

CHLOROPHYLL AND CAROTENOID DISTRIBUTION  
AND PHYTOPLANKTON ECOLOGY IN  
KEYSTONE RESERVOIR,  
TULSA, OKLAHOMA

By

FREDERIC LYNN SPANGLER

Bachelor of Arts  
North Central College  
Naperville, Illinois  
1961

Master of Science  
Oklahoma State University  
Stillwater, Oklahoma  
1965

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Thesis Approved:

*Troy C. Davis*  
\_\_\_\_\_  
Thesis Adviser

*Rudolph J. Miller*  
\_\_\_\_\_

*Glean W. Todd*  
\_\_\_\_\_

*William A. Drew*  
\_\_\_\_\_

*D. D. Murham*  
\_\_\_\_\_  
Dean of the Graduate College

725096

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## TABLE OF CONTENTS

| Chapter  | Page |
|--|------|
| I. INTRODUCTION . . . . .                        | 1    |
| II. KEYSTONE RESERVOIR, THE STUDY AREA . . . . . | 5    |
| III. METHODS . . . . .                           | 9    |
| IV. QUANTITATIVE PIGMENT ESTIMATES . . . . .     | 13   |
| Chlorophyll a . . . . .                          | 13   |
| Chlorophyll b . . . . .                          | 17   |
| Chlorophyll c . . . . .                          | 20   |
| Non-Astacin Carotenoids . . . . .                | 23   |
| Astacin-Type Carotenoids . . . . .               | 27   |
| V. ECOLOGICAL RELATIONSHIPS . . . . .            | 32   |
| Chlorophyll To Plant Carotenoid Ratio . . . . .  | 32   |
| Chlorophyll Fractions . . . . .                  | 32   |
| Light Penetration . . . . .                      | 36   |
| Turbidity . . . . .                              | 36   |
| Euphotic Zone . . . . .                          | 37   |
| Estimated Gross Primary Productivity . . . . .   | 41   |
| Ash-Free Weight . . . . .                        | 45   |
| Chlorophyll a - Dry Weight . . . . .             | 49   |
| Pigment Diversity . . . . .                      | 50   |
| Succession . . . . .                             | 52   |
| Trophic Classification . . . . .                 | 53   |
| VI. SUMMARY . . . . .                            | 55   |
| LITERATURE CITED . . . . .                       | 57   |

## LIST OF TABLES

| Table   | Page |
|---|------|
| I. Annual Means of Concentrations and Amounts of Chlorophyll a . . . . .            | 14   |
| II. Annual Means of Concentrations and Amounts of Chlorophyll b . . . . .           | 19   |
| III. Annual Means of Concentrations and Amounts of Chlorophyll c . . . . .          | 21   |
| IV. Annual Means of Concentrations and Amounts of Non-Astacin Carotenoids . . . . . | 24   |
| V. Annual Means of Concentrations and Amounts of Astacin-Type Carotenoids . . . . . | 29   |
| VI. Annual Means of Pigment Fractions . . . . .                                     | 33   |
| VII. Chlorophyll a - Euphotic Zone Relationships . . . . .                          | 40   |
| VIII. Chlorophyll-Based Estimates of Gross Productivity . . . . .                   | 43   |
| IX. Annual Means of Ash-Free Weight . . . . .                                       | 46   |
| X. Relationship Between Chlorophyll and Ash-Free Weight . . . . .                   | 47   |
| XI. Pigment Diversity Annual Means . . . . .  | 52   |

## LIST OF FIGURES

| Figure  | Page |
|---|------|
| 1. Map of Keystone Reservoir. . . . .   | 6    |
| 2. An Example of an Absorption Curve of an Extract from the<br>Natural Phytoplankton Population . . . . .                   | 10   |
| 3. Variation in Amounts of Chlorophyll a . . . . .  | 15   |
| 4. Variation in Amounts of Chlorophyll b . . . . .  | 18   |
| 5. Variation in Amounts of Chlorophyll c . . . . .  | 22   |
| 6. Variation in Amounts of Non-Astacin Carotenoids . . . . .  | 25   |
| 7. Variation in Amounts of Astacin-Type Carotenoids . . . . .   | 28   |
| 8. Variation in Amounts of Chlorophyll a and Astacin-Type<br>Carotenoids at Stations III and IV . . . . .                   | 30   |
| 9. Variation in Chlorophyll a Fraction. . . . .   | 34   |
| 10. Variation in Chlorophyll b Fraction. . . . .  | 35   |
| 11. Variation in Euphotic Zone Depth . . . . .  | 38   |
| 12. Mean Annual Euphotic Zone Depth and Mean Annual Content<br>of Chlorophyll a Per Square Meter of Euphotic Zone . . . . . | 39   |
| 13. Relative Amount of Chlorophyll a in Euphotic Zone and<br>Relative Extent of Euphotic Zone . . . . .                     | 42   |
| 14. Gross Productivity Estimated from Chlorophyll Data . . . . .  | 44   |
| 15. Pigment Diversity During the Cold Months . . . . .  | 51   |
| 16. The Ratio of Chlorophyll to Biomass at Station IV . . . . .   | 54   |

## CHAPTER I

### INTRODUCTION

From the standpoint of community metabolism, photosynthesis is the most important activity of plants. Study of photosynthetic pigments provides insight into the physiological aspects of aquatic systems and to community structure. Early work relating photosynthesis and chlorophyll was undertaken by Wilstatter and Stoll (1918). According to Odum, et al. (1958) the first use of chlorophyll as a measure of photosynthesis was by Harvey (1934). Since then photosynthesis has been studied extensively (Rabinowitch, 1945, 1951, 1956; Calvin, 1958, and others).

Chlorophyll may be used as an indicator of standing crop but light conditions influence the relationship (Strickland, 1960). Difficulty arises in quantitatively relating chlorophyll to productivity because of the large range in the ratio of photosynthetic rate to chlorophyll (assimilation number). However, assimilation numbers tend to vary around a constant value which may be used to compute gross productivity from chlorophyll and light data (Ryther and Yentsch, 1957).

Odum (1957), Lorenzen (1963), Gibor and Meehan (1961), and others report significant diurnal variation in chlorophyll concentration. Yentsch and Ryther (1957), and Shimada (1958) report chlorophyll maxima at dawn in marine waters. Ichimura (1958) found a diurnal variation in assimilation number. Lorenzen (1963) found diurnal variation in photosynthesis to be due to changes in pigment concentrations in cells. He

also observed diurnal variation in assimilation number. In field studies diurnal variation in chlorophyll cannot satisfactorily be accounted for. Sampling at the same time of day on each collecting trip is assumed to circumvent the problem for the most part.

Chlorophyll typically has a maximum concentration at some depth which may or may not be within the euphotic zone (Lorenzen, 1965). When the maximum concentration occurs at low light intensity deep below the surface the assimilation number is usually low (Steemann Nielsen and Hansen, 1959). Maxima below the euphotic zone may be accounted for by differential sinking rates of cells (Steele and Yentsch, 1960). Shade adaptation may greatly influence chlorophyll concentration in some instances (Yentsch and Lee, 1966). Whether these relationships apply in relatively shallow, well mixed bodies of fresh water is not well established.

A consequence of the aging and sinking of phytoplankters is that pigments begin to be degraded. Available methods for distinguishing between active and detrital chlorophyll are less than adequate. Yentsch and Menzel (1963) proposed a fluorescence method of determining phytoplankton chlorophyll and magnesium-void pigments. Chlorophyll and chlorophyllide (chlorophyll molecule with magnesium but without the phytol group) have the same absorption spectra in the visible light region (Yentsch, 1965a), and a convenient method of separating them is not available.

Phaeophytin is one of the major products of degradation of chlorophyll and is nonphotosynthetic. A phaeophytin is a magnesium-void compound with phytol. Removal of the phytol yields phaeophorbide. Yentsch (1965b) demonstrated that exposure of dark-adapted cells to



light results in a decrease of phaeophytin and an increase in chlorophyll content indicating a direct conversion. Subjecting cells low in phaeophytin to darkness leads to an increase in phaeophytin and a corresponding loss of capacity for light uptake of  $^{14}\text{C}$  and lowered efficiency of pigment.

Chlorophyll amount per unit area tends to be adjusted for maximum absorption of available light (Odum, et al., 1958). Light-adapted cells at the surface tend to have relatively low amounts of chlorophyll and high assimilation numbers (Gessner, 1949). Conversely, shade-adapted cells have relatively larger amounts of chlorophyll and low assimilation numbers. For relatively great surface light intensity the chlorophyll per unit area is expected to be high as are efficiency and assimilation number. This suggests that in the southwestern United States, with long periods of bright light, productivity in aquatic systems may be greater than anticipated in view of the fact that turbidity is typically very high.

Since many aquatic plants have optimum light intensities for photosynthesis, a mid-day reduction in photosynthetic rate may occur (Rabinowitch, 1951). When an extensive chlorophyll containing zone is present the reduction may be obscured by production by shade adapted cells in deep water. Steemann Nielsen (1954) and Verduin (1956) report that community photosynthesis does not drop as low as might be expected under conditions of diminished light. Odum, et al. (1958) recognize the following types of communities based on chlorophyll adaptation to light: stratified, shaded, and mixing communities and thin cultures with bright light. In the mixing community, cells are adapted to

intermediate light. Communities of most lakes of southwestern United States, and Keystone Reservoir in particular, are probably of this type.

The objectives of this study were to observe spatial and temporal distribution of chlorophylls a, b, and c, non-astacin carotenoids (phytoplankton pigments), and astacin-type carotenoids (animal carotenoids), and to examine the results for ecological implications. Quantitative and qualitative pigment determinations reveal numerous relationships which constitute the ecology of a body of water.

Distinct seasonal phenomena were found but events of the year did not fall into distinct units of time which were the same for all of the stations. Therefore, in this report the terms "summer," "winter," etc., are used as approximate designations.

## CHAPTER II

### KEYSTONE RESERVOIR, THE STUDY AREA

Keystone Reservoir was formed in 1964 by construction of a dam across the Arkansas River just below the confluence of the Cimarron and Arkansas Rivers west of Tulsa, Oklahoma, (Figure 1). It was constructed by the U.S. Army Corps of Engineers for multiple uses including flood control, generation of hydroelectric power and recreation. Filling of the reservoir was completed in April, 1965.

Total watershed is  $1.94 \times 10^7$  hectares. Surface area of the reservoir at power pool level (elevation 220 m) is  $1.06 \times 10^6$  hectares. Gross storage capacity at that level is  $8.18 \times 10^8 \text{ m}^3$ . Maximum storage capacity at flood stage (elevation 230 m) is  $2.32 \times 10^9 \text{ m}^3$ .

This study was conducted on the Cimarron branch of the reservoir. Four stations were marked with permanent buoys (Figure 1). The upstream station, Station I, was shallow (0.5 to 4.5 m) with high turbidity, high flow rate, high conductivity, and rapid temperature change relative to other stations. Station II, next downstream, varied in depth from eight to ten meters, was turbid much of the year and had reduced flow rate. One large creek, House Creek, enters between Stations I and II. Chemical stratification developed at Station II but was absent at I. Station III was about 15 meters deep and the water was generally less turbid than at upstream stations. Chemical stratification was better developed than at I and II. Station III was located at a

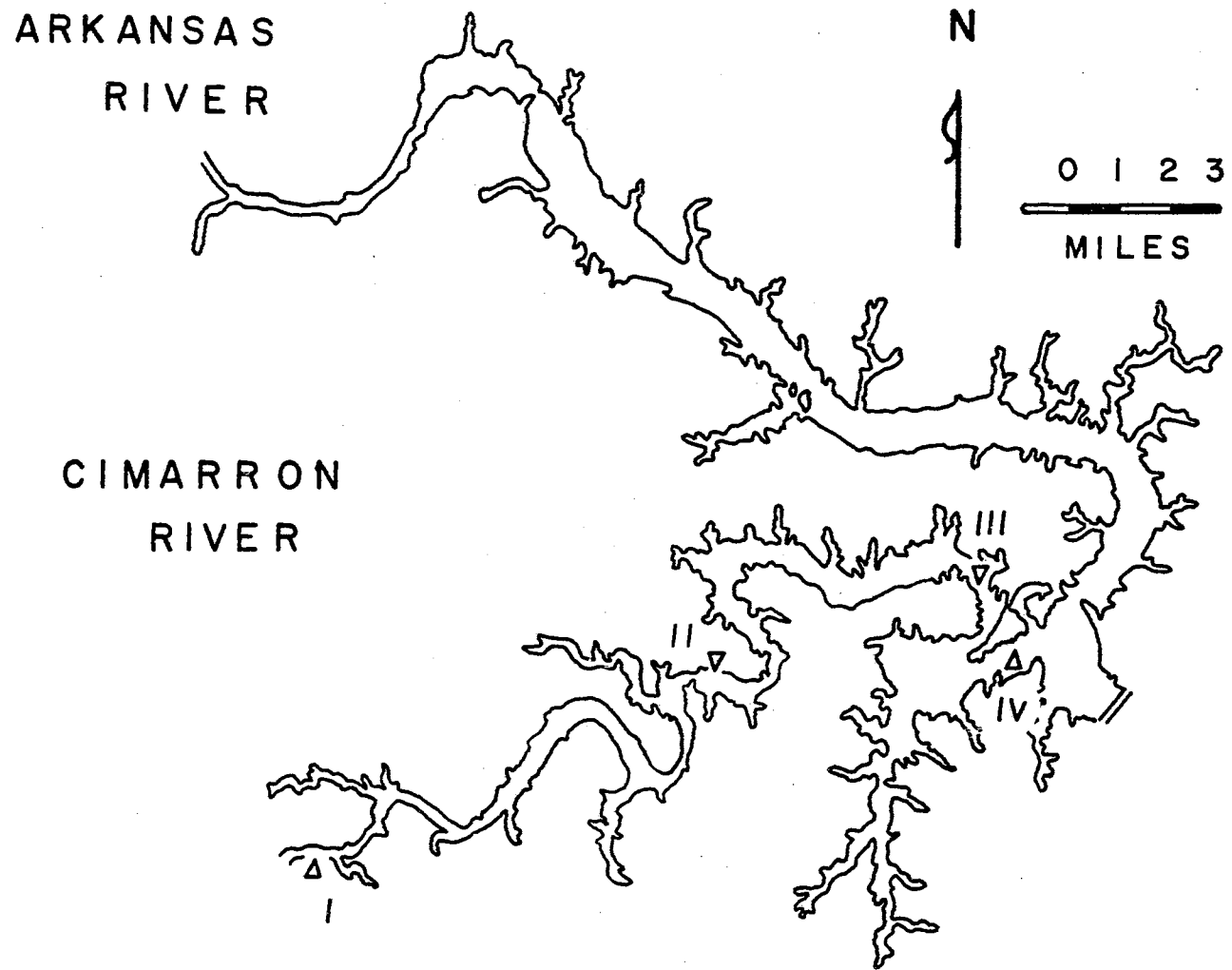


Figure 1. Keystone Reservoir, Tulsa, Oklahoma. Roman Numerals Indicate Locations of the Sampling Stations.

constricted region where the channel makes a sharp bend. Two large backwater areas are located between stations II and III and undoubtedly exert an influence on conditions at III. Large backwaters are also situated between III and IV and adjacent to IV.

