THE UNIVERSITY OF MANITOBA

AN EVALUATION OF A COULTER COUNTER METHOD FOR THE DETERMINATION OF PRIMARY PRODUCTIVITY, AND AN ASSESSMENT OF SEASONAL PHYTOPLANKTON BIOMASS AND SPECIES COMPOSITION AT WEST BLUE LAKE, MANITOBA

by

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ABSTRACT

An evaluation was made of a method of determining primary production by use of an electronic particle counter (Coulter Counter). In order to convert productivity values determined as volume by this method into more meaningful carbon values, it was necessary to establish a relationship between carbon and volume. Although the method was found to be effective, it was also found to be more time consuming than the comparable ^{14}C method. Consequently, it was concluded that the method might serve as an accessory rather than an alternative to the conventional ^{14}C method. Standing crop of the phytoplankton was monitored from May, 1970 through September, 1971, in order to determine the magnitude and species composition of the organisms responsible for primary production. All data contributed to the overall study of the West Blue Lake ecosystem.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

LIST OF APPENDICES

INTRODUCTION

A number of ways have been examined in the past fifty years of measuring primary production in bodies of water. Such methods include the measurement of (a) changes in standing crop; (b) changes of dissolved oxygen content; (c) changes of pH; (d) changes of carbonate content; (e) the uptake of radioactive carbon; (f) changes in total volume of algae. It is the feasibility of using changes in total volume of algae that is examined in this thesis.

Cushing and Nicholson (1966) and Sheldon and Parsons (1967) proposed that the Coulter Counter (Coulter Electronics, Hialeah, Fla.) could be used to measure the change of volume of algae over a definite time period, and their preliminary investigations further supported this view.

It was the intention of this research to determine the applicability of this method to natural populations at West Blue Lake, Manitoba; and to then compare these results with those obtained by the ^{14}C method. In order to express productivity determined by the Coulter Counter method in more meaningful carbon values, it was first necessary to establish a carbon:volume relationship for West Blue Lake algae. In conjunction with primary productivity research, phytoplankton biomass and species composition were monitored. Although the relationship between primary production and

standing crop can be extremely variable as a function of numerous parameters, it was desirable to know as much as possible concerning population fluctuations and species composition of the organisms responsible for this primary production. Furthermore, such monitoring of phytoplankton was expected to yield valuable information relating to an overall investigation of the West Blue Lake ecosystem, of which this study was part.

LITERATURE REVIEW

A. DEVELOPMENT OF THE APPLICATION OF THE COULTER COUNTER

The Coulter Counter first became available in 1953 as an instrument to replace the haemocytometer for the counting of blood cells. Throughout the past eighteen years, the complexity and sensitivity of the instrument have increased significantly, allowing greater diversity of types of particles and particle spectra to be determined.

The principle of operation of the Coulter Counter involves the passage of an electrical current in an electrolyte through an aperture of known dimension. Particles in the known amount of electrolyte drawn throught the aperture interrupt the electrical field, and the magnitude of this interruption is directly proportional to the volume of the particle, within a size range of 2-40% of the aperture diameter. Desired size and volume ranges of particles can be examined by altering current strength or using the system of electrical gates built into the instrument.

During the 1950's, virtually all of the literature published on the Coulter Counter discussed its applicability for counting blood cells. During the 1960's, researchers began using the instrument to count a wider variety of particle spectra.

The first practical evaluation of the Coulter Counter was published by Mattern, Brackett and Olson (1957) who used blood cells as their test particles. They found a good correlation to exist between pulse height and diameter of red blood cells, but not between pulse height and cell volume.

Kubitischek (1958) modified the aperture and obtained the first successful counts of bacteria. His results agreed to within 2% of more laborious haemocytometer counts, and he concluded that the change in resistance of the aperture was proportional to the volume of any particle passing through it. Kubitischek (1958) also proposed that the lower limit of instrument sensitivity was imposed by electrical noise, and he showed experimentally that the upper limit of sensitivity was greater than 30% of the aperture diameter.

Hastings, Sweeney and Mullin (1962) were the first authors to discuss the applicability of the Coulter Counter to the counting and sizing of unicellular marine organisms. They stated that co-incident loss became a negligible source of error when a previously proposed correction procedure had been applied. They supported the results of Kubitischek (1958) in finding that there was only a 2-4% difference between Coulter counts and haemocytometer counts. Their experimental results with algae supported the conclusion of Mattern et al (1957), that pulse height was a function of cell diameter rather than cell volume. They proposed

several other limitations which have been virtually negated by advances in instrument complexity and experimental technique. These were that: (a) the pulse height was markedly affected by the salinity, (b) detritus in the sample caused considerable counting error, and, (c) under normal conditions there were too few cells present in water to allow an accurate count.

Maloney, Donovan and Robinson (1962) tested the suitability of the Coulter Counter in determining the number and size of algal cells, and found it to be effective for this purpose.

In 1963, El Sayed and Lee used the Coulter Counter for the quantitative estimation of cell size and number of several species of unicellular algae. They tested statistically results obtained from the Coulter Counter and concluded that its reliability and reproducibility were very good. They also found that: (a) co-incident loss was easily corrected for by use of tables supplied with the instrument; (b) electrical interference caused false pulses, but that by the correct choice of sensitivity and threshold settings, the major portion of this interference could be screened out; (c) settling of algal cells could be rectified by the use of magnetic stirrers; (d) difficulties incurred by clumping of cells could be overcome by immediate counting with continued stirring.

Parsons (1965) verified the suggestion of El-Sayed and Lee (1963) that the Model B Coulter Counter could be

used to distinguish between a mixture of species of different cell sizes, and further showed that it was effective for measuring the growth rate of chain forming diatoms.

In 1966, Cushing and Nicholson proposed a method whereby the Coulter Counter could be used to measure algal production rates at sea. They stated that the major advantage of this instrument was that very small volumes of water could be used, and so samples could be frequently replicated. In this method they also found that: (a) they were able to determine production and standing crop from the same set of measurements; and (b) living material could be separated from detritus. With this publication, it became feasible to use the Coulter Counter technique as an alternative to the ^{14}C and oxygen evolution methods of measuring primary productivity in planktonic communities.

In order that production values determined by the Coulter Counter in terms of volume could be expressed as mass of carbon fixed, it was necessary to establish a precise relationship between these two variables. Mullin, Sloan and Eppley (1966) made the first real contribution toward the determination of this relationship.

Previously, approximate conversion factors between carbon and volume had been cited in the literature by Cushing (1958), Strickland (1960) and Vollenweider (1969), but these values were imprecise. The values of Strickland and Vollenweider merely set wider limits on Cushings reported

value. Mullin et al (1966) working with pure cultures and determining volumes by optical measurement, found that carbon per unit cell volume varied inversely with cell volume.

Strathmann (1967) conducted further experimentation on carbon: volume relationships, and demonstrated that the common regression equation as given by Mullin et al (1966) was not appropriate for diatoms since they had large vacuoles, and thus had less carbon per unit volume than in other phytoplankton organisms of comparable size. Consequently he felt that plasma volumes gave a more precise estimate of cell carbon in diatoms than did whole cell volumes, and were best estimated separately. Differences among species were also an important source of error in estimating cell carbon from volume.

Sheldon and Parsons (1967) used the Coulter Counter on seawater for the determination of a continuous size spectrum of particulate matter. There they found that (a) particle volume measurements were in good agreement with estimates based on microscopic determination of particle diameter; and (b) highly significant correlations existed between total particle volume and particulate carbon and nitrogen. In 1967, Sheldon and Parsons published a manual describing the theory and possible applications of the Coulter Counter in marine science. They reviewed pertinent literature to this date, and also gave descriptions of their own and other methods.

Sheldon, Evelyn and Parsons (1967) described further measurements of the continuous size spectrum for particulate matter in the sea using the Coulter Counter. They effectively expressed this size spectrum as total particle volume related to the logarithm of particle diameter.

In their 1968 revision of 'A Practical Handbook of Seawater Analysis', Strickland and Parsons describe the electronic counting and sizing of particles by the Coulter Counter. Their description was merely an abbreviated set of instructions taken from a publication by Sheldon and Parsons (1967).

Cushing, Nicholson and Fox (1968) concluded that the relationship between pulse amplitude and particle volume was linear for particles with diameters up to 40% of the aperture diameter. They showed that earlier theories stating that pulse amplitude depended on cell diameter were incorrect. Results from their primary production experiments with the Coulter Counter demonstrated that the instrument could detect minute changes of the total particulate volume in a seawater sample.

Mulligan and Kingsbury (1968) used the Coulter Counter to measure phytoplankton populations in which they found that biomass determined in this way gave a more precise estimate than that obtained by determining chlorophyll 'a' or dry weight. They concluded that the Coulter Counter within certain limits provided a large increase in capability over methods previously available.

Margalef (1969) discussed applications of the Coulter Counter to aquatic science, and concluded that it was practically useless. However, this statement was disputed by Vollenweider (1969) since the errors that Margalef proposed have now been virtually negated by increases of instrument complexity and design.

The development in complexity of the Coulter Counter and the establishment of carbon:volume relationships by other authors, enabled this thesis work to be performed on a stable background of information.

B. THE CARBON-14 (^{14}C) METHOD OF DETERMINING PRIMARY PRODUCTION

Early methods of determining the production of organic matter are now considered to be only of historical value. However, these early techniques were of value in laying the groundwork for more modern methods.

The "oxygen method" introduced by Gaardner and Gran (1927), was the first to gain prominence as an effective method for measuring primary production. After the ^{14}C method was introduced in 1951, many workers attempted to show that the radio isotope method was superior. Although the controversy still exists, it is generally recognized that the difficulty of use and errors inherent in the ^{14}C method are not as great as those of the oxygen method.

In this thesis, since results obtained by the ^{14}C method are compared with values obtained by the Coulter Counter, only publications making a significant contribution

to the development of the former method and directly applicable to this thesis work are reviewed here.

Steemann Neilsen (1951) first proposed in note form, the use of the ^{14}C method as a means of measuring primary production in planktonic communities. In his 1952 publication, he expanded widely on the preparation and use of ^{14}C. Also, he criticized the oxygen technique, stating that the method was useless in oligotrophic situations, whereas the ^{14}C method because of its greater sensitivity was not. He laid the basis for a controversy which still has not been resolved adequately, by stating that the ^{14}C method measured gross production. Riley (1952) refuted Steemann Neilsen's claim, and stated that the ^{14}C method measured something between net and gross production.

Since doubt had been cast on the classical oxygen method as a tool for future studies by Steeman Neilsen, Ryther and Vaccaro (1954) conducted a simultaneous comparison of the ^{14}C and O_2 methods. They agreed that the ^{14}C method was more sensitive, but found the two methods to be comparable if results were extended over a long enough time interval. Vaccaro and Ryther (1954) showed Steeman Neilsen's contention that sunlight exerted bacteriocidal effects in the light bottle to be incorrect. Ryther (1956) critically examined the ^{14}C technique and determined by experimental procedure that net photosynthesis was being measured by this method. The major point supporting this contention was that ^{14}C respired as $^{14}CO_2$ was used

preferentially in photosynthesis to CO_2 already existing in the external medium.

Doty and Oguri (1958) suggested the presence of a physiological daily rhythm of photosynthesis and also presented the experimental design for a plankton incubator. Fogg (1958) discussed the excretion of labelled organics, and considered them not to be a significant loss in short experiments. Rodhe (1958) performed various 'in situ' ^{14}C experiments and found that the sum of the results from consecutive short term experiments was greater than results obtained from a simultaneous series of experiments lasting for a whole day.

In 1958, Rodhe, Vollenweider and Nauwerck found a reasonable correlation to exist between 'in situ' and 'in vitro' productivity experiments. By conducting ^{14}C productivity experiments on a number of consecutive days, they found that as much as one hundred to three hundred per cent difference in productivity values could occur. Consequently, they concluded that productivity experiments performed on a weekly basis would not be accurately extrapolated to a true production value. They also stated that if relative productivity values were required, the ^{14}C method was an unrivalled tool; but they stressed that if absolute values were to be obtained, more comparisons between the ^{14}C and O_2 methods would be necessary.

In 1959, Steeman Neilsen and Hansen attempted to define more accurately the rate of respiration in relation

to light saturated photosynthesis. They determined the respiration rate by extrapolating the linear portion of a photosynthesis:light curve back to the ordinate. Ninety per cent of all such respiration rates measured in this manner were 15% or less of light saturated photosynthesis. Steeman Neilsen (1960) discussed techniques of productivity measurement in the ocean with an emphasis on the ^{14}C method. Points which he emphasized were that: (a) considerable error could be involved in the use of the Geiger Muller counter if samples were not extrapolated to zero thickness; (b) dark bottles should be used to give an estimate of any dark assimilation; (c) the period of the experiment should be kept short, and; (d) excretion losses were likely to be insignificant.

Strickland (1960) published a large report and review discussing all aspects of the measurement of primary production in the sea. In this review he presented all definitions and conversion factors pertinent to phytoplankton; reviewed all work on the chemical composition of phytoplankton with a fair emphasis on the pigments, and also discussed all methods of measuring standing crop and the rate of photosynthesis with an emphasis on the oxygen and ^{14}C methods. He further emphasized primary productivity in terms of the general growth kinetics of phytoplankton and 'in situ' determinations.

Major points relevant to this thesis review are:

(a) his proposed relationship between carbon and

volume;

(b) his support of Ryther's contention that the carbon-14 method measured something close to net photosynthesis;

(c) that a loss of radioactivity on drying could occur in the ^{14}C method;

(d) that significant errors were inherent with the Geiger-Muller counting method;

(e) that a comparison of 'in situ' and light incubator measurements indicated that 'in situ' measurements should be used whenever possible.

McAllister et al (1961) by an 'in situ' study supported the conclusion of Steeman Neilsen and Hansen (1959) that the respiration rate was six to ten per cent of the optimum photosynthetic rate. Simultaneous experiments with ^{14}C and oxygen methods did not give comparable results. However, the authors suggested that the photosynthetic quotient used for the calculation of O_2 values was much too low, and in the ^{14}C method, it was net photosynthesis that was being measured rather than gross photosynthesis.

In 1961, Strickland and Parsons published a "Practical Handbook of Seawater Analysis", which has since been revised in 1965 and 1968. In the 1968 edition, they fully described the uptake of radioactive carbon by algae, and listed careful instructions for the use of this method beginning with the actual preparation of the ^{14}C ampoules in the laboratory to the final measurement of isotope

activity by the most recent methods.

In a consideration of methods of determining uptake of ^{14}C, Geiger-Mueller counting systems were those initially used. Jitts and Scott (1961) used thin films of labelled plastic to compare the counting accuracy of the windowless Geiger-Mueller gas flow counter with that of a liquid scintillation counter. Extrapolations of a self-absorption to 0 mg/cm^2 gave zero thickness activities of 17% and 24% lower than those obtained by the liquid scintillation counter.

Wolfe and Schelske (1967) compared Geiger-Mueller counts of ^{14}C labelled phytoplankton with liquid scintillation counts and concluded that the absolute activity of ^{14}C phytoplankton on filter paper can be determined by direct liquid scintillation counting of the intact sample.

McAllister (1961a) criticized the method used to decontaminate membrane filters containing radioactive phytoplankton over fuming HCl. His results suggested that errors due to these decontamination procedures may exceed those which would result from the contamination. The magnitude of this error would depend on the species composition of the phytoplankton.

McAllister (1961b) measured photosynthesis by the ^{14}C method, and demonstrated that a definite diurnal variation in productivity did occur. He found the magnitude of this diurnal variation to be significantly dampened with depth.

In 1963, the proceedings of yet another conference on primary productivity measurement (ed. Doty, 1963) was published. Again, only those papers making a significant contribution to the measurement of primary productivity by the ^{14}C method will be discussed in this review. Goldman (1963) discussed the most recent developments in the use of ^{14}C, and strongly emphasized the need for an accurate estimate of the CO_2 content and the buffering capacity of the water being tested. He further described his method of nutrient bioassay, emphasizing its reliability and sensitivity. Jitts (1963) provided a comprehensive review in which he attempted to evaluate differences in technique of many workers using the ^{14}C method.

Cassie (1963) tested reproducibility of data from the same water sample and from water samples collected over a small area. He found that results for replicate samples from the same water sampler differed by no greater than 10%, but errors occurring among samples collected over a small area could be as high as 25%. Strickland (1963) stated that whatever may be said in criticizing the radio carbon method, it remained the only technique by which any results could be obtained in the open ocean. Variations in photosynthetic quotients could be so great that the interpretation of results obtained by the oxygen technique were far from simple. The total amount of carbon fixed may be a combination of that fixed photosynthetically and that fixed heterotrophically. The most serious fault in quantitative

photosynthetic rate estimates was the reluctance of workers to state the spectral energy distribution of their light sources, or to measure light intensities in absolute and reproducible energy units.

Vinberg (1960) discussed extensively the measurement of primary production in bodies of water. The ^{14}C method was practically unused in Soviet science at this time and in his discussion of the ^{14}C method, he added no new knowledge to the use of the technique. In fact, he seemed very much biased in favour of the oxygen method.

In 1963, Yentsch reviewed some aspects of primary production measurement. He emphasized that when using the ^{14}C technique to measure photosynthesis, there were two types of problems to be considered. These were the errors inherent in the technique itself, and errors arising from the interpretation of the data.

Antia et al (1963) performed experiments in a large volume plastic sphere and estimated that during the total light period, the plant cells excreted 35 to 40% of their organic matter during growth. In this experiment, comparisons between the O_2 method and the ^{14}C method of measuring production gave excellent agreement.

