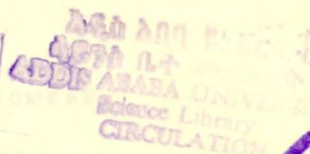
A SEASONAL STUDY ON THE SPECIES COMPOSITION

and

PHYTOPLANKTON BIOMASS

IN LAKE AWASA, ETHIOPIA



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SUMMARY

The species composition and phytoplankton biomass of Lake Awasa, Ethiopia was studied from September 1985 to July 1986, in relation to some environmental factors including thermal, light, and chemical characteristics. During the study period, three phases of thermal stratification were recognized : 1. An unstable stratification period during September to November, followed by complete mixing in December, 2. A stable stratification period during January to April with the beginning of destratification in May, and 3. A mixing period during June to July with an isothermal condition in the whole lake. Complete mixing in June was associated with cooling of air temperature with an influx of cool rain and high rainfall during May to June.

The underwater light penetration showed a similar pattern over the whole period with the highest in the red, and the lowest in the blue spectral region. Euphotic depth varied between 1.6 and 3.0 meters with the highest measurements corresponding to the stable stratification period. The lake water had a fairly high concentration of phosphate (23-45 ug l^{-1}). Low nitrate concentration (7-14 ug l^{-1}) during January to May increased appreciably in June-July with surface values exceeding 100 µg l^{-1} in July. Both nutrients showed increasing values associated with mixing periods and/or the rainy season.

A total of 100 phytoplankton species were identified in Lake Awasa with 48% of the taxa represented by green algae, 30% by blue-green algae, 11% by diatoms, and the rest by chrysophytes, dinoflagellates, cryptomonads and euglenoids. Only 14 species, which comprised about 90% of the phytoplankton biomass, were counted for the whole sampling period. The dominant phytoplankton species were *Lyngbya nyassae*, *Botryococcus braunii* and *Microcystis* species. Seasonal biomass variation was pronounced

in the first two, but not in *Microcystis* species. The total phytoplankton biomass, measured by phytoplankton counting and pigment analysis, increased following the mixing period in December, and thermal destratification during May to July which was also a period with high rainfall and relatively high nutrient concentration. While the seasonal variation of the total phytoplankton community in Lake Awasa was relatively low (coefficient of variation < 20%), it was higher in some of the individual component species.

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CHAPTER I

INTRODUCTION

INTRODUCTION

Phytoplankton are the primary carbon-fixing organisms in the aquatic environment. They provide the base of the aquatic food chain, including the fish population which helps to sustain the ever increasing food demands of man. They are also of great importance in the maintenance of aquatic and terrestrial life in generating about 70% of the earth's atmospheric oxygen.

With the current fast growth of the human population and the advancement of technology, irrational utilization of freshwater resources, eutrophication and toxicity problems, pose a great danger to the ecological balance of the aquatic biota. It is therefore of considerable importance that an understanding of phytoplankton communities, their composition, seasonality and production, as well as the factors which govern their behavior is acquired.

Ethiopia is a developing country with a growing human population depending mostly on agriculture for food, and has been facing drought and famine for some years. In the absence of ecological understanding about the aquatic communities, the need for an alternative source of food will undoubtedly lead to the mismanagement and over-exploitation of the aquatic resources available. If used efficiently and in a rational way, the potential resource can be of great economic importance in providing a continuous supply of food and water and serve in decreasing the burden on the much exploited arable land. Hence the aquatic communities in the country should be given importance and studied in detail.

Although the algal flora of some African lakes have been studied, our knowledge is far from being complete. A number of catalogues and check-lists, as well as detailed investigations on parts of the African flora, have been reviewed by Lemoalle et

al. (1981). The reviewers have pointed out the need for more comprehensive studies on all algal groups covering a wider geographical distribution. They also recommend that phytoplankton studies should not only list the major components of the plankton, but also the rare species so as to get a better knowledge of their distribution and biogeography.

Talling and Talling (1965) have described the chemical composition of some lakes in Africa and discussed the consequences on the distribution of planktonic organisms. The authors have discussed the occurrence of desmids and diatoms in relation to ionic composition, alkalinity and salinity gradients, conductivity and pH. Gasse et al. (1983) later made a systematic study of East African lakes and identified diatom assemblages in relation to some environmental variables, including the ones mentioned above.

There are only a small number of studies made on the phytoplankton communities in Africa dealing with the total biomass as well as the quantitative distribution of the component species. Knowledge of the species composition and the environmental control of their distribution is necessary to understand the spatial and temporal changes in phytoplankton biomass.

The input of solar radiation is the ultimate controlling mechanism in the annual pattern of phytoplankton distribution of temperate lakes. This is both directly through its effect on photosynthesis and growth , and indirectly through its effect on thermal stratification behavior and its subsequent effect on nutrient and phytoplankton distribution. In the tropics where seasonal changes in solar radiation input are minimal, thermal stratification patterns are mainly dependent on lake morphometry, and atmospheric factors such as evaporation, wind regime and humidity. However, influx of cool rain and reduced insolation during wet seasons can also be significant as shown by

Talling (1969) who has examined a number of stratified lakes in Africa, and described some annual cyclic patterns affecting thermal structure, chemical conditions, and the periodicity of planktonic organisms.

Seasonal changes in species composition and biomass have been described for some African lakes including lakes Victoria (Talling, 1966), George (Ganf, 1974c), Tanganyika (Hecky and Kling, 1981), Sibaya (Hart and Hart, 1977), Chad (Compère and Iltis, 1983) and some equatorial lakes (Melack, 1976 cited in Lemoalle et al., 1981). Based on a comparative investigation of available works, Melack (1979) has proposed three patterns of temporal changes in abundance and/or photosynthetic rates of phytoplankton in tropical African lakes :

A. Tropical lakes exhibiting pronounced seasonal fluctuations (coefficient of variation (CV) >20%) usually corresponding with variations in rainfall, river discharge or vertical mixing,

B. Lakes with muted fluctuations (CV <20%) in which diurnal changes often exceed month to month changes, and

C. Lakes where an abrupt change occurs from one persistent algal assemblage and level of photosynthetic activity to another persistent pattern.

Kalff and Watson (1986) have described the temporal patterns of phytoplankton biomass and community structure for lakes Naivasha and Oloiden in Kenya, and made comparison of patterns reported in other tropical and temperate lakes. They have concluded that there is no evidence for any fundamental difference between the freshwater phytoplankton composition and dynamics of tropical lakes, and temperate lakes during the summer.

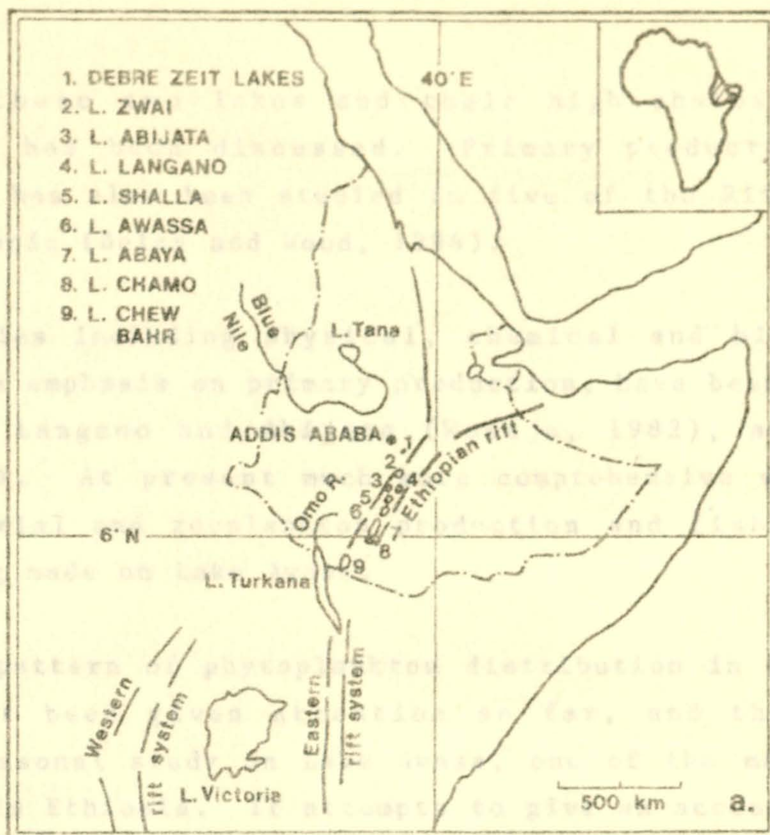
An overview of the seasonality of phytoplankton in African lakes has been given by Talling (1986). He has examined the various

patterns of phytoplankton seasonality described so far, and distinguished between patterns which are dominated by hydrological features (water input-output) and those dominated by hydrographic ones (water column structure and circulation). Different measures of seasonal variability have also been discussed in the comparison of phytoplankton dynamics from different lakes.

Very little is known about the basic limnology of Ethiopian lakes although several investigators have given sporadic reports on morphometric, chemical and biological features. These are being compiled in a bibliography of Ethiopian limnology (Belay, in preparation). Talling and Talling (1965) have reported their own and earlier chemical analyses on some Ethiopian lakes, including the Rift Valley lakes and Lake Tana in the north.

Detailed limnological investigations on Ethiopian lakes include Prosser et al. (1968) and Wood et al. (1976, 1984). They have made an intensive seasonal study on a group of crater lakes within the Rift System, 45 km south-east of Addis Ababa. Their morphometry, thermal and chemical stratification behavior have been described. Based on short term investigations, thermal and chemical stratification patterns of four of the large Rift Valley lakes in Ethiopia - Langano, Abijata, Shalla and Awasa (Figure 1a) have been described by Baxter et al. (1965). These studies have shown that, in general, the moderately deep lakes can have periods of well-marked stratification while the shallow lakes have only diurnal stratification.

Talling et al. (1973), have studied the photosynthetic production by phytoplankton in two Ethiopian soda lakes, Aranguade and Kilole. They reported that Lake Aranguade has an abundant and almost unialgal suspension of _Spirulina platensis_ (Gom.) Geitl., and Lake Kilole contains two abundant blue-green algae, appearing to be _Chroococcus_ and _Spirulina_ species. The high algal



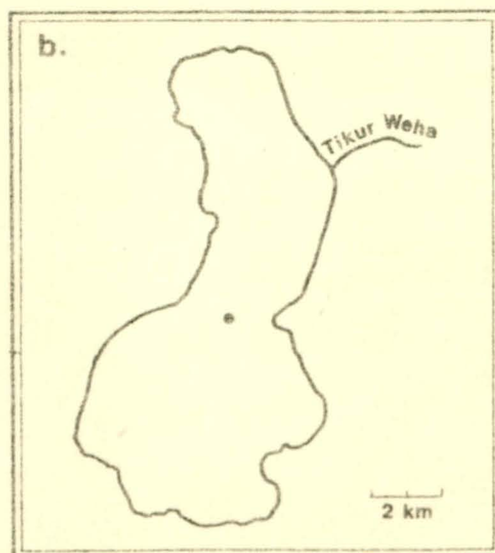


Figure 1. Map of Ethiopia showing the location of the major Rift Valley Lakes (a). Lake Awassa with sampling station indicated (b).

density of these two lakes and their high photosynthetic productivity has been discussed. Primary productivity of phytoplankton has also been studied in five of the Rift Valley lakes in Ethiopia (Belay and Wood, 1984).

Seasonal studies including physical, chemical and biological features, with emphasis on primary production, have been carried out on lakes Langano and Abijata (Wodajo, 1982), and Awasa (Kifle, 1985). At present much more comprehensive work, including bacterial and zooplankton production and fish physiology, is being made on Lake Awasa.

The seasonal pattern of phytoplankton distribution in Ethiopian lakes has not been given attention so far, and this paper presents a seasonal study on Lake Awasa, one of the major Rift Valley lakes in Ethiopia. It attempts to give an account of the seasonal variations in phytoplankton species composition and biomass in relation to some environmental factors.

CHAPTER II

STUDY AREA

STUDY AREA

The Ethiopian section of the Great African Rift Valley runs along the middle of the country in a north-south direction and covers an area of about 150000 km^2. The southern part of the Rift Valley contains seven moderately large lakes covering a total area of 2500 km^2 (Figure 1a). Based on their drainage interconnections, these lakes are divided into three major basins : Zwai-Shalla basin including lakes Zwai, Langano, Abijata and Shalla, Abaya-Chamo-Chew-Bahr basin, and the Awasa basin lying between the two basins.