The reservoir is different from natural lakes in that a channel is well defined throughout most of its length. All sampling stations were located in the channel which was located by depth soundings. Station IV, the downstream station, had a maximum depth of 20 meters. Stratification was most pronounced at IV. Turbidity was consistently much lower at IV than at other stations. Wind undoubtedly caused much greater turbulence and mixing, especially in some seasons, at III and IV with greatest effect at IV.

The Cimarron River headwaters are in a semi-arid region in which New Mexico, Colorado, and Kansas are adjacent to the Oklahoma panhandle. Elevation in this region ranges from 915 to 1,370 meters and average annual precipitation is less than 46 cm (Gray and Galloway, 1959). In northwestern Oklahoma the Cimarron River flows through mixed-grass prairie with average annual precipitation of 76 cm and elevation of 305 to 427 meters. Some soil areas of north-central Oklahoma, particularly the Grant-Pond Creek-Nash association (Gray and Galloway, 1959), have accumulations of soluble salts which result in high conductivity, one of the peculiar features of the Cimarron River. Average annual precipitation in north central Oklahoma is about 97 cm. A wide range of variation occurs from year to year, however.

Keystone Reservoir is a harsh environment for aquatic flora. High turbidity greatly restricts the depth to which photosynthesis may occur. Attached macrophytes are not found at any point although heavy growths

of Cladophora develop at surface level on rocky bluffs. Water level fluctuates greatly thus making even more difficult the establishment of bottom flora. Ice covered Station I to a depth of about two cm on one occasion and to a lesser depth on several others. Ice did not cover the other sampling sites at any time.

## CHAPTER III

### METHODS

The methods of Richards with Thompson (1952) and Creitz and Richards (1955) were combined for concentrating plankton. Water was centrifuged at the rate of one liter per seven minutes with a Foerst plankton centrifuge. Remaining water was removed from the centrifugate with Type AA Millipore filters with pore size  $0.45 \mu$ . Extraction was carried out in darkness in 90 per cent acetone under refrigeration for 18 to 24 hours. Samples were centrifuged for 15 minutes at 2,000 rpm prior to determination of absorbancies.) In some cases a longer centrifugation time was required for removal of turbidity. (A Beckman DB-G recording spectrophotometer was used to determine absorbancies in the wavelength range 400 to  $700 m\mu$ ) (Figure 2). Readings were also taken at  $750 m\mu$  for correction of errors due to turbidity (Strickland and Parsons, 1965). Dilutions frequently were necessary since solutions must have absorbancies less than 0.8. Cells of four cm path length were used except for a short time at the beginning of the study when one cm cells were the only ones available. In cases in which the chlorophyll a peak did not occur at exactly  $665 m\mu$  the readings were taken at the peaks. Other readings were taken relative to the chlorophyll a peak even if its location was displaced laterally (Banse and Anderson, 1967). Pigment quantities were computed by methods of Richards with Thompson (1952) and Parsons and Strickland (1963).

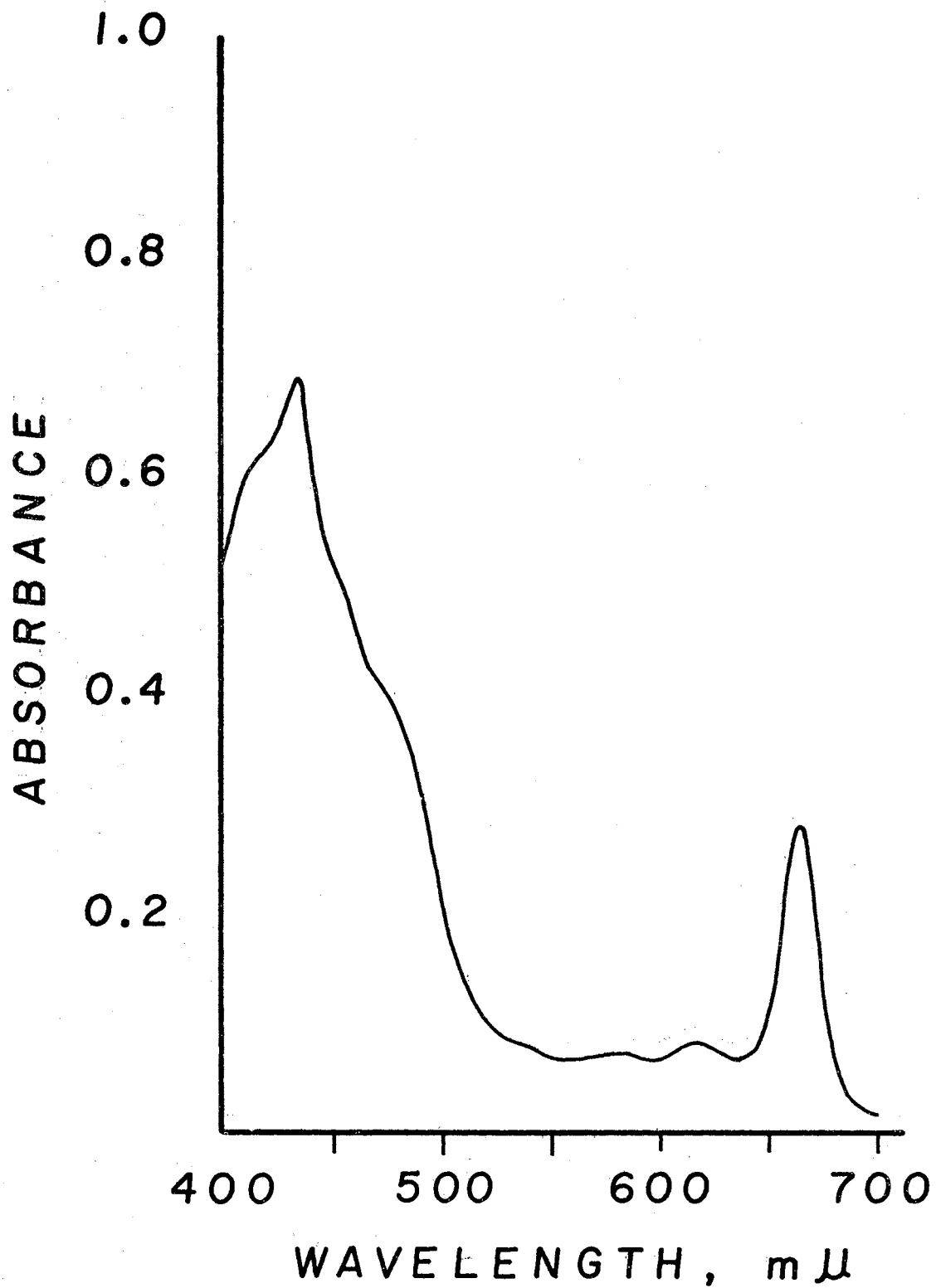


Figure 2. Example of an Absorption Curve of a 90 Per Cent Acetone Extract from the Natural Phytoplankton Population of Keystone Reservoir. Absorbancies Are Read at Wavelengths of 430, 480, 510, 635, 645, and 665 mμ.



Since specific absorption coefficients are unknown for chlorophyll *c* and the carotenoids, results of quantitative determinations are in millisppecific pigment units, represented by the letters MSPU. An MSPU is approximately equal to one mg (Richards with Thompson, 1952).

The Foerst centrifuge is less than 100 per cent efficient in concentration of plankton (Hartman, 1958; Lasker and Holmes, 1957; Reinhard, 1931). Parallel series of samples comparing the centrifuge to the Millipore filter showed that amounts of chlorophyll *a* obtained by the filters were higher by 21 per cent. Therefore, results of quantitative pigment determinations were multiplied by 1.21. Pennak (1949) applied a blanket correction factor of 25 per cent. Hartman (1958) showed that after three centrifugings up to 11 per cent of the organisms may remain in the water. Thus repeated centrifuging was not used in this study.

Ash-free weight (loss on ignition) determinations were made on samples preserved in 5 per cent formalin. One- to five-hundred ml of water were centrifuged and diluted with distilled water and commercial formalin to 10 ml final volume.

Conductivity and temperature were measured in the field with a temperature-compensated Industrial Instruments Solu Bridge, Model RB 3-3341. Some conductivity measurements were made in the laboratory with an Industrial Instruments Model RC1B conductivity meter. Turbidities were determined using a Bausch and Lomb Spectronic-20 colorimeter.

Solar radiation measurements (langleys per day) at Stillwater, Oklahoma, were supplied by the Oklahoma State University Geography Department. Data for some days were not available from that source

and values obtained at Oklahoma City, Oklahoma, were substituted.

Solar radiation data were used to estimate daily production of organic material by the method of Ryther and Yentsch (1957).

Correlation coefficients were computed for some parameters (Steele and Torrie, 1960). The Wilcoxon matched-pairs signed-ranks test (Siegel, 1956) was used to test for significance of differences between annual means of pigment concentrations.

## CHAPTER IV

### QUANTITATIVE PIGMENT ESTIMATES

#### Chlorophyll a

Annual means of chlorophyll a concentrations decreased downstream and with depth (Table I). All but two of the differences tested were significant at the 95 per cent level and all but four were significant at the 99 per cent level. More differences between annual means of concentrations were significant for chlorophyll a than for other pigments. The difference between annual means of chlorophyll a concentrations in surface samples at stations I and II was great but its level of significance was lower than expected on the basis of its magnitude. The same result was found for differences between annual means of concentrations of the other pigments at those stations and can be accounted for by the extreme variability of pigment concentrations, particularly at Station I. The pattern of decrease of annual means of concentrations was the same for all pigments and reflects the long-term spatial distribution. On any given date, however, distribution may have been considerably different. This result was expected on the basis of Kosminski's classic chlorophyll distribution study (1938).

The small water mass at Station I was subject to rapid and large changes in conditions and weekly variation in pigment amount was high (Figure 3). Chlorophyll a concentration exceeded  $100 \text{ mg m}^{-3}$  on ten

occasions at Station I, three at Station II, one at Station III, but never at Station IV. Since Station I was very shallow, changes in concentration of pigment at the surface closely approximated changes in pigment amount on an area basis.

TABLE I  
ANNUAL MEANS OF CONCENTRATIONS ( $\text{MG M}^{-3}$ ) AND  
AMOUNTS ( $\text{MG M}^{-2}$ ) OF CHLOROPHYLL A

| Depth<br>(Meters)  | I        | II       | III      | IV       |
|--------------------|----------|----------|----------|----------|
| 0                  | 84.81 *  | 46.23 ** | 29.81 ** | 23.06 ** |
| 2                  |          | 38.72 ** | 28.36 ** | 20.17 ** |
| 4                  |          | 33.95 ** | 23.25 *  | 18.38    |
| 6                  |          |          | 20.98 ** | 17.60 ** |
| 10                 |          |          | 17.38 ** | 15.01 ** |
| 16                 |          |          |          | 10.81    |
| $\text{mg m}^{-2}$ | 92.30 ** | 272.75   | 281.27   | 264.54   |

One asterisk (\*) between two means indicates that the means are significantly different at the 95 per cent level. Two asterisks (\*\*) indicate differences significant at the 99 per cent level.

Maxima in chlorophyll a amounts were observed at Station I in October, December, March and April (Figure 3). None of the peaks was sustained, however. Each peak consisted of a single observation. Amounts of chlorophyll a were generally less than  $100 \text{ mg m}^{-2}$  at Station I and greater than  $100 \text{ mg m}^{-2}$  at other stations. Changes in amounts were consistently small throughout January, February, and most of March.

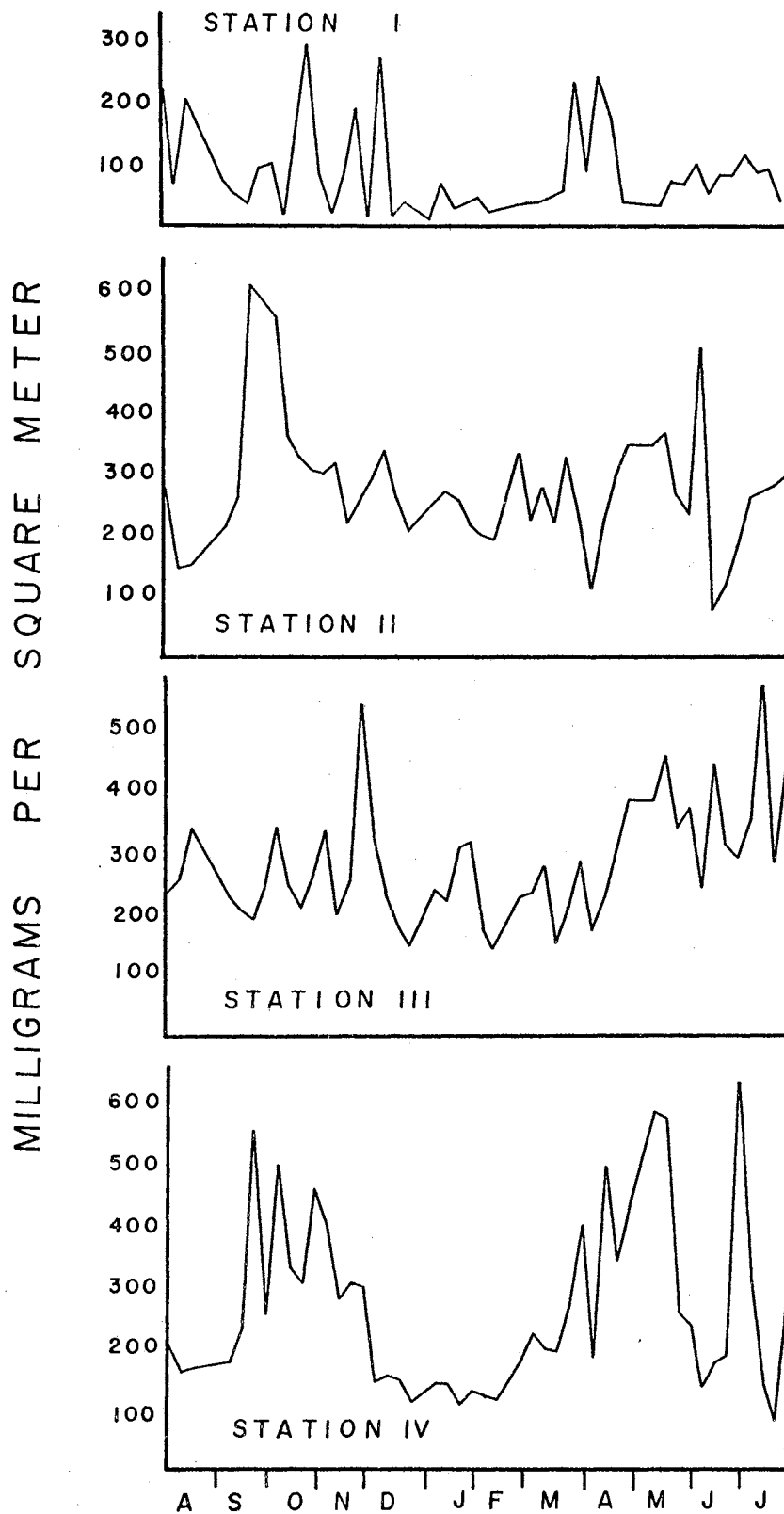


Figure 3. Temporal Variation in Amounts of Chlorophyll a in a Water Column One Meter Square.

