A LIMNOLOGICAL STUDY OF PLANKTONIC PRIMARY PRODUCERS IN A SHALLOW EUTROPHIC RESERVOIR

JOHN HENRY GENTILE

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A LIMNOLOGICAL STUDY OF PLANKTONIC PRIMARY PRODUCERS IN A SHALLOW EUTROPHIC RESERVOIR

BY

JOHN HENRY GENTILE

B. A., Northeastern University, 1962
M. S., University of New Hampshire, 1964

A THESIS
Submitted to the University of New Hampshire
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The Requirements for the Degree of
Doctor of Philosophy

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Department of Zoology
May 1966
This thesis has been examined and approved

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I would like to express my appreciation to Dr. Philip J. Sawyer, Zoology Department, University of New Hampshire, for his countless hours of discussion, numerous suggestions and constructive criticisms during every stage in the preparation of this thesis.

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SECTION I

INTRODUCTION

The investigation discussed in the following pages may best be described as a synecological study of planktonic primary producers in a shallow eutrophic reservoir. Implicit in the word synecological, is a multidimensional study involving many interrelated aspects of a problem and not simply one aspect. In analyzing the planktonic primary producing communities, it is not enough to know what they are (e.g. floristic description), but in addition, what their seasonal and vertical distribution patterns, efficiency, functional attributes, ecological significance, and adaptations are as well. These factors are, in turn, intimately related to morphometry, thermal and chemical stratification of water masses, nutrient availability and regeneration, and light penetration.

The most important function of the primary producing communities is to utilize solar energy for organic synthesis. This aspect of the primary producing communities forms the major unifying concept throughout this investigation. Related to the concept of primary production are several other factors, each of which provides a fertile field for investigation. As a result of such interrelationships, several basic questions guided the paths taken in this study. How is the rate of photosynthesis related to chlorophyll a concentration, not only seasonally but also with depth?
What are some of the ecological adaptations displayed by certain algal groups? Are these adaptations manifested in their functional abilities using the techniques employed in this study? Are the larger algal species more important contributors to organic synthesis than smaller forms, and how does relative importance change with season and depth? What are the seasonal and vertical changes in assimilation coefficients and how are these changes related to the adaptive behavior of chlorophyll a? Since the primary producers utilize solar radiation, what is their efficiency and how does it vary seasonally and with depth? Finally, what are the seasonal and vertical distributions of the algal communities?

Considerable work has been performed on some of these questions, particularly in marine habitats (Ryther, 1956a, Strickland, 1960, and Odum et al., 1959), with a few investigations in some of the larger American lakes (Manning and Juday, 1941, Wright, 1959, and Saunders et al., 1961), and Scandinavian lakes (Rodhe et al., 1958). Unfortunately, a certain amount of contradictory evidence has emerged from these works. It is the intent of this study to investigate these relationships in a small, shallow, eutrophic reservoir and compare these results to those in the literature.

In addition to the basic questions considered above, several other considerations influenced the development of this study. The first was the lack of regional limnological
studies. There have been no systematic limnological investigations performed on any of the lakes and ponds in New Hampshire. Since the techniques used in this study are those which are becoming more widely used in limnological investigations, they are and will be employed on larger and economically important lakes in this State (Sawyer, personal communication).

In addition there are two aspects of the study reported here that deserve special mention. The first is that the sampling schedule covers a period from ice-out to ice-in, thus, it includes several successive communities as well as environmental conditions. The second important aspect is that this study includes vertical distributions of these various phenomena. Both these points, particularly the latter, are noticable by their absence from most limnological studies.

It is hoped that this study will elucidate some of the questions posed above, provide a basis for further investigations, and contribute to the limnology of New Hampshire.
SECTION II
HISTORY AND DESCRIPTION OF THE OLD DURHAM RESERVOIR

History. The Old Durham Reservoir or University Pond (Smith, 1948), is located approximately three-fourths of a mile northwest of the center of the town of Durham, in Strafford County, New Hampshire. The approximate co-ordinates of this location are 43° 08' 30" 'N and 70° 56' 40" W.

This reservoir was constructed in 1893 by blocking Pettee Brook with a 310 foot dam constructed of granite blocks covered with earth (Smith, 1948). The large trees that grew in the original stream bed were cut and many of the stumps left to decay. After its formation, water from this reservoir was used for livestock, fire protection, and for drinking water until 1918, when it was replaced by a well. It is used at present for irrigation purposes by the Horticulture Experiment Station, for fire emergencies, stock watering, and to a limited extent for recreational purposes.