Lake Awasa has a volcano-tectonic origin, and lies in a caldera with a diameter of about 30 km and an area of 1360 km^2 (Makin et al., 1975). The lake basin is totally enclosed by faulting with its western boundary scarp showing signs of some recent reverse movements along its fault zone (Mohr, 1962). It is overlooked from the north by a large volcanic complex Chabbi and Ugri, and the area surrounding the lake is underlain by quartz and pumice (Mohr, 1960).

The Awasa region has a dry, subhumid climate and classified in a rainfall regime which is characterized by one rainy and one dry season (Gamachu, 1977). Rainfall is well distributed throughout the eight rainy months, from March to October, with an annual average rainfall of 1154 mm (Table 1). The annual potential evapo-transpiration for the region is between 1100 and 1250 mm thus incurring a water deficit during the dry period. Gamachu (1977) reported the mean air temperature of the warmest month as 20-24^oC and the coldest month as 16-20^oC. However meteorological data for the sampling period in this work show much higher values (28 - 30^oC) during the dry season.

Lake Awasa is fed by a small river, the Tikur Weha (Figure 1b) which drains a swampy area of about 77 km^2 (Makin et al., 1975),

Table 1. General features of Lake Awassa and the region.

TOPOGRAPHY AND MORPHOMETRY			WATER CHEMISTRY			CLIMATE	
Latitude	6°33'- 7°33' N		TDS	650.4 mg l^{-1}	(d)	Annual rainfall	1154mm
Longitude	38°22'-38°29' E		K_{25}	853 umho cm^{-1}	(e)	Annual evapo-transpiration	1167mm
Altitude	1,680 m a.s.l.		pH	8.85	(e)	Air temperature maximum	24°C
Surface area	90 km^2	(a)	Na	151 mg l^{-1}	(e)	minimum	16°C
Shoreline length	52 km	(b)	K	30 mg l^{-1}	(e)		
Maximum length	17 km	(b)	Ca	11 mg l-1	(e)		
Maximum width	11 km	(c)	Mg	5.7 mg l-1	(e)		
Maximum depth	22 m	(b)	HCO3 + CO3	8.4 meq l-1	(e)		
Mean depth	11 m	(b)	Cl	34.4 mg l-1	(e)		
Volume	1.3 x 109 m3	(b)	SO_4	2.2 mg l-1	(e)		
Drainage area	1250 km2	(b)	SiO_2	75.4 mg l-1	(e)		
Surface inlet	Tikur Weha River		NO_3-N	76.6 ug l-1	(e)		
Surface outlet	Absent		PO_4-P	21.5 ug l-1	(e)		
			Total P	98 ug l-1	(f)		

(a) Makin et al., 1975 (b) Cannicci and Almagia, 1947 (c) Welcome, 1972 (d) Loffredo and Maldura, (e) Kifle, 1985 (f) Talling and Talling, 1965 (g) Gamachu, 1977

which is the remnant of a much greater old lake, Lake Shallo. Although Lake Awasa has a closed basin with no obvious surface outlet, the lake water has remained relatively dilute and it has been suggested by Makin et al., (1975) that there is a subterranean outflow by seepage through the bed of the lake on the south-west and northern side, which may account for a major loss of water. Other authors (Belay and Wood, 1984) have suggested the feeder river draining the swampy area to be the probable cause. The lake water level fluctuates considerably over the years in response to variations in rainfall and evaporation. The maximum depth recorded varies from 21.6 m in 1937, to 17.8 m in 1964 (Baxter et al., 1965) and 22 m in 1986. The surface area of the lake also varies and has been reported to be 129 km^2 (Cannicci and Almagia, 1947), 90 km^2 (Makin et al., 1975) and recently as 88 km^2 (Herrmann, personal communication). The shoreline has a gentle slope with extensive emergent and submergent vegetation almost all around the basin. The macrophyte population includes Paspalidium germinatum, Potamogeton schweinfurthii, Typha latifolia, T. angustifolia and Nymphaea sp. The fish inhabiting the lake include Barbus gregorii, Clarias mossambicus and Oreochromis niloticus. Commercial fishing practiced by a Fishermen's Cooperative depends almost solely on the most common cichlid fish in the lake, Oreochromis niloticus.

Lake Awasa also supports a large bird population including a variety of fishing birds, scavengers and waders. A list of published works on the avifauna of the Rift Valley Lakes is available in Urban (1970). The area around the lake is basically agricultural land except for the growing town of Awasa which runs north-south along the eastern shore of the lake.

CHAPTER III

MATERIALS AND METHODS

MATERIALS AND METHODS

SAMPLING

A single offshore station with a depth of 17 m was chosen as a representative site of the lake for the whole sampling period (Figure 1b). Water samples were collected once a month from seven depths (0,1,2,3,5,10 and 15 m) using a Kemmerer sampler of 2 liter capacity. Sub-samples of water from each depth were transferred to 250 ml bottles and fixed with acid Lugol's solution (0.5 ml/100 ml sample) for quantitative analysis. Samples from the same depths were put in polyethylene bottles and transported in an ice box to the laboratory for pigment and chemical analyses.

A phytoplankton net of mesh size 25 um was used to collect phytoplankton for identification. Duplicate net samples were fixed with acid Lugol's solution and formaldehyde solution.

PHYSICAL PARAMETERS

Vertical distribution of temperature and dissolved oxygen was measured in-situ using a dissolved oxygen probe with a built-in thermistor thermometer and an oxygen meter with a resolution of 0.05 - 0.10 mg l^{-1} (YSI model 57). Underwater light penetration was measured using a selenium barrier-layer cell fitted in a waterproof housing, with different glass color filters and an opal. The color filters covering the range of photosynthetically active radiation (PhAR) were types BG 12, VG 9, and RG 630 (Schott, Mainz, W. Germany) with estimated optical mid-points of 460, 540, and 630 nm respectively.

The vertical extinction coefficient, Ev (ln units m^{-1}) was calculated for the different wavelengths of light by applying the formula:

$$Ev = 1/z \ln Io/Iz$$

where Io is the intensity just below the surface, and Iz is the

intensity at depth z in meters. Euphotic depth (Zeu) was determined using the approximation derived by Talling (1965) for an optically wide range of East African lakes :

$$Zeu = 3.7/Ev\ min$$

where Ev min is the extinction coefficient of the most penetrating wavelength of light. Euphotic depth (Zeu) was also calculated by ascribing 30, 35 and 35% incident PhAR to blue, green and red spectral blocks respectively (Talling, 1957) and taking the depth at which the light intensity equals 1% surface irradiance as Zeu.

Secchi disc transparency was measured and related with the calculated Zeu applying an approximation of Poole-Atkins equation:

$$Z_{SD} = 1.7/Ev$$

where Z_{SD} is the Secchi depth in meters (Idso and Gilbert, 1974).

CHEMICAL PARAMETERS

Measurement of pH for surface water was made in-situ with a portable digital pH meter (Canlab, Model 607) readable to 0.05 pH units. Carbonate-bicarbonate alkalinity was determined by titration against HCl with phenolphthalein and to pH 4.5 with mixed indicator. Electrical conductivity was measured in-situ with a combined conductivity/salinity and thermistor thermometer probe (YSI Model 33 S-C-T meter). Temperature corrections were made to 20°C assuming a mean temperature coefficient of 2.3% per °C (Talling and Talling, 1965).

All further chemical analysis was done on water samples passed through Whatman GF/C glass fiber filters. Nitrate and phosphate were determined about 3 hours after sampling. Nitrate-nitrogen was determined as nitrite after reduction in a cadmium-copper column. Nitrite-nitrogen was determined with a spectrophotometer by diazotization of sulphanilamide and coupling with N-(1-

naphthyl)-ethylenediamine di-HCl according to the method described in Golterman et al. (1978). Nitrite concentration before reduction of nitrate was found to be too low to detect with the method employed. Hence values after reduction were taken as nitrate - nitrogen concentration without correction for nitrite. Soluble reactive phosphorus was determined without extraction according to Mackereth et al. (1978).

SPECIES COMPOSITION

Most of the single-celled species had a size of less than 25 um and would pass through the sampling net. So identification was done both on net and sedimented quantitative samples. The literature referred to in the course of this work included Huber-Pestalozzi (1938-1983), Bourrelly (1966-1970), and Van Meel (1954). The taxa in the list of species are arranged according to Christensen (1962, 1980).

PHYTOPLANKTON BIOMASS

Estimations of phytoplankton biomass were done based on chlorophyll a measurements and cell counting.

Counting - Samples preserved for counting were analyzed at the Laboratory of National Swedish Environment Protection Board, Uppsala, Sweden. All counts were done using a Wild inverted microscope following the Utermohl technique (Utermöhl, 1958).

A preliminary count of common phytoplankton species was made on two samples using sedimentation chambers of 10 ml, and filling just the chamber bottom (2.15 ml). Based on the above results, and considering the amount of time required for counting all samples, 14 species which comprised more than 90% of the total biomass were chosen in all samples. The phytoplankton density was found to be too high to use 10 ml chambers for further counts. So all species except *Botryococcus braunii* were counted in the chamber bottom with an objective of 40x magnification.

Colonies of Botryococcus braunii were counted under 10x objective in a 50 ml sedimentation chamber.

Samples from the upper 0-3 m layer of the lake were initially pooled and counting was done on these pooled, as well as the 5, 10 and 15 m samples for three sampling dates. It was then found more appropriate to include 5 m sample as well in the pool of 0-3 m, and the rest of the samples were treated as such. In counting, the simplified methods described by Willén (1976) and Hobro-Willén (1977) were followed. The total number of individuals counted for all species was at least 60 involving a maximum error of ± 26%, assuming a random distribution. Most of the species were filamentous blue greens, and the cell count was done by measuring their total length, the total length being equivalent to or more than 60 individual trichomes. Colonial plankton such as Microcystis species were however counted as individual cells. For Botryococcus cells, the surface area of the colonies was measured and related to the number of cells per colony area. Since the plankton density on the chamber bottom was high for most species, counting a small number of diagonals was sufficient. Transformation of cell counts to volume was done by fitting the plankton to appropriate stereometric shapes.

Pigment Analysis - Samples were analyzed for pigment concentration about 3 hours after sampling time. Aliquots of 250 ml lake water were passed through Whatman GF/C glass fiber filters. Pigment was extracted with warm 90% methanol , centrifuged, and its absorbancy measured at 665 nm, 480 nm and 750 nm with a Pye Unicam SP6-350 visible spectrophotometer (path length 1 cm). Correction for possible turbidity was made by subtracting readings at 750 nm from the corresponding readings at 665 nm and 480nm. Chlorophyll a estimations were done using the approximate relations derived for 90% methanol by Talling and Driver (1963) : $\text{chl a} = 13.9\ D_{665}$ (path length = 1 cm)
No distinction was made for degradation products.

CHAPTER IV

RESULTS AND DISCUSSION

RESULTS AND DISCUSSION

THERMAL STRATIFICATION

The vertical distribution of temperature and dissolved oxygen during the sampling period was followed from the surface down to 15 m. The results show three phases of thermal stratification (Figures 2 and 3). During the first phase from September to November, thermal discontinuities were relatively unstable with a gentle gradient of about 0.2 to 0.4°C per meter in the lower water column. The temperature difference between the surface and 15 m was between 1.6 and 2.8°C and surface stratification was more pronounced in October. There was complete mixing in December and the lake had an isothermal condition except for the stratification in the upper 0-3 m column of water. This was a superficial gradient formed during the day with increased solar heating, and destroyed during the night due to cooling.

The second phase during January to May is characterized by a strong thermal stratification. The temperature difference between the surface and 15 m varied between 2.7 and 6.6°C with the maximum difference occurring in January. The highest surface temperature recorded during the sampling period (25.4°C) occurred in January producing a steep thermal gradient between the surface and 1 m with a drop of 3°C. At the start of this phase, thermal discontinuity in the deeper water occurred between 5 and 9 m and later moved down below 9 m. During February to April it was oscillating between 9 and 15 m. In May there was a relatively gentle thermal gradient which moved up to 7 m indicating the beginning of thermal stratification. The third phase from June to the end of July was a period of mixing with an isothermal condition in the whole water column except for the surface waters which had a slight temperature gradient. The temperature difference between the surface and 15 m was between 0.5 and 2.5°C.