Unidirectional periods of change in amount of chlorophyll a at Station II lasted longer than at Station I, thus seasonal trends were more distinct. A fall peak of  $606.4 \text{ mg m}^{-2}$  on 21 September was particularly well defined (Figure 3). A general decrease until 8 February followed but minor peaks were distinct in December and January. Variability was high in February and March. A low level was reached in early April but was followed by several weeks of continuous increase. A spring maximum of  $503.9 \text{ mg m}^{-2}$  occurred on 7 June. In one week, however, the amount fell to  $77.3 \text{ mg m}^{-2}$ , the minimum for the year. Five weeks of continuous increase followed.

At Station III unidirectional periods of change in amount of chlorophyll a were usually only one or two weeks long. The result was numerous peaks spaced a few weeks apart. A fall high of  $533.7 \text{ mg m}^{-2}$  occurred in November. A peak in January was well defined at Station III, less evident at II and lacking at I and IV. From the yearly minimum of  $141.6 \text{ mg m}^{-2}$  in February there was a general increase until mid-May. In May, June, and July variability was great but amounts were generally high.

Station IV showed the best defined long-range trends in changes in amount of chlorophyll a (Figure 3). A fall maximum occurred in September and was followed by a general decrease until mid-December. Weekly variation in December and January was low and amounts of chlorophyll a were low. From late February until May amounts increased regularly with few exceptions. After the May peak, amounts were reduced drastically for several weeks. A second spring peak,  $632.2 \text{ mg m}^{-2}$ , observed on 28 June was high for the year and was followed by the yearly low,  $75.3 \text{ mg m}^{-2}$  three weeks later.

## Chlorophyll b

Chlorophyll b occurred in much smaller amounts than the other chlorophylls (Table II). The trend was to lower means downstream and with depth but several notable exceptions occurred. Greatest significance in differences was between means at Stations II and III. Nine pairs of means were different at the 95 per cent level and seven at the 99 per cent level.

Temporal distribution of chlorophyll b at Station I differed from that at other stations (Figure 4). Amounts were very low throughout the year and exceeded  $10 \text{ mg m}^{-2}$  only three times. During fall maxima at other stations chlorophyll b was absent at Station I. A notable peak of  $38.6 \text{ mg m}^{-2}$  occurred on 30 March. The only prolonged period of increase took place from 7 June to 19 July and terminated in a high of  $15.6 \text{ mg m}^{-2}$ .

Changes in amount of chlorophyll b followed a common pattern at the three downstream stations (Figure 4). At the beginning of the study amounts were low. Rapid increase occurred earliest at Station II. A change from  $4.6 \text{ mg m}^{-2}$  to  $53.9 \text{ mg m}^{-2}$  occurred within two weeks in September. Over the next four weeks the amount fell to  $21.3 \text{ mg m}^{-2}$ . A two-week period of increase then resulted in the maximum for the year,  $60.6 \text{ mg m}^{-2}$ , on 9 November. These changes produced two fall peaks. Nine measurements during this time were higher than the highest measurement during the spring. From 2 December to 6 January chlorophyll b fell from  $53.8 \text{ mg m}^{-2}$  to  $0 \text{ mg m}^{-2}$ . An amount greater than  $10 \text{ mg m}^{-2}$  was not observed until 15 March. The pigment nearly disappeared late in December and did not appear in appreciable amounts until March at

MILLIGRAMS PER SQUARE METER

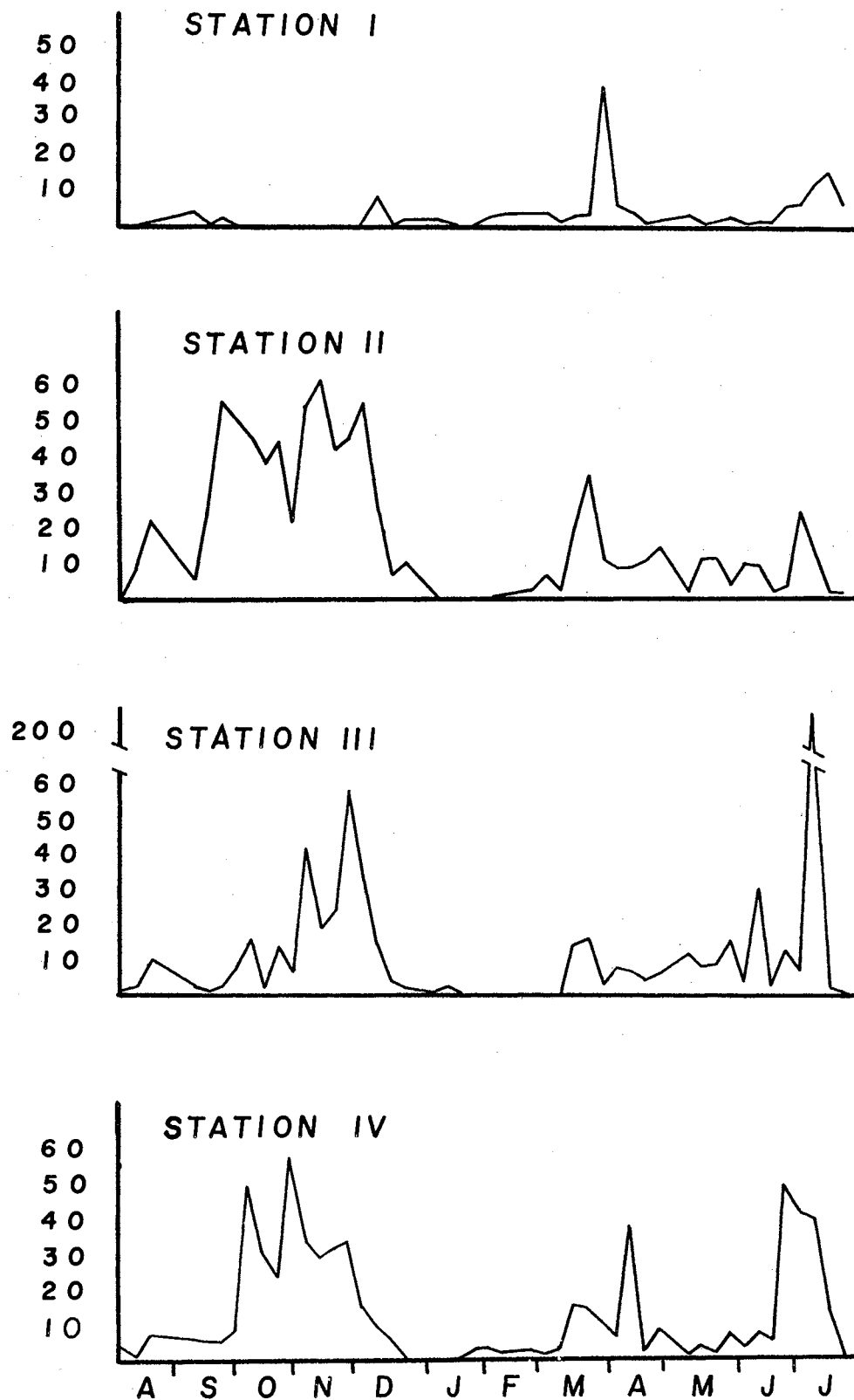


Figure 4. Temporal Variation in Amounts of Chlorophyll b in a Water Column One Meter Square.



each of the downstream stations. A very decided period of decrease preceded this minimum at each station. Coincidence of periods of change at the three stations was great.

TABLE II  
ANNUAL MEANS OF CONCENTRATIONS ( $\text{MG M}^{-3}$ ) AND  
AMOUNTS ( $\text{MG M}^{-2}$ ) OF CHLOROPHYLL B

| Depth<br>(Meters)  | I       | II       | III     | IV      |
|--------------------|---------|----------|---------|---------|
| 0                  | 1.77    | 2.92 **  | 2.05    | 1.30    |
| 2                  |         | 1.93 **  | 2.26 ** | 1.28 *  |
| 4                  |         | 1.34 **  | 1.14 ** | 0.93    |
| 6                  |         |          | 0.68    | 0.82 ** |
| 10                 |         |          | 0.49    | 0.46 *  |
| 16                 |         |          |         | 0.29    |
| $\text{mg m}^{-2}$ | 2.77 ** | 16.33 ** | 12.54   | 12.81   |

One asterisk (\*) between two means indicates that the means are significantly different at the 95 per cent level. Two asterisks (\*\*) indicate differences significant at the 99 per cent level.

An early spring peak of  $34.2 \text{ mg m}^{-2}$  occurred on 22 March at Station II. One week later the amount fell to  $10.3 \text{ mg}$  and it remained at that level until late June except for two occasions. A summer peak of  $24.4 \text{ mg m}^{-2}$  was observed on 5 July. Corresponding peaks occurred at the other stations but were of greater magnitude at Stations III and IV.

Autumn peaks of  $41.3$  and  $57.8 \text{ mg m}^{-2}$  were observed at Station III on 2 November and 25 November. A high September peak corresponding to the one at Station II did not appear. A single, one-week period of

decline occurred between the two fall peaks. From 25 November to 19 December the amount of chlorophyll b fell to  $1.43 \text{ mg m}^{-2}$ . Appreciable amounts did not appear again until 15 March. From then until 15 June amounts were within the range 5 to  $15 \text{ mg m}^{-2}$  except on three occasions when they fell to about  $3 \text{ mg m}^{-2}$ . On 15 June  $29.5 \text{ mg m}^{-2}$  was observed and a decrease immediately followed. The drastic nature of changes in amounts of phytoplankton pigments is exemplified by the occurrence of  $201.9 \text{ mg m}^{-2}$  on 10 July. That measurement is more than three times greater than any other for the entire study. One week later the amount was near zero.

From 30 September to 7 October chlorophyll b increased more than six-fold at Station IV (Figure 4). In two weeks the amount dropped from  $47.8$  to  $21.8 \text{ mg m}^{-2}$  and then increased in one week to  $56.0 \text{ mg m}^{-2}$  on 29 October, the maximum for the year. For about a month, until 25 November, a plateau was maintained at about  $30 \text{ mg m}^{-2}$ . Then a four-week period of decline ended on 19 December when the winter level near zero was reached. In one week chlorophyll b increased from  $2.1$  to  $14.6 \text{ mg m}^{-2}$  on 15 March. Three weeks of gradual decline followed. On 12 April the amount was  $36.4 \text{ mg m}^{-2}$ , an early spring peak. Until 28 June, when  $46.7 \text{ mg m}^{-2}$  was measured,  $8 \text{ mg m}^{-2}$  was not exceeded. A steady decline to zero occurred from 28 June to 25 July.

#### Chlorophyll c

Annual means of chlorophyll c concentration decreased with depth and distance downstream (Table III). Differences between means were significant at the 95 per cent level in only half of the 20 cases tested.

TABLE III  
 ANNUAL MEANS OF CONCENTRATIONS (MSPU M<sup>-3</sup>) AND  
 AMOUNTS (MSPU M<sup>-2</sup>) OF CHLOROPHYLL C

| Depth<br>(Meters)    | I     | II          | III        | IV        |
|----------------------|-------|-------------|------------|-----------|
| 0                    | 18.62 | 11.13 **    | 7.55<br>** | 6.47<br>* |
| 2                    |       | 9.90<br>*   | 6.32<br>** | 5.42      |
| 4                    |       | 9.02 **     | 5.05       | 4.42      |
| 6                    |       |             | 4.90<br>*  | 4.32<br>* |
| 10                   |       |             | 3.53       | 3.11<br>* |
| 16                   |       |             |            | 2.44      |
| MSPU m <sup>-2</sup> | 20.68 | ** 68.16 ** | 58.14      | 63.91     |

One asterisk (\*) between two means indicates that the means are significantly different at the 95 per cent level. Two asterisks (\*\*) indicate differences significant at the 99 per cent level.

Variation in amount of chlorophyll c was low at Station I (Figure 5). Throughout August, September, October, and much of November amounts ranged between 5 and 25 MSPU m<sup>-2</sup>. Twenty-five MSPU m<sup>-2</sup> was exceeded once in November and once in December. In late December, January, and February amounts were below 10 MSPU m<sup>-2</sup>. There was a general increase in March and April with the yearly maximum of 87.4 MSPU m<sup>-2</sup> occurring on 12 April. Two weeks of decline followed the maximum. A gradual, stepwise increase then led to a summer peak in mid-July.

Except for a few one-week periods of decline, the amount of chlorophyll c increased steadily from August until mid-January at Station II (Figure 5). Steady decline until mid-March followed. Two weeks of sharp increase followed by two of decrease resulted in a

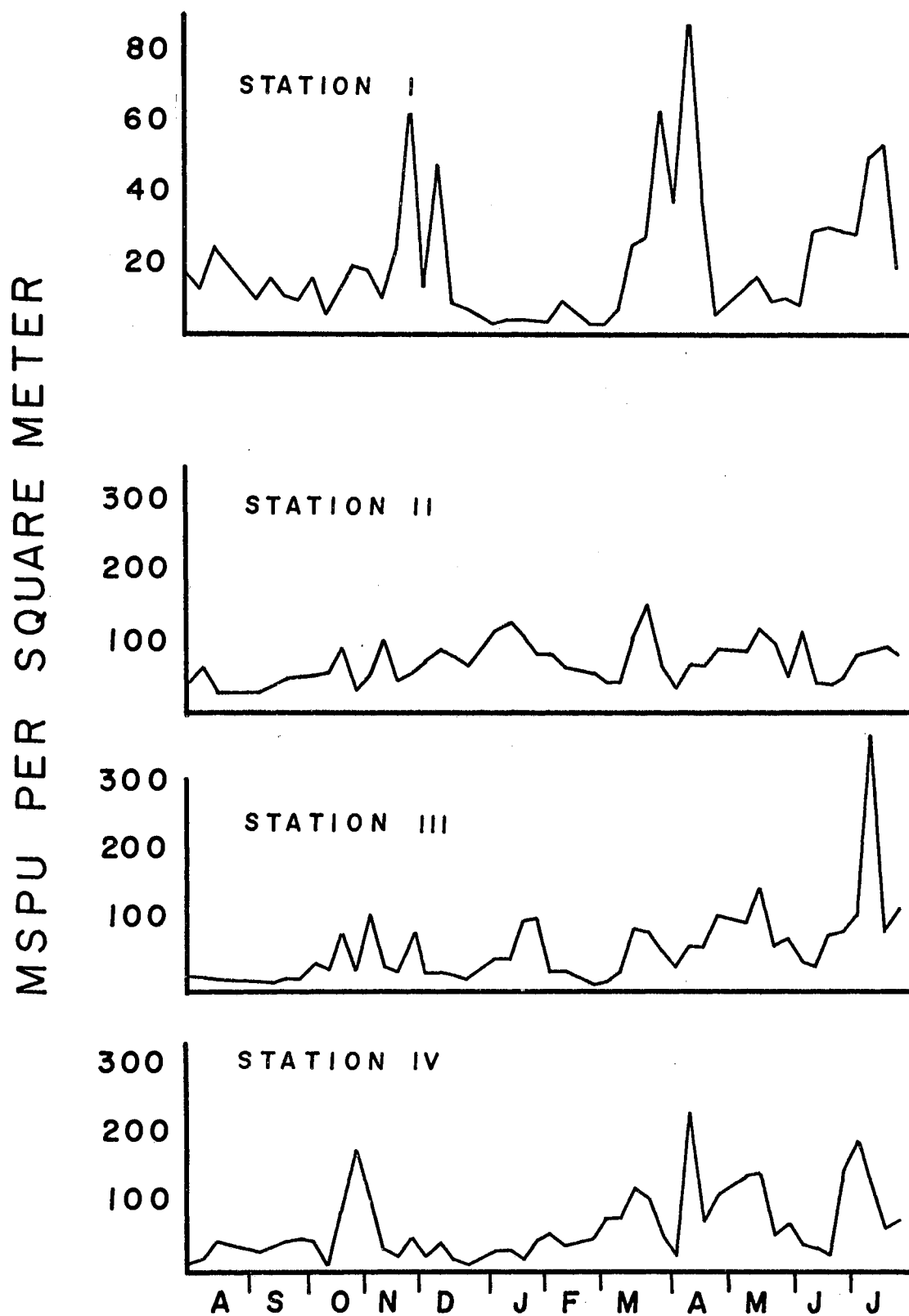


Figure 5. Temporal Variation in Amounts of Chlorophyll c in a Water Column One Meter Square.

distinct peak of 153.9 MSPU  $m^{-2}$  on 22 March. Amounts increased during April and early May but were variable in May and June.