Wetzel (1965) stated that extracellular deposition of inorganic ^{14}C can lead to large overestimates of counts if fuming by concentrated hydrochloric acid was not used. Loss of radioactivity as $^{14}CO_2$ in samples differed among lakes seasonally, and also between illuminated and dark

samples.

Ryther and Menzel (1965) compared the carbon increase as measured by the ^{14}C method with a direct chemical measurement of the carbon change. The agreement between results was extremely good, and they concluded that all previously proposed error factors such as respiration, dark uptake, fuming of filters, drying, filtering and isotope effect were either negligible or self-cancelling.

Bunt (1965) from measurements of photosynthesis and respiration with a mass spectrometer, concluded that where excretion was insignificant, the ^{14}C method gave a measure of net photosynthesis. He was not, however, able to determine the magnitude of the net photosynthesis in comparison to the gross photosynthesis.

Steemann Neilsen (1965) determined the zero thickness activity of filters from aliquots of labelled algal material. The main advantage of this method was that the organisms on the filter paper now had the same geometry as those of the natural phytoplankton. He found this biological technique to give results approximately 31% lower than values obtained by the original $BaCO_3$ technique. In comparing the results of the ^{14}C and O_2 experiments using this new data, he found excellent agreement.

In a symposium held at Pallanza, Italy (ed. Goldman 1965) very few papers dealt specifically with the use of the ^{14}C method. Wetzel (1965) did, however, discuss the advantages and disadvantages of the ^{14}C nutrient enrichment

bioassay technique. He stated that the sensitivity to growth responses and the elimination of a lag in growth response, made the bioassay technique ideal for the elucidation of the role of inorganic nutrients as well as accessory organic growth factors, in regulation of population metabolism. The influence of minor elements was not always direct and caution was necessary in the interpretation of certain stimulatory responses.

In 1966, Schindler was the first to propose a ^{14}C method whereby algal productivity could be determined by the use of a liquid scintillation counter. He stated that the high counting efficiency and low standard deviation, coupled with the individually determined efficiencies and reduced manipulation of filter membranes, made the liquid scintillation method desirable where primary production was very low or erratic.

Arthur and Rigler (1967) showed a relationship to exist between the volume of water filtered and specific activity of the plankton, whereby activity of the plankton per unit volume decreased with increased volume filtered. They attributed this decrease of counts to damage to phytoplankton organisms on the filter as the filtration time increased. They stressed that this effect varied according to the species composition of the phytoplankton.

In 1968, Wallen and Green found that a significant loss of counts occurred during the first 24 hours of dessication of filters. They proposed that the rapid

removal of water from the cells by the dessicant also carried out labelled compounds. This effect varied both with lake type, and with species composition of the phytoplankton.

Vollenweider (1969) edited a reference handbook titled 'A Manual on Methods for Measuring Primary Production in Aquatic Environments', consisting of works by many different authors, describing methods developed up to that time. Fogg (1969) compared the oxygen and ^{14}C methodology, and concluded that the O_2 method was somewhat more reliable in eutrophic situations, but the greater overall sensitivity of the ^{14}C method was stressed. Discussions of bacterial production are given by both Sorokin and Hobbie (1969). Their works indicated how little is known about this field.

Pugh (1970) investigated the internal and external standardization methods of scintillation counting and concluded that the only reliable method for determining the counting efficiencies of algal material was by a channels ratio method, although his curve relating channels ratio to counting efficiency was markedly different from that for homogeneous solutions.

Ward and Nakanishi (1971) found that primary productivity estimated from liquid scintillation counts of the radioactivity of wet ^{14}C-labelled algae on membrane filters was about 30% greater than an estimate from Geiger-Mueller counts of comparable algae, and filters that had been dessicated.

Schindler and Holmgren (1971) demonstrated the use of a method whereby bub ing air was passed through the acidified filtrate, to drive off unlabelled organics. An aliquot of this filtrate could then be placed directly into the fluor, and a measure of excreted organics obtained. In Canadian Shield lakes they found not more than 1% of the fixed carbon to be excreted as organics.

A chronological sequence of literature is given in order to show development in the sensitivity of the ^{14}C and Coulter Counter methods. So far as this author is aware, no comparison between the ^{14}C method and the Coulter Counter method had ever previously been attempted. As was displayed in the literature review, the major error component associated with the Coulter Counter method was the establishment of a carbon: volume relationship accurate for all situations. The major error component of the ^{14}C method was the uncertainty of the magnitude of the Arthur Rigler correction factor. Other problems with both methods may cause significant error at certain times, but none are as pronounced as the two discussed.

METHODS

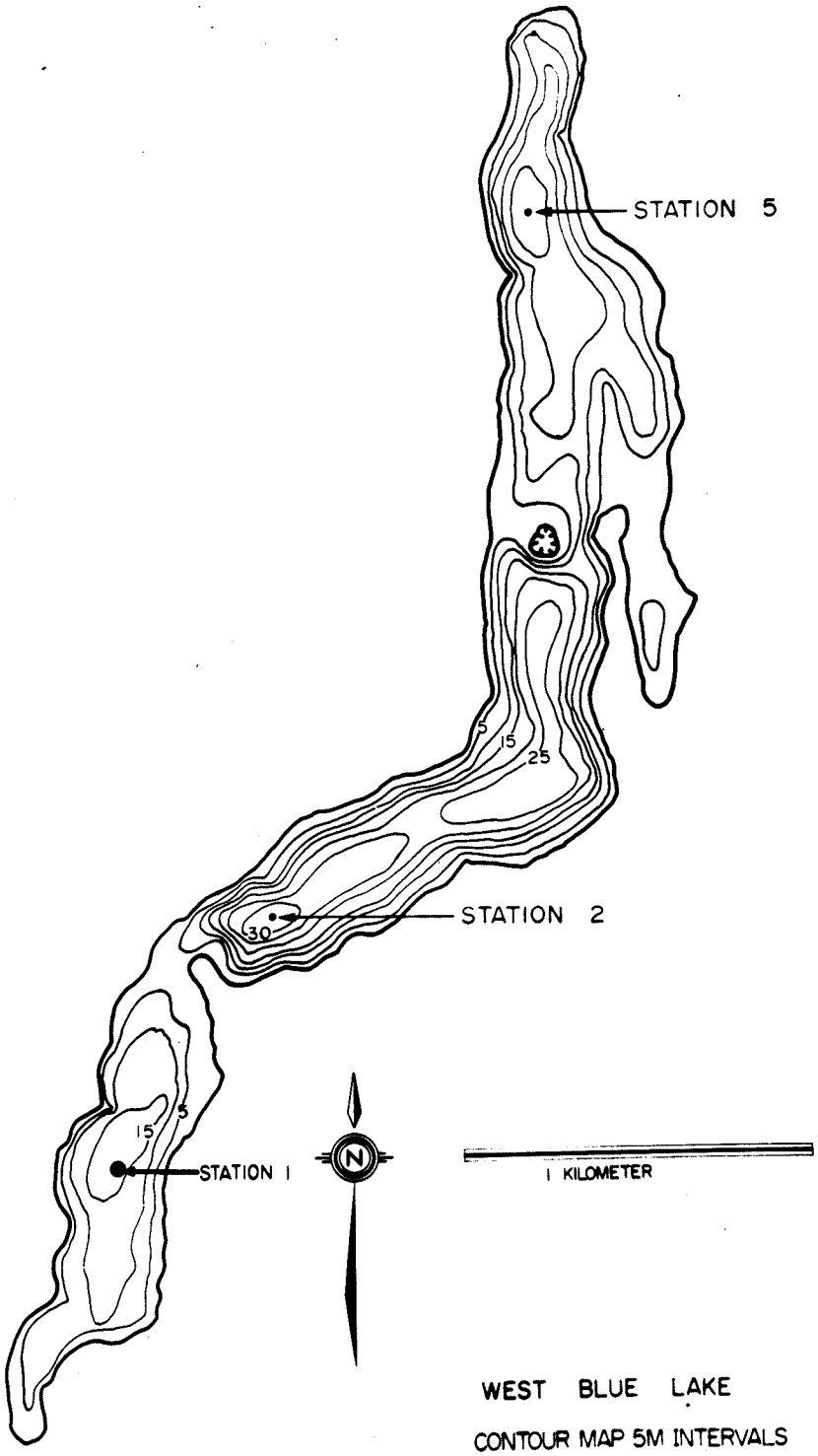
1. Description of West Blue Lake

All sampling and research was conducted at West Blue Lake, Manitoba (Fig. 1) located in the Duck Mountain Provincial Park approximately 300 miles north-west of Winnipeg. The lake is 4.8 kilometers in length, 0.52 kilometers at the widest point and has a shoreline development of 2.87. The lake consists of three basins, the northern-most with a maximum depth of 20 meters; the central basin with a maximum depth of 31 meters and the southern basin with a maximum depth of 18 meters. This lake has a total surface area of 1.6 square kilometers and a mean depth of 11.3 meters. The lake has no outflow, and but a few small inflowing streams carrying water only in the spring.

The majority of the sampling was conducted at Stn. 2, in the central basin (Fig. 1), but various tests were performed at Stn. 1 and 5.

Research was conducted from May 1st, 1970 to September 1st, 1971 on a weekly basis, except during the intervening winter when sampling was undertaken on a monthly basis. Summer samples were analysed immediately at West Blue Lake whereas some winter samples had to be transported to the laboratory in Winnipeg for analysis.

FIG 1 BATHYMETRIC MAP OF WEST BLUE LAKE



2. Seasonal Occurrence of Phytoplankton in West Blue Lake

Phytoplankton samples were collected from Stn. 2 at depths of 0, 3, 7, 12, 17, 20, 25 and 30 meters by use of a 16 litre poly-vinyl chloride van Dorn sampling bottle.

During 1970, samples were passed through a Nitex 153 μ diameter screen to remove most of the zooplankton. However, since this procedure may have removed some large phytoplankton species the procedure was subsequently modified and from May, 1971 onwards each sample was first filtered through a 10 μ mesh net. Phytoplankton retained in the net was flushed into an 8 oz. collecting jar by means of numerous rinses and backwashings in the filtrate. Samples were returned to the laboratory and made up to a volume of 200 ml with lake water, previously filtered through Whatman GF/C glass fiber filters. 10 ml of each thoroughly mixed sample was removed to be enumerated in Sedgewick-Rafter counting cells. The remainder of the sample was then filtered through a 153 μ diameter screen to provide the fraction used for dry and ash weight determinations.

(i) Phytoplankton analysis

One ml of each phytoplankton concentrate was pipetted into a Sedgewick-Rafter counting chamber and allowed to settle for a minimum time of fifteen minutes. By using a 100x magnification, the Sedgewick-Rafter cell could be divided into 35 equal strips. Five of these strips were examined, and species counts were extrapolated

to the whole counting chamber. An analysis of variance was performed on two random five strip samples of a Sedgewick-Rafter cell in order to determine whether five strips were an adequate number. Further tests to determine statistical validity of collection methods and techniques were not performed.

(ii) Determination of Dry and Ash Weights

Screened samples were filtered onto 4.25 cm Whatman GF/A glass fiber filters which had been previously ignited at 450° C to remove any organic material, and then weighed to determine initial filter weights. The wet filters were then placed in foil cups in a drying oven at 105° C for a minimum time of one hour (Strickland and Parsons, 1968). Filters were again weighed and dry weights were determined. These filters were then placed in a muffle furnace at 450° C for four hours (Strickland and Parsons 1968). Filters were again weighed, and ash weights determined.

Values for species count data, dry weights and ash weights were then integrated by plotting the values against depth on standard graph paper and values for each cubic meter were determined and summed to give total values under one square meter of lake surface.

3. Coulter Counter Experiments

(a) Determination of a Carbon:Volume Relationship

In order to express primary productivity, determined

as volume, in terms of carbon, it was necessary to establish a relationship between carbon content and volume of West Blue Lake phytoplankton. Both pure cultures of West Blue Lake species and mixed natural phytoplankton collections were analysed.

For the preparation of unialgal cultures, nutrient agar plates (.8 - 1% agar) were made up with Bristol's (Starr 1964), K-10 (Trelease et al 1935; Chu 1942) or Pringsheim's (Pringsheim 1949) media. Plates were inoculated with 0.1 ml of lakewater and placed in a growth chamber in a 10 hr light - 14 hour dark regime under a light intensity of 2800 lux and a temperature of 10° C, from October through April. From May through September, cultures were placed in a 16 hr light - 8 hr dark regime in a light intensity of 5500 lux and a temperature of 17° C. At irregular intervals the plates were examined by use of a stereomicroscope and algal colonies were picked off with a sterile pipette. Each colony was placed into 10 ml of sterile media, shaken vigorously, and replated onto nutrient agar. After several weeks, colonies growing on these plates were placed into liquid culture in 25 ml glass bottles, in the previously mentioned culture media. If the phytoplankton showed growth, they were first examined for purity and then transferred into 125 or 250 ml erlenmeyer flasks. These flasks were either swirled on a laboratory rotator or aerated. Every two weeks cultures were examined. If good growth was occurring, the algal material was allowed to

settle to the bottom of the flask. The old culture media was decanted off, and fresh culture media was added.

When sufficient growth had occurred, cultures were prepared for volume and carbon determinations by selective screening (Appendix I). Such screening served to concentrate the algae and to remove most detrital material. To permit counting and sizing with a Coulter Counter (Model B, Coulter Electronics, Hialeah, Fla.) appropriate aperture size and instrument sensitivities had to be selected for each species (Appendix I). Similar procedures were also performed on mixed phytoplankton collections.

In the preparation of natural phytoplankton samples, lakewater was passed through a 10 μ mesh net in order to concentrate the algae. The algal concentrate was then passed through a 102 μ mesh screen. Large phytoplankton and detritus retained on this screen were resuspended in a small amount of particle-free lakewater. The phytoplankton and detritus fraction which passed through the screen were then concentrated on a 25 μ mesh screen and resuspended in a small amount of particle-free lakewater. Both concentrates were then examined under the microscope, and the approximate species composition was determined. The selectively screened algae (both natural and cultured) were then in a form suitable for carbon and volume determinations. Three 20 ml fractions were taken from each well mixed algal concentrate, and added to 80 mls of particle-free water in 200 ml jars in order to make a suspension of 100 ml. This

same procedure was used for 10, 5, 2.5 and 1.25 ml of algal concentrate, and each time the sample was made up to 100 ml with particle-free lakewater. Two bottles from each concentration were used for a particulate carbon determination. For this procedure, algae were filtered onto previously ashed 5.5 cm GF/C glass fiber filter papers, frozen and analysed at a later date. Samples for particulate carbon were analysed by the method of Strickland and Parsons (1961).

For determination of particulate volume, 100 ml of Isoton (Coulter Electronics, Hialeah, Fla.) was added to the sample to be analyzed by the Coulter Counter. This Isoton solution containing 0.1% sodium azide in distilled water served two purposes. Primarily it was required to conduct an electrical current through the sample, and secondarily it halted all biological activity until the sample could be analysed. All samples were counted as quickly as possible to avoid any change in sample volume as a function of fixation. The total particulate volume of each sample was then determined.

(b) Productivity Experiments

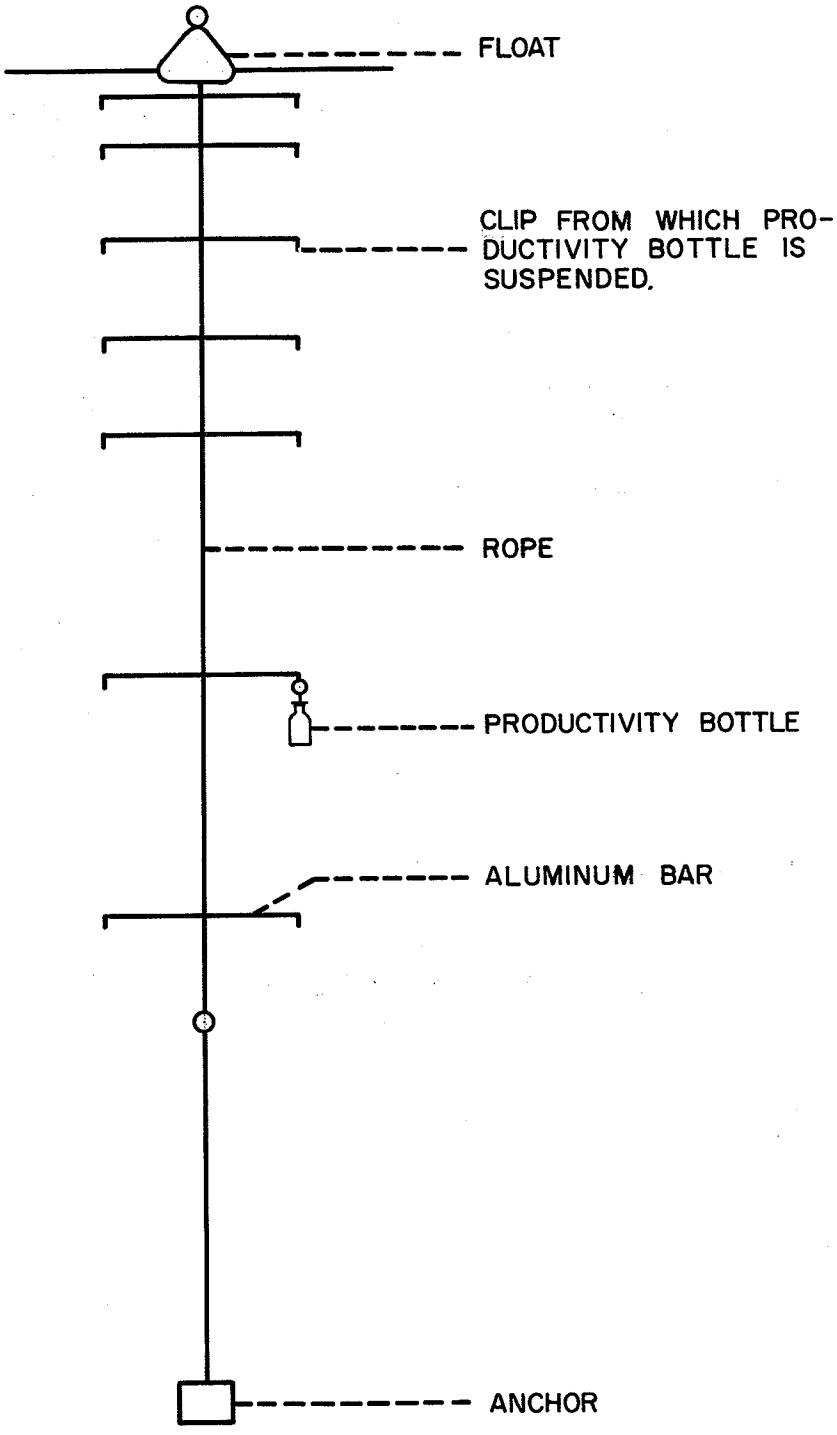
Primary productivity experiments were performed at Stn. 2 at the standard ^{14}C productivity depths of 0, 1, 3, 5, 7, 12 and 17 meters, four times during the summer of 1970 and five times during the summer of 1971. It had previously been determined from ^{14}C experiments and analysis of variance tests that productivity determinations

at Stn. 2 were representative of the whole lake during July 1968 (Ward, Pers. Comm.).