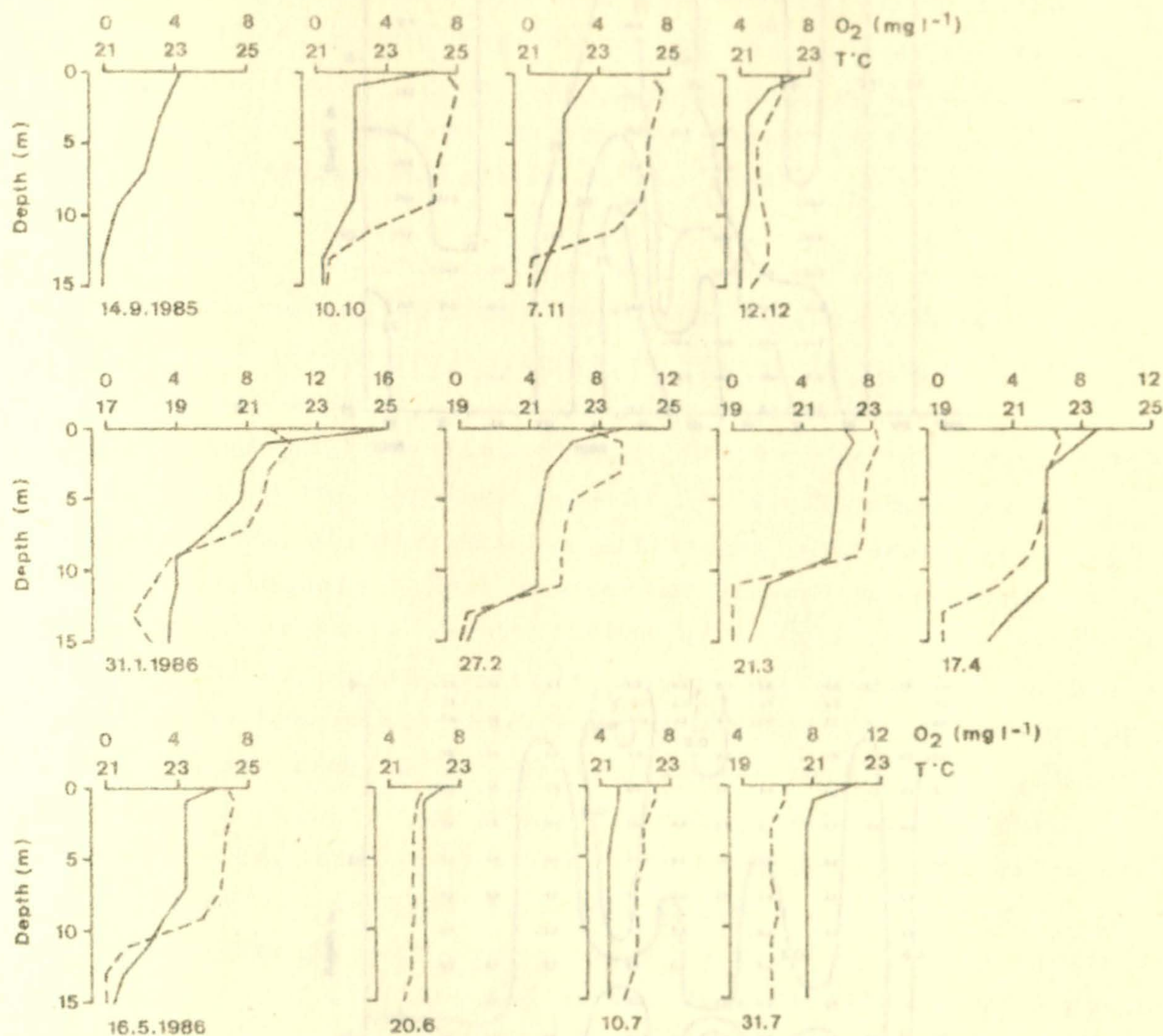
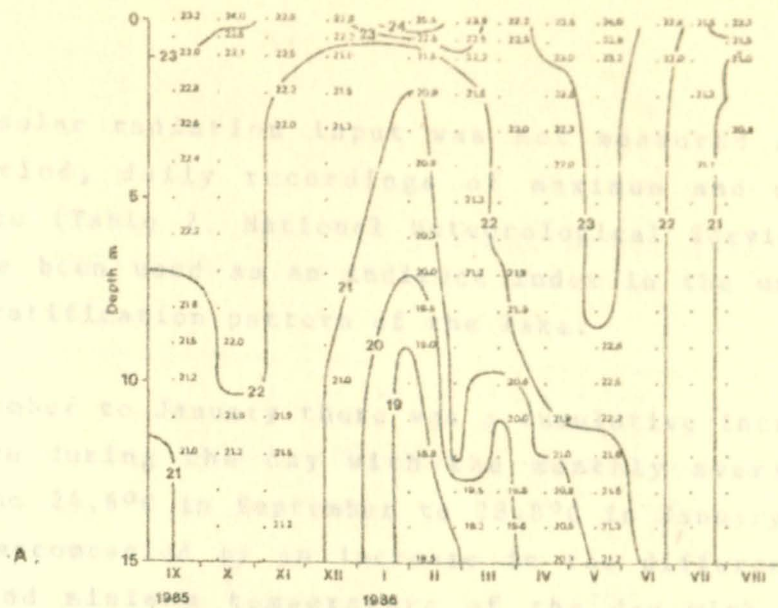


Figure 2. Depth profiles of temperature (—) and dissolved oxygen (---) in Lake Awassa on the sampling date and time indicated.



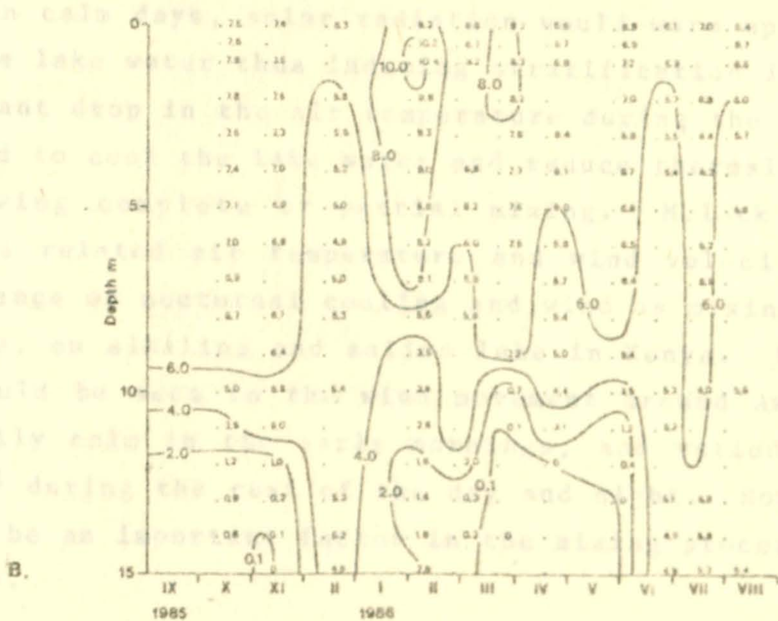


Figure 3. Distribution of temperature (a) and dissolved oxygen (b) wi depth and time showing the stratification pattern in lake Awassa.

Although solar radiation input was not measured during this study period, daily recordings of maximum and minimum air temperature (Table 2, National Meteorological Services Agency, 1986) have been used as an indirect index in the understanding of the stratification pattern of the lake.

From September to January there was a cumulative increase in air temperature during the day with the monthly average maximum rising from 24.6°C in September to 28.8°C in January (Table 2). This was accompanied by an increase in the difference between maximum and minimum temperature of the day with the minimum going down in the evenings from 12.7°C in September to 7.5°C in January. The monthly average difference increased from 11.9°C to 21°C in January. This pronounced diurnal fluctuation in air temperature prevents the formation of stable thermal stratification. On calm days, solar radiation would warm up the air as well as the lake water thus inducing stratification in the lake. A significant drop in the air temperature during the night would be expected to cool the lake water and reduce thermal stability, thus allowing complete or partial mixing. Melack and Kilham (1974) have related air temperature and wind velocity to show the importance of nocturnal cooling and wind as mixing agents in Lake Nakuru, an alkaline and saline lake in Kenya. No seasonal pattern could be seen in the wind movement around Awasa and it was generally calm in the early mornings, and varied between 0 and 6 m s^{-1} during the rest of the day and night. However, wind effect may be an important factor in the mixing process observed in the lake.

Though the air temperature continued to be high during the day, the difference in maximum and minimum air temperature started to decrease in late January (Table 2). This corresponds to the stable thermal stratification phase observed in the lake during January to May. Complete mixing in June was induced by a decrease in solar radiation input, as deduced from air tempera-

Table 2. Monthly averages of maximum and minimum air temperature, and the monthly rainfall in Awassa.

MONTH	TEMPERATURE (°C)			RAINFALL (mm)
	Maximum	Minimum	Maximum-minimum	
September '85	24.6	12.7	11.9	115
October	26.2	10.5	15.7	50
November	27.6	8.8	18.8	13
December	28.1	7.8	20.3	8
January '86	28.8	7.5	21.3	0
February	29.4	11.2	18.2	35
March	28.9	10.5	18.4	70
April	26.3	14.8	11.5	112
May	26.5	13.7	12.8	167
June	23.9	14.4	9.5	193
July	23.5	13.5	10.0	72

ture, and influx of cool rain and high rainfall much as Talling (1969) has shown for other African lakes. The highest amount of rainfall in the region occurred in May and June (Table 2) with the maximum air temperature going down to its lowest value for the sampling period.

Based on measurements taken in Lake Awasa in February, March, and June, Baxter et al. (1965) have observed that deep thermal stratification was rudimentary during February and June, but well marked in March, with thermal discontinuity between 5 and 12 m. Complete or almost complete mixing of the lake was recorded in February, June and December 1984 by Kifle (1985).

The seasonal pattern of thermal stratification observed in Lake Awasa is similar to that described by Talling (1966) for a much larger lake in Africa, Lake Victoria (Figure 1a). He described three phases - a phase with an absence of strong thermal discontinuity from September to December, a second phase of stable stratification from January to May, and a third phase of feeble development of stratification between June and August.

Depth profiles of dissolved oxygen follow the thermal stratification pattern (Figures 2 and 3) with a sharp decrease of oxygen concentration about the region of the metalimnion. During the stratification period, the oxygen concentration above the metalimnion varied from about 4 to 10 mg l^{-1} with a maximum value of 10.4 mg l^{-1} in January. This maximum corresponded to the high chlorophyll and phytoplankton volume measured for that day (Figure 7). During the mixing period, there was an almost uniform distribution of oxygen throughout the water column with concentrations ranging from about 5 to 7 mg l^{-1}. A slight decrease of concentration was found in the surface water on many of the sampling dates, except in December, June and July when the lake was more or less mixing. This decrease can be accounted to high surface temperatures and possibly radiation which by

heating would decrease the solubility of oxygen and/or induce inhibition of photosynthesis.

An anoxic layer of water was present below 13 m in October and November. This was followed by a more or less uniform oxygen distribution in December with values of 4.6 to 6.3 mg l^{-1}. In the second phase of thermal stratification, the anoxic depth oscillated between 11 and 13 m. Baxter et al. (1965) have reported a deoxygenated layer of water in Lake Awasa below about 10 m in their March sample. The depletion of oxygen in the hypolimnetic water reflects its consumption by decomposition of organic matter, and respiration of organisms in deeper waters. In the absence of freely circulating water, there is no replenishment of oxygen from the trophogenic zone; hence the anoxic layer can persist throughout the stratification period.

In all cases of stratification during the sampling period, the metalimnion was below 5 m, and the oxygen distribution in the upper 0-5 m of water was more or less uniform. This, and the fact that the euphotic depth was less than 3 m (Table 3), made it possible to consider the 0-5 m water column as a representative unit of the trophogenic zone. Thus, for all determinations in this study, water samples taken from different depths in this column were either integrated and analyzed, or analyzed and the values averaged by making appropriate corrections for differences in depth.

UNDERWATER LIGHT PENETRATION

The seasonal variation of underwater light penetration expressed by the vertical extinction coefficient (Ev) has been determined for blue, green, and red light at wavelengths of around 460, 540 and 630 nm respectively (Table 3). The same pattern of light extinction was seen throughout the sampling period with the lowest extinction in the red and the highest in the blue spectral regions (Figure 4). Since light penetration is the

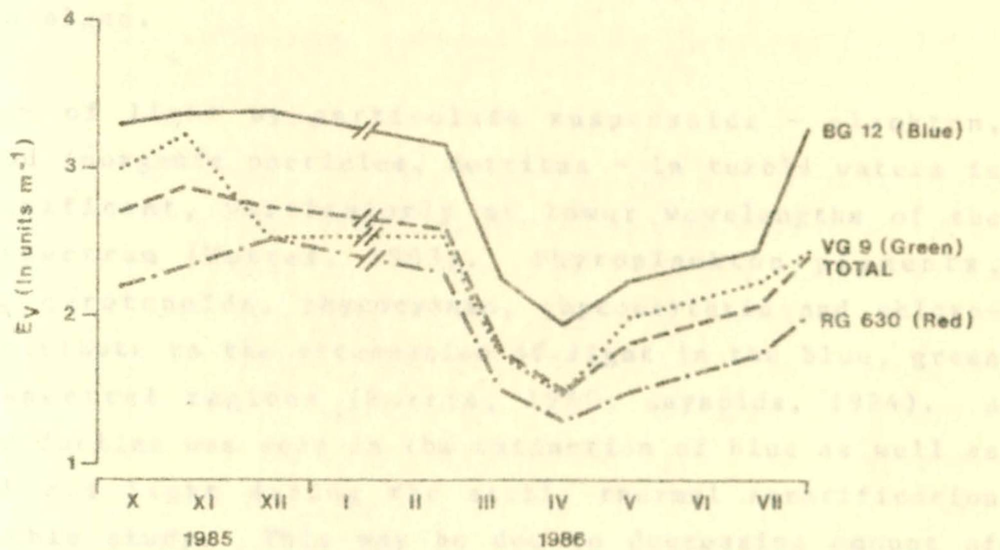


Figure 4. Seasonal variation of light extinction in Lake Awassa express by the vertical extinction coefficient (Ev) for blue, green, red and total light.

reciprocal of extinction, red light penetrates the furthest and blue light is rapidly attenuated in Lake Awasa.