At Station III amounts of chlorophyll c were generally less than 50 MSPU  $m^{-2}$  from August to mid-March (Figure 5). Exceptions occurred in October, November, and January when some values were near 100 MSPU  $m^{-2}$ , suggesting peaks in plankton populations. After 15 March chlorophyll c was present in amounts greater than 50 MSPU  $m^{-2}$  except for some days in April and June. A peak of 142.9 MSPU  $m^{-2}$  occurred on 20 May and was followed by a general decline for four weeks. The maximum for the year was 359.2 MSPU  $m^{-2}$  on 10 July after four weeks of steady increase.

Amounts of chlorophyll c at Station IV were less than 50 MSPU  $m^{-2}$  from August to March except for a three-week period in October and November when a peak of 174.1 MSPU  $m^{-2}$  was attained (Figure 5). December and January had particularly low amounts whereas amounts were relatively high during those months at Stations II and III. At Station IV there was a general increase in amount of chlorophyll c from December to 15 March when a high of 118.2 MSPU  $m^{-2}$  was observed. In late March, as at Stations II and III, a sharp decline occurred until early April. The highest value of the year, 228.2 MSPU  $m^{-2}$ , was observed on 12 April. Amounts decreased to near 25 MSPU  $m^{-2}$  for three weeks in June but rose again to a peak of 186.0 MSPU  $m^{-2}$  in early July.

#### Non-Astacin Carotenoids

Non-astacin carotenoids were present in greater amounts than any pigment except chlorophyll a (Table IV). Concentrations decreased downstream and with depth with no exceptions. Differences between

annual means were significant at the 99 per cent level in most cases. The null hypothesis that surface means at Stations I and II (41.6 and 28.1 MSPU m<sup>-2</sup> respectively) were equal had a probability of 0.29 despite their relatively great difference in magnitude. Differences between four and six meter means at Stations III and IV were not significant at the 95 per cent level nor were they great in relative magnitude.

TABLE IV  
ANNUAL MEANS OF CONCENTRATIONS (MSPU M<sup>-3</sup>) AND  
AMOUNTS (MSPU M<sup>-2</sup>) OF NON-ASTACIN  
CAROTENOIDS

| Depth<br>(Meters)    | I     | II          | III            | IV             |
|----------------------|-------|-------------|----------------|----------------|
| 0                    | 41.57 | 28.09<br>** | ** 16.61<br>** | ** 12.65<br>** |
| 2                    |       | 21.42<br>** | ** 15.46<br>** | ** 10.60<br>** |
| 4                    |       | 19.34<br>** | ** 12.81<br>** | ** 9.66<br>**  |
| 6                    |       |             | 11.43<br>**    | ** 9.33<br>**  |
| 10                   |       |             | 6.85           | * 7.88<br>**   |
| 16                   |       |             |                | 5.21           |
| MSPU m <sup>-2</sup> | 48.74 | ** 153.67   | 150.78         | 134.89         |

One asterisk (\*) between two means indicates that the means are significantly different at the 95 per cent level. Two asterisks (\*\*) indicate differences significant at the 99 per cent level.

Seasonal trends in amount per unit area were apparent but variation within any time period was great, particularly at Station I (Figure 6). Large amounts (up to 163.2 MSPU m<sup>-2</sup>) constituting a fall peak at Station I were observed in October, November, and December but were interspersed with low totals. A general range of 5 to 50 MSPU m<sup>-2</sup> was maintained

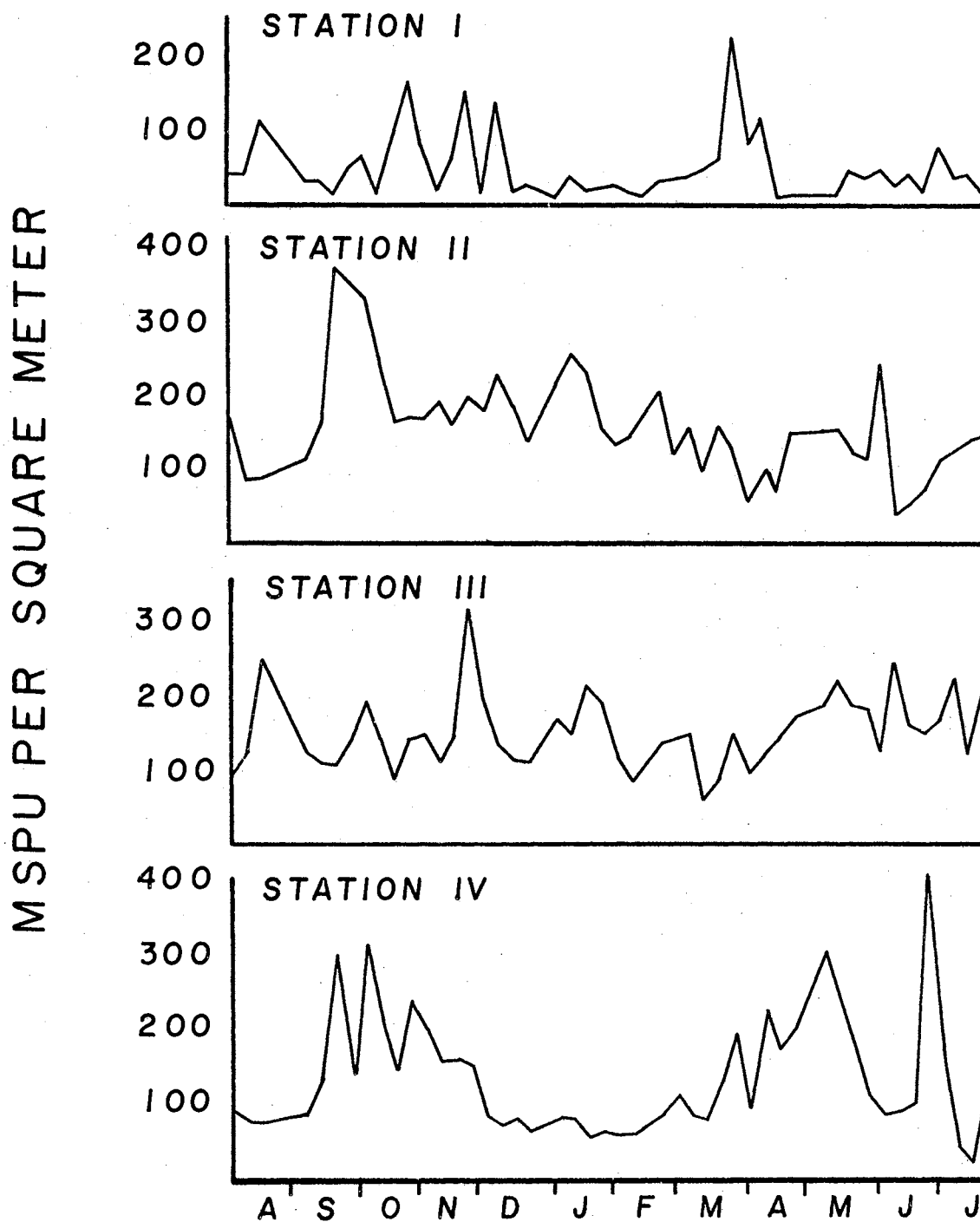


Figure 6. Temporal Variation in Amounts of Non-Astaxin Carotenoids in a Water Column One Meter Square.

from late December to mid-March and from 22 April to the end of the study except for one date in July. From 22 March until 12 April amounts varied between 62.3 and 221.3 MSPU  $m^{-2}$ .

At Station II a well defined peak of 365 MSPU  $m^{-2}$  occurred in September (Figure 6). Two-hundred MSPU  $m^{-2}$  was exceeded only six other times during the year. Three of them constitute a minor but well defined peak in January. From 11 January until 5 April there was a general decrease with the longest interruption being two weeks. Amounts then increased to a high of 236 MSPU  $m^{-2}$  in a single week. Gradual, uninterrupted increase to the end of July followed.

Numerous two- to four-week periods of unidirectional change in amount of non-astacin carotenoids characterized Station III. Amounts greater than 200 MSPU  $m^{-2}$  were observed in August, October, November, January, May and July. Each such peak was preceded by a general increase and followed by a general decrease with few abrupt changes. The maximum for the year, 312.5 MSPU  $m^{-2}$ , occurred on 23 November. Maxima in August, November, January and June may be said to be summer, fall, winter, and spring peaks although division into seasons is not clear.

Three well defined peaks, two extending over more than four weeks each, characterized Station IV. Variation within peaks was great however. Maxima of more than 300 MSPU  $m^{-2}$  occurred in September, October, May, and June. The September and October maxima appeared to be part of a general high with one low observation separating them. A range of 50 to 100 MSPU  $m^{-2}$  was not exceeded from 2 December to 22 February. In contrast, Stations I, II, and III had relative maxima during that time.



### Astacin-Type Carotenoids

This group of pigments is often referred to as the animal carotenoids (Crustacea in particular). They are of special interest in plankton studies because their abundance relative to that of plant pigments, particularly chlorophyll a, may indicate grazing by zooplankters. Grazing may significantly affect the standing crop or influence succession (Fogg, 1965). Wetzel (1964) states that grazing is indicated by an inverse relationship between astacin and plant pigments. Evidence supporting this is given by Anderson, et al. (1955), Langford and Jermolajev (1966) and others.

In most cases concentrations of astacin-type carotenoids decreased downstream and with depth (Table V). However only a few of the differences tested were significant at the 95 per cent level. This result was not unexpected since the means do not differ greatly in magnitude and zooplankton distribution does not have the same controlling factors that phytoplankton distribution has. Variation in astacin-type carotenoid concentration with depth is not expected to vary in the same manner as that of the plant pigments.

Animal carotenoids were absent much of the time early in the study at Station I (Figure 7). High turbidity was suspected as being a cause. Astacin peaks, however, occasionally occurred at times of extremely high turbidity. Amounts of astacin were less than  $5 \text{ MSPU m}^{-2}$  until 15 March with one exception. After 15 March the amount ranged from 4.3 to  $68.5 \text{ MSPU m}^{-2}$  except on four dates, three of which occurred consecutively in late May and early June. The high for the year,  $68.5 \text{ MSPU m}^{-2}$ , followed by one week the spring chlorophyll a maximum. The

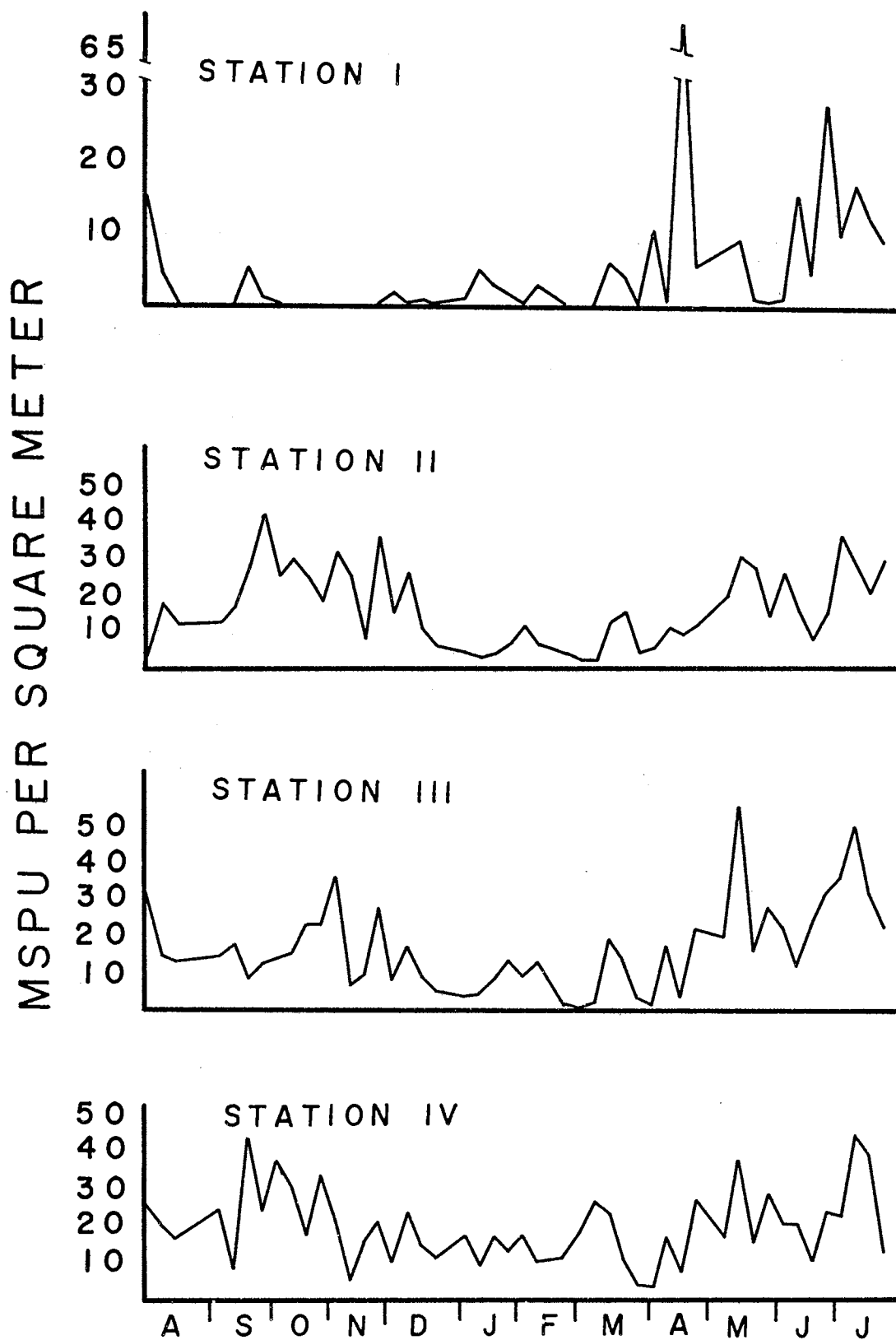


Figure 7. Temporal Variation in Amounts of Astacin-Type Carotenoids in a Water Column One Meter Square.

late May--early June low followed a sharp chlorophyll a decline. Grazing activity is indicated by these relationships.