Samples were taken from each depth with a 4 litre Van Dorn sampling bottle. Water from each depth was passed through a Nitex 153 μ mesh screen in order to remove zooplankton and larger particulate material, then mixed thoroughly in a bucket before being poured into two one litre bottles, one of which had been completely darkened with paint and black tape. The bottles were then suspended at 'in situ' depths on an aluminum bar and float apparatus (Fig. 2) and left for 24 hours. At the end of this period the bottles were collected and taken immediately to the laboratory for analysis. Each sample was thoroughly mixed and then passed through a 100 μ screen so that samples could be counted by use of the 100 μ aperture of the Coulter Counter. Examination of the material retained on the screen showed that some Anabaena and Aphanizomenon chains as well as large Ceratium and Asterionella were lost. However, particles lost by this additional screening were insufficient in number to count by use of any larger aperture tube. 200 ml of lakewater sample was then added to an equal volume of Isoton. The numbers and volume of particles were then determined by use of the Coulter Counter.

For the research conducted during 1970, the Coulter Counter and its accessory Model J plotter were used. However, it was determined in theory and supported by three sets of experimental data that this Model J plotter was

FIG. 2. 'IN SITU' SUSPENSION APPARATUS FOR PRIMARY PRODUCTION BOTTLES



inappropriate for use on natural populations, as will be discussed. These sets of experiments included (i) 1970 productivity data, (ii) growth experiments following the model of Sheldon and Parsons (1967) and (iii) measurements of particle volume at different depths. Consequently, in 1971 the Model B Coulter Counter was used without its accessory Model J plotter.

For a particular aperture and sensitivity selected, the Model J plotter would partition the total particle spectrum into 25 portions and record the relative particle numbers in histogram form. The Coulter Counter, without the plotter, could be made to pefform the same function by merely adjusting the window settings (an electrical gating device that would screen out particles larger or smaller than some pre-determined size) so that the particle spectrum was again partitioned into 25 portions. Each window setting had previously been calibrated with particles of known size and volume in order that volumes could be obtained which were then multiplied by the relative number data obtained (Sheldon and Parsons, 1967).

4. Carbon-14 and Filtration Effect Experiments

Carbon-14 experiments were performed once each week from May through September of 1971 as a matter of routine sampling procedure at West Blue Lake. The five productivity experiments involving the Coulter Counter method were

conducted on the same dates as carbon-14 experiments.

Carbon-14 ampoules were made up into a concentration of 5 μcuries from Amersham-Searle radio-isotope stock (Strickland and Parsons 1968). Water was collected from 0, 1, 3, 5, 7, 12 and 17 meter depths, screened through a 153 μ mesh screen and poured into the appropriate 125 ml light or dark bottle. The bottles were each inoculated with one ampoule (approximately 5 μcuries ^{14}C). A light and a dark bottle were suspended 'in situ' at the above mentioned sampling depths on an apparatus previously described (Fig. 2). The experiment was conducted from 10 a.m. to 2 p.m. At 2 p.m. bottles were retrieved and returned to the laboratory in a light tight box for analysis. The water was filtered immediately through Gelman 0.45 μ pore diameter cellulose acetate filters, arranged in a filtering manifold with a suction no greater than 1/4-1/3 of an atmosphere. These filters were then fumed for one minute over concentrated HCl to remove any inorganic carbon and placed in appropriately labelled scintillation vials containing 10 mls of Brays fluor (Bray, 1960). The cpm's of each sample was determined by a Picker Liquimat 200 Scintillation Counter. Counts were made at a preset statistic of 1.5 ± 2 and dpm's were calculated by the channels ratio method and determination of a quench curve. Carbon fixed by photosynthesis in a day was then calculated according to:

$1.05 \frac{Y}{Z}$. W.A. (mg C/m^3/day) (Strickland 1960).

Values thus obtained per cubic meter were integrated

by plotting these values vs depth on standard graph paper and determining the area under the curve. Values thus obtained gave the total carbon uptake under one square meter of lake surface. Coulter Counter data also converted to carbon uptake under a square meter of lake surface was then directly comparable to the ^{14}C results.

Ten experiments were conducted at West Blue Lake during the summer of 1971 in order to determine the magnitude of the filtration error (Arthur and Rigler 1967; Schindler and Holmgren 1971). A filtering manifold was set up under a vacuum pressure of 1/4-1/3 of 1 atmosphere. Increasing amounts of lakewater (1, 2, 3, 5, 7, 10, 25, 50, 75, 100 and 125 mls) inoculated with ^{14}C for four hours were filtered. A graph of counts plotted against amount of sample added was constructed. Extrapolation of this line to the Y axis gave an estimate of the filtering error for each productivity determination. This correction factor could then be applied to the data.

The above ^{14}C experiments are an on-going part of the overall productivity determinations made on West Blue Lake.

RESULTS

A. Measurements of Phytoplankton Populations in West Blue Lake

A list of the phytoplankton species observed at Station 2 for the period from May 1970 through August 1971 is given in Table 1. The abundance of each phytoplankton species is given on a relative scale from 1-10 for each sampling date and is appended to the text (Appendix II). From these data it can be observed that the most common phytoplankton species are Anabaena spiroides, Aphanizomenon flos-aquae, Asterionella formosa, Botryococcus braunii, Dinobryon sertularia and Stephanodiscus nigariae. Stephanodiscus nigariae was the only species noted on all sampling dates throughout the duration of the sampling interval.

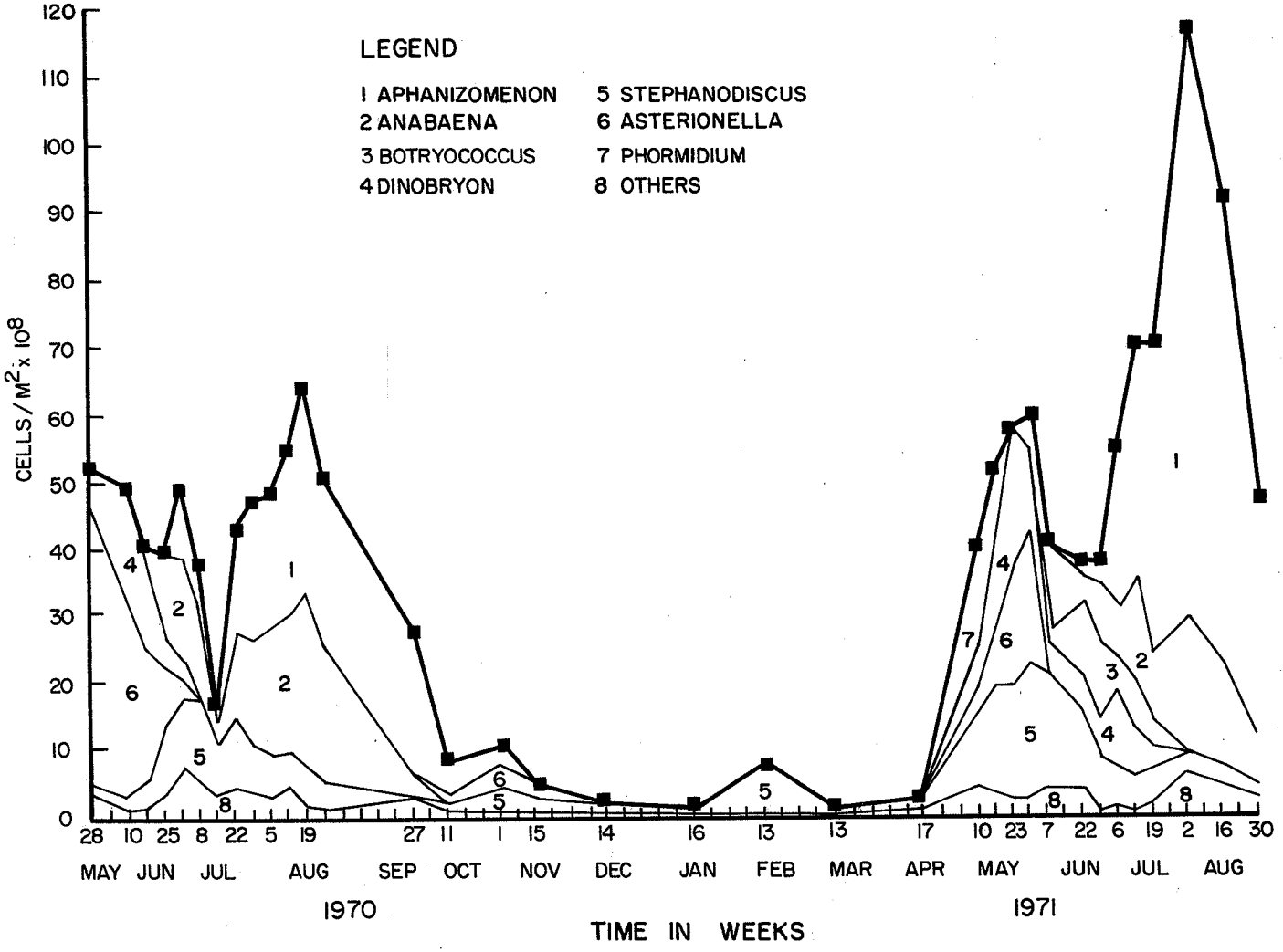
In Fig. 3, the percentage occurrence of each species as a portion of the total species count data is plotted for each sampling date. In both 1970 and 1971, a similar trend of cyclic replacement occurred. The diatoms and flagellates predominated in the spring. As these forms decreased in numbers, they were replaced by larger numbers of blue-green algae. A statistical test was performed to determine whether the number of strips being counted was sufficient. These results are appended to the text (Appendix III). With the onset of fall the numbers of blue-green algae declined

TABLE 1

A List of Phytoplankton Species for West Blue Lake, Manitoba from May, 1970 through August, 1971

Achnanthes sp
Amphora sp
Anabaena spiroides
Ankistrodesmus falcatus
Aphanizomenon flos-aquae
Asterionella formosa
Botryococcus braunii
Ceratium hirundinella
Crucigenia rectangularis
Cyclotella sp
Cymbella sp
Dinobryon sertularia
Eunotia sp
Fragilaria capucina
Fragilaria crotonensis
Gloeotrichia sp
Mallomonas sp
Merismopedia sp
Navicula sp
Nitzschia sp
Oocystis elliptica
Oscillatoria sp
Pediastrum sp
Peridinium sp
Phormidium sp
Pinnularia sp
Pleurosigma sp
Quadrigula chodatii
Rhizosolenia sp
Scenedesmus sp
Staurastrum sp
Stephanodiscus niagarae
Synedra ulna
Synedra incurva
Tabellaria sp

FIG. 3 PHYTOPLANKTON SPECIES COMPOSITION



rapidly. Species count data is recorded per cubic meter for the standard sampling depths on each sampling data; dry weights of suspended material (including both phytoplankton and detritus) are recorded as grams per cubic meter for the standard sampling depths on each sampling dates. The ash weights (obtained by incinerating the dry weight material) are recorded in a similar manner to the dry weights and cell numbers, and all three sets of data have been integrated to numbers of cells beneath a square meter of lake surface, and we appended to the text (Appendix IV). The integrated values for 31 meters at Station 2 are compared in Fig. 4. Dry weight and ash weight data correspond reasonably well, but poorer correspondence is noted between dry weight and species count data, and between ash weight and species count data.

B. Coulter Counter Experiments

(1) Determination of a Carbon:Volume Relationship

Data from carbon and volume determinations are appended to the text (Appendix V). These values were used in the calculation of a regression line (Fig. 5). A number of carbon:volume values were determined for chain forms, or forms with considerable mucous. Inconsistent results were obtained for these species, and consequently they do not appear here, but are appended to the text (Appendix VI). The equation of the line is given in Figure 5. The list of carbon values and their corresponding volumes, together with

FIG. 4. COMPARISON OF DRY WEIGHT, ASH WEIGHT & PHYTOPLANKTON COUNT DATA

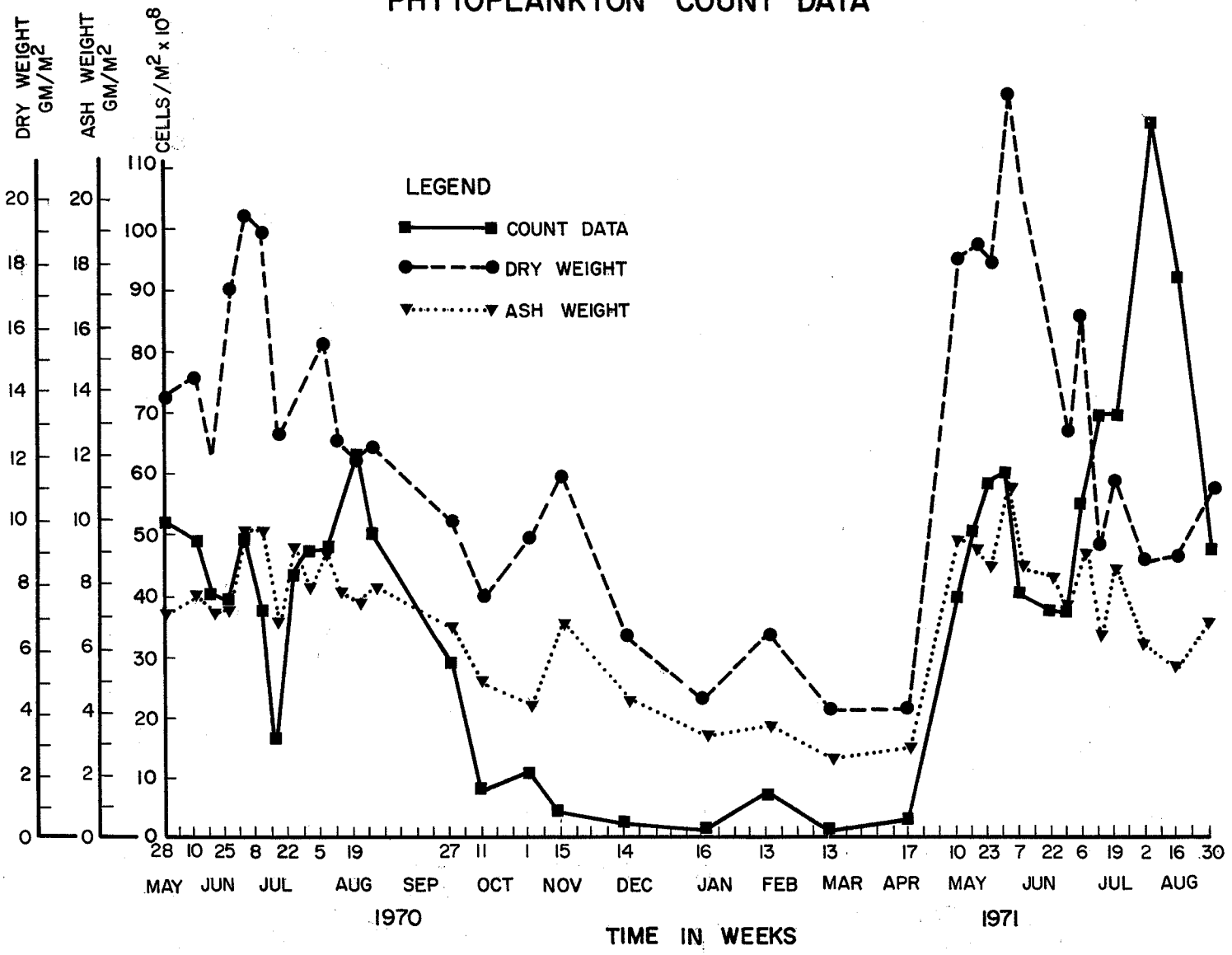
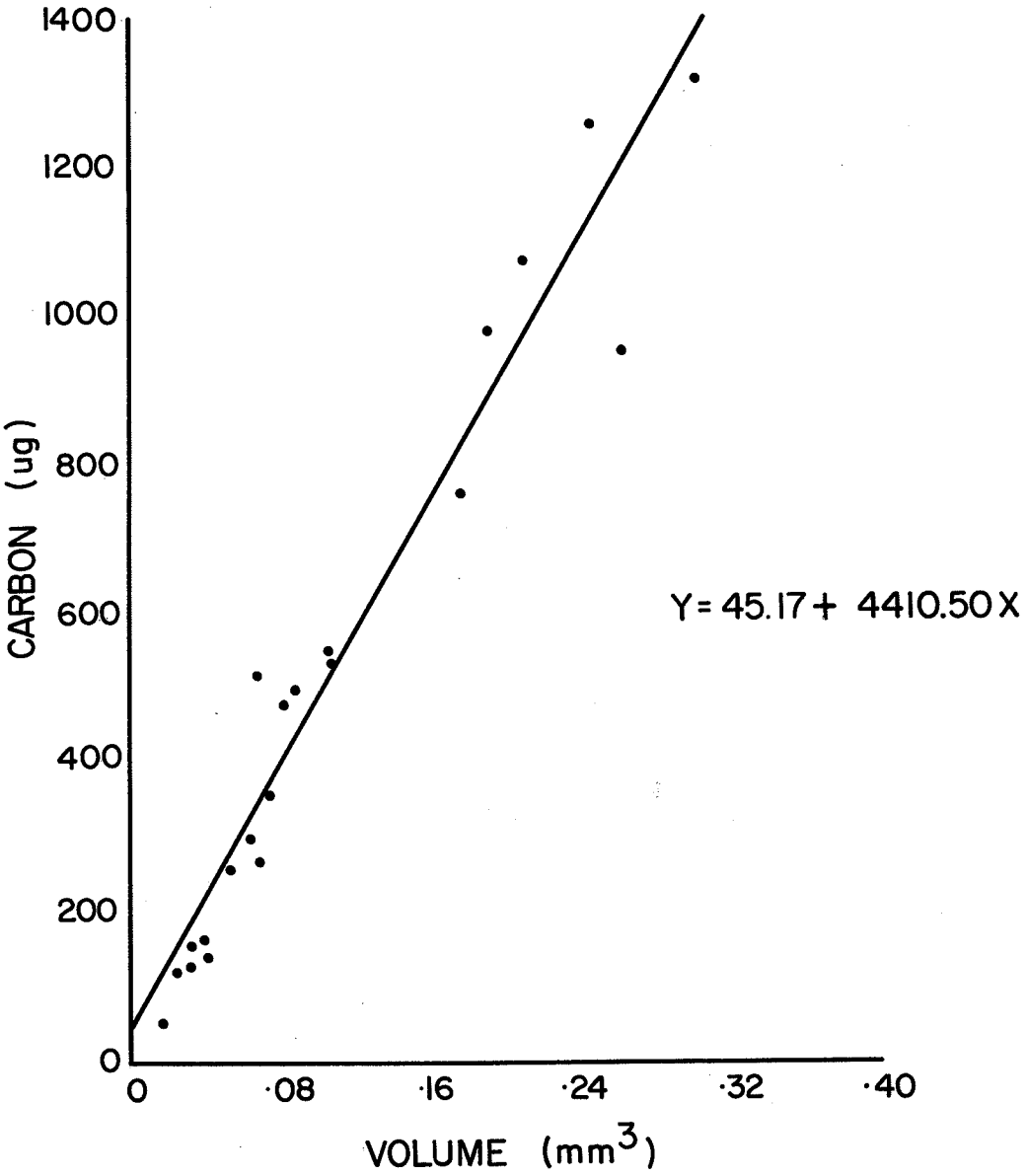