This spectral pattern of light extinction, reported earlier for Lake Awasa (Kifle, 1985), has been found to be typical of lakes with very turbid or colored waters, or dense crops of phytoplankton (Sakamoto and Hogetsu,1963; Ganf, 1974; Melack and Kilham, 1974; Bowling et al.,1986). Talling et al. (1973) have described the same pattern for lakes Aranguade and Kilole, two crater soda lakes in Ethiopia with very dense populations of blue-green algae.

Absorption of light by particulate suspensoids - plankton, organic and inorganic particles, detritus - in turbid waters is quite significant, particularly at lower wavelengths of the visible spectrum (Wetzel, 1983). Phytoplankton pigments, including carotenoids, phycocyanin, phycoerythrin and chlorophyll, contribute to the attenuation of light in the blue, green and red spectral regions (Morris, 1980; Reynolds, 1984). A pronounced decline was seen in the extinction of blue as well as green and red light during the stable thermal stratification phase of this study. This may be due to decreasing amount of suspended matter in the upper column of water. Particulate matter sinking to the bottom can not come back into circulation in the presence of thermal and therefore density gradient. This was also a period of relative decrease in chlorophyll a and phytoplankton volume (Figure 7).

Euphotic depth (Zeu) , the depth at which 1% of the irradiance penetrating the surface water is found, was determined from total light extinction (described in methods). This was compared with the approximation of Zeu calculated from the equation : Zeu = 3.7/Evmin (Talling, 1965), Ev min being the extinction coefficient of the most penetrating light, in this case red. The values from the two determinations were found to

correspond well (Table 3). The annual mean Zeu was about 2 m with the highest values (2.55 to 3.00 m) occurring during the stable thermal stratification phase and the lowest values (1.60 to 2.20 m) during the mixed and unstable thermal stratification phases.

Measurements of Secchi disc transparency, Z_{SD} (Table 3), showed relatively close agreement with Secchi depth approximation by the Poole-Atkins equation : $Z_{SD} = 1.7/Ev$. There was one exception in March, where Z_{SD} measured was much lower than the calculated value, which was possibly due to a subjective error in Secchi disc reading.

The mean euphotic depth for the sampling period, as determined by the total light extinction (Zeu Det.), and as approximated by the minimum extinction coefficient (Zeu Cal.) was 2.12 m and 2.01 m respectively. Dividing these values by the mean Secchi depth value (0.70 m) gives factors of 3.03 and 2.87. Taking an average of 3 as a factor and multiplying with individual Secchi depth readings, gives an approximation of Zeu. These approximated values deviated from values of Zeu (cal.) and Zeu (det.) by about $\pm$ 0.4 m. Kifle (1985) found a mean Zeu of 2.34 m and a mean Z_{SD} of 0.77 m for Lake Awasa. He also determined a factor of 3 to multiply with Secchi depth readings thus approximating the depth of euphotic zone. These values agree well with the present work, and it is suggested here that in future work this factor can be used as an approximation of the euphotic depth in Lake Awasa.

Talling (1971) has described three principal components determining the effective underwater light field for a circulating cell : 1. The time course of surface irradiance, 2. The relative penetration of radiant energy with depth, and 3. The proportion of illuminated and "dark" water in the mixed water column. Duration of surface irradiance around the equator is relatively

Table 3. Optical relationships of extinction coefficient, euphotic and Secchi depth in Lake Awassa.

DATE	Ev (ln units m^{-1})				Zeu (m)		SD (m)	
	Blue	Green	Red	Total	Det	Cal	Det	Cal
14/9/85	-	-	-	-	-	-	0.70	-
10/10/85	3.30	3.00	2.20	2.70	1.68	1.68	0.68	0.63
07/11/85	3.42	3.23	2.33	2.88	1.60	1.59	0.65	0.60
12/12/85	3.38	2.53	2.53	2.73	1.70	1.46	0.69	0.62
31/1/86	-	-	-	-	-	-	0.72	-
27/2/86	3.17	2.55	2.29	2.60	1.77	1.62	0.68	0.65
21/3/86	2.28	1.75	1.47	1.74	2.65	2.52	0.64	0.98
17/4/86	1.95	1.50	1.33	1.53	3.00	2.78	0.80	1.11
16/5/86	2.24	1.99	1.49	1.83	2.55	2.48	0.71	0.93
20/6/86	-	-	-	-	-	-	-	-
10/7/86	2.45	2.25	1.74	2.11	2.20	2.13	0.70	0.80
31/7/86	3.31	2.46	2.03	2.43	1.90	1.82	0.74	0.70
ANNUAL MEAN	2.83	2.36	1.93	2.28	2.12	2.01	0.70	0.78

Ev Total = 30% blue + 35% green + 35% red
Zeu Det = Euphotic depth determined from total light penetration as the depth of 1% surface irradiance
Zeu Cal = Euphotic depth calculated from the relation : Zeu=3.7/Evmin
SD Det = Secchi depth determined with Secchi disc
SD Cal = Secchi depth calculated from the relation : $Ev=1.7/Z_{SD}$ with Ev=Ev Total

constant with about 12 hours of daylight, and this factor does not play such an important role in the tropics as it does in temperate lakes. The relative penetration of radiant energy, which denotes the euphotic depth, is of much more importance in determining phytoplankton physiology and production, particularly in relation to the proportion of illuminated (euphotic zone) to "dark" zone. The proportion will increase in a mixing water column, thus increasing the relative time spent in darkness by the algal cells.

The ratio of mixed depth to euphotic depth (Zmix/Zeu) defined as the optical depth, is a limiting factor in phytoplankton production when it exceeds a critical value (Talling, 1971). Some authors have given a critical value of 4 to 5 (Strickland, 1965; Wood et al., 1978) above which light limitation is expected to prevail. In Lake Awasa, the mean euphotic depth was about 2 m giving a ratio of 5.5 during the mixing and unstable thermal stratification periods (i.e. assuming the mean depth to be an estimate of Zmix (Wood et al., 1978). The ratio would be even higher (7.5) taking the mixed depth of 15 m during June and July (Figure 3a). This would suggest that phytoplankton production can be light limited during the mixing periods. The optical depth would be much less than 5.5 during the stable stratification period and hence light limitation would be minimal. Talling has found limiting optical depths in highly productive lakes such as Lake Kilole (Talling et al., 1973), and in deep lakes during isothermal mixing such as Windermere North Basin, United Kingdom (Talling, 1971). This has also been reported for lakes Shalla (a deep lake), Abijata and Langano (with high amount of particulate suspensoids) in mixing periods (Wood et al., 1978).

Dense populations of phytoplankton absorbing underwater light are said to be "self-shaded". As a measure of their contribution to light extinction, an extinction value -Es- has been deter-

mined to be between 0.01-0.02 ln units per mg chl a m^{-2} for several natural populations (Talling, 1965,1971; Ganf,1974a; Reynolds,1984). Assuming an Es value of 0.015, the extinction of light due to algal biomass, with chlorophyll as an index, in the euphotic zone of Lake Awasa, varied between 0.69 and 1.56 with an average of 1.29 ln units m^{-1}. The mean percentage of light extinction due to algal biomass was 57%. which is much higher than was found for other Rift Valley lakes in Ethiopia. Wood et al. (1978) have found values of 3%, 4 %, 6% and 22% in lakes Zwai, Langano, Shalla and Abijata respectively. However, recent measurements of chlorophyll a in lakes Zwai, Abijata and Shalla (Belay and Wood, 1984) show much higher values in the euphotic zone, which would give a higher percentage of light extinction due to algal biomass.

Self-shading behavior varies with algal size and pigment composition. A considerable decrease below "normal" was found in the Es value of dense populations of Ceratium by Talling (1971). He accounted this decrease to the "sieve effect" - ineffective light interception by some of the cell pigment in large cells. Reynolds (1984) has pointed out that Es decreases as unit volume of phytoplankton increases above about 250 um^3. Colonies of Botryococcus braunii and Microcystis species exceeding this volume make up a considerable proportion of the total phytoplankton in Lake Awasa (Figure 6). This would impart the "sieve effect" mentioned above and would be expected to underestimate Es. Conversely, Es is higher in blue-green algae, containing phycobillins, than in green algae (Kirk, 1975). Blue-green algae making up a major proportion of the phytoplankton in Lake Awasa (Figure 7) would be expected to increase the Es value. In general, it is evident that the attenuation of light by phytoplankton can be significant in determining the underwater light climate of Lake Awasa.

CHEMICAL FEATURES

The results of chemical determinations in Lake Awasa are presented in Figure 5. Alkalinity analysis and pH measurements were done only for the surface water. Soluble reactive phosphate and nitrate analysis included depth samples from 0,1,5,10 and 15 m, but the results did not show a marked difference with depth. Hence only the mean concentration of the upper 0-5 m water column is presented (Figure 5) as a representative value for the trophogenic zone. The same is true for electrical conductivity measurements.

Carbonate and bicarbonate are the predominant anions in the lake, with sodium as the major cation (Talling and Talling, 1965; Kifle, 1985). This is a typical feature of many lakes in Africa, particularly the lakes found in and associated with the East African Rift (Talling and Talling, 1965; Prosser et al., 1968). Carbonate-bicarbonate alkalinity in Lake Awassa showed seasonal variations ranging between 7.33 and 10.52 meq l^{-1}, with the maximum in January and the minimum in late July. High alkalinity values in January may be associated with high evaporation rates during the dry season which would concentrate the ions. January was the driest period of the year (Figure 5) with a very high lake surface temperature (Figure 2). The increase can also be due to an increase in photosynthetic activity of phytoplankton, which had a population peak in January. The concentration of dissolved oxygen was also high during this period (Figure 3b), a possible consequence of high photosynthetic activity.

Electrical conductivity (K_{20}) was between 730 and 825 μmhos cm^{-1} with most of the values being about 100 times the alkalinity in meq l^{-1}. Talling and Talling (1965) found this relationship between conductivity and alkalinity to be true for most lakes in East Africa. Variations in conductivity were relatively small

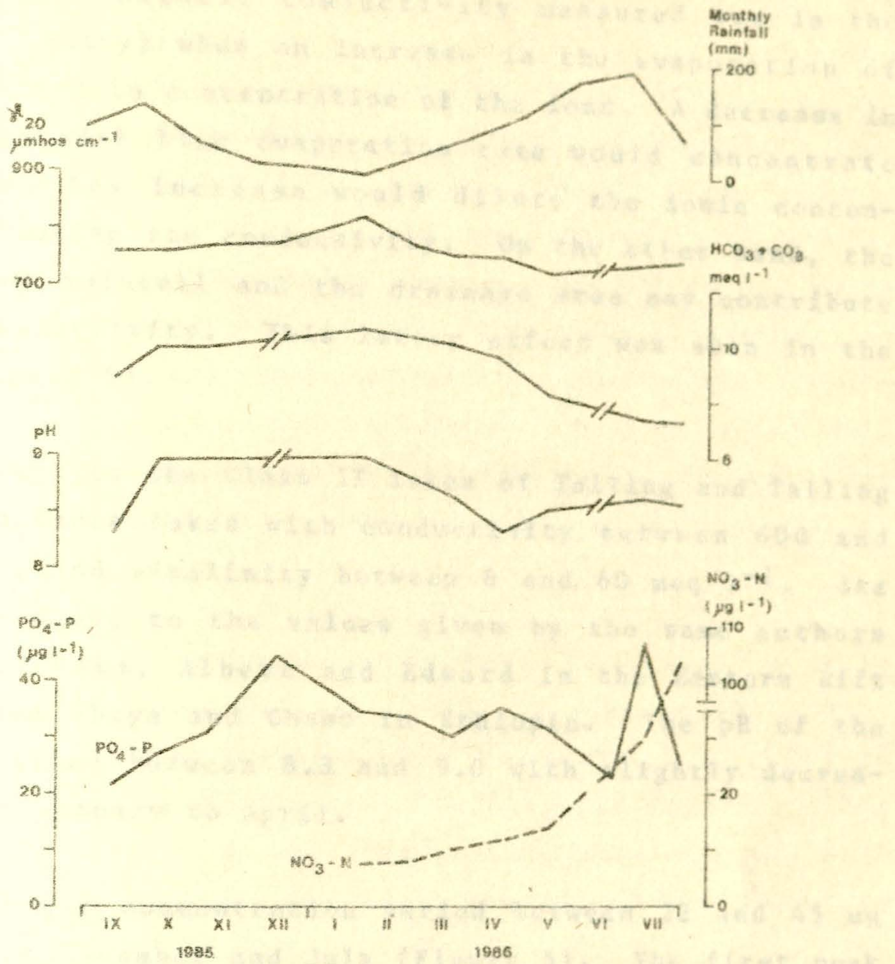


Figure 5. Seasonal variation of some chemical features in Lake Awassa and the average monthly rainfall in the region.

with an increase in the dry and a decrease in the wet seasons (Figure 5). The highest conductivity measured was in the driest month (January) when an increase in the evaporation of lake water resulted in concentration of the ions. A decrease in rainfall coupled with high evaporation rate would concentrate the ions, while its increase would dilute the ionic concentration thus reducing the conductivity. On the other hand, the ionic input from rainfall and the drainage area may contribute to increased conductivity. This latter effect was seen in the July sample (Figure 5).

