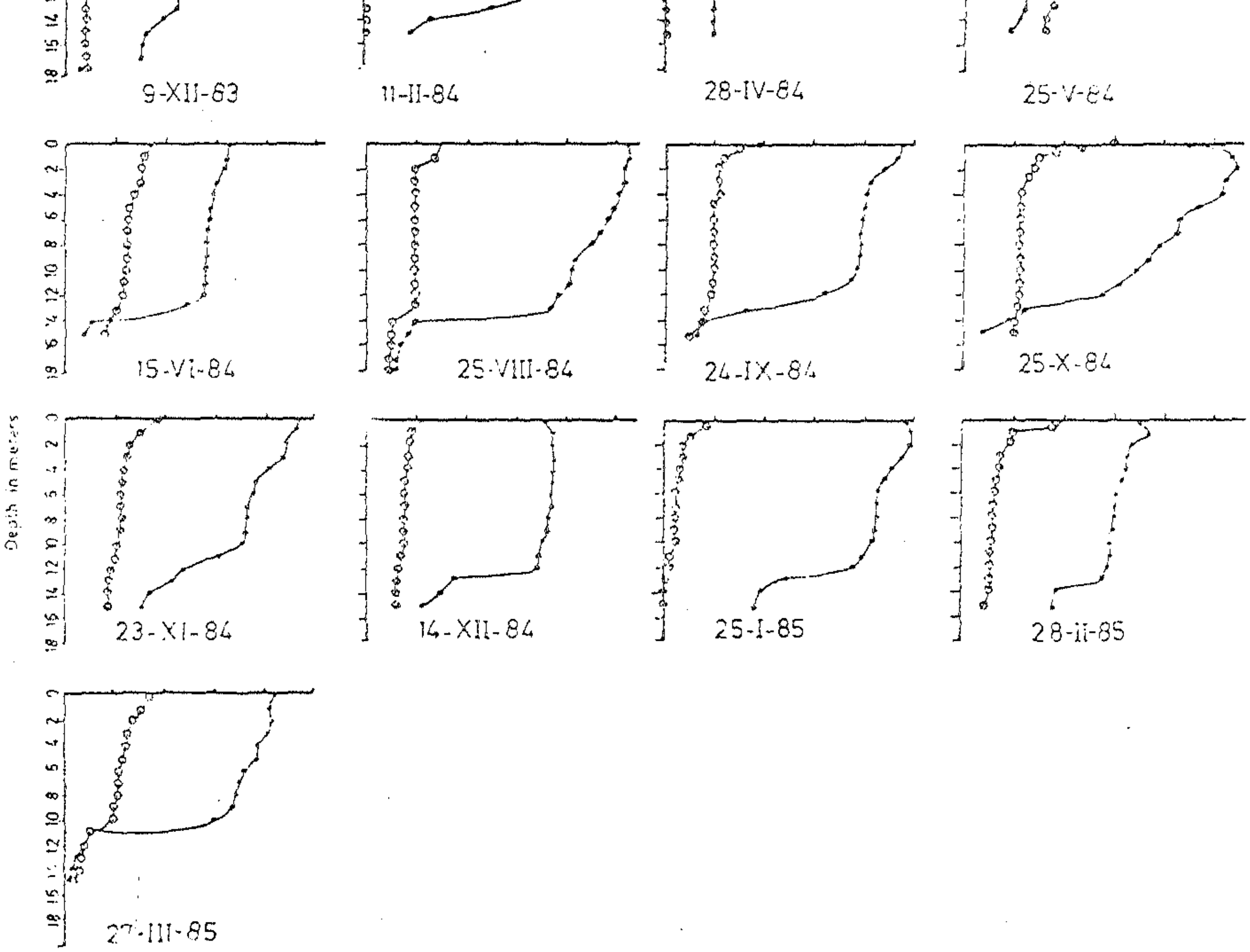

Fig. 2. Depth profiles of temperature(•) & oxygen (•)

indication of strongly developed (deep-seated) therm fication. Instead, there has been thermal stratific of the superficial type described for tropical Afric lakes of moderate altitudes (Baxter et al., 1965). superficial type of stratification which was observe the lake is the expected result of solar heating dur calm periods. Even this stratification affected mai 0-1 m stratum in which steep gradients of temperatur hence of density could develop. There were some cas multiple thermoclines. In such cases the thermal gr were either very gradual, as in December, 1983 or st in April and August, 1984.

But it was noted (Herrman, pers-comm.) that middle of March, 1984, there was a well marked strat with a sharp thermocline and anoxic lower layer. Th same phenomenon was observed in March, 1964 by Baxte (1965) when the thermal discontinuity occupied betwe 5 and 12 m.

According to Baxter _et_ _al_. (1965) thermal st was rudimentary in Lake Awasa during their February samplings, but well-marked during their March sampli

According to Getachew Teffera (unpublished d the superficial stratification that results from sol heating during calm sunny periods seems to be shortfor frequent strong winds from northeast of the lak able to create wave action sufficient to mix it. C or almost complete mixing occurred in Lake Awasa in June and December, 1984. The mixing phenomenon is associated with overcast skies and turbulence.

Generally, the near uniformity of the physi parameters measured along the vertical profiles in afternoon (Getachew Teffera, unpublished data) seem indicative of the frequent occurrence of mixing in the upper half of the water column in Lake Awasa. mixing of lakes is not uncommon in East Africa. Th and exposed East African lakes such as Lake George, (Ganf and Horne, 1975) and Kilole, Ethiopia (Wood e are frequently stirred except in rare periods of ca Well-marked and prolonged stratification has been f the deep and well-sheltered lakes such as Lakes Pawl Bishoftu in Ethiopia (Baxter *et al*., 1965).

Temporal changes in oxygen concentration we during the study period (Fig 2). These fluctuation be the result of the fluctuations observed in phyto photosynthesis or local climatic conditions.

All depth profiles show an oxygen maximum i 0-3 m layer. Seasonal variations in these oxygen m were observed (Fig.2). The concentration of oxyger upper 0-3 m layer lay between 71 and 130% of satura values. The higher concentrations of oxygen were, of the time, associated with higher photosynthetic activity (Fig.4D).

Dissolved oxygen was usually lower at the s lake. The decline of oxygen concentration at the s is attributable to the influence of rising temperat the solubility of oxygen. It could also be the res less contribution of photosynthesis as a consequenc light inhibition, since surface maxima of oxygen co were observed on cloudy days. As a result of the s oxygen produced by photosynthesis in the 0-1 m laye if the weather continues to be calm.