FIG. 5 REGRESSION LINE OF PARTICULATE CARBON vs PARTICULATE VOLUME



the major components of the regression line are appended to the text (Appendix VII). A comparison of this West Blue Lake line with other such regression lines reported in the literature is given in Figure 6.

(2) Determination of Primary Productivity

(i) Coulter Counter

Productivity values were measured in terms of volume and are recorded for 1970 in Table 2, and for 1971 in Table 3. These values were obtained at the standard ^{14}C primary productivity sampling depths, and the values are plotted (Appendix VIII). These graphs were observed to have a number of erratic fluctuations, which will be discussed.

(ii) ^{14}C Experiments

^{14}C data was determined from actual experimentation conducted at West Blue Lake. A mean correction factor of x 2.6 derived from the ten filtration experiments was applied to this data and a comparison of ^{14}C values (uncorrected and corrected) with the Coulter Counter determinations is recorded in Appendix VIII, and plotted in Figure 7. A further comparison of Coulter Counter productivity values with ^{14}C values was made in Table 4. Coulter Counter data is expressed in carbon derived from the experimentally determined regression line relating particulate carbon to particulate volume of West Blue Lake phytoplankton; and for additional comparison, also from the relationship expressed by Mullin, Sloan and Eppely (1966) and by Strathmann (1967).

FIG. 6. COMPARATIVE REGRESSION LINES OF CARBON vs. VOLUME

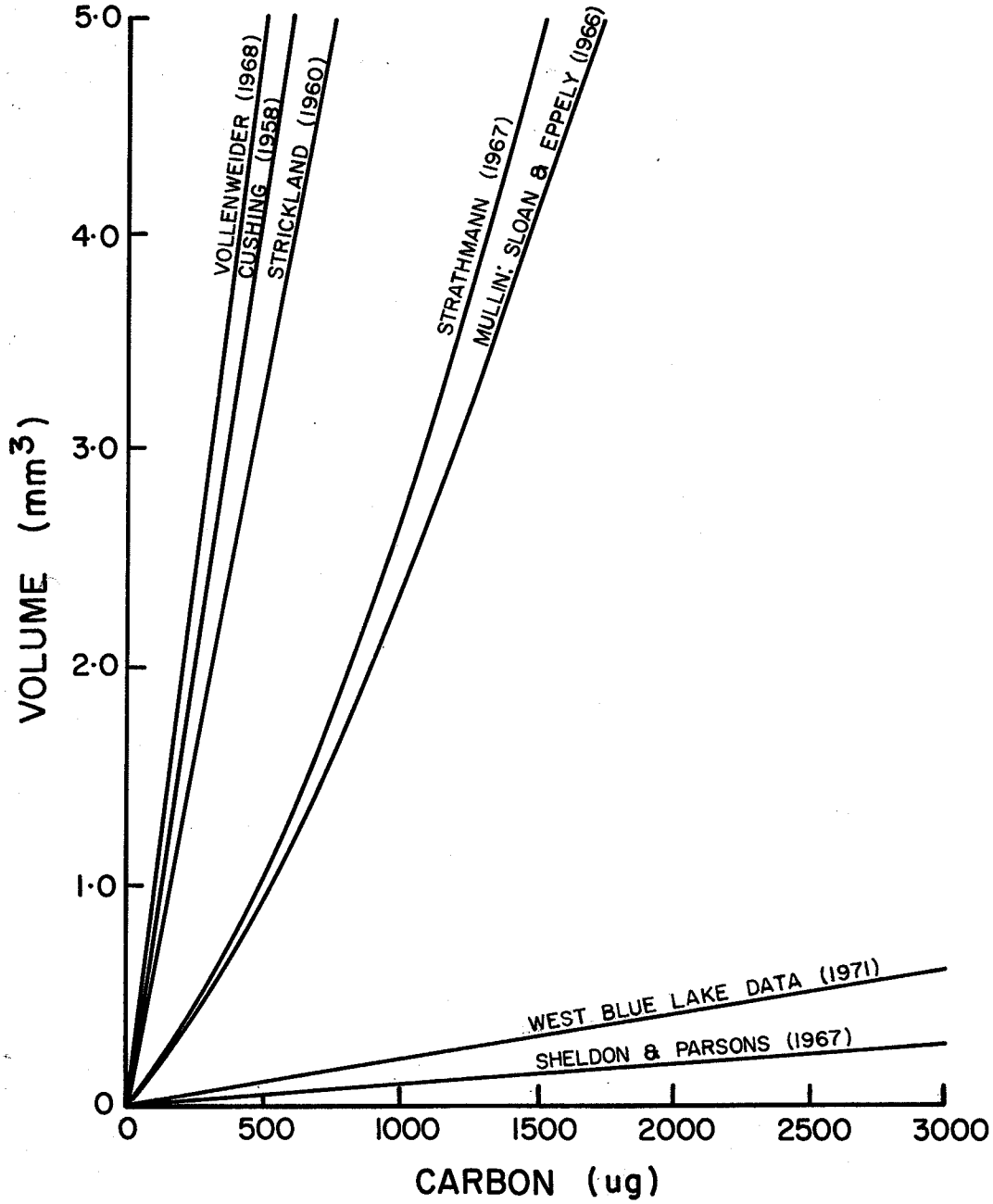


TABLE 2

Primary Productivity Values Determined by the Coulter Counter Method in 1970

Date / Depth (Meters)	July 2, 1970 mm^3/m^3	July 15, 1970 mm^3/m^3	August 12, 1970 mm^3/m^3	October 11, 1970 mm^3/m^3
0	127.32	198.94	76.99	104.65
1	52.02	55.94	-	35.04
3	28.23	114.04	136.33	182.26
5	48.34	182.37	61.54	-
7	30.47	124.94	112.55	8.34
12	- *	-	-	88.10
17	73.66	-	-	-
Integrated Productivity Value Over 17 m mm^3/m^2	596.46	1185.51	828.14	921.57

* Values for Productivity were Negative and Therefore Assumed to be Zero.

TABLE 3

Primary Productivity Values Determined by the Coulter Counter Method in 1971

Date / Depth (Meters)	May 26 1971 mm^3/m^3	June 10, 1971 mm^3/m^3	July 7, 1971 mm^3/m^3	July 21, 1971 mm^3/m^3	August 17, 1971 mm^3/m^3
0	12.50	32.05	28.15	13.18	-
1	19.11	15.86	28.15	-	59.28
3	23.78	26.96	-	11.54	-
5	23.90	12.46	12.64	26.08	33.83
7	19.58	19.92	25.96	-	21.42
12	2.51	2.85	7.67	20.51	-
17	- *	-	.99	3.77	-
Integrated Productivity Value Over 17 m mm^3/m^2	201.83	194.73	199.71	195.67	201.91

*Values for Productivity were Negative and Therefore Asssumed to be Zero.

FIG. 7 DEPTH PROFILES COMPARING PRIMARY PRODUCTIVITY MEASURED BY ^{14}C, ^{14}C (CORRECTED FOR FILTRATION ERROR) AND COULTER COUNTER METHODS

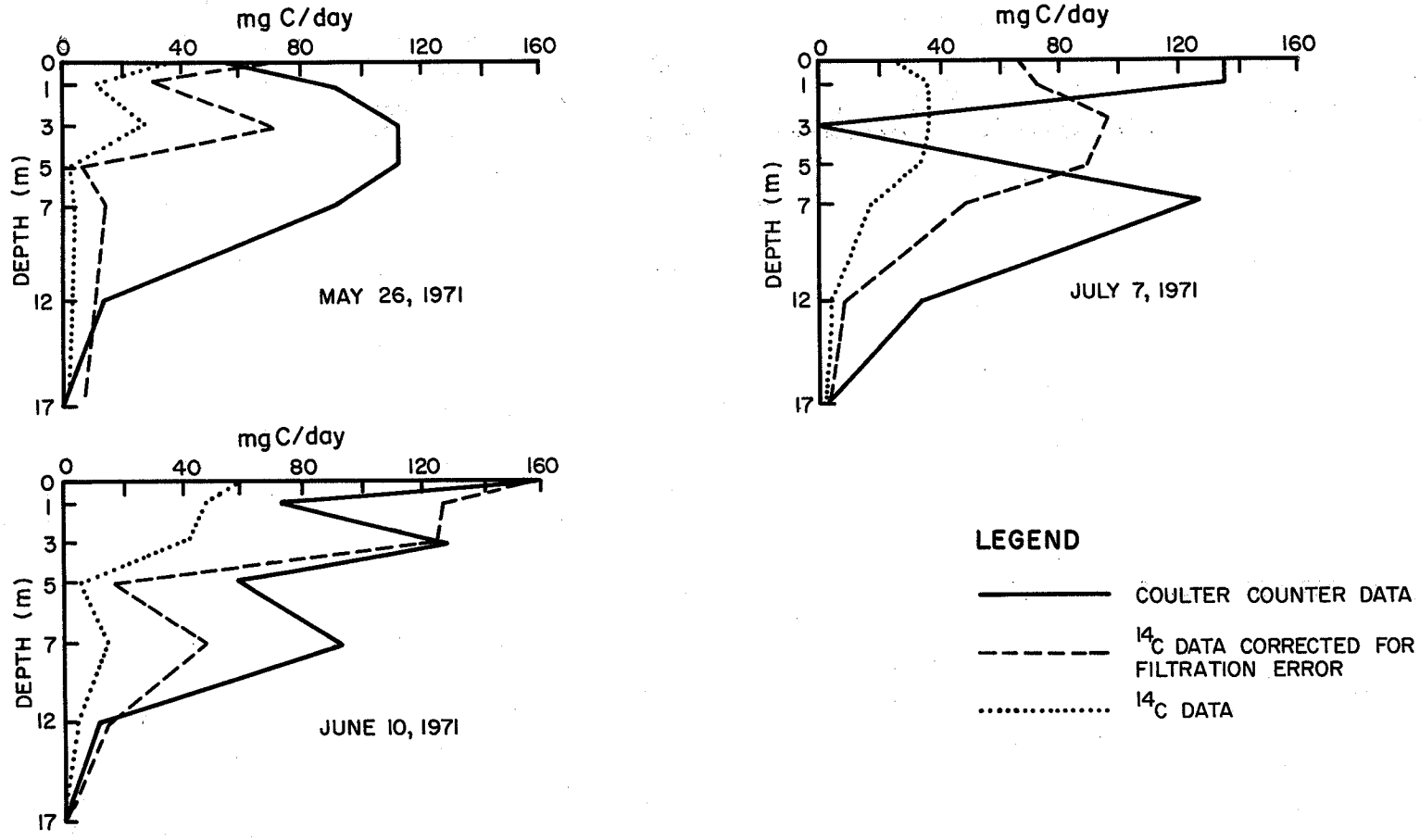
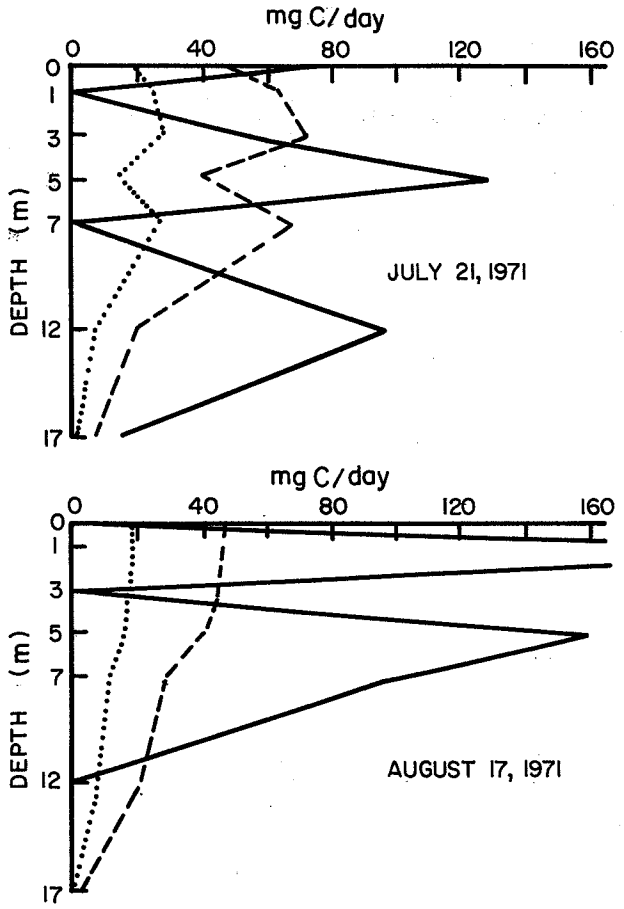


FIG. 7 DEPTH PROFILES COMPARING PRIMARY PRODUCTIVITY MEASURED BY ^{14}C, ^{14}C (CORRECTED FOR FILTRATION ERROR) AND COULTER COUNTER METHODS



LEGEND

——— COULTER COUNTER DATA

– – – – ^{14}C DATA CORRECTED FOR FILTRATION ERROR

..... ^{14}C DATA

TABLE 4

Comparison of ^{14}C values (corrected and uncorrected for filtration error) with Coulter Counter determinations in which carbon was determined from regression lines derived experimentally and from the literature relating particulate carbon and particulate volume.

	West Blue Lake Phyto-plankton	Mullin, Sloan & Eppely (1966)	Strathmann (1967)	Carbon 14	Carbon-14 Corrected for Arthur-Rigler Effect
May 27, 1971	0.960*	0.096	0.086	0.130	0.338
June 11, 1971	0.945	0.088	0.079	0.335	0.871
July 8, 1971	0.950	0.092	0.082	0.285	0.741
July 22, 1971	0.940	0.085	0.078	0.260	0.676
Aug. 19, 1971	0.970	0.097	0.088	0.159	0.413

* Units for all values are mg $C/m^2/day$

DISCUSSION

A. Phytoplankton Analysis

For this thesis work, it was decided that studies of primary production should be supported by data which assessed the population magnitude and species composition of the primary producers. Phytoplankton data was not only supportive to this and other productivity studies at West Blue Lake, but was an essential component to the development of an ecosystem concept in which energy flow was being measured.