Lake Awasa belongs to the Class II lakes of Talling and Talling (1965) which includes lakes with conductivity between 600 and 6000 μmhos cm^{-1}, and alkalinity between 6 and 60 meq l^{-1}. Its conductivity is close to the values given by the same authors for lakes Tanganyika, Albert and Edward in the Eastern Rift system, and lakes Abaya and Chamo in Ethiopia. The pH of the surface water varied between 8.3 and 9.0 with slightly decreasing values from January to April.

Phosphate-phosphorus concentration varied between 22 and 45 μg l^{-1} with peaks in December and July (Figure 5). The first peak can be associated with the complete mixing in the lake whereby an accumulation of phosphate in the hypolimnion released from decaying organisms could have been brought into circulation. No marked increase of phosphate was found in the hypolimnion during the stable stratification period, but it is possible that accumulation takes place deeper in the lake, i.e. below 15 m. The decrease of phosphate in January and June, following the mixing periods, may be attributed to its consumption by the increasing population of phytoplankton (Figure 7).

The second peak in July is associated with the rainfall, which was at its maximum for the sampling period, and hence an increased nutrient loading from the drainage area. Phyto-

plankton assimilation of phosphate could again be a possible cause for the sharp decline found at the end of the month. Its incorporation by phytoplankton and bacteria can cause a very rapid depletion of available phosphate (Wetzel, 1983). Another possible cause is the decrease in the release of phosphate from the sediments in the presence of oxygen. The lake was completely mixed from June to the end of July during which time dissolved oxygen at 15 m increased from 4.2 mg l^{-1} to 5.2 mg l^{-1}. Though there was no measurement for the sediment surface, it seems highly probable there was oxygenated deeper water affecting phosphate release from the sediments. Wood et al. (1984) have found the lowest phosphate concentration in the group of Debre Zeit lakes (Figure 1a) to occur during, or at the end of, their mixing periods.

High phosphate concentrations have been reported for many African lakes (Talling and Talling, 1965; Prosser et al., 1968; Talling et al., 1973; Melack, 1978; Wood et al., 1984) as opposed to their low nitrate content (Talling and Talling, 1965; Prosser et al., 1968). In the previous seasonal work on Lake Awasa (Kifle, 1985), soluble reactive phosphate was found to vary between 5 and 45 $\mu g\ l^{-1}$.

Nitrate analysis was made from January to the end of July, during which time the concentration increased gradually (Figure 5). In most cases the values were low, varying between 7 and 20 ug l^{-1}. At the end of July a pronounced increase occurred in the surface waters with concentrations of above 100 ug l^{-1}. This could be due to the high rainfall and nutrient loading from the drainage area at the time. Some amount might also be attributed to nitrogen fixation by the blue-green alga _Anabaenopsis raciborskii_ which had a major biomass peak in July with relatively high concentration in the surface waters (Figure 6). In Lake Victoria, a population maximum of _Anabaena flos-aquae_, which occurred in a slight-stratification period, was associated

with high concentrations of nitrate in the lake (Talling, 1966). Unfortunately there is no biomass data for the other nitrogen-fixing algae in Lake Awasa.

Wood et al. (1984) have shown for the Debre Zeit lakes in Ethiopia that ammonium is the predominant form of nitrogen, and nitrate is in low concentrations. Ammonia and ammonium nitrogen (NH_3 + NH_4-N) values for Lake Awasa (Gebre Mariam, unpublished data) showed that in March, 1986 there was a concentration of about 5 times the nitrate-nitrogen in the upper 0-5 m of water, and 10 and 25 times in 10 and 15 m respectively. This is an indication of the high proportion of reduced to oxidized forms of nitrogen in the lake, particularly in the deeper water during the stratification period. Though there are no ammonium values available for the rest of the sampling period, the increase of nitrate in the trophogenic zone during July could have been due to the oxidation of the reduced forms in the deeper water which have been brought into circulation. But the low nitrate concentrations found in deeper oxygenated waters make this reason unlikely. Kifle (1985), has reported nitrate concentrations of 25 to 165 µg l^{-1} for Lake Awasa, which are relatively higher than the values found in this study. This is possibly due to the difference in the methods used for nitrate reduction (Zn as opposed to Cd-Cu reduction).

No determinations were made in this study on total nitrogen and phosphorus which would have given a much better picture of the status of the two nutrients in the lake. In the absence of this information it is not possible to discuss the nitrogen to phosphorus ratio which plays an important role in phytoplankton physiology. However the nitrate to phosphate ratio was very low during most of the sampling period (Figure 5). The consequences of this feature will be discussed later in relation to seasonality of phytoplankton.

SPECIES COMPOSITION

A total of 100 phytoplankton species were identified in the samples collected over a year from the pelagic zone of Lake Awasa (see Species List below). The qualitative composition of the algal flora shows that the green algae have the highest number of taxa representing 48% of the total taxa of which 34% belong to the Chlorococcales group. Desmids constituted only 9% of the total, which is equal to the percentage composition of a single genus of the Chlorococcales, Scenedesmus. The Chlorophyta also contributed the highest number of taxa in all the tropical lakes compared by Kalff and Watson (1986). While planktonic Chlorococcales are widely distributed in waters of differing alkalinity and salinity (Wetzel, 1983), most species of desmids are characteristic of fresh waters low in total ions (Talling and Talling, 1965; Wetzel, 1983). Reduced representation of desmids in the phytoplankton of Lake Awasa may be due to the relatively high ionic concentration (K_{20} 728-826 umho cm^{-1}) and alkalinity (7.3-10.5 meq l^{-1}) of the lake. Talling and Talling (1965) have reported that desmids are numerous in the Class I lakes (K_{20}<600 µmho cm^{-1}) but uncommon in Class II (K_{20} 600-6000 µmho cm^{-1} corresponding to an alkalinity of about 6-60 meq l^{-1}) African lakes. According to these authors, the upper limit of alkalinity at which an appreciable desmid plankton exists was reached in Lake Malawi (Nyassa) (2.5 meq l^{-1}) and this limit may be extended in most African lakes with a usually high ratio of monovalent to divalent cations. Thus, though the alkalinity of Lake Awasa (7.3-10.5 meq l^{-1}) is higher than the limit reported, the ratio of monovalent to divalent cations is about 10:1 (Kifle, 1985) which can allow the occurrence of some desmid population in the lake.

The blue-green algae composed 30% of the identified taxa, with Microcystis as the genus with the highest number of taxa among the group. Microcystis was also quantitatively the second most important genus in the lake, next to Lyngbya. The blue-green

algae have a wide geographical distribution, even though there are some species characteristic of higher or lower latitudes. Examples are Oscillatoria species which seem more characteristic of temperate zones, Spirulina and Anabaenopsis species which occur more frequently at lower latitudes (Gibson and Smith, 1982). It is also true that planktonic blue-green algae, e.g. Microcystis species, are more commonly associated with eutrophic lakes (Gibson and Smith, 1982) and usually alkaline waters (Wetzel, 1983).

Identification of the diatom flora, which consisted of only 11 taxa, was done mostly to the genus level. The list is rather incomplete because it is likely that there are more than one species in the genera identified so far. Among the diatom populations in Lake Awasa, Nitzschia and Melosira species appeared to have an appreciable number, with the former being more common. This may be related to the alkalinity of the lake, a factor which Talling and Talling (1965) have considered as important in determining the diatom communities of the African lakes they compared. Thus, they have reported that species of Melosira are numerous in most lakes of relatively low alkalinity and salinity (Class I), and that species of Nitzschia are often abundant in lakes of intermediate alkalinity (Class II) to which Lake Awasa belongs. Gasse et al. (1983) have identified the diatom community of Lake Awasa as transitional between a Melosira-dominated and a Nitzschia-dominated diatom assemblage, with a richer Nitzschia flora.

Cryptophyceae, Dinophyceae, Chrysophyceae, Euglenophyceae and Tribophyceae contributed to only 11% of the taxa identified from the lake. Identification of species on preserved samples (5-16 months) did not allow much taxonomic work on flagellates which has underestimated the number of taxa in these groups. The low representation of chrysophytes and cryptophytes in Lake Awasa can be related to the relatively productive nature of the lake.

Some authors have reported that these groups are associated with oligotrophic lakes (Hecky and Kling, 1981; Kalff and Watson, 1986). Lewis (1978a) has emphasized the importance of chrysophytes in temperate lakes reporting that the group is virtually absent in the plankton of the lowland tropics. However, Hecky and Kling (1981) have shown that it does not apply to Lake Tanganyika where chrysophytes and cryptophytes make up 13% and 5% of the total taxa and 30% and 10% of the total biomass respectively. They have also reported that the groups are co-dominants during periods of low biomass, and have associated the occurrence of these groups with the oligotrophic nature of the lake. This view has also been supported by Kalff and Watson (1986) who have compared tropical and temperate lakes, and deduced that the relative importance of chrysophytes is a function of the trophic status of the lakes rather than of latitude.

The total number of taxa found in Lake Awasa is comparable to that reported for the tropical lakes Tanganyika (Hecky et al., 1978), Naivasha and Oloiden (Kalff and Watson, 1986) and the subtropical lake Lanao (Lewis, 1978b) which had 103,143,94 and 70 taxa respectively. There is also a similarity with respect to the relative contribution of the taxonomic groups to the total number of taxa. They all have a dominance of green algae (35-63%), followed by the blue-green algae (18-30%). Lake George, a shallow equatorial lake, shows a different picture with a total of 58 taxa (Ganf, 1974a) and a dominance of blue-green algae (50%) followed by green algae (31%).

SPECIES LIST

CYANOPHYTA, blue-green algae

Nostocophyceae (=Cyanophyceae)

Aphanothece microspora (Men.) Rbh.

A. sp.

Chroococcus limneticus Lemm.

C. minutus (Kütz.) Nag.

C. turgidus (Kütz.) Nag.

C. sp.

Coelosphaerium minutissimum Lemm.

Eucapsis alpina Clem. and Schantz

Merismopedia glauca (Ehr.) Näg.

M. punctata Meyen

M. tenuissima Lemm.

Microcystis aeruginosa (Kütz.) Kütz.

M. delicatissima (W. and G.S.West) Starm.

M. elachista (W.and G.S.West) Starm.

M. elachista f. planctonica (G.M.Sm.) Starm.

M. wesenbergii (Kom.) Starm.

Synechococcus elegans (Wolosz.) Kom.

Anabaenopsis raciborskii Wolosz.

A. tanganyikae (G.S.West) Wolosz. and Miller

Aphanizomenon aphanizomenoides (Forti) Horecka and Kom.

A. flos-aquae f. gracile (Lemm.) Elenk

Lyngbya hieronymusii Lemm.

L. nyassae Schmidle

Oscillatoria bornetii (Zukal) Forti

O. lacustris (Kleb.) Geitl.

O. tenuis C.A.Ag.

O. sp.

Pseudanabaena mucicola (Hub.-Pestal. and Naum.) Schwabe

Spirulina laxissima G.S.West

S. sp.

CHROMOPHYTA

Cryptophyceae, cryptomonads

Cryptomonas sp.