This reservoir is 1,000 meters long and from 32 to 140 meters wide. Its longitudinal axis runs northwest to southeast, thus coinciding with the direction of the prevailing winds.

The reservoir may be divided into an upper portion which runs northwesterly from the road leading to the
Horticulture Experiment Station, and into a main lower portion which runs southeasterly from this road (Figure 1). The upper section of the reservoir has been characterized by Smith (1948) as being in a dystrophic stage in its evolution (pH 5.9), extensively invaded by higher aquatic plants, and rapidly evolving into a swamp. No investigations were performed by this author on this portion of the reservoir.

This upper area is connected to the lower, main portion of the reservoir by a three-foot culvert which runs under the above-mentioned road. It is this larger, main body of water which is the subject of the investigations reported here. Unless otherwise specified, it is this portion that is being referred to whenever the term reservoir is used.

Examination of the morphometric map (Figure 1), shows that more than 50 per cent of the adjacent watershed is composed of forest, primarily white pine (Pinus strobus), with one area bordered by pasture and the opposite shore with brush and shrubs. There are three small streams draining into this pond on the northeast side. Only during early spring were these streams actively contributing to the reservoir and by early June they were completely dry. A spillway functions at the easterly end during and for a few weeks after ice-out. By the end of May, the water level of the reservoir had dropped enough so that no further spillage was observed until the next spring. Since little water was added via tributaries or from rainfall after early
Figure 1. The morphometry of the Old Durham Reservoir at maximum depth.
May in 1964 and again in May of 1965, the reservoir was essentially a closed system with the water level gradually receding throughout the summer and fall. The water level ceased dropping only after ice formation. A permanent ice cover had formed over the reservoir by December 1, 1964, and January 1, 1966, at which times the reservoir was at its lowest levels. Its maximum depth at these times was only 2.2 meters.

Morphometry. The morphometric map (Figure 1) and hypsographic curve (Figure 2), show that the basin of this reservoir is very shallow, with more than 80 per cent of the maximum volume being contained within the top two meters of depth. Only at the eastern end of the reservoir, where the sampling station for this study was located, did the depth exceed three meters. When vertical distribution of the total reservoir volume is expressed as a per cent of the total volume, 49.2 per cent of the total volume is contained within the zero to one meter contour, 32.7 per cent within the one to two meter contour, 15.2 per cent within the two to three meter contour, and only 2.9 per cent within the three to four meter contour. The total area of the reservoir is slightly more than ten acres (four hectares) with a spring maximum volume of 21,500,000 gallons (80,000 cubic meters). During the two autumns covered in this study, the volume of the reservoir at the time of freezing was only 41 per cent of its capacity. Therefore, more than 14,500,000 gallons of water were lost by evaporation or used for irrigation.
Figure 2. A hypsographic curve of the Old Durham Reservoir at maximum depth.
purposes during the summer.

Within the one meter contour, large beds of submerged aquatic vegetation were present throughout the summer. Though a systematic study of these plants was not undertaken, the following dominant species were identified: the yellow water lily (Nuphar advena), coontail (Ceratophyllum sp.), an aquatic moss (Mnium sp.), and water milfoil (Myriophyllum sp.). All of the above species were found everywhere around the pond except Nuphar which was restricted to the area within the two meter contour on the southern bank of the reservoir. It is interesting to note that while Nuphar advena was the only water lily in the lower portion of the reservoir, the more acid upper section of the reservoir contained the white water lily (Nymphaea odorata). This distribution exemplifies the ecological preference for slightly acid waters displayed by Nymphaea, while Nuphar tolerates a wider range of hydrogen ion concentrations.

One method of assessing the effect of morphometry on the movement and mixing of water masses is by the study of the vertical stratification of temperature and dissolved gases. The principle force responsible for mixing of water masses in this reservoir is wind, particularly from the southeast and northwest. Since both these winds are coincidental with the longitudinal axis of the reservoir, their effects are accentuated. It appears from my observations that the northwesterly winds are most effective
in the movement and circulation of water, because their path is unobstructed as they travel the full length of the reservoir. The easterly end of this reservoir is well protected by dense stands of white pine. As a result, any wind coming from the south or east has little effect on the movement of water near the sampling station but may be important at the northwestern end of the reservoir.