Seasonal trends were more apparent at Station II with astacin-type carotenoids present at all times. Amounts were lowest from late December to the end of March with two distinct minor peaks, both inversely related to chlorophyll a changes observed during that period. Highest amounts (greater than 20 MSPU  $m^{-2}$ ) occurred in the intervals from September to December and May to June. Maxima were not maintained although levels were generally higher than in the winter.

TABLE V  
ANNUAL MEANS OF CONCENTRATIONS (MSPU  $M^{-3}$ ) AND  
AMOUNTS (MSPU  $M^{-2}$ ) OF ASTACIN-TYPE  
CAROTENOIDS

| Depth<br>(Meters) | I       | II      | III     | IV     |
|-------------------|---------|---------|---------|--------|
| 0                 | 3.35    | 2.44 *  | 1.34 ** | 1.74   |
| 2                 |         | 1.98 ** | 1.25    | 1.50 * |
| 4                 |         | 1.95 ** | 1.30    | 1.26   |
| 6                 |         |         | 1.25    | 1.23   |
| 10                |         |         | 1.17    | 0.98   |
| 16                |         |         |         | 1.15   |
| MSPU $m^{-2}$     | 5.25 ** | 15.77   | 16.33   | 20.17  |

One asterisk (\*) between two means indicates that the means are significantly different at the 95 per cent level. Two asterisks (\*\*) indicate differences significant at the 99 per cent level.

Changes in astacin amounts at Station III corresponded to those at Station II. High values for the year were observed in August, November,

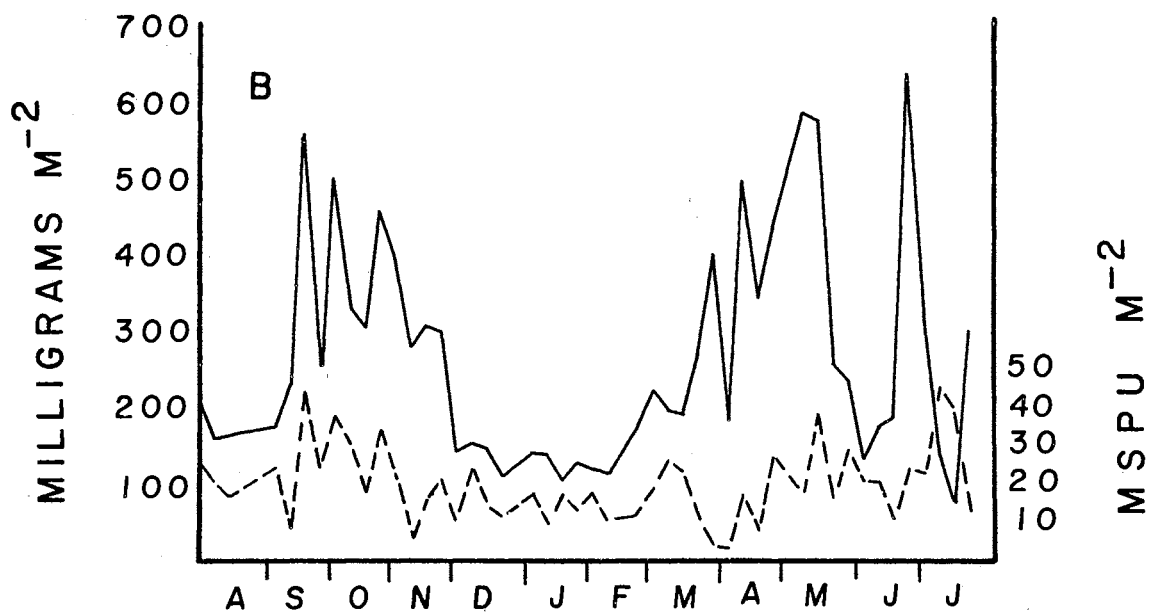
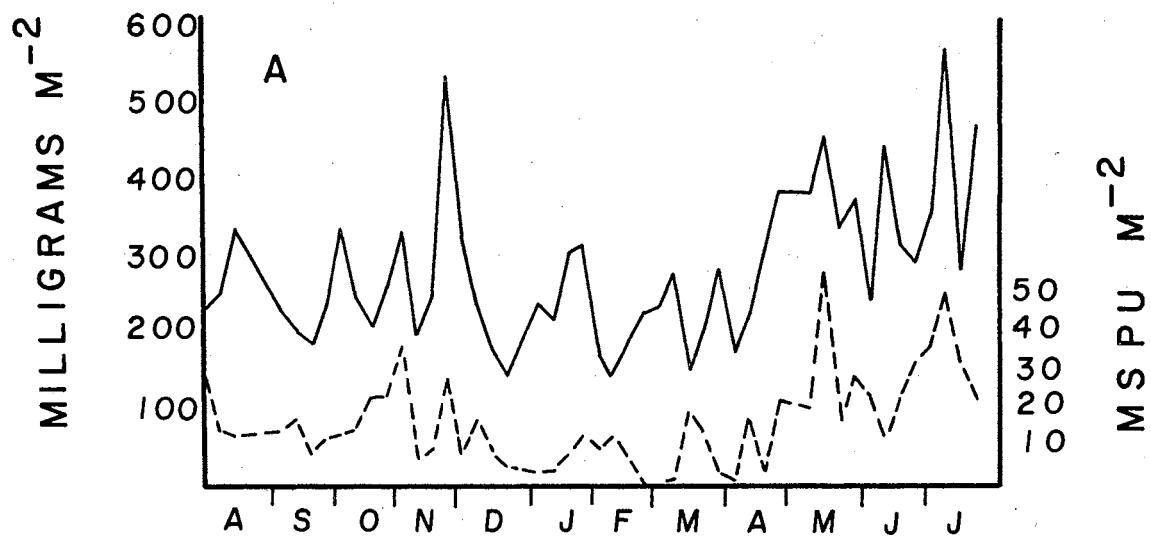


Figure 8. Temporal Variation in Chlorophyll a (—) and Astacin-Type Carotenoids (- - -) at A--Station III and at B--Station IV.

May and July. Several distinct lesser peaks appeared. Lowest values occurred in the period from December to March. Astacin--chlorophyll a relationships indicating grazing are illustrated in Figure 8.

At Station IV amounts of astacin were high in September, October, and July. Well defined peaks also occurred in March and May. Unidirectional periods of change were usually not longer than two weeks, the longest being three and four weeks. As with plant pigments, greatest variability was in the fall and spring when amounts were generally highest. Evidence of grazing by zooplankton is given by the inverse relationship to chlorophyll a (Figure 8).

## CHAPTER V

### ECOLOGICAL RELATIONSHIPS

#### Chlorophyll To Plant Carotenoid Ratio

Non-astacin carotenoids constituted about 40 per cent of the total phytoplankton pigment amount (Table VI). Maximum ratios for Stations I to IV were 6.96, 5.10, 4.95, and 7.52. Minimum ratios were 1.35, 1.58, 1.43, and 1.74. Large ratios indicate relatively low amounts of carotenoid pigment. Although seasonal differences were not great, there was generally relatively less carotenoid pigment in the spring and summer and relatively more in fall and winter months. This result is consistent with the anticipated ecological succession in which high ratios prevail at times favorable to phytoplankton growth (Yentsch, 1959). Before 30 September only one ratio lower than 1.9 was observed. From October through March ratios less than 1.9 were very common. Only one ratio less than 2.0 occurred at any station after 5 April. Wetzel (1964) found that concentrations of chlorophylls a and c and non-astacin carotenoids maintained constant proportions throughout the year.

#### Chlorophyll Fractions

The fraction of a particular chlorophyll at a given time is defined as the amount (or concentration) of the chlorophyll divided by the sum of the amounts (or concentrations) of all of the chlorophylls at that time (Table VI). Units for the numerator and denominator must

be the same but may be either on an area or volume basis. Some long-term similarities are apparent in changes in chlorophyll fractions among stations (Figures 9 and 10).

TABLE VI  
ANNUAL MEANS OF PIGMENT FRACTIONS

NATC = Non-Astacin Type Carotenoids; ATC = Astacin Type Carotenoids

| Station | Chlorophylls |       |       | Carotenoids |       | Total Chlorophyll<br>NATC |
|---------|--------------|-------|-------|-------------|-------|---------------------------|
|         | A            | B     | C     | ATC         | NATC  |                           |
|         | Total        | Total | Total | Total       | Total |                           |
| I       | 0.793        | 0.022 | 0.185 | 0.122       | 0.878 | 2.675                     |
| II      | 0.759        | 0.043 | 0.198 | 0.103       | 0.897 | 2.520                     |
| III     | 0.825        | 0.027 | 0.148 | 0.098       | 0.902 | 2.350                     |
| IV      | 0.784        | 0.034 | 0.182 | 0.154       | 0.846 | 2.685                     |

In late September and early October the chlorophyll a fraction was higher than its annual mean (Figure 9). At Station I the "a fraction" fell below its annual mean for several weeks beginning in early November. At other stations reduction of the "a fraction" began late in October. Then a period during which it was higher than the annual mean for several consecutive weeks during December and January was observed at each station except Station II. Pronounced reductions in the "a fraction" occurred simultaneously at all stations in early March. Increases followed at all stations until values reached the annual means around which they varied until mid-June. At that time general dropoffs occurred, particularly at Stations I, III, and IV.

At Station I the "b fraction" was not appreciable until February. Chlorophyll b appeared then and was present for several weeks during

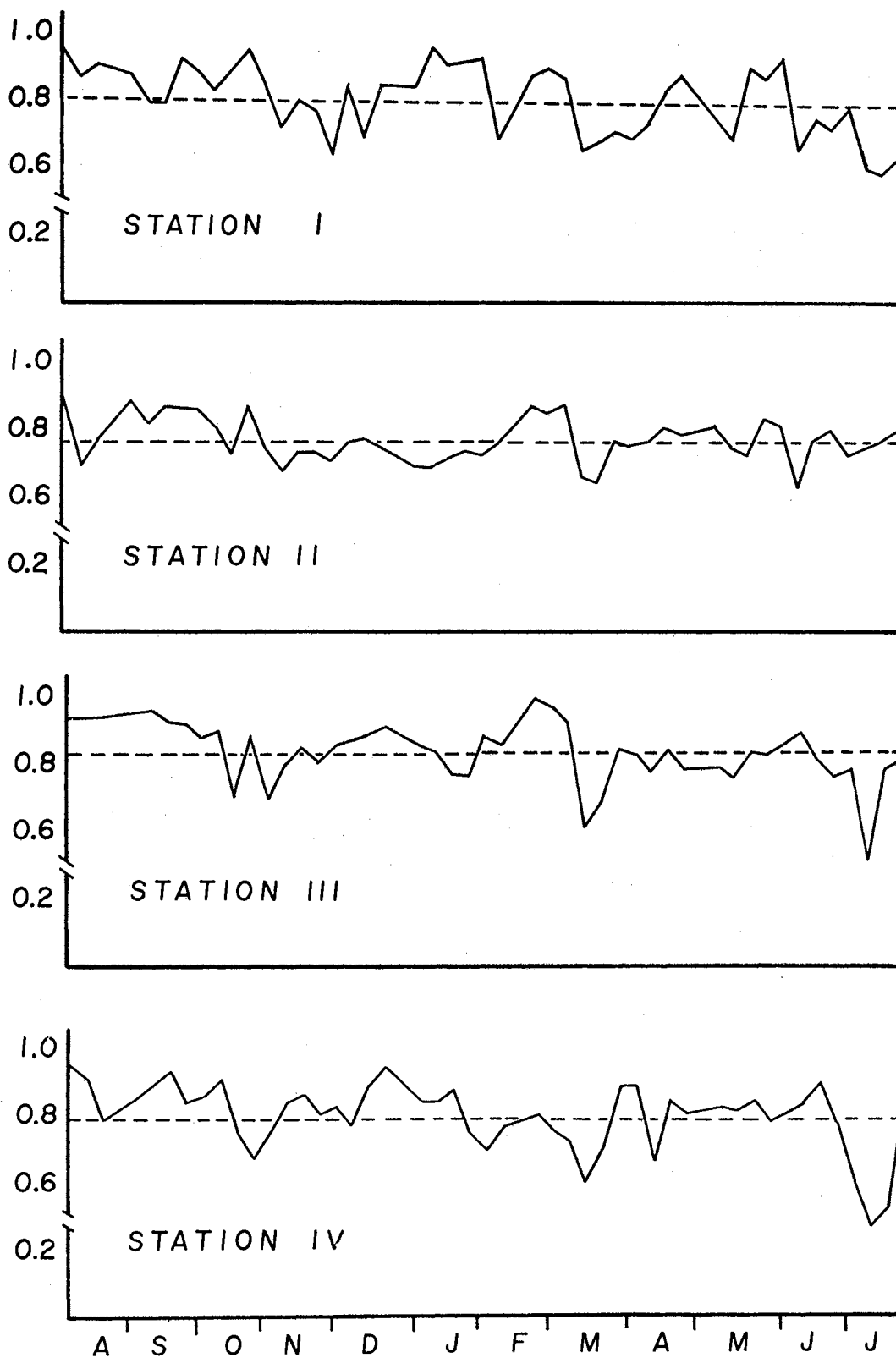


Figure 9. Temporal Variation in Chlorophyll a Fraction (Amount of Chlorophyll a Relative to Total Chlorophyll Amount) in a Column of Water.