The particle spectrum in the water column at West Blue Lake ranged from the bacteria and nannoplankton less than 1 μ in diameter to the large zooplankters often greater than 250 μ in diameter. It was practically impossible to separate this particle spectrum into distinct groups since considerable overlap occurred. In order to concentrate the phytoplankton for counting and weighing, it was necessary to pass lakewater samples through a 10 μ mesh net. Consequently, most nannoplankton and bacteriophyta of smaller diameter were lost. The importance of these groups in the phytoplankton of West Blue Lake has not yet been assessed. In order to obtain comparability between biomass (dry and ash weights) and species count data, it would have been necessary to adjust species count data according to the

volume of individual species present. For example, one Stephanodiscus cell is equal in volume to fifty Anabaena cells. Nalawejko (1966) stated that numerical records of phytoplankton abundance may result in a misrepresentation of the true importance of certain species because of the large differences in size of various planktonic algae. Lund (1964) pointed out that counts of phytoplankton could be made more valuable if data were available on the relationship between cell numbers and dry weight and volume in these species. Observations of count data, dry weight and ash weight data (Figure 4) clearly supported the statements of Nalaweijko and Lund. It was not, however, amongst the purposes of this investigation to pursue this matter further.

Only 35 species are presently recorded (Table 3) in West Blue Lake, but undoubtedly more than this actually were present. Species not observed were from the nannoplankton and bacteriophyta groups, having a diameter of less than 10 μ. It is suspected that the sedimentation method of Utermohl would be superior to the Sedgewick-Rafter method used. It was apparent that not only did the Sedgewick-Rafter method miss the small forms, but that it considerably underestimated many of the colonial blue-green algae. Although an analysis of variance indicated that the sampling method used at Station 2 was adequate for that location, it was beyond the scope of this thesis to assess population magnitude and species composition over the whole lake.

The phytoplankton displayed a very marked pattern of cyclic replacement, and some general trends were observed. Ice was present on West Blue Lake from mid-November until early May. During this time algal cell numbers and biomass fell to their lowest levels. As the ice left the lake in the spring, stratification in the water column quickly occurred before a complete spring turnover had occurred. A rapid increase of diatoms and dinoflagellates was observed. These species were replaced by green and blue-green algae as water temperature increased. In the fall as light and temperature decreased, the phytoplankton biomass and cell numbers also decreased sharply. A complete mixing of the lakewater then occurred before ice re-formed. It was impossible to speculate any further how factors such as light, temperature, nutrients and zooplankton grazing affected species composition and rate of reproduction of the phytoplankton.

It can be concluded, however, that the primary productivity at West Blue Lake must be of moderate proportion in order to develop such large phytoplankton biomass and algal cell numbers. This conclusion is further supported by the ^{14}C and Coulter Counter productivity data. It has been stressed in the literature that poor relationship exists between the standing crop and primary productivity (Strickland 1960; Ruttner 1969). It is explained that a small population (kept small by grazing or flushing) may have high rate of production, whereas, an extremely

large population may have a very low rate of production as a function of nutrient exhaustion or cell senescence. Dickman (1969) supported the contention that it is necessary to obtain standing crop values, since little can be speculated about the primary productivity unless such information is known.

Too few Coulter Counter measurements of primary production were taken to permit an assessment of how closely primary production and standing crop data were related at West Blue Lake. On the basis of the above hypothesis, it is expected that the relationship would be poor.

B. Coulter Counter and Carbon-14 Experiments

1. Carbon:Volume Relationship

The regression line relating carbon and volume ($F_{.001}(1 \& 19 \text{ df}) = 10.07^{**}$) determined experimentally at West Blue Lake differed considerably from the carbon:volume relationships determined by other workers. Cushing (1958) first reported such a carbon:volume relationship whereas Strickland (1960) and Vollenweider (1968) merely reported the same relationship, but with considerably wider limits. In Cushing's (1958) work, carbon was determined by a wet oxidation method whereas volume was determined by microscope analysis of natural populations. Mullin, Sloan and Eppley (1966) performed extensive experiments on cultured populations of algae, and found the relationship between carbon and volume to be slightly allometric. Their regression line

supported their conclusion that algal carbon per unit of algal volume decreased slightly with increasing cell volume. Strathmann (1967) claimed that the line of Mullin et al was not entirely correct. He proposed that as diatom cell size increased, each cell contained proportionately less carbon per cell volume due to the increasing size of the cell vacuole. He then gave the equation which best represented this occurrence. This line deviated considerably from the line of Mullin et al (Figure 6). Sheldon and Parsons (1967) determined the total spectrum of particulate material in seawater samples including both phytoplankton and detritus, and obtained a line very different from that of Mullin et al (1966) and Strathmann (1967).

The carbon:volume line determined from West Blue Lake data lies very close to that of Sheldon and Parsons (Figure 6). The slight deviation may simply be a function of the difference between a marine population and a freshwater one and the different species present. Several explanations may account for the significant difference between the data obtained by Sheldon and Parsons (1967) and at West Blue Lake as compared with that of Mullin et al (1966) and Strathmann (1967). Primarily, two different types of algal populations were being measured. Mullin et al (1966) and Strathmann (1967) measured the volume and carbon of cultured populations of phytoplankton only, containing no detritus, whereas Sheldon and Parsons (1967) and West Blue Lake data gave the carbon:volume relationship of

natural populations of phytoplankton containing considerable amounts of detritus.

The manner in which these carbon:volume relationships were determined by the different authors may also have been of some significance. A Coulter Counter was used to determine volume at West Blue Lake and by Sheldon and Parsons, whereas Mullin et al and Strathmann estimated volume with a Model A Coulter Counter and visually, and possibly more arbitrarily. In a phytoplankton population, if growth only were occurring, then the amount of carbon per unit volume could be expected to decrease, and the relationship proposed by Mullin et al (1966) and Strathmann (1967) would best represent the actual occurrence; but, if cell division only were occurring, then the carbon per unit volume would increase considerably and the West Blue Lake line and that of Sheldon and Parsons (1967) would then be more appropriate. However, since the actual growth and division pattern in natural populations is a combination of both of these events, then the true carbon:volume relationship must be a continually fluctuating parameter between these two sets of lines. Such a parameter may well alter with different situations, and would be expected to relate to the proportion of actively growing cells. Consequently, the integrated Coulter Counter results presented may be too high by a factor of two. This, combined with the lack of variability of integrated Coulter Counter results due to non-replication of samples, would give even closer

correlation between corrected ^{14}C values and integrated Coulter Counter results.

(2) Productivity Experiments

Since it was the intention of this research to compare productivity values obtained by the Coulter Counter and ^{14}C methods, both procedures were applied in comparable situations, and at comparable times.

In the 1970 productivity experiments, use of the Model J plotter and clumping of particles, together caused very significant error. Strickland (1960) discussed this settling and clumping of phytoplankton, and stated that it could cause distortion of photosynthesis:depth profiles in both the oxygen and ^{14}C methods. However, it was found that this error was even more serious in the Coulter Counter method in which volume changes were being measured. In 1970, some difficulty was experienced with the ^{14}C primary productivity experiments due to contamination of the ^{14}C ampoules by particulate material (Platt and Irwin, 1968). The errors in the ^{14}C and Coulter Counter methods made it impossible to attempt any comparison between these methods for 1970.

1970 productivity values as determined by the Coulter Counter (Appendix VII) displayed many erratic patterns, although in several cases predictable trends of surface inhibition were apparent. Also, expected decreases of productivity with depth were present. These 1970 values

were, however, some three times greater than those obtained in 1971 (Appendix VII). Both the erratic patterns in 1970 and differences in overall magnitude between the two years were attributed to the use of the Model J plotter in the first year of this study.

In 1971, the Model J plotter was not used. As previously explained by a slight modification of the counting method, it was possible to obtain more accurate results by use of the Model B Coulter Counter only. Considerable error still occurred due to clumping of particles, but considerably fewer erratic values were obtained, and trends in the depth profiles of productivity were more pronounced. Had the samples been more frequently replicated, less erratic results would have been obtained making the integrated productivity results considerably higher and more variable. The trend of surface light inhibition was observed on several graphs, and the decrease of productivity values with depth was distinct on all graphs. On May 26, an almost symmetrical depth profile of productivity was obtained. On other sampling dates erratic values attributed to clumping errors tend to distort these profiles. When productivity values were determined to be negative, it was assumed that an error had occurred, and a zero value was recorded in the table and on the graph. When the values for each sampling date were integrated under one square meter of lake surface, they were found to be extremely similar. It was concluded by extrapolation of the line

relating cpm's and volume filtered to the Y axis for the ten experiments conducted at West Blue Lake, that a mean filtration correction factor of 2.6 must be applied. Such a procedure is well documented in the literature (Arthur and Rigler, 1967; Schindler and Holmgren 1971). Severe limitations must be placed on such results since filtration effect is known to vary radically with filtration pressure, species composition of phytoplankton and time (Arthur and Rigler 1967; Schlinder and Holmgren 1971). Variations of filtration effect with depth have not yet been reported in the literature. Filtration effect has been definitely shown to occur, but its magnitude remains unknown; consequently all ^{14}C values were adjusted by the above filtration factor. Both corrected and uncorrected ^{14}C values were compared to Coulter Counter data.

Comparisons of the productivity-depth profiles for each sampling date (Figure 7) displayed some close correlations, but there were also numerous erratic discrepancies. ^{14}C values corrected for filtration error agreed much more closely with Coulter Counter values. This is considerably more apparent in Table 4, where all productivity values have been integrated, so as to give the amount of carbon fixed under one square meter of lake surface per day. Poor relationship existed between the uncorrected ^{14}C values and the Coulter Counter values. It had been established that the primary production in previous years was too low to account for the carbon consumed by secondary

production, (Ward, Pers. Communication). Although it cannot be concluded with certainty what correction factor should be applied to the ^{14}C data, the case for applying such a factor is strong.

The integrated Coulter Counter values are similar. This does not indicate insensitivity of the method, but was perhaps caused by clumping of particles in some bottles and errors were accentuated by lack of replication of samples.

Productivity values calculated from the West Blue Lake line were ten times larger than the Mullin, Sloan and Eppley (1966) line and eleven times larger than the Strathmann (1967) line. As previously expressed, none of the carbon:volume relationships given are expected to represent the true carbon:volume relationship for all situations. The West Blue Lake relationship possibly over-estimates the amount of carbon per unit volume. If this were true, then an even closer correlation could be expected between ^{14}C data and Coulter Counter data.

This work with the Coulter Counter has been preliminary experimentation with a new method of assessing primary production. It is made clear in this discussion that there are many unknown quantities in attempting a comparison between ^{14}C and Coulter Counter methods. These limitations include (a) the true carbon:volume relationship, (b) the magnitude of the filtration error over time and depth, (c) the lack of variability of Coulter Counter results, and (d) the clumping of particles in productivity

bottles. Consequently no more than a very approximate agreement between the two methods could be expected.

(3) An Assessment of the Coulter Counter Method as a Tool for Primary Productivity Measurement

The Coulter Counter method of determining the primary productivity is concluded to be of limited value.

The method has several strong attributes. These include ease of replication of samples with the development of the model T Coulter Counter, a further possibility of extending the Coulter Counter method to obtain an indication of phytoplankton groups primarily responsible for the production, and finally that the extent of accuracy of the ^{14}C-O_2 methods is as yet unknown, and therefore the Coulter Counter method may serve as a valuable tool in the actual elucidation of this problem.

Two major sources of error arise in the Coulter Counter method. These include firstly the clumping and settling of particles in the light and dark bottles, and secondly the establishment of a carbon:volume relationship which is suspected to be different for every situation. Also, a considerable amount of time is required to analyze both the samples and the data.

CONCLUSIONS

The conclusions arising from this thesis work were as follows:

(a) Algae smaller than 10 μ in diameter, and colonial blue-green algae of large size were omitted by the Sedgewick-Rafter method of counting phytoplankton.

(b) A similar trend of cyclic replacement occurred during the two years that the phytoplankton were monitored, with diatoms and flagellates predominating in the spring followed by a pulse of green and blue-green algae in the summer and fall.

(c) Moderately high phytoplankton biomass data is supported by moderately high primary productivity values.

(d) The carbon:volume relationship given by Mullin, Sloan and Eppley (1966) and Strathmann (1967) for pure cultures was considerably different from that given by Sheldon and Parsons (1967) or determined at West Blue Lake for mixed populations containing considerable amounts of detritus.

(e) The accessory Model J plotter to the Coulter Counter is an inappropriate instrument for the assessment of natural populations of phytoplankton.

(f) Distinctive trends of surface light inhibition and decrease of productivity values with depth existed in

productivity:depth profiles determined by the Coulter Counter.

(g) ^{14}C data, uncorrected for filtration error did not agree well with Coulter Counter values. However, after the filtration correction had been applied, considerably closer agreement was observed.

(h) Although the Coulter Counter method could never equal the speed and sensitivity of the ^{14}C method, it is felt that it could serve as a valuable check on ^{14}C methodology and experiments.

SUMMARY

1. Phytoplankton biomass (dry and ash weights) and species composition were monitored from May, 1970 to August, 1971. Standing crop values were high in the spring and summer and low in fall and winter; primary productivity values followed a similar pattern. A similar trend of cyclic replacement of phytoplankton occurred in 1970 and 1971. Reasons for this manner of replacement were discussed. Of particular note was the presence of diatoms and dinoflagellates in the spring and a large increase of blue-green algae in the summer and fall.

2. A carbon:volume relationship was determined for West Blue Lake phytoplankton. This relationship was found to differ considerably from other such relationships reported in the literature. Reasons for these discrepancies are discussed at length. The equation for the line was determined to be $Y = 45.1736 + 4410.5X$. The line had the following highly significant F value; $F_{.005}$ (1, 19 df) = 10.07**.

3. Primary productivity values determined during 1970 were presented (Appendix VII) but considered invalid due to the use of the Model J plotter (Coulter Electronics, Hialeah, Fla.). Some noticeable trends in the data are discussed.

4. Primary productivity values determined during 1971 were presented, Appendix VII, and noticeable trends in the data are fully discussed. These included surface light inhibition, and decrease of productivity values with depth.

5. Primary productivity values determined by the Coulter Counter were converted to carbon by the use of several of the carbon:volume relationships reported in this thesis (Figure 6 and Tables 2 and 3). These data were then compared with ^{14}C data (both uncorrected and corrected for filtration error),(Figure 7 and Table 4). The true carbon: volume relationship was concluded to be a continually fluctuating parameter for different situations.

6. The feasibility of using the Coulter Counter method to determine primary productivity is discussed. This method was found to be far more time consuming than the comparable ^{14}C method, but the method could serve as an accessory rather than an alternative to this conventional ^{14}C method. Advantages of the method are ease of replication of samples and possible determination of the size ranges of organisms responsible for the production. Disadvantages include clumping of particles in productivity bottles, and difficulty of obtaining a precise carbon: volume relationship.

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APPENDIX I

Screen sizes used to concentrate algae and sensitivity, volume range and aperture diameter used of the Coulter Counter for the determination of particulate volumes and carbon.

APPENDIX I

Screen Sizes Used to Concentrate Algae for the Determination of Particulate Volumes and Carbon

Approximate Species Composition	Size Range
1. Pure Culture *Chlorella vulgaris*	>10 μ
2. Pure Culture *Ankistrodesmus falcatus*	>10 μ - > 35 μ
3. Pure Culture *Navicula* sp	>10 μ
4. Pure Culture *Anabaena spiroides*	>35 μ - >102 μ >102 μ- >243 μ
5. Natural Phytoplankton (May 17, 1971) 40% *Stephanodiscus* 10% *Asterionella* 10% *Dinobryon* 5% Others 35% *Detritus*	>25 μ - >102 μ
6. Natural Phytoplankton (June 4, 1971) 40% *Stephanodiscus* 10% *Asterionella* 20% *Dinobryon* 30% *Detritus*	>25 μ - >102 μ
7. Natural Phytoplankton (June 4, 1971) 40% *Asterionella* 5% *Stephanodiscus* 5% *Ceratium* 20% *Dinobryon* 30% *Detritus*	>102 μ- >243 μ
8. Natural Phytoplankton (July 26, 1971) 35% *Stephanodiscus* 20% *Dinobryon* 10% Blue-greens 10% Others 25% *Detritus*	>25 μ - >102 μ

APPENDIX I

Sensitivity, Volume Ranges and Aperture Diameter Used of the Coulter Counter for the Determination of Particulate Volumes and Carbon

Type of Sample	Aperture	Sensitivity and Volume Range	
Chlorella vulgaris	100μ	1/32	$14.2\mu^3$ - $284\mu^3$
Ankistrodesmus falcatus	100μ	1/32	$28.4\mu^3$ - $710\mu^3$
Navicula sp	100μ	1/32	$14.2\mu^3$ - $710\mu^3$
Anabaena spiroides	100μ	1/16	$28.4\mu^3$ - $1,430\mu^3$
		1/2	$1,430\ \mu^3$ - $11,400\mu^3$
	400μ	1/32	$10,088\ \mu^3$ - $50,440\mu^3$
		1/16	$50,440\ \mu^3$ - $252,000\mu^3$
Natural Phytoplankton (May 17, 1971)	100μ	1/8	$228\ \mu^3$ - $2,850\mu^3$
		1	$2,850\ \mu^3$ - $22,800\mu^3$
Natural Phytoplankton (June 4, 1971)	100μ	1/2	$456\ \mu^3$ - $11,400\mu^3$
		2	$11,400\ \mu^3$ - $45,600\mu^3$
	400μ	1/4	$21,880\ \mu^3$ - $1,009,400\mu^3$
Natural Phytoplankton (July 26, 1971)	100μ	1/4	$456\ \mu^3$ - $5,700\mu^3$
		1	$5,700\ \mu^3$ - $22,800\mu^3$
Primary Productivity (1970)			
1. July 2, 1970	100μ	1/32	$85.2\mu^3$ - $710\mu^3$
		1/4	$710\ \mu^3$ - $5,700\mu^3$
2. July 15, 1970	100μ	1/32	$85.2\mu^3$ - $710\mu^3$
		1/4	$710\ \mu^3$ - $5,700\mu^3$
3. August 12, 1970	100μ	1/32	$85.2\mu^3$ - $710\mu^3$
		1/4	$710\ \mu^3$ - $5,700\mu^3$
4. October 11, 1970	100μ	1/32	$85.2\mu^3$ - $710\mu^3$
		1/4	$710\ \mu^3$ - $5,700\mu^3$
Primary Productivity (1971)			
1. May 26, 1971	100μ	1/32	$85.2\mu^3$ - $710\mu^3$
		1/4	$710\ \mu\mu^3$ - $5,700\mu^3$
		1	$5,700\ \mu^3$ - $22,800\mu^3$

APPENDIX I

Type of Sample	Aperture	Sensitivity	and Volume Range
2. June 10, 1971	100μ	1/32	$85.2\mu^3$ - $710\mu^3$
		1/4	$710\ \mu^3$ - $5,700\mu^3$
		1	$5,700\ \mu^3$ - $22,800\mu^3$
3. July 7, 1971	100μ	1/32	$85.2\mu^3$ - $710\mu^3$
		1/4	$710\ \mu^3$ - $5,700\mu^3$
		1	$5,700\ \mu^3$ - $22,800\mu^3$
4. July 21, 1971	100μ	1/32	$85.2\mu^3$ - $710\mu^3$
		1/4	$710\ \mu^3$ - $5,700\mu^3$
		1	$5,700\ \mu^3$ - $22,800\mu^3$
5. August 17, 1971	100μ	1/32	$85.2\mu^3$ - $710\mu^3$
		1/4	$710\ \mu^3$ - $5,700\mu^3$
		1	$5,700\ \mu^3$ - $22,800\mu^3$

APPENDIX II

Relative abundance of each phytoplankton species from May 1970 to August 1971.