The action of these winds has been assessed from two types of data; the changes in vertical distribution of dissolved gases and temperature, and the distribution of surface objects (e.g. pollen grains, blue-green algae, dead leaves). As will be discussed later, the vertical distribution of oxygen and carbon dioxide exemplify the effects of internal mixing, particularly the partial re-oxygenation of deeper waters after anaerobic conditions have been established. Weather data indicate only moderate winds are required to upset the stability of the water column. That the predominant winds operative in this reservoir are northwesterly can be deduced from the accumulation of floating objects at the eastern end of the reservoir. Pollen from the surrounding pines accumulate in such densities as to color the water yellow at the eastern shore. Further, blooms of Anabaena planktonica Brunnthaler are often blown into windrows along the eastern shore as are dead leaves and other objects. We may conclude then, that northwesterly winds of moderate velocity (10-20 m.p.h.) have an important effect upon the movement
of surface and subsurface water masses, and consequently on the limnology of this reservoir.

This reservoir has an extensive littoral zone confined to the zero to one meter contour level but it does not support aquatic plants across the entire basin. Stratification does occur at the deepest end and remains for more than four months. Due to its shallow basin, only an epilimnion and a metalimnion forms, the latter becoming devoid of oxygen during summer stratification. No estimation of littoral productivity was made, but the limnetic area, as will be discussed later, was highly productive and its primary production most likely exceeded that of the littoral area. According to Hutchinson's (1957) classification, this man-made reservoir closely approximates his Type 73.

In summary, this reservoir may be considered as a small lake, with sustained summer stratification, and showing the classic dimictic circulation pattern common to temperate lakes. Though its littoral zone is fairly extensive, it does not coincide with the accepted definition for ponds (Welch, 1952, Odum, 1959, and Reid, 1961). The very high limnetic primary production is characteristic of a lake rather than a pond.

This body of water is unmistakably eutrophic with rich phytoplankton communities and a high sustained productivity from early July to September. The high rates of productivity indicate ample supplies of nutrients in the
epilimnion throughout the summer, even when there is no exchange with the deeper waters where rapid decomposition and nutrient regeneration is occurring. The contribution of allochthonous nutrients seems unlikely in view of the lack of surface run off and non-existent tributary contribution during the two summers covered in this study. Therefore, one must look to autochthonous sources of nutrients or nutrient regeneration to explain the high sustained productivity characteristic of the summer phytoplankton populations. The relationship between morphometry and nutrient regeneration will be discussed later.
SECTION III

MATERIALS AND METHODS

GENERAL

**Sampling Schedule.** Sampling dates were chosen deliberately to be clear to partly cloudy, and only on two occasions were studies performed on overcast days. The sampling schedule commenced March 17, 1965 and terminated January 4, 1966, with sampling frequency varying from one day a month to every seven to ten days during the summer. All plankton and physical data collections, pigment analysis, and productivity studies were performed on samples collected from one station at the deep, east end of the reservoir. Except for *in situ* productivity determinations, which were incubated for four hours, all data were collected between 0900 and 1030 hours EST and processed the same day.

**Temperature.** Temperature profiles were constructed by using a Tele-Thermometer (Model 43H, 0-37°C, Yellow Springs Instrument Co.). Readings were taken in air, at the surface, and at 0.5 meter intervals to the bottom. This thermometer was checked weekly in the lab against a mercury thermometer and once in the field against a reversing thermometer.

**Subsurface Illumination.** Measurements of subsurface illumination were made with a Whitney Underwater Daylight
Meter (Whitney Underwater Instrument Co.) which contained a Weston 856 RR photovoltaic cell sensitive to the visible range of the electromagnetic spectrum. All measurements were performed with a neutral density filter which reduced the light by a factor of forty. This permitted the use of lower in-line resistances and placed the readings in the optimum sensitivity range of the instrument. Readings were taken in air, at the surface, and then at 0.5 meter intervals to the point of extinction. The readings were re-checked as the photosensing unit was raised.

Incident Solar Radiation. Total incident solar radiation was obtained from an Epply Pyrethiometer with an automatic recorder maintained by the UNH weather station. The total incident radiation was calculated by planimetry for the total photosynthetic day as well as for the four hour incubation period. A Keuffel and Esser (Model 620005) metric planimeter was used. One unit area on the pyrethiometer recording was equivalent to 3.12 langley (gm cal/cm²)

Since photosynthetic pigments utilize only wave lengths from 4000 to 7000Å, it is necessary to correct the total incident radiation to that which is photosynthetically active. Forseythe (1954) calculated that 50.4-52.3% of the total solar radiation is within the 4000 to 7700Å range while List (1951) stated that 42.5-45.25% falls within the range 4000 to 7000Å. Ryther (1956) agreeing with Edmondson (1955) considers 50% to be photosynthetically active. In
all my calculations I have used 50%.