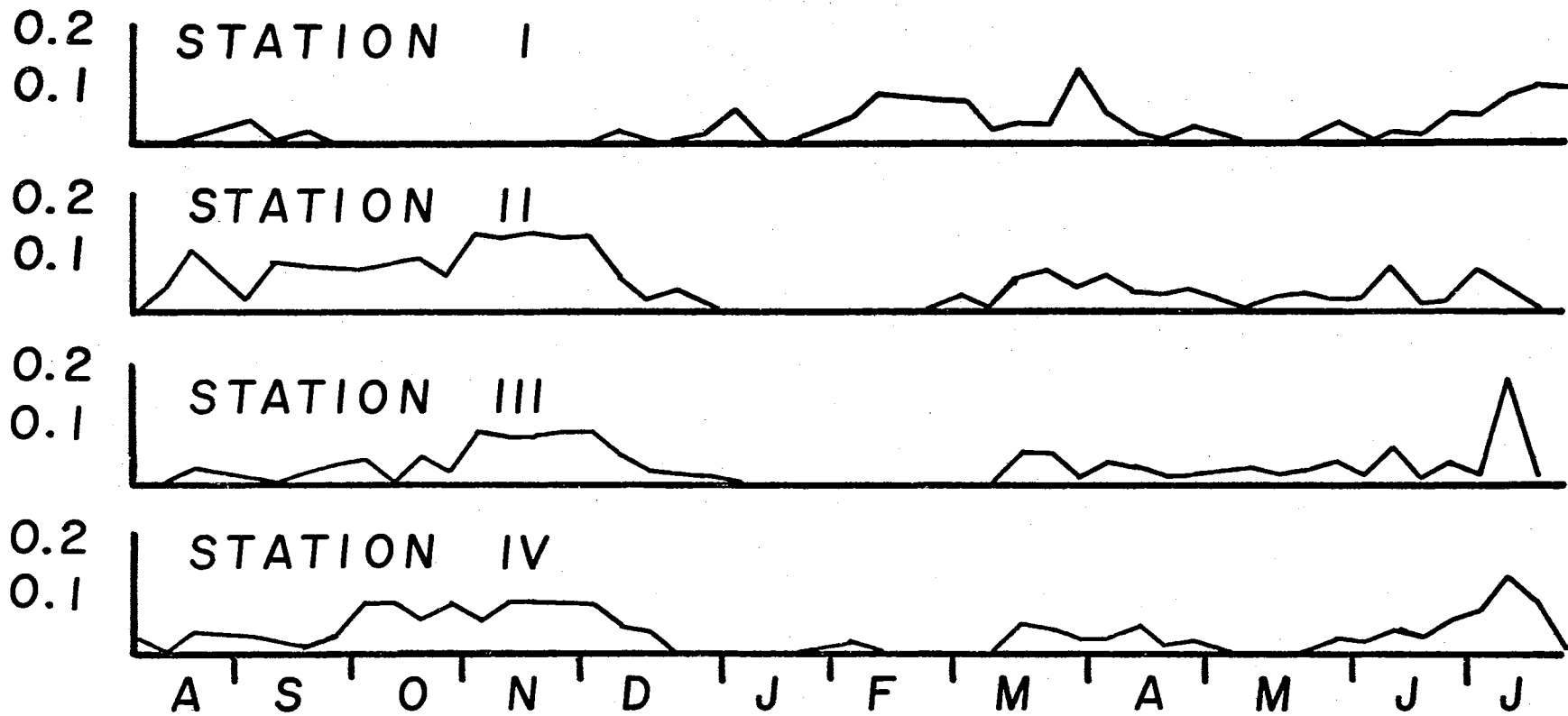


Figure 10. Temporal Variation in Chlorophyll b Fraction (Amount of Chlorophyll b Relative to Total Amount of Chlorophyll) in a Column of Water.

which it was absent at other stations. The "b fraction" was maximum for the year at Station I on 30 March but decreased to zero over the next three weeks. It remained low until June and then increased until the end of July.

Changes in the "b fraction" paralleled each other closely at the three downstream stations (Figure 10). High values near 0.10 were maintained during November at Stations II, III, and IV and simultaneous lowering followed in December. Most striking was the absence of chlorophyll b for several weeks in December, January, and February at Stations II to IV. In late March and early April minor plateaus near 0.05 were observed for several weeks. Values near zero separated the plateaus from June and early July highs. The "b fraction" was near zero at all three downstream stations in July.

The chlorophyll c fraction, when graphed, appears to be nearly a mirror image of the "a fraction" because of the low contribution of b to the total.

### Light Penetration

#### Turbidity

Turbidity--standing crop relationships are not well understood although there is general agreement that turbidity is limiting in some cases (Verduin, 1954). Harris and Silvey (1940) found maximum production and minimum turbidity in some cases and minimum production and maximum turbidity in others in Texas reservoir lakes. In a study of Oklahoma waters, Claffey (1955) found that numbers of algal cells decreased with increasing turbidity. In Japanese lakes Ichimura (1956) found a curvilinear relationship between transparency and chlorophyll

content except in cases in which organic matter content was extremely high or wind resulted in large amounts of suspended inorganic material.

In Keystone Reservoir turbidity changed rapidly, particularly at Stations I and II. Mean turbidity decreased downstream as evidenced by increase in euphotic zone depth. On some dates when standing crop was high turbidity was great. The opposite was also observed. It is possible that the first result was observed because a large crop was produced in relatively clear water which suddenly became turbid. Verduin (1954) suggests that a large crop may develop in a shallow euphotic zone if circulation is great enough to maintain organisms in the euphotic zone a sufficient part of the daylight hours.

#### Euphotic Zone

Euphotic zone depth showed long-term changes at all stations (Figure 11). Changes at Stations I and II paralleled each other closely as did those at Stations III and IV. Annual mean euphotic zone depth increased downstream (Figure 12).

At Station II there was a general increase in euphotic zone depth until 1 March. A general decrease followed until 10 May. At other stations changes in one direction were less continuous. Stations III and IV had the most pronounced seasonal differences with well defined lows in September, October, and April and prolonged maxima in the winter.

Pigment amounts, particularly of chlorophyll a, were generally inversely related to euphotic zone depth. A possible explanation is that large plankton populations contribute greatly to turbidity. In some cases, particularly at Stations I and II, there were deep euphotic zones and low chlorophyll indicating that clay was the major source of

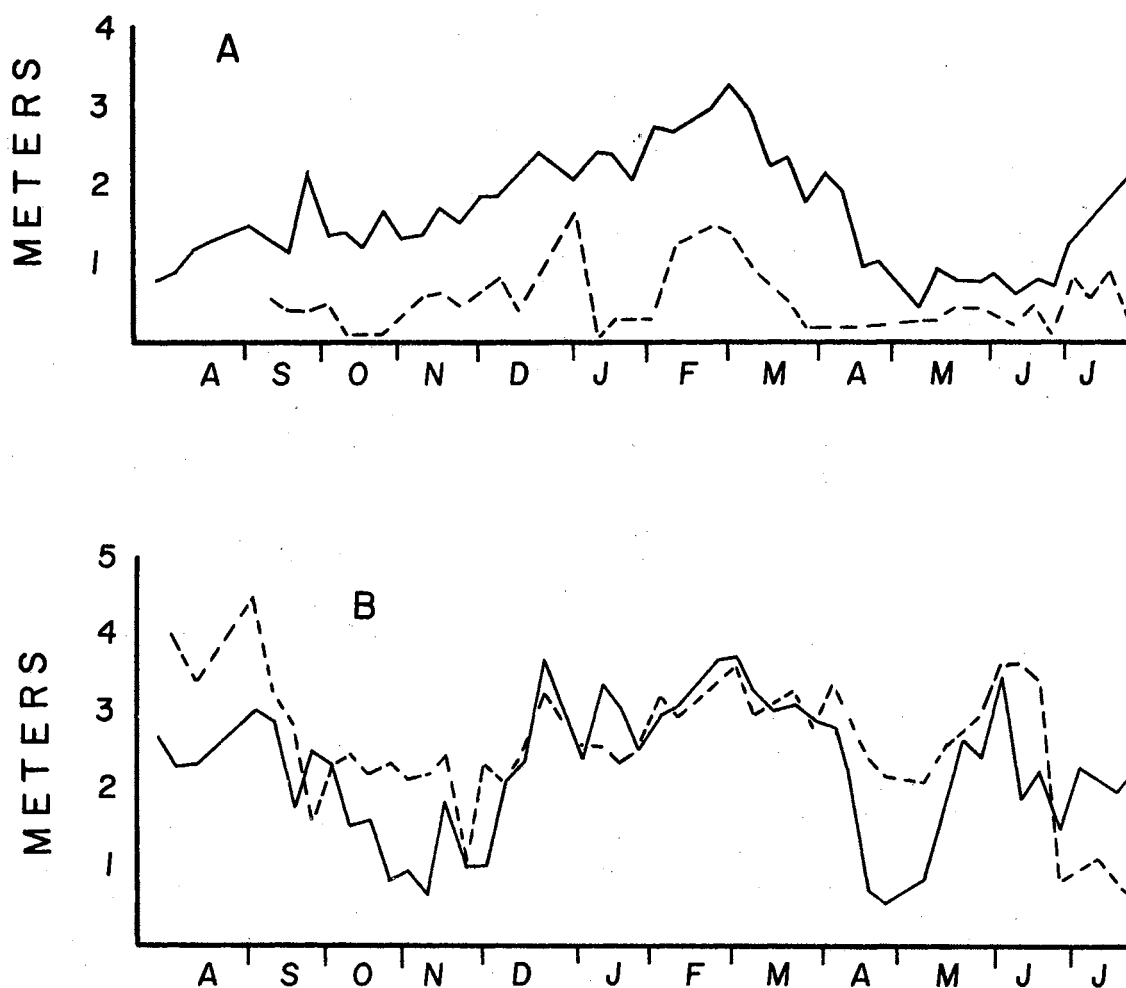


Figure 11. Temporal Variation in Euphotic Zone Depth at A--Station I (---) and Station II (—), and at B--Station III (—) and Station IV (---).

turbidity. Pigment maxima when euphotic zone is shallow probably are allowed by changes in other conditions. Table VII summarizes some of the relationships between euphotic zone depth and chlorophyll a.

At Station I the euphotic zone extended to the bottom on several occasions. Differences between fraction of chlorophyll a in the euphotic zone (relative to total chlorophyll a in the water column) and the euphotic zone fraction of the water column may be regarded as evidence of unequal vertical distribution of pigment. At Station I the euphotic zone comprised more than half of the water column but possessed

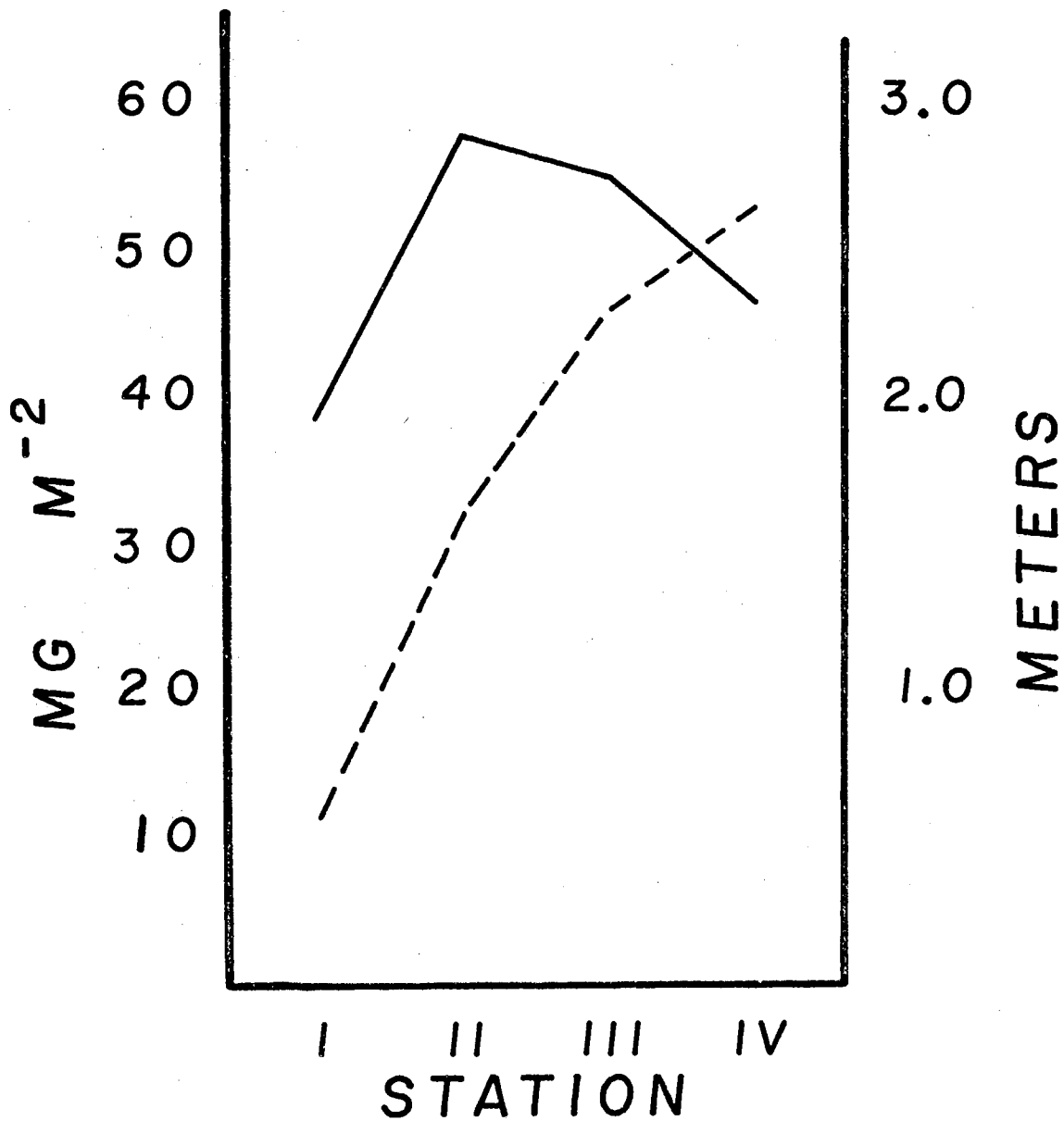


Figure 12. Mean Annual Euphotic Zone Depth in Meters (- - -) and Mean Annual Chlorophyll a Content in mg Per Square Meter of Euphotic Zone (—).

TABLE VII  
CHLOROPHYLL A--EUPHOTIC ZONE RELATIONSHIPS

| Station | Maximum Euphotic<br>Zone Depth<br>meters | Minimum Euphotic<br>Zone Depth<br>meters | Mean Depth Of<br>Euphotic Zone<br>meters | Euphotic Zone<br>As Fraction Of<br>Total Depth | Chlorophyll a In<br>Euphotic Zone As<br>Fraction Of Total<br>In Water Column |
|---------|--|--|--|--|--|
| I       | 1.67                                     | 0.03                                     | 0.55                                     | 0.55   | 0.45   |
| II      | 3.29                                     | 0.41                                     | 1.63                                     | 0.23   | 0.26   |
| III     | 3.75                                     | 0.57                                     | 2.32                                     | 0.15   | 0.21   |
| IV      | 4.52                                     | 0.63                                     | 2.64                                     | 0.15   | 0.20   |

less than half of the chlorophyll a. At Station IV the euphotic zone was 15 per cent of the water column but has 20 per cent of the chlorophyll a. Chlorophyll a probably was equally distributed between euphotic zone and the lower water mass at some point near Station II (Figure 13).

#### Estimated Gross Primary Productivity

Since chlorophyll a is the major photosynthetic pigment there is good reason to seek a relationship between it and gross photosynthesis and light intensity. Several authors have investigated the relationship (Strickland, 1960). In this study the method of Ryther and Yentsch (1957) was applied. The method is based on an average ratio of 3.7 mg carbon fixed per hour to 1.0 mg chlorophyll. Strickland (1960) reported a range of about 1 to 10 mg carbon fixed per hour for each mg chlorophyll with an average of about four. Results must be considered with this range of variability in mind.

Productivity increased downstream to Station III and then decreased at Station IV (Table VIII). These findings might have been expected on the basis of the changes in euphotic zone depth and chlorophyll a in the euphotic zone from upstream to downstream. From Station II to III euphotic zone depth increased 52.3 per cent, amount of chlorophyll a decreased 12.7 per cent, and productivity increased 4.5 per cent. The increase in productivity occurred despite lower chlorophyll a amount because of the proportionately large increase in the zone in which light was sufficient for photosynthesis.