Below the 0-3 m layer the oxygen concentrat very gradually to above 10 meters, whereupon the de becomes sharp to 13 m and the concentration becomes negligible at about 15 meters. The oxygen concentr below the trophogenic zone was always below saturat suggesting probably that consumption of oxygen per area was higher than the net rate of influx from th trophogenic zone.

The substantial oxygen deficit that existed times in the deeper water columns should be expecte occur in a productive lake water. In a lake like A where there is a fairly abundant organic matter for and decomposition, depletion of oxygen in the deepe of the water column is to be expected.

2. The optical characteristics of Lake Awasa.

The photosynthetically active radiation (Ph on the lake surface on days of primary production m is given in Table 6. and its seasonal trends are in in Fig. 7A. The Ph.A.R. was high (29-30 cal cm^{-2}h^{-} for the low value (13.5 cal cm^{-2}h^{-1}) recorded in Se under cloudy conditions.

The vertical extent of underwater illuminat hence of the photosynthetic zone is controlled to a extent by the minimum extinction coefficient, ε_{min} (Talling, 1957b). The vertical extinction coeffici three spectral blocks red, green and blue as appro RG 630, VG9 and BG12 respectively are given in Tabl vertical extinction coefficients are very high for low for red and green indicating that the long wave penetrate the farthest and blue light is attenuated This pattern is similar to that reported for other dense standing crops of phytoplankton or in which t is very turbid due to non-algal materials (Dvihally Vollenweider, 1961; Sakamoto and Hogestu, 1963, Tal

Table 2

Samplin Date
27.XI.8
9.XII.
11.II.8
25.V.84
15.VI.8
25.VII
24.IX.8
25.X.84
23.XI.8
14.XII
25.I.85
28.II.8
27.III

1965a; Talling *et al* ., 1973., Ganf, 1974b; Ganf and 1975). The reason why blue light is the least penet component in the lakes just considered is that phyto have marked effects on light in the blue region of t (Talling, 1960a, 1970; Ganf, 1974b) and attenuation solids is usually highest for blue light (Westlake,

Similar results were reported for Lake Awasa (Amha Belay and Wood, unpublished), the four norther lakes in the Ethiopian rift valley (Wood *et al*., 197 for Lakes Chammo and Abaya (Amha Belay and Wood, 198 Lake Hayq, Ethiopia, the situation is different. Th in Lake Hayq has the greatest transparency for green least for red (Baxter and Golobitsch, 1970).

The minimum vertical extinction coefficients (the extinction coefficient of the most penetrating (Talling, 1957b) showed some seasonal variations (Fi with the highest values in December, 1983, September and March, 1985. These values coincided with period relatively high algal crops or increased concentrati dissolved materials or both (see Fig 4 and 7).

By adopting an appropriate value for increme change in extinction coefficient per unit changes in a concentrations (specific extinction coefficients, (Talling, 1960a), it is possible to calculate the p of light extinction due to algae and the depth of t zone at 0 chlorophyll a concentrations, Zeu_{max} (Wood *et al.*, 1978). E_s values were frequently found bet and 0.02 in units per mg chl a m^{-3} (Talling, 1965a; loss, 1974; Ganf, 1974 b; Berman, 1976; Jewson, 197

Here an E_s value of 0.015 has been used to the percentage light extinction due to algae and th depth at 0 chlorophyll a concentrations $Zeu_{(max)}$ (T The percentage extinction due to algae is always le 50% and seems to indicate that the background atten light is more important than attenuation by chlorop The percentage of light extinction due to algae sho values in August, November and December, 1984 durin algal crops were relatively high (Table 3).

Lake Abiata, with an algal crop of 56.6 mg was found to have only 22% of light extinction due (Wood *et al.*, 1978). According to Wood *et al.* (197 percentage light extinction due to algae in Lake Zi and Shalla was less than 10, and the calculated Zeu each of these lakes was only a little greater than measured Zeu. In Lake Abiata and Awasa, the $Zeu_{(ma}$ be as much as 50% (Wood *et al.*, 1978) and 40% respe

greater than the measured Z_{eu}. Light attenuation d non-algal causes is large in all lakes of the north Ethiopian rift valley as the % light extinctions du algae suggest (Wood et al., 1978). In lake Awasa, ground attenuation is more apparent at the low valu crop. In lake George, Uganda, non-algal attenuatio was found to be high (Ganf, 1974 b). In Lake Arang et al. 1973) the extinction of light due to algae important than in any other Ethiopian lakes.

The transparency of the lake as approximate a standard Secchi disc varied between 65 and 95 cm High Secchi disc readings (> 88 cm) were found in M December, 1983 and December, 1984. The lake is of high transparency though not as transparent as lake Ethiopia (S_D=8-9m) (Baxter and Golobitsch, 1970) an Shalla (Z_{eu}, 3.7-4.93)(Wood et al., 1978; Amha Bel Wood, 1984). In the very productive alkaline salin in Africa, Nakuru and Elementeita, Kenya, Secchi di readings of only 15 and 17 cm were found (Melack an 1974). In these lakes extinction coefficients (in

for blue were as high as 50 and 10-12 for red and
These values are high in comparison with most natu
produce very shallow euphotic depths (Talling <u>et</u>

The relation of Secchi depth to the compens
has received attention in the literature since Poo
(1929) calculated an approximate ratio of $\frac{1.7}{SD}$ in w
the Secchi depth in meters. The quotient gives th
extinction coefficient of light absorption. Limno
also tried to find factors which can be used to tr
euphotic depth by determining the ratio Zeu/$_{SD}$.
the mean depth of the euphotic zone (2.34m) and th
depth (0.77m) in lake Awasa is a quotient very clo
factor, when multiplied by the Secchi depth in met
depth of the approximate compensation point for La

Among four Kenyan freshwaters the average Se
of Lake Awasa is closer to Lake Oloidien (Melack, 1
Lakes Naivasha and Winam Gulf have Secchi depths ra
1-1.5 meters, whereas L. Crescent Island Crater has
depth of 4.6 meters (Melack, 1979a).

The Euphotic depth (m) (i.e. the depth at wh
of the surface light intensity is found) (Talling,
Talling, 1960b; Fogg, 1980) varied between 1.59 and
(see table 2). These values were in close agreemen
Zeu taken as equal to $\frac{3.7}{\epsilon_{min}}$ in which ϵ_{min} is the exti

(Talling, 1957b; Talling, 1965a; Ganf, 1974b). The values (Zeu cal) were, of course always greater th measured (Zeu det). The average of Zeu of lake Aw is more than twice that of Lake George, Uganda (Ga about 5-10 times that of the most productive lakes Lakes Aranguadi and Kilole (Talling *et al*; 1973).