Dinophyceae, dinoflagellates

Gymnodinium sp.

Peridinium inconspicuum Lemm.

Chrysophyceae, golden algae

Mallomonas sp.

Spiniferomonas sp.

Chrysococcus sp.

Diatomophyceae, diatoms

Melosira distans (Ehr.) Kütz.

M. nyassensis v. victoriae O.Müll.

Stephanodiscus sp.

Achnanthes sp.

Cymbella sp.

Eunotia zasuminensis (Cab.) Korn.

Fragilaria sp.

Navicula sp.

Nitzschia sp.

Surirella sp.

Synedra ulna v. amphirhynchus (E.) Grun.

Tribophyceae, yellow-green algae

Goniochloris fallax Fott

Tetraedriella regularis (Kütz.) Fott

CHLOROPHYTA

Euglenophyceae, euglenoids

Phacus longicauda (Ehr.) Duj.

Trachelomonas spp.

Chlorophyceae, green algae

Astrephomene gubernaculifera Pocock

Chlamydomonas sp.

Eudorina elegans Ehr.

Gonium pectorale O.F.Müll.

Pandorina morum (O.F.Mull.) Bory
Actinastrum sp.
Ankistrodesmus bernardii Kom.
Botryococcus braunii Kütz.
Coelastrum astroideum De-Not.
Crucigenia quadrata Morr.
C. tetrapedia (Kirchn.) W. and G.S.West
Crucigeniella neglecta (Fott and Ettl) Kom.
Dictyosphaerium ehrenbergianum Näg.
D. pulchellum Wood
Golenkinia paucispina W. and G.S.West
Kirchneriella aperta Teil.
Lagerheimia subsalsa Lemm.
Oocystis marssonii Lemm.
O. parva W. and G.S.West
Pediastrum boryanum v. brevicone A.Br.
P. boryanum (Turp.) Menegh. v. boryanum
P. duplex Meyen v. duplex
P. tetras (Ehrenb.) Ralfs
Quadricoccus verrucosus Fott
Scenedesmus acuminatus (Lagerh.) Chod.
S. acutiformis Schrod. v. acutiformis
S. caudato-aculeolatus Chod.
S. dimorphus (Turp.) Kütz.
S. disciformis f. disciformis (Chod.) Fott and Kom.
S. gutwinskii v. heterospina Bodrogk.
S. microspina Chod.
S. obliquus (Turp.) Kütz.
S. quadricauda (Turp.) Bréb.
Schroederia setigera (Schrod.) Lemm.
Selenastrum bibraianum Reinsch
Tetradesmus wisconsinensis G.M.Smith
Tetraedron caudatum (Corda) Hansg.
T. minimum (A.Br.) Hansg.
T. triangulare Kors.

- Tetrastrum glabrum (Roll) Ahlstr.and Tiff.
Dicoleon nordstedtii Kleb.
Closterium acutum v. variabile (Lemm.) Krieg.
C. moniliferum v. moniliferum
Cosmarium capense v. nyassae
C. contractum v. minutum West
C. wembaerense Schmidle
C. sp.
Euastrum Turneri v. simplex Forster
Staurastrum brachioprominens
S. tetracerum (Kutz.) Ralfs

Table 4. Phytoplankton species counted in the study, and their unit size.

SPECIES	Length (um)	Breadth (um)	Height (um)	Diam (um)	Vol (um^3)
Anabaenopsis raciborskii				1.8	
Lyngbya nyassae				1.3	
Merismopedia punctata				3.0	14
Microcystis aeruginosa				4.5	48
M. elachista				1.8	3
M. elachista f. planctonica				3.0	14
M. wesenbergii				4.5	48
Spirulina laxissima				0.8	
S. sp.				0.8	
Synechococcus elegans				1.0	
Botryococcus braunii					142
Oocystis parva	5.5		2.5		18
O. marssonii	8.0		4.5		85
Tetraedron minimum	4.6	4.6	2.3		49

PHYTOPLANKTON BIOMASS

Seasonal variation of phytoplankton species - The phytoplankton of Lake Awasa was characterized by a large variety of species, with a frequent dominance of coccoid and filamentous blue-green algae, and colonies of Botryococcus braunii. A preliminary observation of some samples showed a common occurrence of some diatoms including Melosira nyassensis, Surirella and Navicula species, green algae including Scenedesmus species and Cosmarium contractum, and the dinoflagellate Peridinium inconspicuum. Though their number was sufficient for a proper count, they comprised only about 10% of the total phytoplankton volume, and were not considered for further count. The 14 species counted in this study include 10 blue-green and 4 green algae (Table 4), and their seasonal distribution pattern is illustrated in Figure 6, where the taxa have been presented in order of their relative contribution to the total phytoplankton biomass.

Blue-Green Algae - The population of blue-green algae was relatively low during September-November. Microcystis species, Anabaenopsis raciborskii and Synechococcus elegans showed an increase during the mixing period in December. Lyngbya nyassae and Spirulina species, on the other hand, showed a decline of population in December followed by a slight increase in January. All phytoplankton species showed an increase of population in May. The peak was most pronounced in Lyngbya, Microcystis, Spirulina and Synechococcus species. This population maximum occurred when the lake was in the process of destratifying (Figures 2 and 3) which involves resuspension of plankton as well as nutrient replenishment in the water column, followed by fast utilization by the growing population.

Among the major phytoplankters of Lake Awasa, the individual species with the highest biomass was Lyngbya nyassae, a filamentous alga with very narrow trichomes (ca 1.3 µm). Except on a

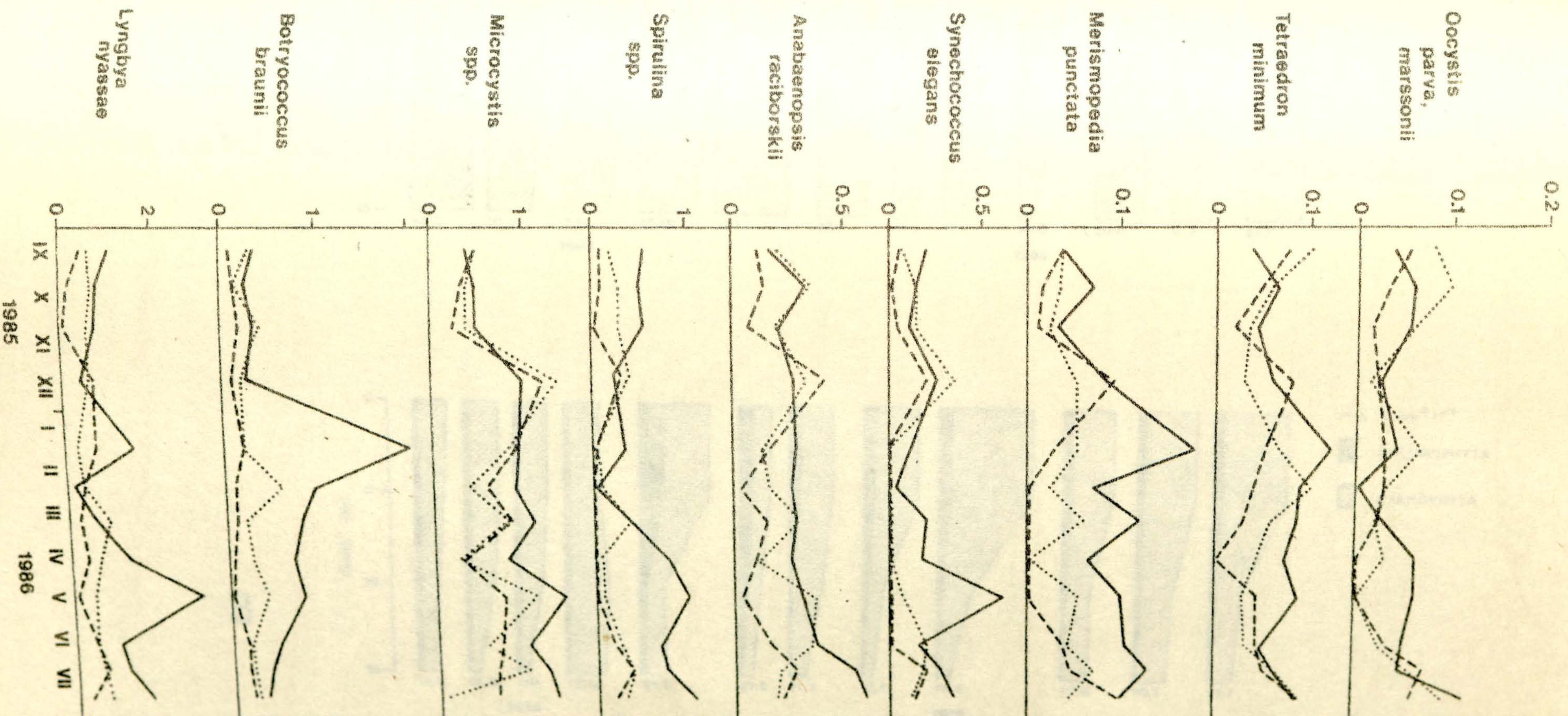
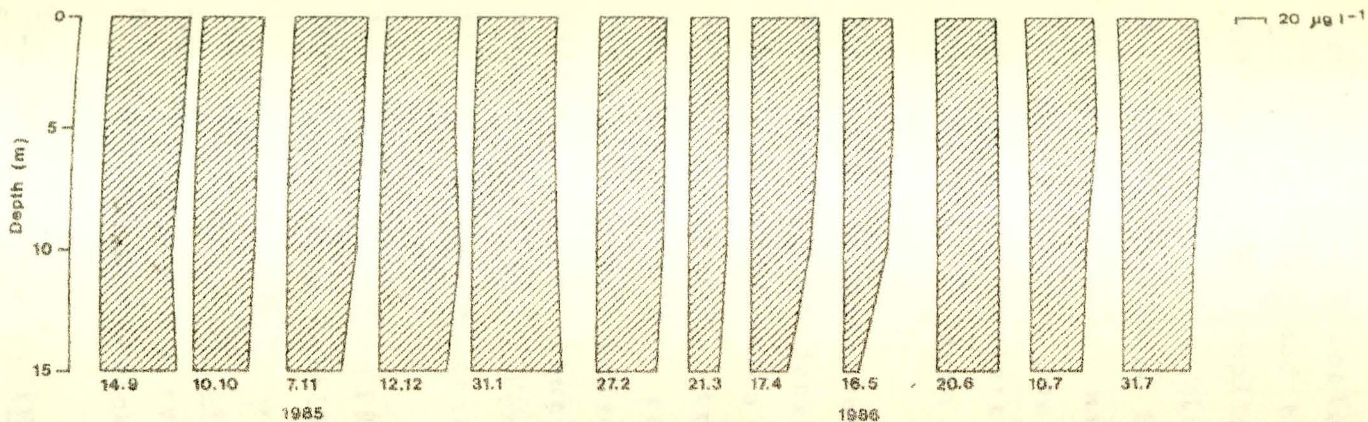


Figure 6. Seasonal variation in phytoplankton biomass (mm³l⁻¹) of Lake Awassa at depths of 0 – 5 meters (—), 10 m. (....), and 15 m(---). *Microcystis* spp. includes *M. aeruginosa*, *M. elachista f. planctonica*, *M. elachista*, *M. wesenbergii*. *Spirulina* spp. includes *S. laxissima* and *Spirulina* sp.

A



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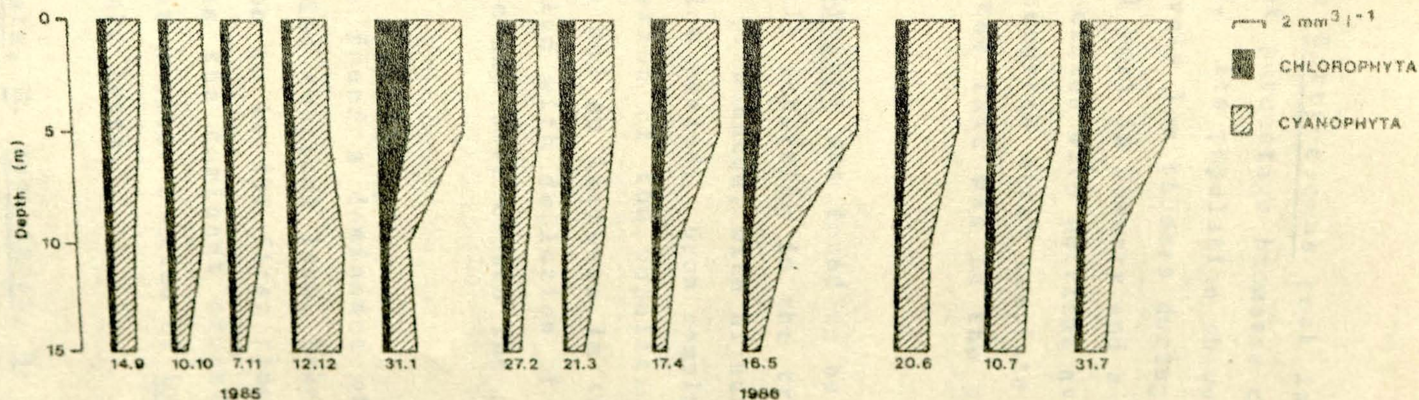

Figure 7. Variation of chlorophyll a (a) and phytoplankton volume (b) with depth and time in Lake Awas<u>s</u>a.

few occasions, including the Botryococcus peak in January, Lyngbya nyassae had the highest percentage biomasss composition throughout the sampling period. Its population showed distinct seasonal variation with relatively low biomass during September to December followed by a small peak in January and a major peak in May. Both peaks may be associated with nutrient availability (Figure 5) since the former occurred after complete mixing in December and the latter when the lake was in the process of destratifying (Figure 3).