From Station III to IV euphotic zone depth increase was only about one-fourth as great as between II and III. Chlorophyll a in the euphotic zone decreased 14.6 per cent, and productivity decreased 12.7

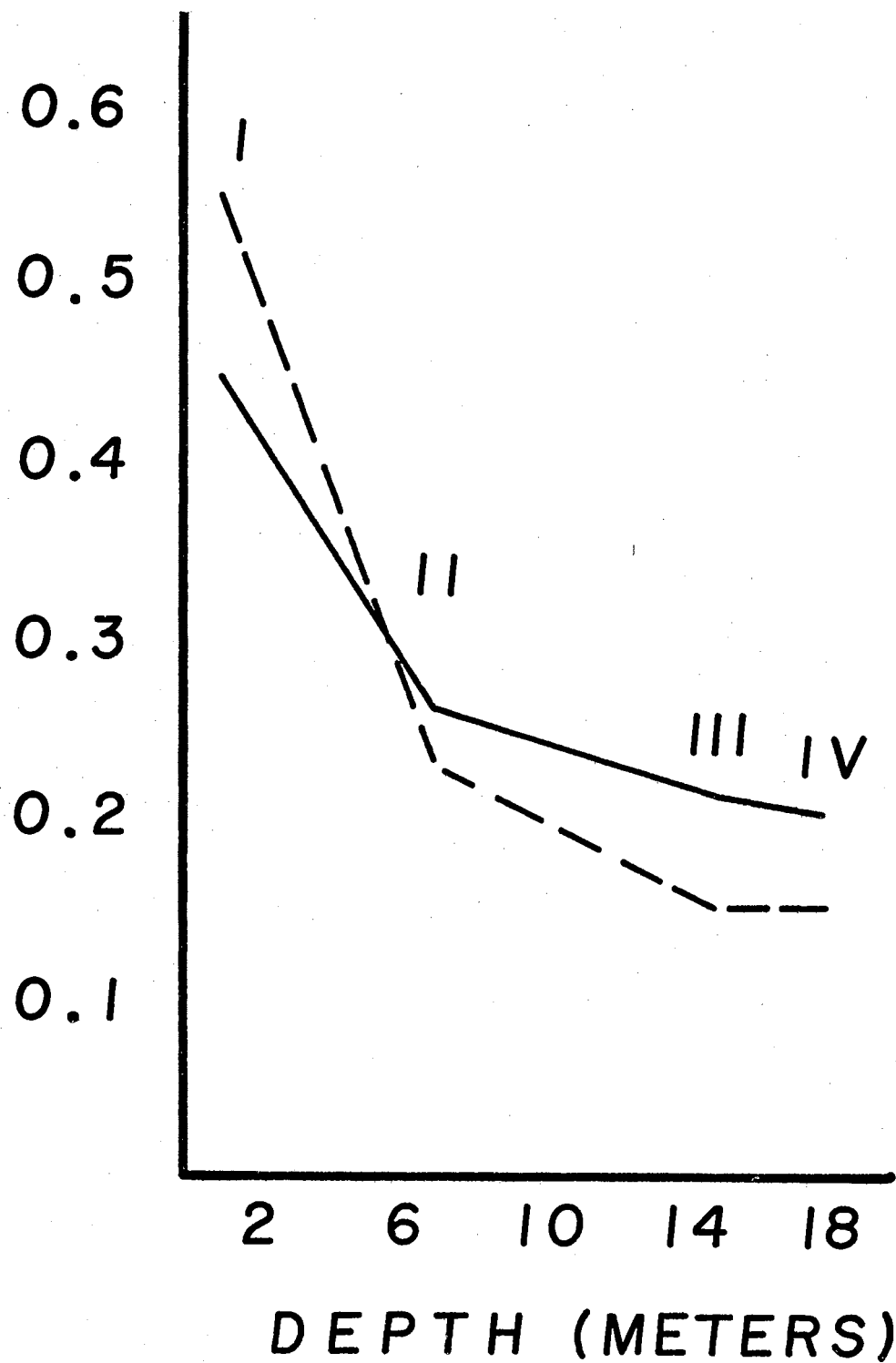


Figure 13. Amount of Chlorophyll a in the Euphotic Zone as a Fraction of the Total Amount of Chlorophyll a in the Water Column (—). Depth of the Euphotic Zone as a Fraction of the Total Depth of the Water Column (---).



per cent because the relative increase in extent of photosynthetic zone was not great enough to allow it to increase.

TABLE VIII

## CHLOROPHYLL-BASED ESTIMATES OF GROSS PRODUCTIVITY

| Station | grams of carbon fixed $m^{-2} day^{-1}$ |         |                     |
|---------|---|---------|---------------------|
|         | Means                                   | Maximum | Extremes<br>Minimum |
| I       | 0.592                                   | 3.071   | 0.010               |
| II      | 0.852                                   | 2.985   | 0.044               |
| III     | 0.890                                   | 2.184   | 0.069               |
| IV      | 0.768                                   | 2.184   | 0.069               |

Seasonal trends in gross productivity (Figure 14) were indicated at all stations but were not well defined. Since they were computed using chlorophyll amounts as a factor, rates varied much the same as pigment varied. Daily incident solar radiation values were low in December and January (18 to 309  $ly day^{-1}$ ) with values as high as 710  $ly day^{-1}$  in other times of the year. Day to day variations in solar radiation were great, especially in spring and summer and did not correlate well with variations in pigment amounts. However, pigment amounts and production rates were low during the months when radiation was low. Correlation coefficients were computed with surface samples of chlorophyll a and the means of incident solar radiation for sample dates and the four days preceding each. By station, going downstream, correlation coefficients were -0.01, -0.28, 0.32, and 0.32.

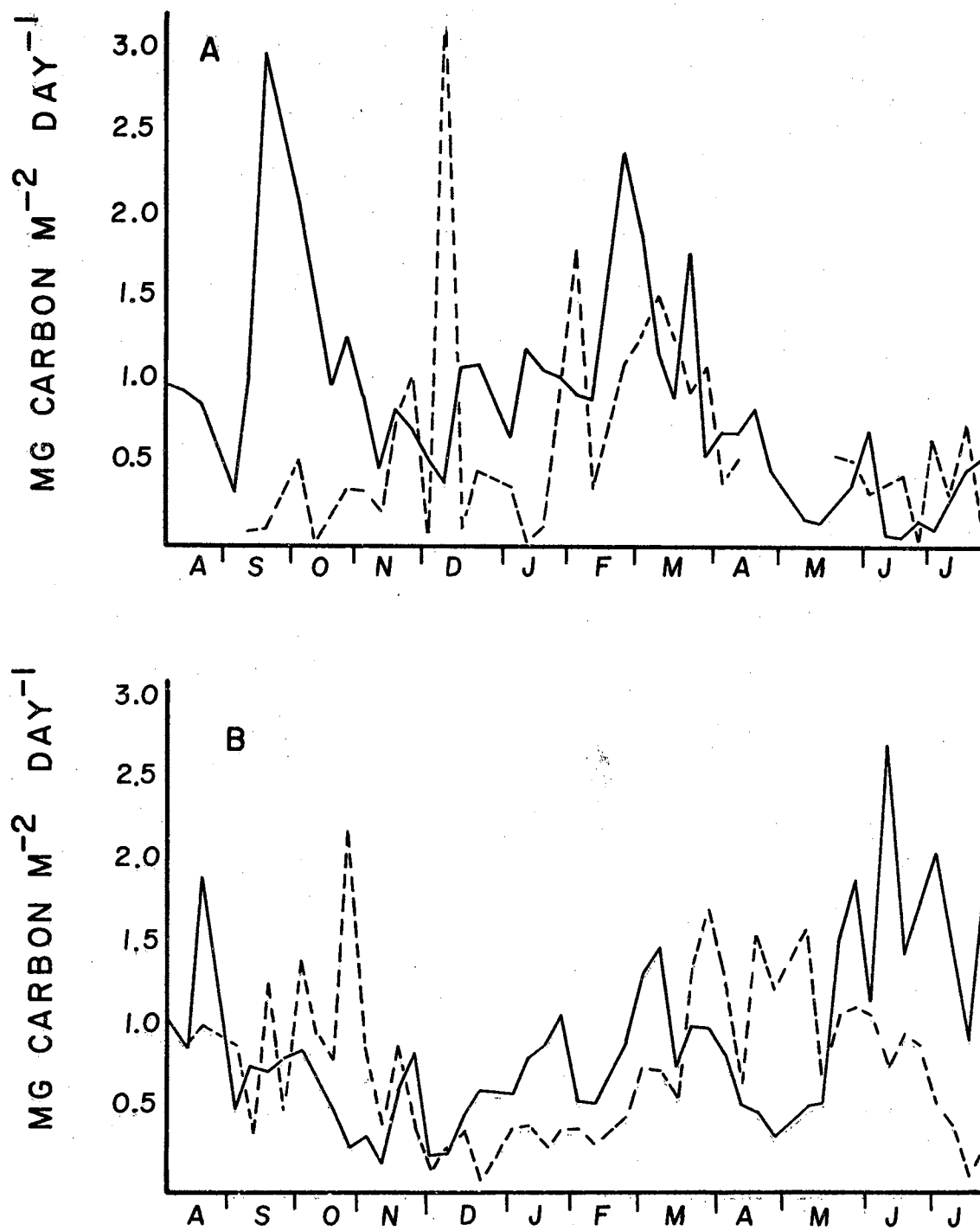


Figure 14. Temporal Variation in Rate of Gross Production as Calculated from Chlorophyll and Light Data. A-- Station I (---) and Station II (—). B-- Station III (—) and Station IV (---).

Eley (personal communication) studied productivity in Keystone Reservoir using the light--dark bottle method from August, 1965, to April, 1966, and found monthly means of productivity ranging from zero to 1.50 grams carbon fixed  $m^{-2} day^{-1}$ .

#### Ash-Free Weight

Ash-free weight was determined once or twice a month at each depth at each station. Annual means displayed the same pattern of spatial and temporal distribution displayed by the pigments. There was a general decrease downstream and with depth (Table IX). Some irregularities in the pattern occurred however. The surface mean at Station I was nearly four times greater than the next highest mean. Undoubtedly much of the organic material at Station I was allochthonous.

Ash-free weight at Station I showed different temporal variation than at the other stations. The minimum amount was observed at the same time as at other stations, however, and an April 26 peak corresponded to peaks at Stations III and IV. Even though ash-free weight per unit volume was relatively much greater at Station I, the amount per unit area was considerably lower than at any other station except on two occasions. On 26 April ash-free weight at Station I exceeded that at all other stations and on 21 June it exceeded that at stations II and III.

Clay turbidity was frequently high at Station I and may have interfered with ash-free weight determinations. Clay particles may retain moisture in oven dried samples. Retained moisture is lost on ignition and the weight loss is credited to loss of organic material.

TABLE IX  
ANNUAL MEANS OF ASH-FREE WEIGHT, GRAMS M<sup>-3</sup>

| Depth<br>(Meters) | Station |       |      |      |
|-------------------|---------|-------|------|------|
|                   | I       | II    | III  | IV   |
| 0                 | 41.12   | 11.61 | 7.31 | 6.78 |
| 2                 |         | 9.49  | 6.29 | 7.36 |
| 4                 |         | 9.15  | 5.18 | 5.74 |
| 6                 |         |       | 5.63 | 6.56 |
| 10                |         |       | 6.86 | 6.51 |
| 16                |         |       |      | 5.23 |

In order to separate the contributions of detritus and zooplankton from the total ash-free weight it was assumed that 35 per cent of the ash-free weight was contributed by phytoplankton (Pennak, 1955; Wright, 1959). This must be considered to be a rough approximation of a factor which undoubtedly varies with time and location.

The general relationship  $1.0 \mu\text{g chlorophyll } a = 0.14 \text{ mg ash-free weight}$  was arrived at. Ash-free weights of all surface samples for the year were summed and 65 per cent was subtracted. The result was divided by the corresponding sum of chlorophyll a determinations. This relationship agrees well with ratios of 0.12 and 0.11 reported by Wright (1959). Worthy of note, however, is that the ratio computed for the three downstream stations alone is only  $1.0 \mu\text{g chlorophyll } a = 0.09 \text{ mg ash-free weight}$ .

The ratio of chlorophyll a and ash-free weight increases distinctly with depth (Table X) and can be accounted for by the presence of large amounts of detritus at lower depths and by degradation of chlorophyll

TABLE X  
RELATIONSHIP BETWEEN CHLOROPHYLL AND ASH-FREE WEIGHT

| Depth (meters) | Station          |                  |                  |                  |
|----------------|------------------|------------------|------------------|------------------|
|                | I                | II               | III              | IV               |
| 0              | 0.47<br>83<br>35 | 0.23<br>42<br>35 | 0.26<br>41<br>35 | 0.31<br>45<br>35 |
| 2              |                  | 0.26<br>30       | 0.25<br>36       | 0.46<br>24       |
| 4              |                  | 0.35<br>23       | 0.24<br>37       | 0.39<br>28       |
| 6              |                  |                  | 0.30<br>31       | 0.47<br>23       |
| 10             |                  |                  | 0.45<br>22       | 0.64<br>17       |
| 16             |                  |                  |                  | 0.68<br>16       |

in lower water masses. Since no correction could be made for detrital chlorophyll it is assumed that the relationship  $1.0 \mu\text{g chlorophyll a} = 0.14 \text{ mg ash-free weight}$  applies at all depths. That being the case, computation of degree of reduction of phytoplankton contribution, or of increase of zooplankton-detritus contribution to ash-free weight was possible. Results are shown in Table X as decreasing phytoplankton contribution to ash-free weight with increased depth.

Strickland (1960) approached the chlorophyll--ash-free weight relationship through the equations

$$\text{mg C} = F \times \text{mg chlorophyll}$$

and

$$\text{mg C} = (0.5 \pm 0.05) \times \text{mg ash-free weight}$$

where mg C is organically combined carbon and F is a constant to be computed for each situation. Values of F are a means of comparing data reported in the literature. By computing mg C from ash-free weights and using pigment data, an F was found for each station (Table X). Strickland reports F values of 20 to 130 for mixed populations and suggests that, as a rule of thumb,  $F = 30$  for natural populations without nutrient deficiencies. For Wright's data (1959) yielding the relationship  $1.0 \mu\text{g chlorophyll a} = 0.12 \text{ mg ash-free weight}$  Strickland found that  $F = 60$ . The value  $F = 82$  at Station I in this study is about twice as high as that for the other stations. It may be a representative value but the data suggest that the arbitrary assignment of 35 per cent to the phytoplankton contribution to ash-free weight is questionable.

### Chlorophyll a - Dry Weight Relationship

Using Strickland's (1960) equation

$$\text{mg ash-free organic matter} = F \times \text{mg dry weight}$$

where  $F = 0.6 \pm 0.2$  for mixed populations, the chlorophyll a relationship to dry weight was examined. Using annual means of pigment estimates in surface samples chlorophyll a was found to be in the range 0.23 to 0.94 per cent of dry weight. For the stations in order downstream the ranges determined were 0.23 to 0.48, 0.46 to 0.91, 0.46 to 0.94, and 0.40 to 0.77 per cent. Of particular interest is that even though the ranges are rather wide, that for Station I barely overlaps those of the other stations which coincide quite completely. If the relationship  $1.0 \mu\text{g chlorophyll a} = 0.14 \text{ mg ash-free weight}$  is used for the calculation, the range is found to be 0.28 to 0.57 per cent. The same calculation on Wright's data (1959) yields a range of 0.33 to 0.67 per cent.