A further correction has been incorporated which accounts for reflection and backscatter. Hutchinson (1957) cited empirical determinations (Poole and Atkins, 1926, Powell and Clarke, 1936, Whitney, 1938) indicating that six to eight per cent of the incident light is reflected from an overcast sky. Davis (1941) working on Wisconsin lakes found values of six per cent for a diffuse sky and 5.2-5.5 per cent for clear skies during July and August. These values were the same for rough or smooth surfaces when the sun was at a zenith angle of 50° or less. At zenith angles greater than 50° the loss was greater from a smooth than from a rough surface. Except for conditions under ice or in diurnal studies a value of six per cent was used in this study. In the special cases cited above, values obtained from light meter readings in air and under ice were used to estimate reflectance and absorbance.

To calculate the quantity of radiation penetrating to various depths, the surface light meter value was arbitrarily taken as 100% of available illumination and all depths were calculated with reference to the surface as per cent transmission. The corrected radiation values were considered equivalent to 100% transmission at the surface and for various depths the proper percentages of this value were used. This, according to Hutchinson (1957), corresponds to the vertical extinction coefficient values as determined by the slope of the line resulting when photometer readings
are plotted logarithmically against depth. This permitted quantitative estimation of the amount of radiation available for photosynthesis at each depth. Qualitative changes in spectral composition resulting from differential absorption within the water column were not assessed. The spectral distribution of light at a depth is a function of the nature of the water itself and the kinds and quantities of substances dissolved and suspended in it (Beeton, 1962). In the study reported here, the water had a high concentration of suspended solids, which according to Strickland (1958) selectively absorb radiation in the blue and ultraviolet range. It would be expected, from comparisons with studies on spectral distribution in other lakes (Beeton, 1962), that the spectral composition of this pond at depths below one meter would be in the 550-650 mu range. If this is true, a large percentage of the high energy portion of the spectrum is excluded. Since radiation values calculated above are based on the assumption that the whole spectral range penetrates equally to all depths, the values reported here are higher than the true values. Consequently, efficiency values at 1.5 and 2.5 meter depths are probably low.

**Water Chemistry.** The following analyses were performed on water samples from each depth on each sampling date. Dissolved oxygen (Alsterberg Modification of the Winkler Technique), free carbon dioxide, carbonate and bicarbonate alkalinity were performed according to procedures described in Standard Methods for the Examination of Water
and Wastewater (American Public Health Association, Eleventh Edition, 1960). Total hardness, Ca\textsuperscript{++} and Mg\textsuperscript{++}, were determined by the modified titrimetric method of Patton and Reeder (1965). Conductivity measurements were made with a Model RA-2A, conductivity meter (Industrial Instruments Inc.), and all values were corrected to 18°C (Smith, 1962). Measurements of pH were made with a Beckman Zero-Matic pH Meter (Beckman Instrument Co.).

**Chlorophyll Determinations.** Differential chlorophyll determinations were performed separately on total phytoplankton and nannoplankton from 0.5, 1.5 and 2.5 meter water samples. The original spectrophotometric technique developed by Richards and Thompson (1952) was used as a basis for these determinations, but with the following modifications. Plankton samples were collected on membrane filters (Schleicher and Schuell Co., Bact-T-Flex, B-3) and treated as described by Creitz and Richards (1955). Refinements and integration of these two techniques as well as a discussion of collection and storage procedures are described by Strickland and Parsons (1961). There has been considerable criticism of the specific absorption coefficients used by Richards and Thompson and estimating equations derived from them (Humphrey, 1961, Strickland, 1960). Consequently a new, more accurate series of equations for the quantitation of chlorophylls a, b, and c have been developed by Parsons and Strickland (1963) and were used in this study. The field procedure employed was as follows.
Samples for analysis were collected with an opaque water bottle and placed in one liter translucent polyethylene bottles to which MgCO$_3$ was added to maintain alkalinity and retard phaeophytin formation. The samples were shaded from intense sunlight and processed within one hour of collection at the laboratory. The separation of nannoplankton from net phytoplankton was accomplished by prefiltering a sample of water through #25 plankton net which removed phytoplankton greater than 60 microns. Therefore, nannoplankton is arbitrarily defined in this study as those chlorophyll-bearing organisms less than 60 u in size. The resulting filtrate was then filtered through a membrane filter. For the estimation of total chlorophyll, a water sample was filtered through a membrane filter. This procedure permitted the direct estimation of total phytoplankton chlorophyll and nannoplankton chlorophyll and the indirect estimation of netplankton chlorophyll. Analysis of extracts were performed with a Beckman DU Spectrophotometer using a 5cm light path.