Talling (1957b) defined the limit of the e as equal to the depth at which 1% of the surface p irradiance is detected. It was, however, found he elsewhere (Talling, 1965a; Talling *et al*., 1973; B 1976; Grobellar and Stegmann, 1976) that some evol O_2 still takes place below the 1% level of the inc irradiance. Although there is little doubt as to lity of assessment of the euphotic zone by means o synthetic profile, expression of the euphotic zone of the incident irradiance penetrating to the vari depths will undoubtedly persist since it is more e quickly measured. Moreover, since light is a cruc for primary production, the determination of the e zone by the penetration of the Ph.A.R. in natural seems to be justifiable.

For most of the study period the euphotic Lake Awasa were somewhat intermediate between the deep lake Shalla and optically shallow lakes Zwei, and Langano in Ethiopia (Wood *et al*., 1978).

In lake Abiata, the shallowness of the eup is due to high algal crops whereas in Lake Langano colloidal-based turbidity is responsible for the s of the euphotic zone. In lake Awasa, the underwat is determined by the extinction of light due to ph and non-algal materials as in any other lakes. Bu crops seem (Table 3) to contribute a lot to the at of light. The euphotic zone of lake Hayq is expec very deep as can be implied from the very low mini coefficient (0.17 in units m^{-1}) (Baxter and Golobi

In spite of what the cause of light attenu a lake is, the absolute depth of the euphotic zone is of less significance than the ratio of freely m (Z mix) to euphotic depth (Zeu), which is known as depth (Wood *et al*., 1978).

There has been no indication of strongly d stratification in lake Awasa for most of the study It, therefore, seems reasonable to assume the freq of mixing in lake Awasa and consider that its mixe is equal to the mean depth $(\bar{Z})$ as done by Wood *et* for other Ethiopian rift valley lakes. In line wi

assumption, the optical depths (Z_{mix}/Z_{eu}) were calc
given in Table 2. It can be seen that for most of
period the optical depth of Lake Awasa was less tha
taken by Wood *et al.* (1978) for the light-limitatio
production. The optical depths of Lake Awasa seem
the absence of light limitation as compared to lake
and Shalla for which values in excess of 15 and 26
were found (Wood *et al.*, 1978). The optical shallo
Awasa is not, of course, comparable to that of Lake Z
optical depth values were found to fall for below t
The optical depths of Kenyan freshwaters range from
Island Crater) to 6.9 (Oloidien) with an intermedia
5.1 for Naivasha (Melack, 1979a).

In light of the calculated optical depths,
assumed that relatively larger proportions of the w
columns in Lake Ziway, Awasa and Crescent Island Cra
illuminated as compared to the other lakes just con

2. The surface water chemistry of Lake Awasa

The major chemical constituents of the sur of Lake Awasa are given in Table 4A.

The total ionic concentration was approxima the concentrations in milliequivalents per litre (m of both the principal cations ($Na^+ + K^+ + Ca^{++} + Mg^{++}$) principal anions ($HCO_3^- + CO_3^= + CL^- + SO_4^=$) (Talling 1965; Wetzel and Likens, 1979; Wetzel, 1983). The the concentrations of the anions and cations were f agree fairly closely with each other.

The salinity of Lake Awasa water is express sum of the eight major cations and anions in mass p ($mg\ 1^{-1}$). The salinity of the lake is very low, al than 1 gm, and is only one-twentieth of the salinit Shalla ($16\ g\ 1^{-1}$) (Baumann et al., 1975). Since th discernible outlet, the low salinity of the lake is to subterranean outflow by seepage through the bed lake (Beadle, 1981). According to Richardson and R (1972) and Gaudet and Melack (1981), various freshe mechanisms may have operated in African rift valley during the past 5000 years, including burial of alk layers, underground seepage and ion removal by aqua

[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Electrical conductivity (K_{25}) is not well cor (R=-0.03) with the estimates of total ionic concent This is to be expected in light of the non-liner r between the concentration of solutes and conductivi 1963) especially for minor constituents of lakewate (Wetzel, 1983).

The lake is basically similar to other Afric with sodium as the major cation and bicarbonate + the predominant anions. This pattern of ionic domi characteristic of many African lakes studies (see Wood, 1965; Talling and Talling, 1965; Prosser et Baxter and Golobitsch, 1970). Potassium is always amounts than sodium and its concentration usually in a manner parallel with the increase in salinity is always in excess of magnesium as in Lake Chammo (Amha Belay and Wood, 1982), Lakes Zwei and Tana and Talling, 1965) an Tikur Wiha river all in Ethi (Tilahun Kibret, 1985). This dominance pattern is from that of Lake Hayq, Ethiopia (Baxter and Golob and Bale mountain lakes, Ethiopia (Loffler, 1978) magnesium is present in higher proportions by equi than calcium. For lake Awasa, the cations are the in the order Na K Ca Mg.

Among the cations, Mg and Ca were found to ch very little seasonally. The concentrations of sod potassium showed seasonal variations with peaks of concentrations during the periods from April to Ju and from January to March, 1985.

The hardness of the lake water was calcula plying the concentrations (mg 1^{-1}) of the two har cations (Ca and Mg) by appropriate factors (Wetzel Likens, 1979). The products were summed to obtain hardness. The average total hardness was found t 1^{-1} $CaCO_3$. According to the classification by Br (1970) the lake water is soft.

Some ionic ratios involving cations deserv As seen in Table 4B, the ratio of monovalent to di cations (Na + K)/(Ca + Mg) are frequently in th 11.0-15.0. These values are much higher than the limit of the ratio (1.5) considered to favor the by diatoms of the algal flora (Wetzel, 1983). Th ratio of calcium to magnesium is very close to 2.