APPENDIX II

Relative Abundance of Each Phytoplankton Species From May, 1970 - August, 1971

	May 28 1970	June 10 1970	June 19 1970	June 25 1970	July 1 1970
Achnanthes sp.	0	0	0	0	0
Amphora sp.	0	0	0	0	0
Anabaena spiroides	0	3	0	7	8
Ankistrodesmus falcatus	0	0	0	3	2
Aphanizomenon flos, aquae	0	1	2	0	7
Asterionella formosa	9	9	9	7	5
Botryococcus braunii	0	0	2	0	0
Ceratium hirundinella	0	0	0	1	2
Crucigenia rectangularis	1	0	1	3	6
Cyclotella sp.	0	0	0	0	0
Cymbella sp.	1	1	0	1	0
Dinobryon sertularia	3	8	8	6	4
Eunotia sp.	0	0	0	0	0
Fragilaria capucina	1	2	0	0	0
Fragilaria crotonensis	3	1	2	0	0
Gloeotrichia sp.	3	0	0	0	0
Mallomonas sp.	0	1	0	0	0
Merismopedia sp.	0	0	0	0	0
Navicula sp.	2	2	2	2	3
Nitzschia sp.	0	0	0	0	0
Oocystis elliptica	0	2	1	2	6
Oscillatoria sp.	0	0	0	3	0
Pediastrum sp.	1	0	1	0	0
Peridinium sp.	2	1	1	0	0
Phormidium sp.	0	0	0	0	0
Pinnularia sp.	1	0	0	0	0
Pleurosigma sp.	1	1	0	0	0
Quadrigula chodatii	0	0	1	4	3
Rhizosolenia sp.	0	0	1	1	2
Scenedesmus sp.	1	0	0	0	0
Staurastrum sp.	1	0	0	3	2
Stephanodiscus niagarae	5	5	6	7	7
Synedra incurva	3	1	1	2	2
Synedra ulna	2	1	1	1	2
Tabellaria sp.	0	0	0	0	0

Legend:
0 - absent
1 - > 200/1
2 - >1000/1
3 - >5000/1
4 - >10,000/1
5 - > 20,000/1
6 - > 50,000/1
7 - > 100,000/1
8 - > 200,000/1
9 - > 200,000/1

(continued)

Relative Abundance of Each Phytoplankton Species
From May, 1970 - August, 1971

	July 8 1970	July 15 1970	July 22 1970	July 29 1970	Aug. 5 1970	Aug. 12 1970	Aug. 19 1970
Achnanthes sp.	0	0	0	0	0	0	0
Amphora sp.	0	0	0	0	0	0	0
Anabaena spiroides	7	6	8	8	8	8	8
Ankistrodesmus falcatus	2	4	3	2	0	3	2
Aphanizomenon flos. aquae	6	2	7	8	8	8	9
Asterionella formosa	3	3	4	4	4	4	4
Botryococcus braunii	6	4	4	5	6	6	6
Ceratium hirundinella	2	2	2	3	2	1	1
Crucigenia rectangularis	5	3	5	3	5	0	2
Cyclotella sp.	0	0	0	0	0	1	0
Cymbella sp.	0	0	0	0	0	0	0
Dinobryon sertularia	4	4	4	0	3	6	0
Eunotia sp.	0	0	0	0	0	0	0
Fragilaria capucina	0	0	0	0	0	0	0
Fragilaria crotonensis	2	0	0	0	0	0	0
Gloeotrichia sp.	0	0	0	0	0	0	0
Mallomonas sp.	0	0	0	1	3	0	0
Merismopedia sp.	0	0	0	0	0	0	0
Navicula sp.	2	1	1	2	0	2	0
Nitzschia sp.	0	0	0	0	0	0	0
Oocystis elliptica	4	5	4	4	4	4	3
Oscillatoria sp.	0	0	0	0	0	0	0
Pediastrum sp.	0	0	1	1	0	1	0
Peridinium sp.	0	0	0	0	0	0	0
Phormidium sp.	0	0	0	0	0	0	0
Pinnularia sp.	0	0	0	0	0	0	0
Pleurosigma sp.	0	0	0	1	0	1	0
Quadrigula chodatii	3	3	2	2	3	2	0
Rhizosolenia sp.	2	0	0	0	0	0	0
Scenedesmus sp.	0	0	0	0	0	0	0
Staurastrum sp.	0	0	0	0	0	0	0
Stephanodiscus niagarae	7	6	7	6	6	6	6
Synedra incurva	2	2	2	0	0	0	0
Synedra ulna	1	2	0	1	1	2	0
Tabellaria sp.	0	0	0	0	2	0	0

Legend:
0 - absent
1 - >200/1
2 - >1000/1
3 - >5000/1
4 - >10,000/1
5 ->20,000/1
6 ->50,000/1
7 ->100,000/1
8 ->200,000/1
9 ->200,000/1

(continued)

Relative Abundance of Each Phytoplankton Species
From May, 1970 - August, 1971

	Aug. 26 1970	Sept. 27 1970	Oct. 11 1970	Nov. 1 1970	Nov. 15 1970	Dec. 14 1970	Jan. 16 1971
Achnanthes sp.	0	0	0	0	0	0	0
Amphora sp.	0	0	1	0	0	0	0
Anabaena spiroides	8	6	4	3	0	0	0
Ankistrodesmus falcatus	2	0	1	1	0	1	0
Aphanizomenon flos. aquae	8	8	6	5	0	0	0
Asterionella formosa	3	4	4	6	4	2	1
Botryococcus braunii	6	4	3	0	0	0	0
Ceratium hirundinella	2	2	0	0	0	0	0
Crucigenia rectangularis	3	0	0	0	3	2	0
Cyclotella sp.	0	0	0	0	1	0	0
Cymbella sp.	0	0	0	0	0	0	0
Dinobryon sertularia	3	3	3	0	3	0	2
Eunotia sp.	0	0	0	0	0	0	0
Fragilaria capucina	0	0	0	0	0	0	0
Fragilaria crotonensis	0	0	1	2	0	0	0
Gloeotrichia sp.	0	0	0	0	0	0	0
Mallomonas sp.	0	0	0	0	1	0	0
Merismopedia sp.	0	0	0	0	0	0	0
Navicula sp.	1	1	1	0	2	1	1
Nitzschia sp.	0	0	1	0	0	0	0
Oocystis elliptica	0	0	1	0	0	0	0
Oscillatoria sp.	0	0	0	0	0	5	0
Pediastrum sp.	0	0	0	0	0	0	0
Peridinium sp.	0	0	1	0	0	0	0
Phormidium sp.	0	0	0	0	5	0	5
Pinnularia sp.	0	0	0	0	0	0	0
Pleurosigma sp.	1	0	0	0	1	0	0
Quadrigula chodatii	0	0	0	0	0	0	0
Rhizosolenia sp.	0	0	0	0	0	0	0
Scenedesmus sp.	0	0	0	0	0	0	0
Staurastrum sp.	0	0	1	0	0	0	0
Stephanodiscus niagarae	5	3	4	5	4	3	3
Synedra incurva	0	0	0	3	2	1	0
Synedra ulna	0	0	0	1	0	0	0
Tabellaria sp.	0	2	0	0	0	0	0

Legend:
0 - absent
1 - >200/1
2 - >1000/1
3 - >5000/1
4 - >10.000/1
5- >20,000/1
6- >50,000/1
7- >100,000/1
8- >200,000/1
9- >200.000/1

(continued)

Relative Abundance of Each Phytoplankton Species
From May, 1970 - August, 1971

	Feb. 13 1971	Mar. 13 1971	Apr. 17 1971	May 10 1971	May 17 1971	May 23 1971	May 31 1971	June 7 1971
Achnanthes sp.	0	0	0	0	1	0	0	0
Amphora sp.	0	0	0	0	0	0	0	0
Anabaena spiroides	0	0	4	0	3	3	4	8
Ankistrodesmus falcatus	0	0	0	0	3	0	0	1
Aphanizomenon flos. aquae	0	0	0	4	0	0	4	6
Asterionella formosa	0	0	0	6	7	8	8	6
Botryococcus braunii	0	0	0	0	0	0	5	5
Ceratium hirundinella	0	0	0	0	0	1	2	2
Crucigenia rectangularis	0	0	0	0	2	3	0	0
Cyclotella sp.	0	0	0	1	0	0	0	0
Cymbella sp.	0	0	0	0	0	0	0	0
Dinobryon sertularia	0	0	0	6	8	9	8	6
Eunotia sp.	0	0	0	1	0	0	0	0
Fragilaria capucina	0	0	0	0	0	0	0	0
Fragilaria crotonensis	0	2	1	3	4	3	2	3
Gloeotrichia sp.	0	0	0	0	0	0	0	0
Mallomonas sp.	0	0	0	0	1	0	0	0
Merismopedia sp.	0	0	0	0	0	0	4	0
Navicula sp.	0	0	0	2	3	3	2	3
Nitzschia sp.	0	0	0	0	0	0	0	0
Oocystis elliptica	0	0	0	4	0	0	4	0
Oscillatoria sp.	2	0	0	0	0	0	0	0
Pediastrum sp.	0	0	0	0	0	0	0	0
Peridinium sp.	0	0	0	1	3	1	0	0
Phormidium sp.	0	0	0	4	8	0	0	0
Pinnularia sp.	0	0	0	0	0	0	0	0
Pleurosigma sp.	0	0	0	0	1	0	0	0
Quadrigula chodatii	0	0	0	2	0	2	3	4
Rhizosolenia sp.	0	0	0	1	2	1	0	0
Scenedesmus sp.	0	0	0	0	0	0	0	0
Staurastrum sp.	0	0	0	0	0	0	0	0
Stephanodiscus niagarae	4	6	5	7	7	7	8	8
Synedra incurva	0	0	0	2	4	3	3	0
Synedra ulna	0	0	0	2	1	2	0	0
Tabellaria sp.	0	0	0	0	0	0	0	0

Legend:
0 - absent
1 - >200/1
2 - >1000/1
3 - >5000/1
4 - >10,000/1
5 - > 20,000/1
6 - > 50,000/1
7 - >100,000/1
8 - >200,000/1
9 - >200,000/1

(continued)

Relative Abundance of Each Phytoplankton Species
From May, 1970-August, 1971

	June 22 1971	June 28 1971	July 6 1971	July 12 1971	July 19 1971	Aug. 2 1971	Aug. 16 1971	Aug. 30 1971
Achnanthes sp.	0	0	0	0	0	0	0	0
Amphora sp.	0	0	0	0	0	0	0	0
Anabaena spiroides	5	7	6	8	8	8	8	6
Ankistrodesmus falcatus	0	0	0	4	1	0	0	0
Aphanizomenon flos. aquae	6	6	9	9	9	9	9	9
Asterionella formosa	3	3	3	3	2	3	6	6
Botryococcus braunii	7	8	6	7	6	6	3	3
Ceratium hirundinella	2	1	2	2	2	2	2	2
Crucigenia rectangularis	4	0	0	0	0	0	0	0
Cyclotella sp.	0	0	0	0	0	0	0	0
Cymbella sp.	0	0	0	0	0	0	0	0
Dinobryon sertularia	7	7	8	6	6	3	4	5
Eunotia sp.	0	0	0	0	0	0	0	0
Fragilaria capucina	0	0	0	0	0	0	0	0
Fragilaria crotonensis	0	0	0	0	0	0	0	0
Gloeotrichia sp.	0	0	0	0	6	0	0	0
Mallomonas sp.	0	0	0	0	0	0	0	1
Merismopedia sp.	0	0	0	0	0	0	0	0
Navicula sp.	3	3	4	3	2	1	1	0
Nitzschia sp.	0	0	0	0	0	0	0	0
Oocystis elliptica	3	0	0	0	0	3	3	1
Oscillatoria sp.	0	0	0	0	0	0	0	0
Pediastrum sp.	0	0	0	0	0	0	0	0
Peridinium sp.	0	0	0	0	0	0	0	0
Phormidium sp.	0	0	0	0	0	0	0	0
Pinnularia sp.	0	0	0	0	0	0	0	0
Pleurosigma sp.	0	0	0	0	1	0	0	0
Quadrigula chodatii	0	0	1	2	2	0	0	0
Rhizosolenia sp.	0	0	0	0	0	0	0	0
Scenedesmus sp.	0	0	0	0	0	0	0	0
Staurastrum sp.	0	0	0	0	0	0	0	0
Stephanodiscus niagarae	6	6	6	6	6	5	5	4
Synedra incurva	0	2	2	3	2	0	0	1
Synedra ulna	0	0	1	1	0	0	0	0
Tabellaria sp.	2	0	0	2	0	0	0	0

Legend:
0 - absent
1 - > 200/1
2 - >1000/1
3 - >5000/1
4 - >10,000/1
5 - > 20,000/1
6 - > 50,000/1
7 - >100,000/1
8 - >200,000/1
9 - >200,000/1

APPENDIX III

Statistical evaluation of phytoplankton counting technique.

APPENDIX III

Set I

Cell Type \ Strip	1	2	3	4	5
Unicells	23	24	20	22	21
Colonial Blue Greens	3681	3413	2309	1505	2610
Total (all)	3757	3462	2429	1560	2675

Unicells: $o^2 = 2.4998$

Blue-greens $o^2 = 763,876$

Totals $o^2 = 760,384$

Set II

Cell Type \ Strip	1	2	3	4	5
Unicells	21	16	23	18	21
Colonial Blue-Greens	2824	2248	913	4323	2237
Total (all cells)	3003	2278	1029	4350	2352

Unicells: $o^2 = 7.6995$

Blue-greens: $o^2 = 1,517,824$

Totals: $o^2 = 1,464,100$

Unicells: $F = \frac{7.6995}{2.4998} = 3.0800^*$

Blue-greens: $F = \frac{1,517,824}{763,867} = 1.9870^*$

Total cells: $F = \frac{1,464,100}{760,384} = 1.9254^*$

*Significant at the 5% level.

APPENDIX IV

Seasonal species count data, dry weight and ash weight determinations of phytoplankton.