The vertical distribution of Lyngbya was found to be variable, with the highest density usually occurring in the trophogenic zone. Stratification was more pronounced, with higher biomass, during the thermal stratification period. Upon complete mixing in June there was redistribution of the population with a decrease in the surface waters and an increase in the deeper waters. Redistribution coupled with depletion of available nutrients in the water column could have caused the population fall in the trophogenic zone.

Reynolds et al. (1983) have found a dominance of Lyngbya limnetica in a stably stratified tropical lake, Lake Carioca. They believe their observation to be the first time anywhere that a species of Lyngbya was the dominant organism. The present study also, reveals that another species of Lyngbya was the dominant phytoplankter in lake Awasa.

Microcystis species (M. elachista, M. aeruginosa, M. elachista f. planctonica, M. wesenbergii) showed a very similar distribution pattern; hence their total volume is presented in Figure 6 as Microcystis spp. Fluctuations of Microcystis population did not show a marked seasonality and appeared to be random. However, there was a relatively low density from September to November and January to April, both prior to mixing conditions in the lake. Their biomass over the whole lake column was

relatively high in December and May when the lake was in an almost isothermal condition and at the start of thermocline breakdown respectively. This population increase could be caused by resuspension of colonies located in the sediments in the stable periods. In Lake Victoria, Talling (1966) found that seasonal fluctuations in the numbers of Microcystis wesenbergii were not pronounced, but showed a small increase upon loss of stratification. In his qualitative observations, he has also found an appreciable increase in the number of another Microcystis species at the same time of mixing. Reynolds and Rogers (1976) have shown for temperate lakes that Microcystis colonies pass the winter months on the bottom muds and migrate up to the epilimnion in the summer. Ganf (1974 a) has also shown in a tropical lake (Lake George) that large numbers of Microcystis colonies reside within the lake sediments in calm conditions and are brought back into circulation by turbulence. The fluctuation of the Microcystis population observed in Lake Awasa may be due to this phenomenon. In Lake George, a shallow, tropical lake with a diurnal stratification cycle, Ganf (1974 a) has reported two dominant Microcystis species with large but random density fluctuations which he suggested were due to changes from calm to turbulent conditions in the lake.

Next to Lyngbya and Microcystis species, Spirulina species (S. laxissima and S. sp.) were the most important blue-green algae in their contribution to the phytoplankton volume of Lake Awasa. A decline of their population from September to February was followed by a marked increase from March to July, with the highest values in May and late July. Their distribution with depth showed variation with time. Distinct stratification of the population was found during March to May with very low density in the deeper waters, thus corresponding to the stable thermal stratification period. Relatively similar densities were recorded in the whole water column during September to December. This pattern of stratification in algal biomass was

more evident in Synechococcus elegans which also showed a seasonal pattern similar to Spirulina species.

No distinct pattern of seasonality was found in the distribution of Anabaenopsis raciborskii except for the pronounced increase of population in the surface waters in July. Samples in July had unusually long trichomes of both the spiral and straight forms of the alga which indicates a growing population prior to division. It appeared that it was the volume rather than the number of individual trichomes that resulted in the biomass increase.

Fluctuations in Merismopedia punctata were irregular with a relatively low population during September to December, and a peak in January. Stratification of this phytoplankton species was evident during January to May with almost no cells at 15 m during February to May.

Among the blue-green algae counted, distinct seasonal minima (February) and maxima (May) were found only in the filamentous species - Lyngbya nyassae, Synechococcus elegans and Spirulina species. Anabaenopsis raciborskii, and the coccoid colonies of Merismopedia punctata and Microcystis species showed fluctuations with relatively higher populations at times, but no definite minima were obvious during this work. Differences could arise from differences in their nutritional requirements, as well as buoyancy regulation mechanisms which can be important in the efficient utilization of available nutrients. Hart and Hart (1977) have reported a similar behavior in Lake Sibaya, where three filamentous species of blue-green algae showed population maxima and minima almost concurrently while other colonial blue-green algae, diatoms and desmids showed a different picture. They report this as an indication that the environmental requirements of all three blue-greens were very similar. Selective grazing by zooplankton can also be one

possible cause for differences in seasonal behavior between phytoplankton species of different morphological features (Wetzel, 1983).

Green Algae - The four species counted in this study include Tetraedron minimum, Oocystis parva, O.marssonii and Botryococcus braunii with the latter being the most important in contributing to the phytoplankton biomass of the lake (Figure 6). Botryococcus braunii showed a distinct seasonal pattern with a conspicuous peak in January in the surface waters. During the unstable stratification period (September to November) and the mixing period (December, and June to July), it had low biomass and very similar values at all depths. The peak in January was followed by generally decreasing values up to the end of the sampling period in July. Stratification of the plankton was distinct during the stratification period (January to May) with lower values in deep water. In the absence of turbulence Botryococcus colonies, which have a high lipid content, can be buoyant and concentrate in the surface waters. Brown masses of these colonies are usually seen on the lake surface sometimes forming streaks at places. Pooling samples from 0-5 m for counting reduces the errors in biomass estimation which would have been considerable due to horizontal variations on the surface with slight wind movement.

The population maxima in Botryococcus occurred in the driest period, and when alkalinity, conductivity (Figure 5) and surface temperatures were the highest for the sampling period. A similar behavior was also reported for Lake Turkana (Harbott, 1982) where Botryococcus braunii is one of the dominant algae in the open water. It showed a dominance when the lake level was at a seasonal minimum. The alga has been reported to live and grow successfully under an extremely wide range of physical conditions in natural waters (Belcher, 1968). With the onset of stratification following periods of mixing, phytoplankton with

efficient buoyancy mechanisms can make better use of the nutrients (Figure 5) and light available in the surface waters, although positive buoyancy is not necessarily of a selective advantage to the plankton since it exposes the cells to strong light at the surface. However, the buoyancy of Botryococcus colonies, coupled with their carotenoid pigmentation which has a screening effect from high light intensities found at the surface, can make them more competitive with the other species, thus enhancing their growth in the surface waters.

Oocystis and Tetraedron species were present in low concentrations and showed small variations in time with no distinct pattern. Their vertical distribution which also showed slight variations at times was almost uniform during the mixing period in June and July. This was also true in December when their biomass values were similarly low at all depths. Concentrations at 15 m were generally low for both Oocystis and Tetraedron species. Most of the irregular fluctuations of their population with time may be attributed to redistribution in the water column due to turbulence.

Seasonal variation of phytoplankton pigment - The distribution of chlorophyll a in the whole water column is presented in Figure 7a. The concentration varied seasonally with relatively high values (41-58 $\mu g\ l^{-1}$) from September to January. This was followed by decreasing values during February-May which coincides with the stratification period. There was an increase from June to the end of July which corresponds to the mixing period in the lake. The lowest chlorophyll values for the whole water column (23 $ug\ l^{-1}$) were measured in March. This is about 42% of the highest chlorophyll value (55 $ug\ l^{-1}$) measured in January. This maximum occurred at the onset of stratification following the mixing in December, which had likely raised the phosphate concentration to its highest value for the sampling period (Figure 5).

The mean chlorophyll a concentration for the trophogenic zone (0-5 m) of Lake Awasa was 43 ug l^{-1} which is much higher than concentrations in lakes Langano (7 ug l^{-1}) and Shalla (6 ug l^{-1}), Ethiopia (Belay and Wood, 1984), and Lake Victoria which has 1.2-5.5 mg m^{-3} (Talling, 1966) and Tanganyika which has a mean of 1.2 mg m^{-3} (Hecky and Kling, 1981). The algal crop in Lake Awasa is comparable to lakes Abijata (65 ug l^{-1}) and Zwai (91 ug l^{-1}) in Ethiopia (Belay and Wood, 1984), and lakes Naivasha and Oloiden in Kenya which had seasonal means of 27 ug l^{-1} and 23 ug l^{-1} respectively (Kalff and Watson, 1986).

The ratio of carotenoid to chlorophyll a was calculated by comparing absorption of pigment extracts at 480 nm and 665 nm representing the absorption peaks of carotenoids and chlorophyll respectively (Talling, 1966). The ratio which varied between 2.00-4.76 (Figure 8c) is relatively higher than the values given for Lake Victoria (Talling, 1966) and Lake Sibaya (Hart and Hart, 1977). This high ratio may be attributed to Botryococcus braunii which was one of the dominant phytoplankters in Lake Awasa. Botryococcus is known to have high amount of carotenoid, particularly β-carotene, which gives the colony its red color (Belcher, 1968). This author has also reported an accumulation of carotenoids in the alga with ageing, high temperatures and high light intensities, and during nitrate and phosphate starvation. Considering the generally high temperatures and light intensity in the tropics, it is likely that colonies of Botryococcus in Lake Awasa will tend to accumulate carotenoids, thus increasing the carotenoid:chlorophyll ratio. Carotenoids are believed to have a protective role against inhibiting light intensities (Krinsky, 1966, cited by Belay, 1974).

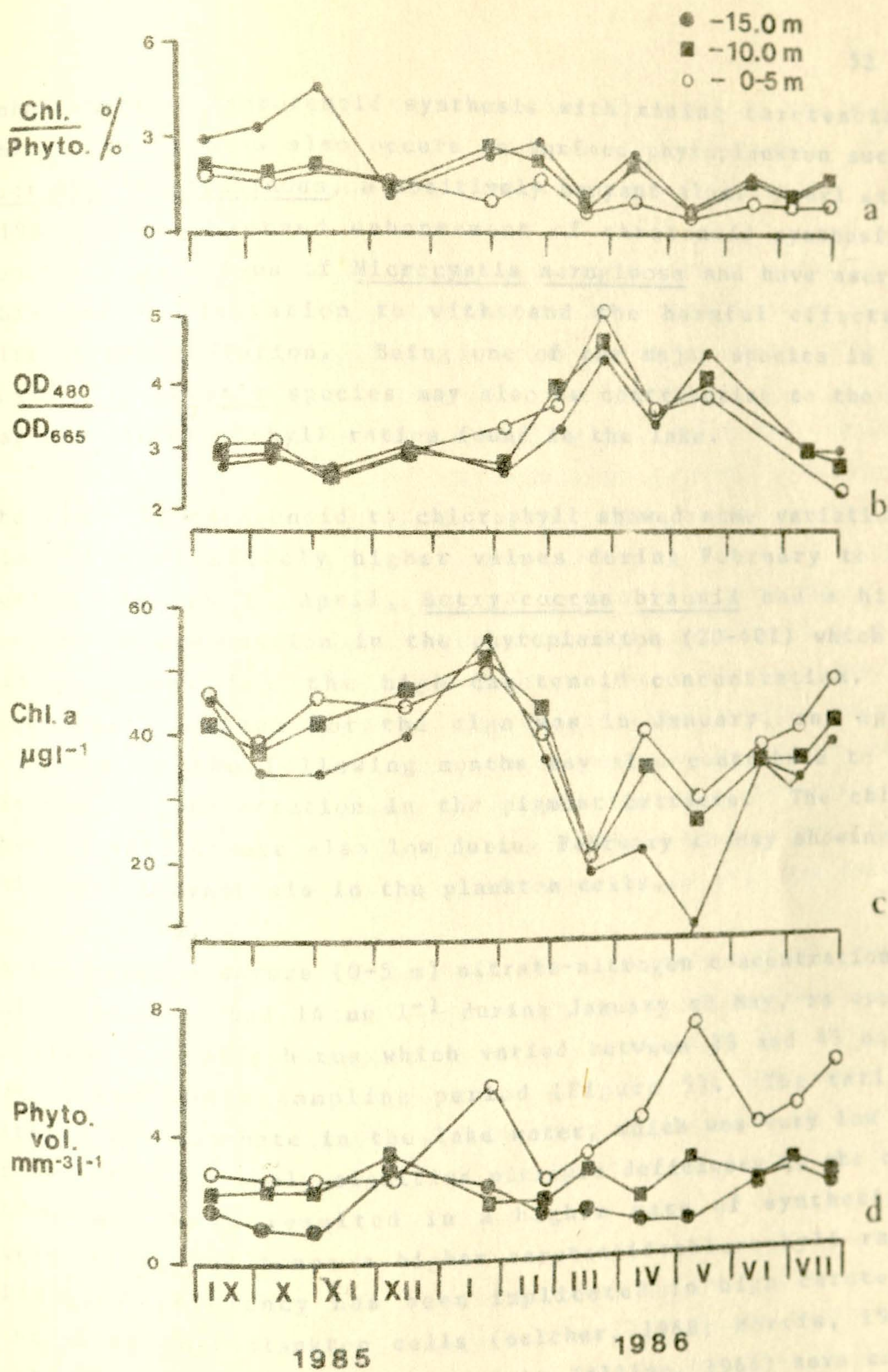

Figure 8. Seasonal variation in phytoplankton biomass and related ratios. a) The ratio of chlorophyll a to phytoplankton volume expressed as a percentage. b) The ratio of carotenoid to chlorophyll a (OD 480/OD 665). c) Chlorophyll a concentration. d) Phytoplankton volume.