As already indicated, $CO_3 + HCO_3$ is the pr anion. The anionic proportions follow the order This pattern of anionic dominance is characteristi aquatic systems over large areas of the temperate (Wetzel, 1983) including praire ponds (Driver and 1977) and other African lake waters (Talling and 1965; Prosser *et al.*, 1968; Baxter and Golobitsch,

Table 4B. Cation ratios

Date	Monovalent: Divalent	Calciu
27-XI-83	5.7	
28-IV-84	12.0	
25-V-84	14.0	
15-VI-84	13.3	
25-VIII-84	9.1	
24-IX-84	11.9	
25-X-84	10.3	
23-XI-84	6.9	
14-XIII-84	9.2	
25-I-85	11.9	
28-II-85	14.7	
27-III-84	11.6	

Melack and Kilham, 1974; Amha Belay and Wood, 1982

Alkalinity (HCO_3 + CO_3) showed some seasona (Fig 3) with the highest concentrations in Septembe 1984 and February-March, 1985. The $_p$H of the surf water is between 8.7 and 9.05. The highest PH valu observed in April and September, 1984 and March, 19 These values coincided with relatively high alkalin and low free carbondioxide concentrations. The cor (r=0.244) between Alkalinity and PH was poor. This be due to the accumulation of CO_2 from respiration decomposition as well as due to its removal by phot The trend of variation of both $_p$H and Alkalinity is shown in Fig 3. As can be seen in Fig. 3, an incre Alkalinity did not result in a concomitant increase This is probably due to the accumulation of dissolv carbondioxide which tends to reduce the $_p$H. Likewi alkalinity value was found to coincide with high $_p$H is probably the result of the removal of CO_2 from w aquatic plants. This removal increases the carbona which hydrolyze to yield hydroxyl ions and raise th (Boyd, 1979).

Chloride showed little seasonal variation (As has been found for other African lakes (see Beac Talling and Talling, 1965; Baxter and Golobitsch, 1

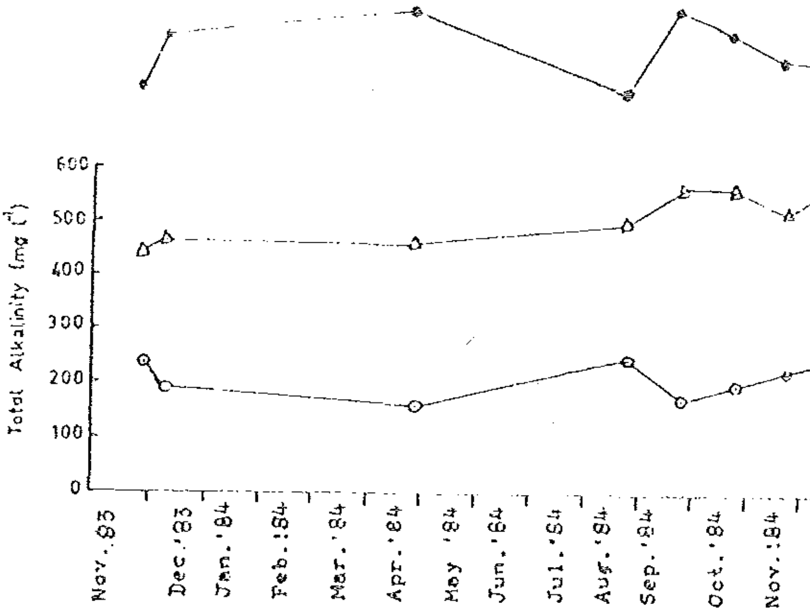

Fig.3 The relationship between Total Alkalinity(Δ
and PH(⊛) .

sulphate concentrations were always low (<5 mg 1^{-1})
has been indicated by Talling and Talling (1965) th
estimation of sulphate by precipitation with barium
might have contributed to the low levels observed.
are, of course, certain African lakes like Lake Mah
Uganda (Melack and Kilham, 1972) and Lake Kitagata,
(Kilham, 1984) in which exceptionally high concentr
of sulphate were found (61000 and 62370 meq 1^{-1} SO_4

Among the major mineral nutrients, silica i
relatively high concentrations (see Table 4A). Thi
have resulted from either the relatively insignific
ribution which diatoms make to the phytoplankton c
or from the dominance by quartz of the rock at the
bottom (Mohr, 1962). Very high concentrations of s
were also reported for Bishoftu crater lakes (Pross
1968) L. Nakuru, Kenya (Melack and Kilham,1974) and
Malawi (Moss, 1969b). Silica was found to change s
with the highest concentrations in December, 1983,
and November, 1984 (Fig. 4).

Nitrate-nitrogen and nitrite-nitrogen are g
in Tropical African saline lakes (Hammer, 1981). L
concentrations of nitrate and nitrite were also rep
many other African lakes (Talling and Talling, 1965
et al., 1968; Amha Belay and Wood, 1982). Lake Awa

concentrations less than $200\ \mu g\ l^{-1}$ is not an excep Nitrate-nitrogen was found to show seasonal variati peaks of concentrations in January, February and Ma (Fig. 4). This is probably associated with evapora ntrations since these months are relatively dry.

High concentrations of phosphate are not at African lakes (Talling and Talling, 1965) especiall lakes including those in Kenya (Nakuru and Magadi; and Kilham 1974) and in Ethiopia (Aranguadi and Chi Concentrations as high as $300\ \mu g\ l^{-1}$ of phosphate we reported for Lakes Chammo and Abaya (Amha Belay ar 1982). But in Lake Awasa reactive phosphate was al than $50\ \mu g\ l^{-1}$. The low concentration of phosphate water could be the result of luxury consumption by (Mackreth, 1953). Phosphate analysis was done with For this analytical reason, it is also likely that has underestimated the concentration of phosphate i Awasa. Phosphate showed seasonal variations, with values during the relatively wet months (June and S The high levels of phosphate in these months could result of phosphate loading of the lake through ru coming from the surrounding agricultural lands dur precipitation.

The seasonal trends of silica, phosphate, a

(Fig.4) probably reflect various stages of runoff, (precipitation), phytoplankton uptake and evaporati processes.

It is intersting to note that the concentra almost all mineral elements in the river that feeds lake, Tikur Wiha (Table, 5) is very low as compare lake. It is likely that the swamp through which th flows can act as nutrient filter with a consequent in the salinity of the river. The higher salinity lake is also the expected result of evaporative con of a closed basin receiving inflows. It is, therefo reasonable to assume that inflows coming through Ti have a dilution effect on the lake water.

In the river, as in the lake, sodium is in concentrations than the other cations, and HCO_3^- is predominant anion. The anionic dominance pattern f same order as in the lake, but the cation proportio different with calcium being in excess of both pota magnesium.

Chemical analyses of lake waters donot nece indicate potentially limiting factors since the aqu environment is a dynamic system in which chemical i between the diversity of organisms and abiotic fact taking place. It is not, therefore, wise to talk o limiting nutrients at this point.

4. Standing crop and photosynthesis of phytoplank Lake Awasa

The phytoplankton of Lake Awasa includes m of diatoms, greens and blue greens. The colonial <u>Botryococcus</u> was frequently seen at the lake surfa streaks. The appearance of high concentrations of at the surface may not necessarily be the result o growth, but of localized events resulting from the effect of wind combined with its buoyant condition fat production.