APPENDIX IV

Depth	Date	May 28, 1970	June 10, 1970	June 19, 1970	June 25, 1970	July 1, 1970
0 m	cells/m^3	2.47×10^8	4.17×10^8	1.43×10^8	1.83×10^8	2.33×10^8
	dry wt gm/m^3	.356	.525	.431	.650	.925
	ash wt gm/m^3	.231	.288	.238	.306	.419
3 m	cells/m^3	3.44×10^8	3.05×10^8	2.29×10^8	1.92×10^8	3.39×10^8
	dry wt gm/m^3	.538	1.038	.469	.569	.819
	ash wt gm/m^3	.313	.481	.250	.288	.369
7 m	cells/m^3	1.99×10^8	3.02×10^8	3.40×10^8	1.98×10^8	1.98×10^8
	dry wt gm/m^3	.469	.619	.581	.631	.725
	ash wt gm/m^3	.313	.344	.288	.275	.331
12m	cells/m^3	1.60×10^8	1.19×10^8	1.06×10^8	1.39×10^8	1.52×10^8
	dry wt gm/m^3	.431	.394	.400	.619	.550
	ash wt gm/m^3	.194	.188	.244	.238	.275
17m	cells/m^3	1.62×10^8	$.55 \times 10^8$	$.68 \times 10^8$	$.97 \times 10^8$	1.46×10^8
	dry wt gm/m^3	.476	.313	.288	.713	.488
	ash wt gm/m^3	.206	.144	.169	.269	.244
20m	cells/m^3	1.81×10^8	$.54 \times 10^8$	$.52 \times 10^8$	$.94 \times 10^8$	$.90 \times 10^8$
	dry wt gm/m^3	.544	.181	.331	.381	.406
	ash wt gm/m^3	.269	.081	.200	.163	.225
25m	cells/m^3	$.44 \times 10^8$	$.63 \times 10^8$	$.48 \times 10^8$	$.35 \times 10^8$	$.31 \times 10^8$
	dry wt gm/m^3	.319	.281	.269	.388	.369
	ash wt gm/m^3	.144	.138	.194	.125	.206
30m	cells/m^3	$.58 \times 10^8$	$.62 \times 10^8$	$.38 \times 10^8$	$.68 \times 10^8$	$.44 \times 10^8$
	dry wt gm/m^3	.306	.431	.263	.381	.788
	ash wt gm/m^3	.088	.263	.169	.181	.375
Integrated Data /m^2						
	cells/m^2	5.21×10^9	4.85×10^9	4.02×10^9	3.88×10^9	4.86×10^9
	grams/m^2	13.74	14.45	11.96	16.81	19.44
	grams/m^2	6.90	7.38	6.98	7.14	9.39

APPENDIX IV

Depth	Date	July 8, 1970	July 15, 1970	July 22, 1970	July 29, 1970	Aug. 5, 1970
0 m	cells/m^3	1.97×10^8	$.50 \times 10^8$	1.39×10^8	1.58×10^8	1.58×10^8
	dry wt gm/m^3	.781	.494	.475	.363	.544
	ash wt gm/m^3	.406	.300	.281	.206	.325
3 m	cells/m^3	2.14×10^8	$.91 \times 10^8$	1.26×10^8	2.18×10^8	1.33×10^8
	dry wt gm/m^3	.906	.563	.569	.556	.513
	ash wt gm/m^3	.481	.319	.338	.313	.306
7 m	cells/m^3	1.87×10^8	1.07×10^8	3.60×10^8	2.79×10^8	2.97×10^8
	dry wt gm/m^3	.575	.544	.819	.638	.531
	ash wt gm/m^3	.281	.294	.463	.381	.313
12m	cells/m^3	1.95×10^8	$.54 \times 10^8$	1.78×10^8	2.78×10^8	2.48×10^8
	dry wt gm/m^3	.831	.313	.569	.575	.650
	ash wt gm/m^3	.413	.156	.319	.306	.413
17m	cells/m^3	$.68 \times 10^8$	$.54 \times 10^8$	1.38×10^8	1.07×10^8	2.01×10^8
	dry wt gm/m^3	.413	.363	.594	.319	.531
	ash wt gm/m^3	.231	.200	.356	.181	.325
20m	cells/m^3	$.52 \times 10^8$	$.20 \times 10^8$	$.74 \times 10^8$	$.82 \times 10^8$	$.63 \times 10^8$
	dry wt gm/m^3	.413	.356	.350	.400	.325
	ash wt gm/m^3	.194	.181	.175	.213	.185
25m	cells/m^3	$.35 \times 10^8$	$.12 \times 10^8$	$.33 \times 10^8$	$.45 \times 10^8$	$.52 \times 10^8$
	dry wt gm/m^3	.569	.269	.325	.375	.350
	ash wt gm/m^3	.300	.138	.181	.175	.169
30m	cells/m^3	$.21 \times 10^8$	$.26 \times 10^8$	$.22 \times 10^8$	$.13 \times 10^8$	$.26 \times 10^8$
	dry wt gm/m^3	.338	.350	.319	.300	.456
	ash wt gm/m^3	.119	.188	.175	.138	.206
Integrated Data /m^2						
	cells/m^2	3.68×10^9	1.65×10^9	4.34×10^9	4.74×10^9	4.77×10^9
	grams/m^2	18.96	12.59	16.14	14.33	15.48
	grams/m^2	9.47	6.79	9.16	7.76	8.92

APPENDIX IV

Depth	Date	Aug. 12, 1970	Aug. 19, 1970	Aug. 25, 1970	Sept. 27, 1970	Oct. 11, 1970
0 m	cells/m^3	1.68×10^8	1.77×10^8	2.50×10^8	1.12×10^8	$.24 \times 10^8$
	dry wt gm/m^3	.250	.294	.281	.231	.219
	ash wt gm/m^3	.194	.194	.213	.206	.175
3 m	cells/m^3	1.57×10^8	1.49×10^8	1.59×10^8	$.93 \times 10^8$	$.38 \times 10^8$
	dry wt gm/m^3	.313	.331	.269	.231	.250
	ash wt gm/m^3	.225	.206	.206	.206	.175
7 m	cells/m^3	2.55×10^8	2.36×10^8	3.05×10^8	1.73×10^8	$.60 \times 10^8$
	dry wt gm/m^3	.481	.338	.450	.231	.219
	ash wt gm/m^3	.331	.219	.300	.200	.119
12m	cells/m^3	3.33×10^8	3.73×10^8	2.11×10^8	1.46×10^8	$.37 \times 10^8$
	dry wt gm/m^3	.413	.431	.388	.306	.238
	ash wt gm/m^3	.281	.281	.250	.244	.131
17m	cells/m^3	2.28×10^8	2.85×10^8	1.19×10^8	1.11×10^8	$.15 \times 10^8$
	dry wt gm/m^3	.469	.438	.425	.344	.206
	ash wt gm/m^3	.281	.275	.263	.244	.131
20m	cells/m^3	$.98 \times 10^8$	2.23×10^8	1.13×10^8	$.44 \times 10^8$	$.14 \times 10^8$
	dry wt gm/m^3	.394	.438	.469	.288	.213
	ash wt gm/m^3	.244	.251	.269	.175	.150
25m	cells/m^3	$.71 \times 10^8$	$.70 \times 10^8$	$.85 \times 10^8$	$.32 \times 10^8$	$.08 \times 10^8$
	dry wt gm/m^3	.356	.306	.331	.375	.300
	ash wt gm/m^3	.188	.175	.194	.200	.169
30m	cells/m^3	$.30 \times 10^8$	$.65 \times 10^8$	$.50 \times 10^8$	$.14 \times 10^8$	$.006 \times 10^8$
	dry wt gm/m^3	.343	.381	.413	.419	.263
	ash wt gm/m^3	.169	.219	.219	.207	.188
Integrated Data /m^2						
	cells/m^2	5.46×10^9	6.37×10^9	5.04×10^9	2.88×10^9	$.79 \times 10^9$
	grams/m^2	12.46	11.99	12.35	9.93	7.70
	grams/m^2	7.78	7.36	7.71	6.72	4.88

APPENDIX IV

Depth		Date Nov. 1, 1970	Nov. 15, 1970	Dec. 14, 1970	Jan. 16, 1971	Feb. 13, 1971
0 m	cells/m^3	$.28 \times 10^8$	$.23 \times 10^8$	$.24 \times 10^8$	$.05 \times 10^8$	$.05 \times 10^8$
	dry wt gm/m^3	.231	.244	.150	.094	.100
	ash wt gm/m^3	.131	.181	.125	.075	.063
3 m	cells/m^3	$.40 \times 10^8$	$.18 \times 10^8$	$.04 \times 10^8$	$.13 \times 10^8$	$.03 \times 10^8$
	dry wt gm/m^3	.194	.194	.219	.138	.075
	ash wt gm/m^3	.131	.150	.181	.100	.056
7 m	cells/m^3	$.39 \times 10^8$	$.14 \times 10^8$	$.03 \times 10^8$	$.04 \times 10^8$	$.02 \times 10^8$
	dry wt gm/m^3	.281	.188	.244	.088	.125
	ash wt gm/m^3	.144	.150	.188	.063	.075
12m	cells/m^3	$.40 \times 10^8$	$.12 \times 10^8$	$.04 \times 10^8$	$.04 \times 10^8$	$.03 \times 10^8$
	dry wt gm/m^3	.213	.225	.181	.081	.169
	ash wt gm/m^3	.081	.106	.131	.063	.113
17m	cells/m^3	$.49 \times 10^8$	$.08 \times 10^8$	$.05 \times 10^8$	$.02 \times 10^8$	$.02 \times 10^8$
	dry wt gm/m^3	.244	.244	.144	.100	.106
	ash wt gm/m^3	.119	.188	.100	.075	.063
20m	cells/m^3	$.34 \times 10^8$	$.10 \times 10^8$	$.44 \times 10^8$	$.02 \times 10^8$	$.02 \times 10^8$
	dry wt gm/m^3	.300	.356	.163	.150	.144
	ash wt gm/m^3	.075	.238	.100	.125	.081
25m	cells/m^3	$.35 \times 10^8$	$.20 \times 10^8$	$.11 \times 10^8$	$.04 \times 10^8$	$.02 \times 10^8$
	dry wt gm/m^3	.350	.681	.281	.188	.344
	ash wt gm/m^3	.144	.369	.156	.125	.188
30m	cells/m^3	$.04 \times 10^8$	$.13 \times 10^8$	$.08 \times 10^8$	$.01 \times 10^8$	$.04 \times 10^8$
	dry wt gm/m^3	.550	.644	.175	.250	.450
	ash wt gm/m^3	.213	.281	.106	.163	.188
Integrated Data /m^2						
	cells/m^2	1.10×10^9	$.45 \times 10^9$	$.22 \times 10^9$	$.13 \times 10^9$	$.81 \times 10^9$
	grams/m^2	9.56	11.49	6.39	4.39	6.39
	grams/m^2	4.11	6.73	4.37	3.11	3.49

APPENDIX IV

Depth	Date	Mar. 13, 1971	Apr. 17, 1971	May 10, 1971	May 17, 1971	May 23, 1971
0 m	cells/m^3	$.23 \times 10^8$	$.08 \times 10^8$	1.31×10^8	2.58×10^8	3.38×10^8
	dry wt gm/m^3	.225	.106	.438	.463	.513
	ash wt gm/m^3	.175	.094	.250	.294	.288
3 m	cells/m^3	$.11 \times 10^8$	$.15 \times 10^8$	1.20×10^8	2.59×10^8	3.77×10^8
	dry wt gm/m^3	.119	.081	.594	.563	.569
	ash wt gm/m^3	.100	.063	.338	.300	.338
7 m	cells/m^3	$.01 \times 10^8$	$.18 \times 10^8$	1.06×10^8	1.97×10^8	4.17×10^8
	dry wt gm/m^3	.875	.131	.513	.625	.719
	ash wt gm/m^3	.056	.113	.294	.344	.394
12m	cells/m^3	$.009 \times 10^8$	$.14 \times 10^8$	1.02×10^8	1.44×10^8	1.30×10^8
	dry wt gm/m^3	.119	.150	.450	.656	.463
	ash wt gm/m^3	.050	.125	.238	.381	.219
17m	cells/m^3	$.01 \times 10^8$	$.07 \times 10^8$	1.09×10^8	1.83×10^8	1.09×10^8
	dry wt gm/m^3	.094	.119	.638	.619	.588
	ash wt gm/m^3	.038	.063	.350	.306	.200
20m	cells/m^3	$.01 \times 10^8$	$.05 \times 10^8$	$.80 \times 10^8$	$.48 \times 10^8$	$.62 \times 10^8$
	dry wt gm/m^3	.081	.113	.406	.563	.538
	ash wt gm/m^3	.038	.075	.206	.200	.244
25m	cells/m^3	$.01 \times 10^8$	$.05 \times 10^8$	2.21×10^8	$.80 \times 10^8$	$.72 \times 10^8$
	dry wt gm/m^3	.144	.112	.713	.531	.631
	ash wt gm/m^3	.081	.075	.313	.175	.275
30m	cells/m^3	$.02 \times 10^8$	$.05 \times 10^8$	$.97 \times 10^8$	1.97×10^8	$.62 \times 10^8$
	dry wt gm/m^3	.150	.112	.738	.706	.494
	ash wt gm/m^3	.087	.075	.344	.287	.188
Integrated Data /m^2						
	cells/m^2	$.11 \times 10^9$	$.31 \times 10^9$	3.92×10^9	5.15×10^9	5.83×10^9
	grams/m^2	3.89	3.87	18.21	18.64	18.20
	grams/m^2	2.36	2.78	9.38	9.14	8.52

APPENDIX IV

Depth	Date	May 31, 1971	June 7, 1971	June 22, 1971	June 28, 1971	July 6, 1971
0 m	cells/m^3	2.96×10^8	2.18×10^8	1.33×10^8	1.53×10^8	2.03×10^8
	dry wt gm/m^3	.875	1.060	.419	.656	.281
	ash wt gm/m^3	.475	.444	.300	.294	.213
3 m	cells/m^3	2.58×10^8	1.57×10^8	2.12×10^8	2.25×10^8	2.58×10^8
	dry wt gm/m^3	.875	1.044	.444	.488	.594
	ash wt gm/m^3	.394	.444	.294	.263	.375
7 m	cells/m^3	4.05×10^8	3.21×10^8	2.24×10^8	2.13×10^8	2.21×10^8
	dry wt gm/m^3	1.080	.956	.538	.475	.788
	ash wt gm/m^3	.513	.431	.294	.375	.425
12m	cells/m^3	2.65×10^8	1.50×10^8	1.30×10^8	1.03×10^8	1.51×10^8
	dry wt gm/m^3	.725	.644	.488	.369	.594
	ash wt gm/m^3	.356	.256	.238	.206	.313
17m	cells/m^3	$.98 \times 10^8$	$.88 \times 10^8$	$.96 \times 10^8$	$.79 \times 10^8$	5.13×10^8
	dry wt gm/m^3	.644	.438	.456	.394	.638
	ash wt gm/m^3	.313	.188	.219	.206	.300
20m	cells/m^3	1.02×10^8	$.59 \times 10^8$	$.68 \times 10^8$	1.50×10^8	$.54 \times 10^8$
	dry wt gm/m^3	.594	.369	.388	.437	.413
	ash wt gm/m^3	.288	.150	.212	.269	.288
25m	cells/m^3	$.70 \times 10^8$	$.36 \times 10^8$	$.47 \times 10^8$	$.36 \times 10^8$	$.18 \times 10^8$
	dry wt gm/m^3	.613	.394	.500	.294	.369
	ash wt gm/m^3	.244	.169	.256	.131	.194
30m	cells/m^3	$.44 \times 10^8$	$.21 \times 10^8$	$.52 \times 10^8$	$.22 \times 10^8$	$.30 \times 10^8$
	dry wt gm/m^3	.538	.394	.588	.231	.325
	ash wt gm/m^3	.275	.169	.263	.100	.163
Integrated Data /m^2						
	cells/m^2	5.97×10^9	4404×10^9	3.76×10^9	3.75×10^9	5.55×10^9
	grams/m^2	23.45	20.04	15.46	12.73	16.50
	grams/m^2	11.17	8.51	8.20	7.18	9.08

APPENDIX IV

Depth		Date July 12, 1971	July 19, 1971	Aug. 2, 1971	Aug. 16, 1971	Aug. 30, 1971
0 m	cells/m^3	3.31×10^8	2.74×10^8	5.54×10^8	4.25×10^8	5.48×10^8
	dry wt gm/m^3	.238	.232	.244	.194	.313
	ash wt gm/m^3	.206	.200	.213	.113	.194
3 m	cells/m^3	3.25×10^8	3.73×10^8	2.99×10^8	1.18×10^8	$.64 \times 10^8$
	dry wt gm/m^3	.306	.281	.231	.188	.331
	ash wt gm/m^3	.231	.231	.200	.113	.200
7 m	cells/m^3	3.18×10^8	3.20×10^8	5.00×10^8	1.41×10^8	$.72 \times 10^8$
	dry wt gm/m^3	.294	.306	.275	.225	.350
	ash wt gm/m^3	.206	.243	.213	.138	.219
12m	cells/m^3	4.17×10^8	3.78×10^8	5.39×10^8	8.98×10^8	2.41×10^8
	dry wt gm/m^3	.344	.338	.188	.319	.381
	ash wt gm/m^3	.238	.288	.125	.219	.250
17m	cells/m^3	$.65 \times 10^8$	2.98×10^8	3.25×10^8	$.46 \times 10^8$	$.77 \times 10^8$
	dry wt gm/m^3	.288	.438	.250	.300	.331
	ash wt gm/m^3	.194	.344	.169	.175	.231
20m	cells/m^3	2.40×10^8	$.33 \times 10^8$	3.20×10^8	4.21×10^8	3.19×10^8
	dry wt gm/m^3	.375	.438	.319	.275	.313
	ash wt gm/m^3	.231	.331	.194	.175	.206
25m	cells/m^3	$.78 \times 10^8$	$.81 \times 10^8$	3.35×10^8	1.50×10^8	$.36 \times 10^8$
	dry wt gm/m^3	.263	.381	.344	.350	.381
	ash wt gm/m^3	.138	.256	.256	.194	.212
30m	cells/m^3	$.16 \times 10^8$	$.12 \times 10^8$	$.17 \times 10^8$	$.26 \times 10^8$	$.08 \times 10^8$
	dry wt gm/m^3	.300	.350	.294	.275	.250
	ash wt gm/m^3	.144	.225	.175	.150	.156
Integrated Data /m^2						
	cells/m^2	6.99×10^9	6.98×10^9	11.75×10^9	9.17×10^9	4.70×10^9
	grams/m^2	9.13	11.32	8.65	8.77	10.74
	grams/m^2	6.29	8.63	6.14	5.30	6.73

APPENDIX V

Particulate volume and carbon determinations for serial dilutions of algal species.