Enhancement of carotenoid synthesis with rising carotenoid to chlorophyll ratios also occurs in surface phytoplankton such as Microcystis aeruginosa, a positively buoyant alga. Paerl et al. (1983) have observed enhancement of carotenoid synthesis in buoyant populations of Microcystis aeruginosa and have ascribed this as an adaptation to withstand the harmful effects of ultraviolet radiation. Being one of the major species in Lake Awasa, Microcystis species may also be contributing to the high carotenoid:chlorophyll ratios found in the lake.

The ratio of carotenoid to chlorophyll showed some variation in time with relatively higher values during February to May. During January to April, Botryococcus braunii had a higher percentage composition in the phytoplankton (20-40%) which may also account for the high carotenoid concentration. The population maximum for the alga was in January, and ageing colonies in the following months may also contribute to high carotenoid concentration in the pigment extracts. The chlorophyll a values were also low during February to May showing low chlorophyll synthesis in the plankton cells.

In the surface waters (0-5 m) nitrate-nitrogen concentration was only between 7 and 14 ug l^{-1} during January to May, as opposed to phosphate-phosphorus which varied between 23 and 45 ug l^{-1} during the whole sampling period (Figure 5). The ratio of nitrate to phosphate in the lake water, which was very low most of the time, probably signifies nitrogen deficiency in the cells which may have resulted in a higher rate of synthesis of carotenoids, and hence a higher carotenoid:chlorophyll ratio. Nitrogen deficiency has been implicated in high carotenoid content of phytoplankton cells (Belcher, 1968; Morris, 1980). Yentsch and Vaccaro (1958, cited by Talling, 1966) have considered the nitrogen content of marine phytoplankton to be an important determinant of the carotenoid:chlorophyll ratio. This explanation seems likely considering the drop in ratio in July,

when the lowest value for the year was recorded in the surface waters (Figure 8b). The drop coincides with the highest nitrate concentration measured in the surface waters (Figure 5).

Vertical distribution of chlorophyll showed less variation than the phytoplankton volume (Figure 7a,b). The latter shows a pronounced stratification of algae in most cases, with much lower biomass values below the trophogenic zone. Pigment concentration however, remained fairly similar throughout the water column for most of the sampling period. During the stratification period (January to May) the decline of the algal population with depth was clearly seen with the phytoplankton volume, particularly at times of higher biomass values. This was not so obvious with the chlorophyll a, but it is better illustrated in Figure 8 which includes the concentrations in 0-5 m, and at 10 m and 15 m. It shows fairly similar values at all depths during September to December, and an almost uniform distribution during January to March. The concentration at 15 m was relatively lower in April, and declined more in May when the lowest chlorophyll a at a single depth (10 $\mu g\ l^{-1}$) was detected.

With complete mixing in June, phytoplankton volume showed an increase at 15 m with a decrease in the upper column of water, thus showing the distribution of the plankton in the trophogenic zone over the whole column of water. This is also discernible from Figure 6, where most species show an increase in biomass at 15 m from May to June. Chlorophyll a, however, showed an increase at all depths.

Under stable conditions, phytoplankton tend to accumulate in the trophogenic zone provided they are not negatively buoyant. The dominant blue-green algae in Lake Awasa, Lyngbya, Microcystis and Spirulina species, are all known to possess gas vacuoles in their cells which give them positive buoyancy. The other dominant alga Botryococcus braunii, is also buoyant due to its

high accumulation of lipid. Considering the composition of the phytoplankton which are mostly buoyant (Figure 6), stratification of plankton is expected to occur, specially during stable periods.

In the chlorophyll a analysis, no distinction was made for degradation products of chlorophyll. The contribution of phaeopigments to the absorbance of pigment extracts, which can be considerable in deep waters, can exaggerate the chlorophyll values thus masking a possible decrease with depth. Diatoms which have cell walls of silica are most dense, with a specific gravity of as much as 0.06 g ml^{-1} in excess of that of water (Moss, 1980). Thus they would be expected to concentrate in deep water under stable conditions. The diatom population in Lake Awasa, which has not been estimated in this work but contributes to the pigment concentration, may be another reason for the differences found between chlorophyll a and phytoplankton volume.

A comparison was made between the two measures of total phytoplankton density - chlorophyll a (Figure 8c) and phytoplankton volume (Figure 8d). The ratio of chlorophyll a to phytoplankton volume in percentage is shown in Figure 8a. On all occasions except one, the ratio was higher in deeper than in the surface waters. Possible reasons which have been discussed earlier, i.e. degradation products and the diatom population not included in the phytoplankton count, may again contribute to the high ratio in deep water. It may also be because the chlorophyll a content per cell increases with depth. Phytoplankton cells residing in deeper waters can have a relatively higher pigment content than cells in the surface waters exposed to high light, to make maximum utilization of the low light available in deep water (Reynolds, 1984). This low light adaptation has been exhibited in a metalimnetic Lyngbya population which had a high chlorophyll a content (11 ug mm^{-3}) as a photosynthetic adapt-

ation to extremely low light intensities (Reynolds et al., 1983).-

The ratio of chlorophyll a to phytoplankton volume in the upper 0-5 m water column varied between 0.43 and 1.81. The two lowest values recorded, 0.43 and 0.62, were in May and March respectively. These ratios correspond to the two highest ratios determined for carotenoid to chlorophyll. The overall reciprocal relationship of the two ratios (cf. Figures 8a,b) suggests that low rate of chlorophyll synthesis is associated with high carotenoid synthesis in the plankton.

SEASONALITY OF PHYTOPLANKTON

Temporal distribution of phytoplankton seemed to be most influenced by the thermal stratification behavior of the lake. Total biomass increased with the onset of stratification following complete mixing in December, and with the beginning of destratification in May. This increase may be associated with vertical mixing in the water column which redistributes suspended matter and influences the temperature and light climate, and nutrient availability which in turn determine the fate of the phytoplankton. Rainfall and drainage from the catchment area during the rainy season also contributed to the nutrient supply of the lake, enhancing growth of phytoplankton during the mixing period in June-July.

The magnitude of seasonal changes, in the phytoplankton biomass of Lake Awasa expressed as chlorophyll a, is low when compared with other tropical lakes presented in Melack (1979). He has applied the coefficient of variation (CV) to assess the range of seasonal variability in the abundance and photosynthetic rates of phytoplankton among tropical lakes, and proposed three temporal patterns. According to Kifle (1985), and the present work which gave a CV of 20% with the chlorophyll a data, Lake Awasa falls in pattern B. Melack describes this pattern as one

in which the phytoplankton assemblage is constant, and the species are adapted to the full range of environmental conditions; as conditions change in the environment, species better adapted attain numerical dominance. This conforms with the findings in Lake Awasa where the phytoplankton composition was the same throughout the sampling period and some species had a population peak under different environmental conditions.

Seasonality of phytoplankton in Lake Awasa was also assessed by applying the ratio of seasonal population maxima to minima (Kalff and Watson, 1986). Total phytoplankton gave a ratio of 2.8 for cell volume and 2.4 for the chlorophyll a content in the trophogenic zone. Expressing this ratio as the log 10 derivative in orders of magnitude (Talling, 1986), the amplitude of variation was found to be only 0.45 and 0.38 respectively. This is very similar to the annual amplitude observed in Lake Sibaya (Hart and Hart, 1977) and Lake George (Ganf, 1974c). The total community showed an amplitude of 0.42 in Lake Sibaya, and about 0.2-0.4 in Lake George (Talling, 1986). Measurement of chlorophyll a for 5 years in Lake Naivasha show very similar amplitude of variation with the above lakes (0.34, 0.38, 0.40, 0.65, and 1.08) with the two exceptional values for the Lake (0.65 and 1.08) suggesting that changes in environmental conditions are sometimes greater (Kalff and Watson, 1986). Most values are slightly lower than the seasonal amplitude of variation (0.58) in the chlorophyll a content of the productive zone in Lake Victoria (Talling, 1986).

The seasonal amplitude of variation in the component species of Lake Awasa was higher than was found in the total community, although it was still less than one order of magnitude for all species except Lyngbya nyassae (1.28), Spirulina spp. (1.20) and Synechococcus elegans (1.16). Among the green algae, seasonal amplitude was highest (0.88) in Botryococcus braunii. The magnitude of seasonal variation in the total community was

masked to a certain extent by the difference in the major peak periods of the dominant phytoplankton Botryocococcus braunii and Lyngbya nyassae. Considering that the amplitude of variation was relatively lower in the pigment concentration than in the total cell volume, variation in total phytoplankton community could have also been masked due to uncounted phytoplankton species which contributed to the pigment concentration. Relatively low community values as compared to component species were also found in lakes Victoria (Talling, 1966), Sibaya (Hart and Hart, 1977) and George (Ganf, 1974c). Talling (1986) accounts this difference of pattern in Lake Victoria to the influence of abundant but less variant and uncounted Aphanocapsa spp., and the complementary patterns of occurrence of some diatoms and blue-green algae. Small and uncounted species have been suggested to be the probable cause in Lake Sibaya (Hart and Hart, 1977).

Grazing is one of the factors influencing the temporal and spatial distribution of phytoplankton. The abundance of the grazing population, selective grazing and their feeding habit influences the species abundance and seasonal behaviour of the phytoplankton on which they feed. The most important fish in the commercial fishery of Lake Awasa, Oreochromis niloticus, is a phytoplankton feeder. Among the four species of zooplankton which make up 98% of the total biomass in Lake Awasa (Mengistu, unpublished data), Thermocyclops consimilis, Diaphanosoma excisum and Alona diaphana, and juveniles of Mesocyclops aequatorialis similis are herbivorous. Mengistu's data show differences in the seasonal pattern of abundance among these populations, with Mesocyclops species more abundant during January-March and July-September, and Thermocyclops species during April-June. This pattern of seasonality among the grazers could very well affect the seasonal behaviour of the phytoplankton population, either by masking a possible variation

or by inducing one, due to intensive or selective grazing in some period.

CONCLUSION

CONCLUSION

The overall distribution pattern of phytoplankton biomass in Lake Awasa was generally influenced by the hydrographic structure of the water column with an increase of biomass upon partial mixing or following complete mixing. Inorganic phosphate was relatively high during the sampling period while nitrate concentration, determined during January-July, was low except during the rainy season in June and July. The pigment extracts showed a generally high carotenoid to chlorophyll ratio indicating the possibility of nitrogen deficiency in the phytoplankton cells. However, detailed investigation needs to be carried out on the nitrogen status of the algae, as well as on the nitrogen and phosphorus dynamics of the lake, to confirm this suggestion.

The phytoplankton community of Lake Awasa, dominated by blue-green algae and one species of green algae, shows some seasonal pattern of distribution. The range of seasonal variability, which was relatively low when compared to some tropical lakes with marked seasonality, was different among the component species counted in this study. This is a reflection of differences in morphological and physiological behavior of the species in relation to the environmental conditions prevailing in the lake. Grazing by zooplankton and fish can be one important factor in determining or modifying the seasonal behavior of total phytoplankton biomass and/or component species. Hence studies of the fish and zooplankton community should be integrated with phytoplankton studies to get a better picture of the seasonal pattern.

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DECLARATION

I, the undersigned declare that this dissertation is my own work and that all sources of material used for the thesis have been correctly acknowledged.

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