The seasonal trends of algal crops in Lake measured by chlorophyll a concentrations) in relat inorganic nutrients is illustrated in Fig. 4. Lake exhibited fairly high algal crops for most of the period. The low algal crops observed in November- 1983, and in April-May, 1984 built up in June and 1984. For the low algal crops observed in the fir months of the study period, the possible explanati is that integrated samples taken for the first fou are likely to give lower values as compared to sur in which a very high concentration of <u>Botryococcus</u>

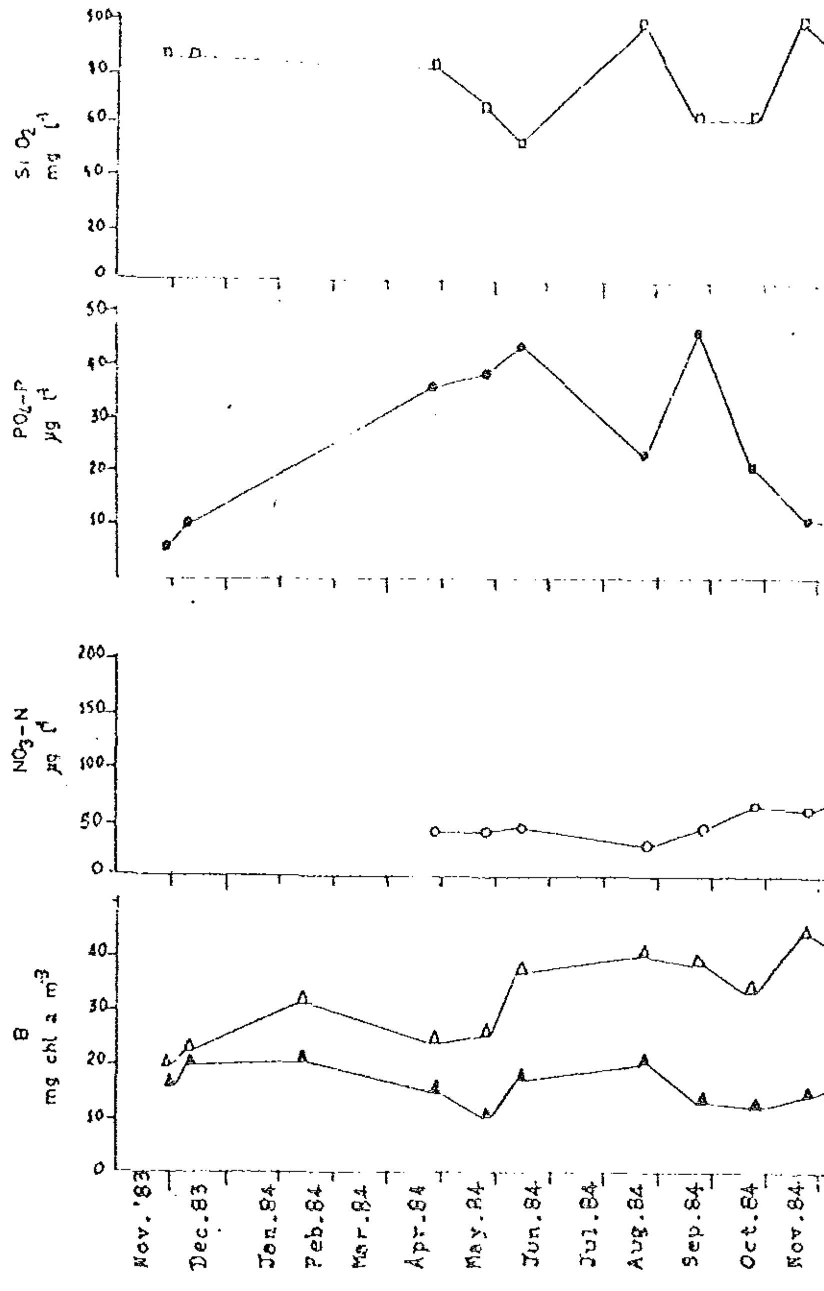

Fig.4. Seasonal variation in phytoplankton standing
light-saturated rate of gross photosynthesis
to inorganic nutrients including
A. SiO_2 (mg l^{-1}, □) B. PO_4-P (µg l^{-1}, ■) C. NO_3-

There was no pronounced variation in the a
from November, 1984 to March, 1985. Generally, th
algal crops observed seem to be the result of incr
concentration of phosphate as a result of runoff c
the lake during periods of precipitation (July-Sep
and of nitrate as a result of the evaporative conc
of lake water during the driest months (November-J
and months of the 'small rains' (February-March).

The high algal crops (as measured by chlor
concentrations) of Lake Awasa are many times highe
those of lakes Langano and Shalla and are a little
that of Zwei and only half of Lake Abiata (Amha Be
1984). The algal crops of Lake Awasa are signific
than those algal crops reported for Ethiopian soda
(225-300 mg chl a m^{-2}) (Talling _et al._, 1973), Lak
Uganda (400 mg chl a m^{-2}) (Ganf, 1974a) and Lake
Kenya (330 mg chl a m^{-3}) (Melack, 1976). The amou
chlorophyll in the euphotic zone is comparable to
zone chlorophyll content of most African lakes lis
Melack (1979a).

It is well established that considerable v
occurs in day-to-day productivity in lakes. The g
productivity picture, however, does emerge from mo
determinations with the degree of loss of precisio

upon the magnitude of population oscillations withi

The measurement of primary production by p in lake Awasa can be compared in a time sequence w interpretation of the results of measurements made relation to temporal changes of population density chemical and physical aspects of **the** lake and its

The depth distribution of gross photosynth unit water volume (A: mg O_2 $m^{-3}h^{-1}$) is given in fi vertical distribution of photosynthetic activity p volume of water was of a typical pattern for phyto (Talling, 1965a; Ganf, 1974a). The depth profiles synthesis measured in the lake showed variations b the maximum rate (A_{max}) attained and in the extent occupied by the euphotic zone. Because surface or samples were used, the depth variations observed w expression of varying phytoplankton densities but responses of uniform algal material to different l intensities.