APPENDIX V

Particulate Volume and Carbon Determinations for Serial Dilutions of Stephanodiscus sp May 17, 1971

Sample Dilution	Particulate Volume/100 ml (mm^3)	Optical Density at 440 nm	Particulate Carbon/100 ml (µgms)
1	0.2456	0.380	1260 µgms C
1/2	0.0878	0.154	500 µgms C
1/4	0.0717	0.083	278 µgms C
1/8	0.0254	0.038	128 µgms C

Particulate Volume and Carbon Determinations for Serial Dilutions of Chlorella sp May 28, 1971

Sample Dilution	Particulate Volume/100 ml (mm^3)	Optical Density at 440 nm	Particulate Carbon/100 ml (µgms)
1	0.3026	0.400	1320 µgms C
1/2	0.1774	0.230	770 µgms C
1/4	0.0733	0.110	370 µgms C
1/8	0.0395	0.046	152 µgms C

APPENDIX V

Particulate Volume and Carbon Determinations for Serial Dilutions of Natural Phytoplankton - June 4, 1971

Sample Dilutions	Particulate Volume/100 ml (mm^3)	Optical Density at 440 nm	Particulate Carbon/100 ml (µgms)
1	0.2632	0.292	960 µgms C
1/2	0.1083	0.169	558 µgms C
1/4	0.0638	0.092	303 µgms C

Particulate Volume and Carbon Determinations for Serial Dilutions of Asterionella sp and Large Phytoplankton - June 4, 1971

Sample Dilutions	Particulate Volume/100 ml (mm^3)	Optical Density at 440 nm	Particulate Carbon/100 ml (µgms)
1	0.1820	0.295	985 µgms C
1/2	0.0802	0.146	483 µgms C
1/4	0.0346	0.048	163 µgms C

APPENDIX V

Particulate Volume and Carbon Determinations for Serial Dilutions of Ankistrodesmus sp - July 7, 1971

Sample Dilutions	Particulate Volume/100 ml (mm^3)	Optical Density at 440 nm	Particulate Carbon/100 ml (µgms)
1	0.0688	0.1585	525 µgms C
1/2	0.0379	0.0505	167 µgms C
1/4	0.0172	0.0195	65 µgms C

Particulate Volume and Carbon Determinations for Serial Dilutions of Natural Phytoplankton - July 26, 1971

Sample Dilutions	Particulate Volume/100 ml (mm^3)	Optical Density at 440 nm	Particulate Carbon/100 ml (µgms)
1	0.2107	0.324	1080 µgms C
1/2	0.1099	0.1630	538 µgms C
1/4	0.0509	0.0815	268 µgms C
1/8	0.0296	0.0390	133 µgms C

APPENDIX V

Particulate Volume and Carbon Determinations for Serial Dilutions of *Navicula* sp - August 7, 1971

Sample Dilution	Particulate Volume/100 ml (mm^3)	Optical Density at 440 nm	Particulate Carbon/100 ml (µgms)
1	0.0670	0.292	634 µgms C
1/2	0.0466	0.115	342 µgms C
1/4	0.0288	0.080	187 µgms C
1/8	0.0192	0.005	21 µgms C
1/16	0.0085	0.002	11 µgms C

PARTICULATE VOLUME AND CARBON DETERMINATIONS FOR SERIAL DILUTIONS OF SMALL ANABAENA

August 2, 1971

Sample Dilution	Particulate Volume/100 mls (mm^3)	Optical Density at 440 nm	Particulate Carbon/100 mls ugms
1	.0913	.3480	1160 ugms C
1/2	.0443	.1850	610 ugms C
1/4	.0264	.0705	233 ugms C

PARTICULATE VOLUME AND CARBON DETERMINATIONS FOR SERIAL DILUTIONS OF LARGE ANABAENA

July 26, 1971

Sample Dilution	Particulate Volume/100 mls (mm^3)	Optical Density at 440 nm	Particulate Carbon/100 mls ugms
1	.1284	.393	1310 ugms C
1/2	.0755	.217	712 ugms C
1/4	.0609	.120	398 ugms C

PARTICULATE VOLUME AND CARBON DETERMINATIONS FOR SERIAL DILUTIONS OF SMALL ANABAENA

July 26, 1971

Sample Dilution	Particulate Volume/100 mls (mm^3)	Optical Density at 440 nm	Particulate Carbon/100 mls ugms
1	.0824	.4185	1380 ugms C
1/2	.0528	.2475	815 ugms C
1/4	.0289	.1005	333 ugms C
1/8	.0158	.0805	266 ugms C

PARTICULATE VOLUME AND CARBON DETERMINATIONS FOR SERIAL DILUTIONS OF OOCYSTIS SP.

July 7, 1971

Sample Dilution	Particulate Volume/100 mls (mm^3)	Optical Density at 440 nm	Particulate Carbon/100 mls ug ms
1	.0067	.3505	1160 ugms C
1/2	.0038	.1825	600 ugms C
1/4	.0033	.0870	290 ugms C

APPENDIX VI

Table of X and Y values and determination of the 'F' value.

APPENDIX VI

Table of X and Y values and calculation of the regression equation

X (volume mm^3)	Y (μgms C)
1. .01723	65
2. .02542	128
3. .02958	133
4. .03457	163
5. .03794	167
6. .03952	152
7. .05087	268
8. .06384	303
9. .06882	525
10. .07166	278
11. .07329	370
12. .08016	483
13. .08775	500
14. .10827	558
15. .10993	538
16. .17736	770
17. .18203	985
18. .21068	1080
19. .24557	1260
20. .26320	960
21. .30263	1320

$\Sigma X = 2.28033$ $\Sigma Y = 11006$

$n = 21$ $n = 21$

$\bar{x} = 0.10859$ $\bar{y} = 524$

Regression equation $Y = a + bx$

$b = 4410.5$

$a = 45.1736$

$\therefore Y = 45.1736 + 4410.5X.$

Analysis of variance for data of Appendix III.

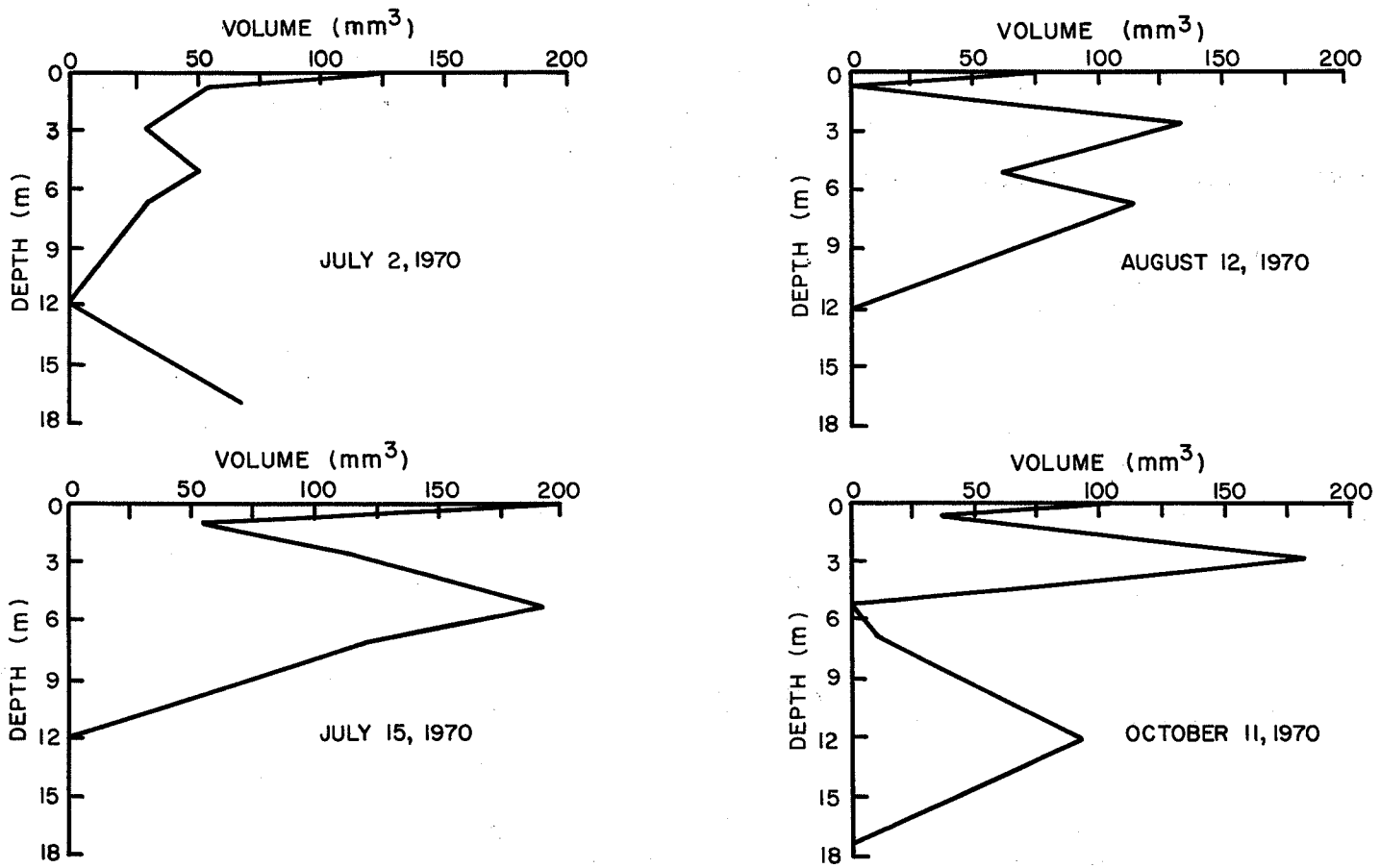
Source	df	df	SS	MS	F
X	1	1	0.3875	0.3875	891**
Residual	n-2	19	0.0087	0.000435	
Total	n-1	20	0.3962		

$$F_{.005}(1 + 19 \text{ df}) = 10.07$$

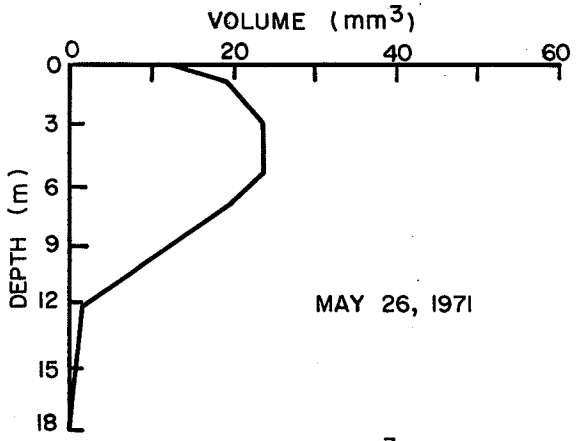
APPENDIX VII

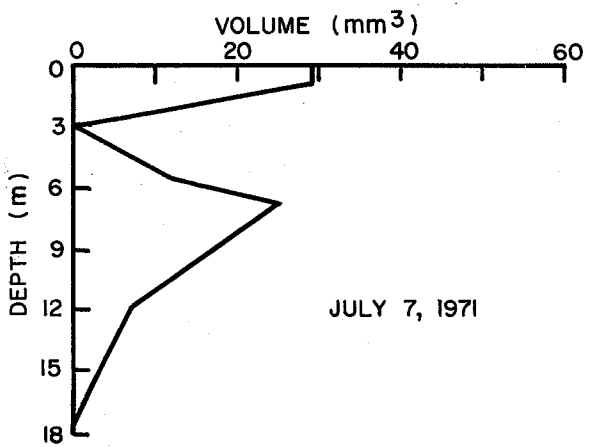
Depth profiles of production measured by the Coulter Counter.

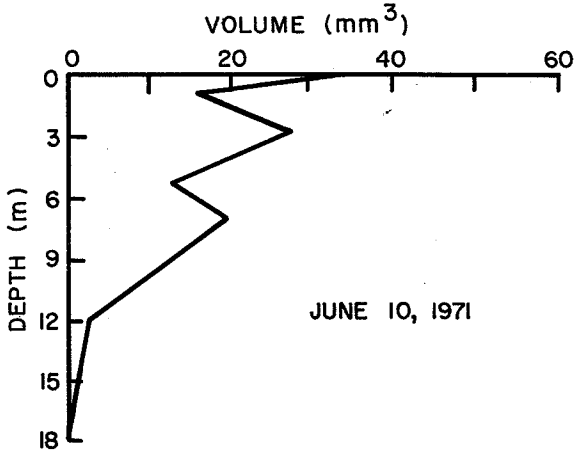
DEPTH PROFILES OF PRIMARY PRODUCTION MEASURED BY THE COULTER COUNTER



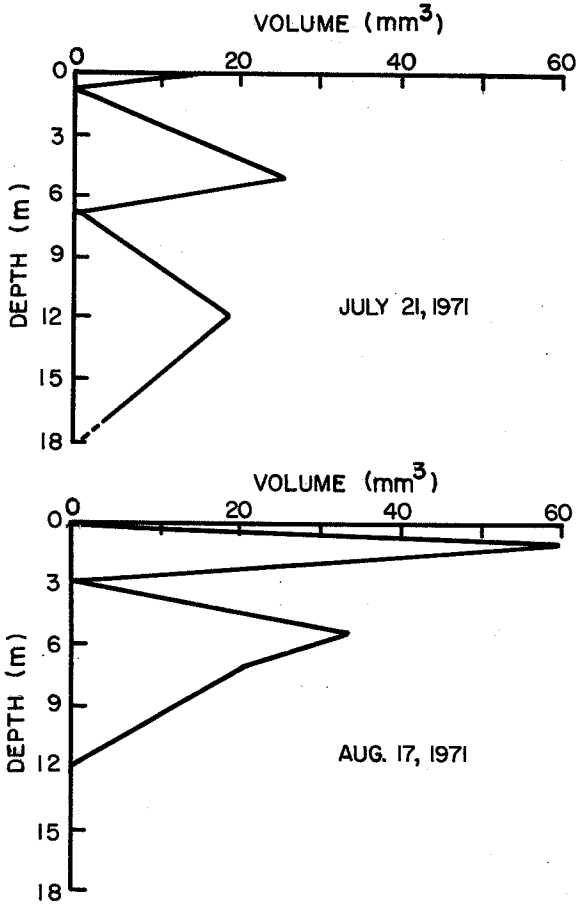
DEPTH PROFILES OF PRIMARY PRODUCTION MEASURED BY THE COULTER COUNTER







DEPTH PROFILES OF PRIMARY PRODUCTION MEASURED BY THE COULTER COUNTER



APPENDIX VIII

Comparison of ^{14}C (both corrected and uncorrected for filtration error) and Coulter Counter values of determining the primary productivity.

APPENDIX VIII

Comparison of ^{14}C (both corrected and uncorrected for filtration error) and Coulter Counter Values of Determining the Primary Productivity
(May 27, 1971)

Depth (meters)	^{14}C Values mgmsC/m^3/day	^{14}C (corrected for filtration error) mgmsC/m^3/day	Coulter Counter Values mgmsC/m^3/day
0	28.95	62.50	59.81
1	10.43	27.10	91.68
3	26.75	69.55	114.14
5	1.28	3.33	114.67
7	5.43	14.10	93.98
12	4.00	10.40	12.05
17	3.60	9.35	0

APPENDIX VIII

Comparison of ^{14}C (both corrected and uncorrected for filtration error) and Coulter Counter Values of Determining the Primary Productivity
June 10, 1971

Depth (meters)	^{14}C Values mgms $C/m^3/day$	^{14}C (corrected for filtration error) mgms $C/m^3/day$	Coulter Counter Values mgms $C/m^3/day$
0	57.25	148.85	153.84
1	49.15	127.80	76.13
3	47.65	123.90	129.41
5	6.75	17.55	59.81
7	17.75	46.15	95.66
12	6.75	17.50	13.68
17	0	0	0

APPENDIX VIII

Comparison of ^{14}C (both corrected and uncorrected for filtration error) and Coulter Counter Values of Determining the Primary Productivity
(July 8, 1971)

Depth (meters)	^{14}C Values mgms $C/m^3/day$	^{14}C (corrected for filtration error) mgms $C/m^3/day$	Coulter Counter Values mgms $C/m^3/day$
0	25.50	66.30	135.12
1	35.75	71.50	135.12
3	37.50	97.50	0
5	34.75	90.35	60.67
7	19.00	49.40	124.61
12	3.75	9.75	36.82
17	2.25	5.85	4.75

APPENDIX VIII

Comparison of ^{14}C (both corrected and uncorrected for filtration error) and Coulter Counter values of determining the Primary Productivity
(July 22, 1971)

Depth (meters)	^{14}C Values mgms $C/m^3/day$	^{14}C (corrected for filtration error) mgms $C/m^3/day$	Coulter Counter Values mgms $C/m^3/day$
0	19.50	50.70	63.26
1	24.00	62.40	0
3	28.00	72.80	55.39
5	15.25	39.65	125.18
7	25.25	65.65	0
12	8.50	22.10	98.45
17	3.00	7.80	18.10

APPENDIX VIII

Comparison of ^{14}C (both corrected and uncorrected for filtration error) and Coulter Counter Values of Determining the Primary Productivity
(August 17, 1971)

Depth (meters)	^{14}C Values mgms $C/m^3/day$	^{14}C (corrected for filtration error) mgms $C/m^3/day$	Coulter Counter Values mgms $C/m^3/day$
0	17.75	46.15	0
1	17.50	45.50	284.54
3	17.25	44.85	0
5	15.50	40.30	162.38
7	11.25	29.25	102.82
12	8.50	22.10	0
17	6.00	1.55	0