Rabinowitch (1945) reports a range of 0.09 to 2.0 per cent of dry weight according to a tabulation of results of several workers. McConnell and Sigler (1959) found chlorophyll a to be 0.15 to 2.4 per cent of dry weight in river algae. Wetzel (1964) gives a range of 0.25 to 2.0 per cent for Borax Lake, California. The per cent in green algae is reported to range as high as 6.0 (Atkins and Jenkins, 1953). Margalef gives a range of 0.31 to 0.64 per cent for some artificial lakes in Spain.

### Pigment Diversity

A pigment diversity index proposed by Margalef (1957) was applied in this study. The index is the ratio of optical density readings on 90 per cent acetone extracts at 430 and 665 mu. Yellow pigments absorb heavily at 430 mu and green pigments (chlorophyll a) absorb heavily in the 665 mu region. Thus, the ratio is a "yellow/green" ratio and gives an indication of the number of molecules of one type relative to those of the other. Physiological states of populations and successional changes are reflected in changes in the pigment diversity index. Aging and nutrient conditions are the major factors influencing both total and relative amounts of pigments (Ketchum, et al., 1958). Pigment proportion is more dependent on aging than on light (Margalef, 1958, 1963). The ratio  $D_{430}/D_{665}$  tends to be highest in old, stable ecosystems and lowest for young, growing populations (Odum, 1963). Margalef (1964) reported ratios of 4.32 to 6.98 during summer for artificial lakes in Spain. Knudson (unpublished) found ratios as high as nine for clear ponds in north central Oklahoma.)

Pigment diversity was computed for all samples collected during the study period. The greatest differences between stations occurred during the cold months (Figure 15). Pigment diversity values were highest in January and February with the highest ratio (4.15) at Station II early in January. Stations III, IV, and I had successively lower peaks of 3.55 late in January, 3.25 early in February, and 2.80 late in December, respectively. The ratio decreased rapidly at all stations early in March during which time biomass began to increase after a steady, winter-long decline (Figure 15). Throughout the study pigment diversity was consistently lower at Station I than at other stations. Except in



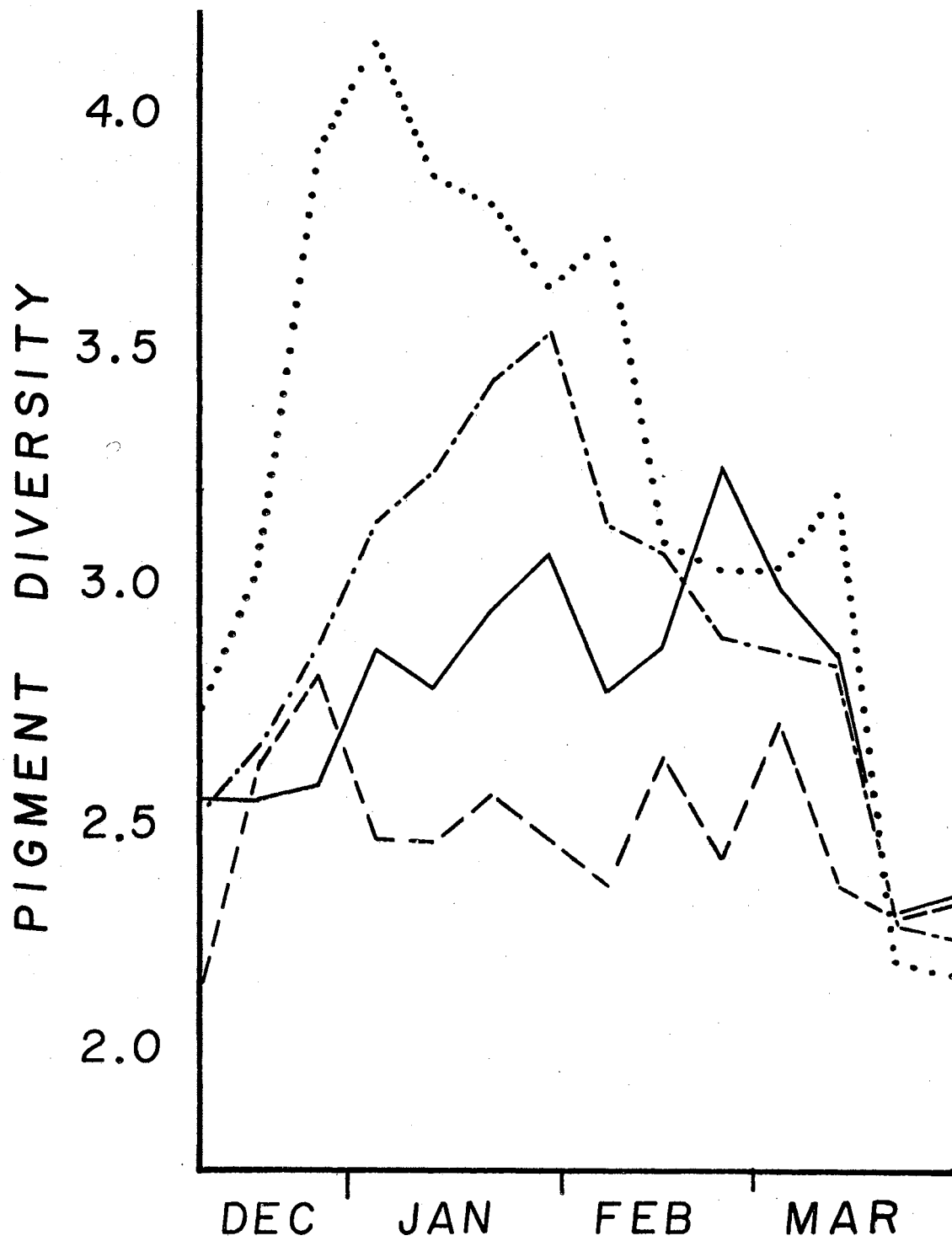


Figure 15. Pigment Diversity ( $D_{430}/D_{665}$ ) During the Cold Months. Station I (---), Station II (···), Station III (-·-·-), Station IV (—).

winter months there were only small differences in pigment diversity among stations. Table XI gives annual means of pigment diversity.

TABLE XI  
PIGMENT DIVERSITY ANNUAL MEANS

| Depth<br>(Meters) | Station |      |      |      |
|-------------------|---------|------|------|------|
|                   | I       | II   | III  | IV   |
| 0                 | 2.53    | 2.82 | 2.73 | 2.81 |
| 2                 |         | 2.76 | 2.72 | 2.78 |
| 4                 |         | 2.77 | 2.73 | 2.77 |
| 6                 |         |      | 2.79 | 2.79 |
| 10                |         |      | 2.72 | 2.79 |
| 16                |         |      |      | 2.98 |

Low diversity at Station I may be an effect of high turbidity. Knudson (unpublished) found that diversity did not reach high values at any time throughout the year in turbid Oklahoma farm ponds. Succession may be prevented from proceeding to maturity. River currents at Station I could have the same effect, however.

### Succession

Seasonal variation in pigment amounts is partly a result of changes in species composition. The Richards with Thompson method, however, does not give adequate differentiation of pigments for taxonomic sorting (Strickland, 1960). Margalef (1958) showed that chlorophyll a relative to biomass decreases with natural development of a plankton community. He divided succession into three stages and found the ratio to be indicative of the stage. In this study only Station IV yielded

ratios changing in a manner suggesting succession (Figure 16). Ash-free weight data were probably not obtained frequently enough for thorough analysis. Well defined maxima occurred in December and June. The yearly minimum was in March at about the middle of a long general increase in amount of chlorophyll a. The December peak occurred early in the prolonged winter chlorophyll a minimum. Changes in the chlorophyll a to ash-free weight ratio suggest succession but numerically do not fall into Margalef's categories.

The expected succession is: diatoms, green algae, bluegreen algae (Blum, 1956; Fogg, 1965). Chlorophyll c peaks occurred at the upper three stations in December and January indicating relatively great abundance of diatoms. Greatest amounts of chlorophyll b occurred in late fall at Stations III and IV giving evidence of relatively great abundance of Chlorophyta or Euglenophyta at that time.

#### Trophic Classification

The reservoir may be classified with regard to trophic state on the basis of chlorophyll data. In general, deep, oligotrophic lakes have less chlorophyll and shallow, eutrophic lakes have more (Sakamoto, 1966). Aruga and Monsi (1963) regarded lakes having 30 to 120 mg m<sup>-2</sup> in the euphotic zone as being eutrophic. Ichimura (1956) classified Japanese lakes having 10.6 to 57.5 mg chlorophyll m<sup>-3</sup> above the compensation point as eutrophic. Keystone Reservoir falls into this category with annual mean chlorophyll a in the euphotic zone ranging from 33 to 59 mg m<sup>-2</sup>.

Aruga (1966) considered the ratio between annual maximum and minimum to be a clue to trophic type with higher ratios characteristic

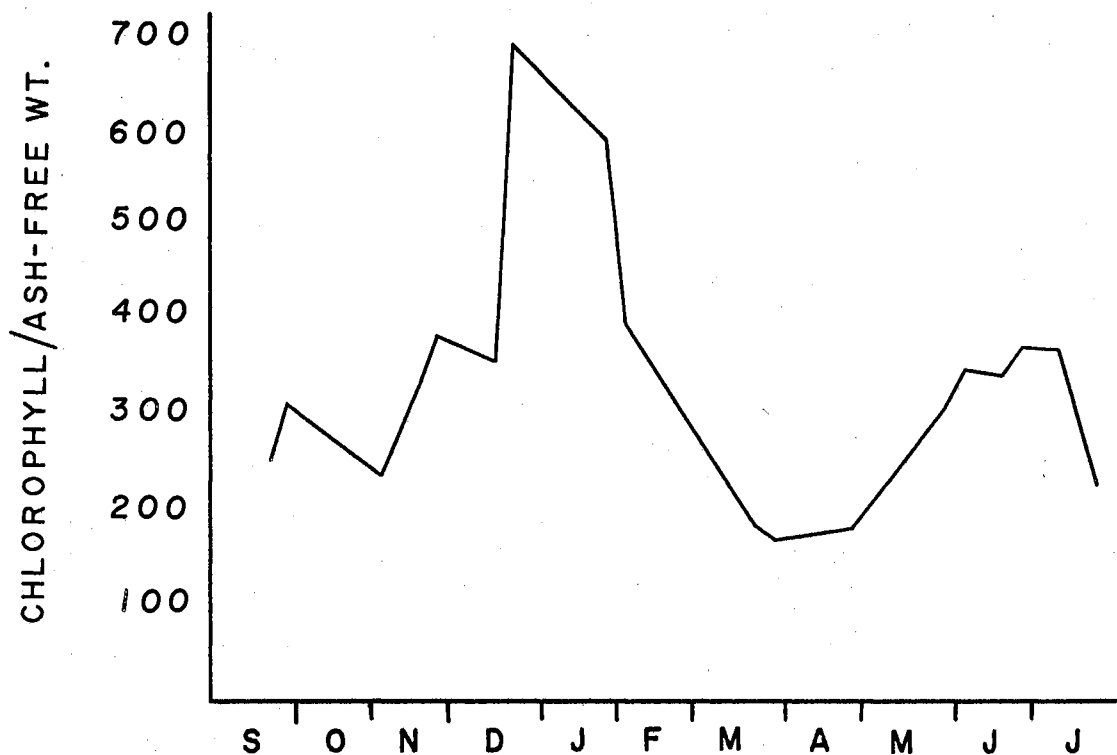


Figure 16. The Ratio of Chlorophyll to Ash-Free Weight at Station IV.

of eutrophic lakes. Ratios for Stations I to IV were 18.8, 7.9, 4.0, and 8.5 respectively.

Oligotrophic waters are characterized by ultraplanktonic forms and larger organisms are more predominant in eutrophic waters (Wetzel, 1964). In Keystone Reservoir large organisms appeared frequently at Station I and seldom at Station IV.

Evidence indicates that the degree of eutrophication decreases downstream. However, physical conditions differ greatly among the stations, particularly between Station I and the others, and criteria must be applied judiciously.

## CHAPTER VI

### SUMMARY

1. Weekly plankton pigment concentrations were measured at depth intervals at four stations on Keystone Reservoir, Tulsa, Oklahoma. Ash-free weight (loss on ignition) was determined once or twice each month. Light, temperature, and turbidity were measured each week. Daily river discharge and solar radiation records were obtained from the U.S. Geological Survey and the Geography Department of Oklahoma State University.
2. The contributions of chlorophylls a, b, and c to total chlorophyll were 75 to 82, 2 to 4, and 14 to 20 per cent respectively.
3. Astacin-type carotenoids made up 9.8 to 15.4 per cent of total carotenoids.
4. Annual means of chlorophyll a in the euphotic zone ranged from 33 to 59 mg m<sup>-3</sup>. On the basis of these values and literature reports of eutrophic lakes, Keystone Reservoir must be considered to be eutrophic.
5. Chlorophyll a was estimated to have constituted 0.23 to 0.94 per cent of dry weight of phytoplankton.
6. The relationship 1.0 µg chlorophyll a = 0.14 mg ash-free weight (surface samples) was arrived at. It was applied

at all depths in computing relative contributions of plankton and detritus to ash-free weight. Phytoplankton contributed less to ash-free weight as depth increased.

7. Pigment diversity was usually lowest at Station I.

Most pronounced differences between stations occurred in January and February when Station II had the highest values.

8. Gross productivity (grams C fixed  $\text{m}^{-2} \text{day}^{-1}$ ), estimated from chlorophyll a data, increased downstream to Station III but was lower at Station IV than at III. The range of annual means was 0.01 to 2.98  $\text{g C m}^{-2} \text{day}^{-1}$ .

9. Mean temperature of the water mass varied seasonally but did not change much in any short time period. Thus, division of the year into seasons was not warranted on the basis of temperature.

10. Turbidity decreased and depth of the euphotic zone increased progressively downstream.

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VITA

Frederic Lynn Spangler

Candidate for the Degree of

Doctor of Philosophy

Thesis: CHLOROPHYLL AND CAROTENOID DISTRIBUTION AND PHYTOPLANKTON  
ECOLOGY IN KEYSTONE RESERVOIR, TULSA, OKLAHOMA

Major Field: Zoology

Biographical:

Personal Data: Born at Streator, Illinois, August 1, 1939, the  
son of Carol F. and Irene A. Spangler.

Education: Graduated from Fort Atkinson Senior High School,  
Fort Atkinson, Wisconsin, 1957; received the Bachelor of  
Arts degree from North Central College, Naperville, Illinois,  
with a major in General Biology, June, 1961; attended the  
University of Wisconsin, Madison, Wisconsin, summer, 1960;  
attended Northwestern University, Evanston and Chicago,  
Illinois, summer and evening, 1962; received the Master of  
Science degree from Oklahoma State University, May, 1965,  
with major in Natural Science; completed requirements for  
the Doctor of Philosophy degree at Oklahoma State University  
in May, 1969.

Professional Experience: Biology teacher, Naperville Community  
High School, Naperville, Illinois, 1961-1963; Public Health  
Service Research Trainee, Zoology Department, Oklahoma State  
University, 1964-1967; Research Assistant, Zoology Depart-  
ment, Oklahoma State University, 1967-1968.

Professional and Honorary Organizations: Phi Sigma and Beta  
Beta Beta Biological Honor Societies and American Society  
of Limnology and Oceanography.