For measurements taken on bright sunny day a general tendency in many profiles for the highes rates to be at depths below the surface. The dept production was, of course, dependent upon the lake and amount of surface radiation. The depression o

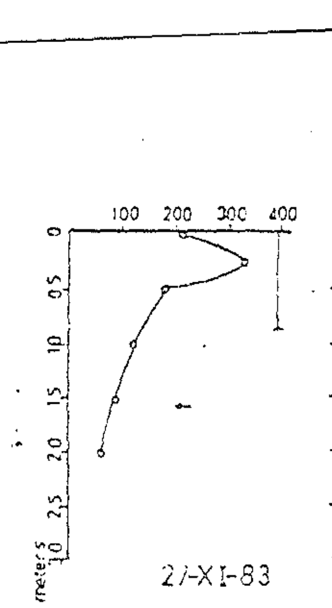
100
200
300
400
0
0.5
1.0
1.5
2.0
2.5
3.0
Depth in meters
27-XI-83
0
0.5
1.0
1.5
2.0
2.5
3.0
24-IX-84

Fig.5. De
Se

surface may be attributable to light inhibition (
Nielsen, 1952, 1962; Ryther, 1956; Goldman et al.
and Kok, 1966 a,b; Soeder and Stengel, 1974) whic
in the inactivation of enzymes involved in photos
(Steemann-Nielsen, 1952; Steemann-Nielsen and Jor
1962). Lower surface photosynthetic activity has
been observed by many workers (Talling, 1957a; Go
Talling, 1965a, 1966a; Lewis, 1974 and Ganf and H
But it is intersting to note that on 14 December,
irradiance of 27 cal $cm^{-2}h^{-1}$ produced a 62% reduc
P_{max} at the surface, whereas on 23 November, 1984
irradiance of 26.8 cal $cm^{-2}h^{-1}$ caused only a 22%
in P_{max}. On February 28 and March 22, 1985 an ir
of 27.09 cal $cm^{-2}h^{-1}$ produced 67 and 50% reductio
respectively. It is, therefore, safe to draw the
that the degree of surface depression of photosyn
in lake Awasa is not a function of only the incid
Similar trends were reported for Kinnego Bay by J

In some cases the zone of inhibition was
to only 25cm from the surface. In others, the zo
was deeper and was found to extend as far as 1.5
from the lake surface. In the latter cases, the
inhibition constitutes a significant fraction of
genic zone, with a consequential reduction of the
photosynthetic activity per unit area.

On the other hand, for measurements taken under cl conditions with intensities less than 1500 $\mu Em^{-2}s$ was no inhibition at the lake surface. In other w maximum photosynthetic activity took place at the with gradual decline in oxygen production because linear decrease in light intensity with increasing

For photosynthetic profiles with light inh the surface, the depth of maximum production (Opti was frequently at 1.00m corresponding to a light i (400-700 nm) of 10 to 20% of the surface irradianc 330$\mu Em^{-2}s^{-1}$) as measured by the underwater photom

From the relationship between the photosyn expressed as a % of the maximum rate of photosynth and irradiance expressed as a % of the intensity j the surface I_o (400-700 nm), the light intensity t the onset of light saturation (Ik, Talling, 1957a) determined . The values obtained were between 8 t sub-surface irradiance (400-700 nm). The % range to 1.2-3 cal $cm^{-2}h^{-1}$ with most values close to 2.4 The incident irradiance (400-700 nm varied with of 29.3-30.1 cal $cm^{-2}h^{-1}$ apart from one lower value $cm^{-2}h^{-1}$) measured on a very cloudy day (September

The light saturated rates of photosynthesi fairly high ranging from 217 to 425 $mgO_2\ m^{-3}h^{-1}$, w about a twofold variation. These maximum rates ar equivalent to a fixation of carbon amounting to 68 mg C $m^{-3}h^{-1}$ if a photosynthetic quatient of 1.2 is

The maximum rates of photosynthesis (A_{max}) Awasa are usually higher than those reported for l Naivasha and Crescent Island Crater in Kenya (100- 50-180 mg O_2 $m^{-3}h^{-1}$ respectively) (Melack, 1979a). highest maximal rates of photosynthesis (mg O_2 m^{-3} Lake Oloidien and Winam Gulf (750 and 640 respecti however, much greater than that of Lake Awasa (425

The highest and most efficient photosynthet tropical soda lakes occur during the blooms of *Sp* *platensis* (Hammer, 1981). Very high, light-satur of phytoplankton photosynthesis have been reported Aranguadi and Kilole in Ethiopia (10000 and 3420 m C $m^{-3}h^{-1}$, respectively) (Talling *et al.*, 1973), fo Mariut in Egypt (40000 mg C $m^{-3}h^{-1}$) (Aleem and Sam and Lake Simbi, Kenya (4300 mg C $m^{-3}h^{-1}$) Melack,

Several seasonal trends are indicated in Fi Higher maximum rates of gross photosynthesis were during periods of relatively high phosphate or nit concentrations (Fig. 4). It seems that there is a stimulation of growth and photosynthetic activity

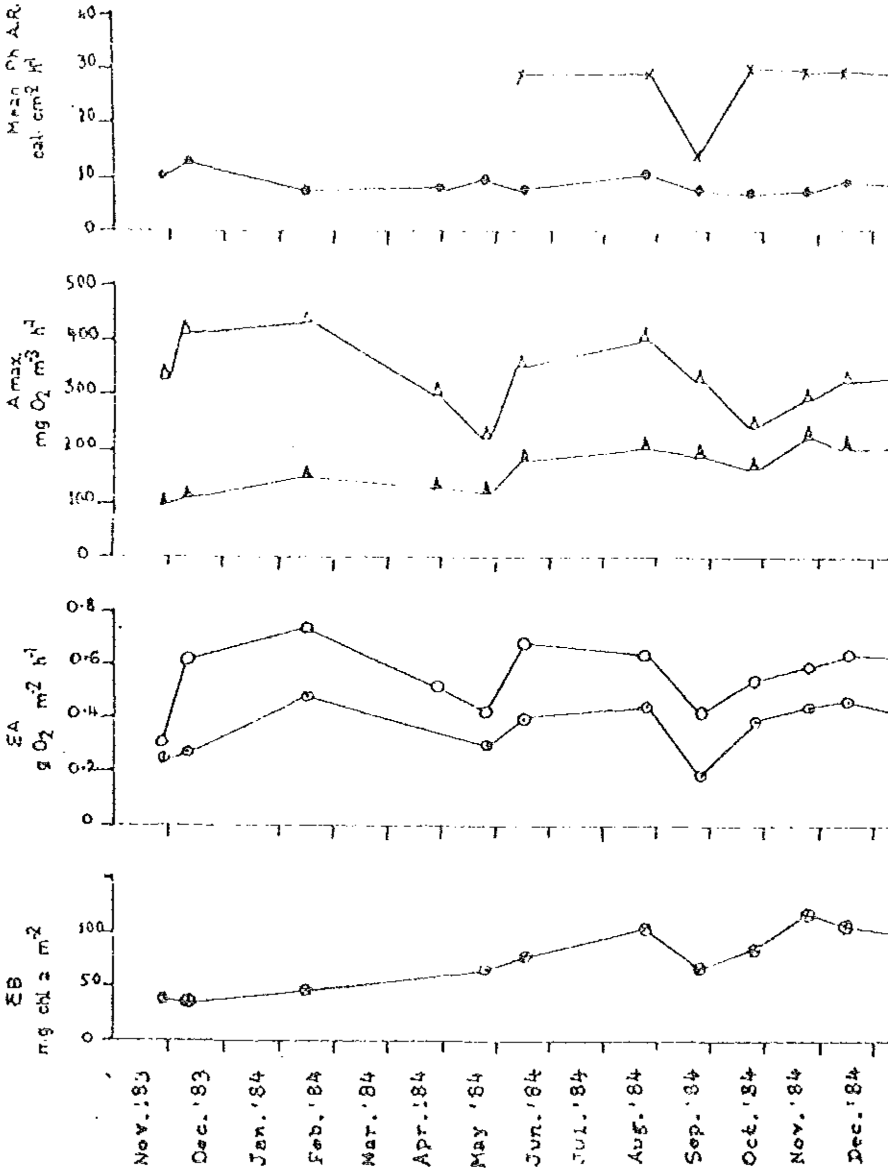

Fig.7. Seasonal changes in factors controlling photosyn
Awasa including A. Mean Ph.A.R. falling on the
(cal cm^{-2}h^{-1}, X), with the minimum extinction coe
B. Maximum rates of gross photosynthesis per uni
(A_{max}, △) with corresponding estimates of popul
C. The ratio $A_{max}/\varepsilon_{min}$ (⊙) in relation to int
per unit area(ΣA , O) ; D. The content of chlorop
tic zone (ΣB, ⊗).

of phytoplankton by nitrate alone or in combinatio phosphorus. The limitation of algal growth in Eas lakes and rivers has frequently been associated wi as the comprehensive studies in the rivers of Nile Talling, 1958; Talling and Rzoska, 1967), in Lake (Talling, 1966a) and in Central African waters (Mo suggest.

The maximum photosynthetic rates are not co (r=-0.008) with the standing crop. But there is a general tendency (Fig 7B) in A_{max} to increase with in Biomass. Pentecost and Happey-Wood (1978) have higher correlations (r= +0.450 and + 0.671) betwee (light-saturated) photosynthesis and chlorophyll c for welsh lakes.

Higher photosynthetic rates in Kenya freshw found to occur with high chlorophyll concentration 1979a). But Talling et al. (1973) found relativel saturated rates of photosynthesis with high algal mg chl a m^{-3}) and the relatively low algal crop(1 chl a m^{-3}) was found to yield the highest A_{max} in Aranguadi. Likewise in Lake Awasa, relatively low were found to yield the highest maximum rates in D 1983 and February, 1984. The observed maximum rat be the result of high photosynthetic efficiency (φ (mg chl a) $^{-1}h^{-1}$) (Hammer, 1981).

Sampli date
27.XI.
9.XII.
11.II.
28.IV.
25.V.8
15.VI.
25.VII 84
24.IX.
25.X.8
23.XI.
14.XII
25.I.8
28.II.
27.III

In all depth-profiles of photosynthesis in
at a certain depth below the optimal depth (depth
photosynthetic activity), the oxygen production fa
a point where it is just equal to the amount consu
respiration and decomposition. This depth, known
compensation depth, was frequently found between 2
meters. For some depth-profiles, the compensation
clearly located. This is probably due to the inad
spacing of the depths of incubation. This depth
found to move upward with decreases and downward w
in penetration of light and surface radiation.

The lower limit of the euphotic zone, as de
by the photosynthetic profiles was found to some w
the corresponding limit of the euphotic zone deter
depth of 1% of the available sub-surface radiatio

Specific rates of photosynthesis (ϕ =
Fig 6) gave depth-profiles similar to those of pho
rates expressed per unit water volume. The specif
low at the surface for measurements taken on days
intensity. The photosynthetic efficiency (ϕ max =
(mg chl a) $^{-1}h^{-1}$; Table 6) for Lake Awasa approa
with most values between 6 and 10 and with high va
during periods of low algal crops. High photosynt
efficiency with low algal crops were also reported

Kinneret in Israel (Berman and Pollinger, 1974) and fo
lakes (Pentecost and Happey-Wood, 1978). High alg
values need not effect high photosynthetic activit
1981). Evidence also exists (Wright, 1960; Finde
Cooper, 1970) for an inverse relationship between c
concentration and photosynthetic capacity.

The highest photosynthetic efficiency value
mg O_2 (mg chl a) $^{-1}h^{-1}$) are greater than those re
lakes Ziway (9.6) and Abiata (14.8) Amha Belay and
1984) but are close to the values reported for La
Uganda (17-18) (Ganf and Horne, 1975) and other E
lakes (25 ± 6) (Talling, 1965a).

The estimation of net primary production is
importance since only the amount of carbon fixed
the respiratory requirements of phytoplankton is
to higher trophic levels. The maximum net photosy
activity (Table 6) averaged 214.6 mg O_2 (66.95 m
with a minimum of 130 mg O_2 (40.56 mg C) $m^{-3}h^{-1}$
maximum of 325 mg O_2(101.4 mg C) $m^{-3}h^{-1}$

Calculation by planimetry of the area encl depth profiles allows an estimate of the areal p activity. The values obtained planimetrically ar in Table 6. Integral photosynthesis ranged from 0.73 g O_2 $m^{-2}h^{-1}$ (0.094 to 0.226 g C $m^{-2}h^{-1}$). Th seem to be more indicative of the maximum rates (mg $O_2m^{-3}h^{-1}$) (Fig 7B and 7C) of photosynthesis t differing depths of the euphotic zone and the pos variations in the specific rates of photosynthesi saturation (ϕ max, see table 6).

Talling (1957b) has shown that if the phot algal population is evenly distributed and not ma differentiated with depth, the ratio $A_{max}/\varepsilon_{min}$ i determinant of the integral photosynthesis per un (i.e ΣA in g O_2 $m^{-2}h^{-1}$). Fig 7C presents the gen between the seasonal variations of these two quan Since ε_{min} tends to increase with the population increase in B would be expected to result in a le increase in the ratio $A_{max}/\varepsilon_{min}$ and hence in the productivity (Talling, 1965a). This divergence a to Talling (1965a) is a seasonal expression of se effects in the algal population. This feature ha **described for** algal populations in an English lak Talling (1960b).

Integral photosynthesis showed some variat variation seems to be dominated by the changes in the variation in population density (Fig 4B)

The seasonal variation of the photosynthet radiation falling on the lake surface (Fig 7A) is apart from the unusually low record on a very clo Its significance for integral photosynthesis is, very much reduced by the effects which light satu on the depth profiles of photosynthesis.

To make the data more comparable to many A the hourly rates were converted to daily rates by used by Talling (1965a) for other East African la empirically derived factor of 0.9 was multiplied of hours of sunlight and the product multiplied by rate. The estimated values of integral photosynt ($\Sigma\Sigma A$, $g_2O\ m^{-2}d^{-1}$) are listed in Table 6. The ca values ranged from 3.3 to 7.8 g O_2 (1.03 to 2.4 g They are very close to those reported for Lake Na Oloidien and crescent island craters in Kenya (Me and are greater than those of Lake Zwei and Abiat Belay and Wood, 1984).

The value (g $Cm^{-2}d^{-1}$) for lake Awasa cor with the highest values recorded for temperate lakes (1 - 3 g $Cm^{-2}d^{-1}$) Talling, 1965a).

Talling (1965a) estimated daily integral
($\Sigma\Sigma A$) that ranged from 2.2-4.8 g O_2 (0.8-1.8 gC)
for the small highland lakes of Bunyoni and Mule
intermediate values of 5.4-10.5 g O_2 (2-4 gC) m
most experiments in other lakes, to a few values
10.5-16 g O_2 (4.6 gC) $m^{-2}d^{-1}$ from Lake George, E
Albert and offshore Victoria water. Melack (197
a daily integral close to 36 g O_2 (11.3 gC) m^{-2}d
Simbi in Kenya.

The efficiency of utilization of photosyn
available radiation by phytoplankton photosynthe
calculated on energy basis as in Lind (1979). T
values indicate that 1.7 to 2.9% of the photosyn
available radiation was utilized in gross photos
production. The very high efficiency of light u
corresponds to measurements taken on very cloudy
Similar results were found by Talling (1965a) fo
water of Lake Victoria. At low light intensity
be high efficiency of light utilization in the a
light saturation effects, because there is a pro
between light intensity and rate of photosynthes
Nielsen, 1957). Moreover, elimination of the re
inhibition would usually increase overall effici
(Tilzer *et al.*, 1975).

High efficiencies appear to be characteri

production with heavy plankton concentration (Mel
In dense phytoplankton suspensions, such as those
of African soda lakes, high efficiencies of light
are possible. This is because a larger proportio
insolation is absorbed by photosynthetic pigments
because surface inhibition and light limitation a
are reduced per cell as the phytoplankton circula
steep gradients of light (Tilzer *et al*., 1975).
lake of Australia-Red Rock Tarn-light utilization
were found to be between 3 to 8% (Hammer, 1981).

The annual mean primary productivity in la
1.88 g C$m^{-2}d^{-1}$ (21.13k cal if an approximate equ
of 3.5 k cal (g $O_2)^{-1}$ is assumed (Cole, 1983). M
taken have shown that the values recorded vary to
within the range of 1.03 g C $m^{-2}d^{-1}$ to 2.43 g C m
calculated annual productivity of the lake is 686
hectare. This value must be viewed as an approxi
because of the monthly interval of sampling and t
variation in porductivity within a month and in d
parts of the lake.

Melack (1979 b) recognized three patterns
variability of phytoplankton primary production i
lakes. The classification of tropical lakes into
patterns recognized was based on calculated coeff

variation (CV, standard deviation divided by mean), Accordingly, the monthly CV of Lake Awasa primary was calculated. The calculated CV value of Lake Av puts it under pattern B with Lakes Naivasha (Melack and Nakuru (Melack and Kilham, 1974) in Kenya and in Ethiopia (Talling et al., 1973) in which there i coupling of primary production and biomass to the s of the weather. Lake Awasa can be best compared to freshwater, Lake Naivasha, fringed by papyrus swam papyrus swamps are believed to have a buffering ef acts of the seasonal rains and effect a regular nu (Melack, 1979a).

According to Melack (1979a) the productivity of Lake Naivasha increased from June to September remained constant. The overall pattern in lake Na corresponded with the rate of change in the lake l

Lake Awasa has an extensive littoral vegeta extends as far as 100 meters towards the centre of littoral vegetation in combination with the swamp which the Tikur Wuha river flows to the lake, may a nutrient filter that reduces the amplitude of the variation in pelagic phytoplankton photosynthesis.

The productivity (g O_2 $m^{-2}h^{-1}$) of lake Awa from November, 1983 to February, 1984 before decli a value in September. Near constancy in primary p was observed from November, 1984 to March 1985. T seem to be associated with the conditions of the d wettest periods. In the former, the evaporative c of lake water and in the latter an increased suppl through runoff from the lake surroundings during p of precipitation seem to be responsible for the hi synthetic rates observed. Both have, of course, d on the lake water level.

In Lake Elementeita, Kenya, the initiation biological change (Melack, 1976; Livingstone and M coincided with a period of rapid lake-level declin evaporative concentration. Other lakes with a coi of primary productivity and rain-induced lake leve include Lake Chad (Lemoalle, 1975) and a fish-pond Ife, Nigeria (Imevbore et al., 1972).

There is comparatively little variation in variation reaching the lake surface. Thus the sea of rainfall seems to play a predominant role in de the nutrient status, algal crop and primary produ phytoplankton in Lake Awasa.

Conclusions and Recommendations

Though not pronounced, spatial (vertical) a variations of phytoplankton standing crop and pri were observed. The vertical variations appear to of variation in the underwater radiation which is the lake's transparency and amount of surface rad observed temporal variations in phytoplankton sta primary production seem to be controlled more by than energy supply. The seasonality of rainfall to play the predominant role in determining the n and extent of algal growth and primary production

Various indices of the nutritional status o plankton production should be included in order t an evidence for nitrogen or phosphorus limitation tion of changes in primary production in response enrichment as a direct measure of the limitation plankton production is, therefore, desirable. Mo our approach is broadened to include sediment che the study will be of greater utility in explainin nutrient limitation of phytoplankton primary prod

It is well known that considerable variation day-to-day productivity in lakes. The general pr picture, however, does emerge from monthly determ in order to get a better picture of the seasonal

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