METHODS USED IN THE ESTIMATION OF PRIMARY PRODUCTIVITY

**Preparation of Sodium C$^{14}$-Carbonate.** The preparation Na$_2$C$^{14}$O$_3$ from BaC$^{14}$O$_3$ was basically similar to the procedure of Steemann-Nielsen (1952). Modifications of this technique were of two types; changes in the basic apparatus and changes and clarification of the concentrations of the reactants in the conversion process.

The apparatus used in this study (Figure 3) has three modifications not present in the original. The function of
Figure 3. Apparatus employed in the conversion of BaC\textsubscript{14}O\textsubscript{3} to Na\textsubscript{2}C\textsubscript{14}O\textsubscript{3}.
these is as follows. After the conversion reaction has been completed, nitrogen is introduced into the chamber while the stopcock connecting the reaction flask with the sodium hydroxide trap is opened. This permits flushing the chamber of any residual $\text{C}^{14}\text{O}_2$ which is then absorbed as it bubbles through the trap. A second change involves the suspension of the reaction flask within the evacuated chamber. The use of cotton alone, as recommended originally, was found to be inadequate to support the flask when all the acid was added. Further, the cotton must be completely immersed in the acid to insure that any particles of carbonate that might have been entrapped during the initially violent reaction are converted to $\text{CO}_2$. Efforts to soak the cotton with extra acid resulted in the reaction flask sliding off the delivery tube. To prevent this, the reaction flask was covered by a tightly fitting, perforated polyethylene cap which was attached firmly to the delivery tube. This arrangement proved very reliable. A final modification was the use of a magnetic stirrer to agitate the sodium hydroxide solution and facilitate the absorption of the radioactive carbon dioxide. This precluded the formation of a pH gradient within the sodium hydroxide that might reduce the efficiency of the conversion (Goldman, 1961).

In order to facilitate the expansion and transfer of $\text{C}^{14}\text{O}_2$ evolved in the reaction flask into the chamber, a quantity of non-radioactive barium carbonate was added as a carrier. In selecting the proper amount of carrier
to be added, two relationships had to be observed. The ratio of milliequivalents between carrier and radioactive barium carbonate and between sodium hydroxide and total barium carbonate should be approximately eight to one (Amell, 1964, person communication). To satisfy both these requirements, 30mgs of carrier were added to 3.5mgs of radioactive barium carbonate (1mc). To insure complete combustion of both carrier and radioactive carbonate, 0.75N HCL was employed rather than the suggested 0.5N HCL. Except for the above alterations, the conversion procedure was the same as that described by Steemann-Nielsen (1952).

**Determination of Absolute Activity.** After completion of the conversion of lmc of BaC\(^{14}\)O\(_3\) to Na\(_2\)C\(^{14}\)O\(_3\), the flask was thoroughly rinsed with ion-free, glass distilled water and the contents diluted to 500ml in a volumetric flask. The pH of this solution was adjusted to 9.5 and then it was autoclaved. Phenolphthalein was added as a visual indicator to insure that the pH remained above 8.3. This resulted in an activity of 2uc/ml assuming that the conversion process was 100% efficient. Since that latter assumption is untenable, it is necessary to obtain the precise activity of a milliliter of this solution. The knowledge of this activity is a prerequisite for the accurate calculation of the amount of carbon assimilated.

There are three basic techniques employed for the determination of the absolute activity of an unknown sample. The classical approach entails the preparation of a
self-absorption curve and its extrapolation to zero thickness (Steemann-Nielsen, 1952). In this procedure, the activity in an aliquot of the unknown sample is measured by precipitating BaC\textsuperscript{14}O\textsubscript{3} from Na\textsubscript{2}C\textsubscript{14}O\textsubscript{3} on a tared membrane filter. A series of such samples are prepared with various densities of precipitate. The specific activities are then plotted against density (g/cm\textsuperscript{2}) and the scatter extrapolated to zero thickness either empirically or mathematically. This technique has three important weaknesses. The first is the preparation of very thin films of BaCO\textsubscript{3}, and the second is the accurate determination of the weight of the precipitate. The latter can be predicted from the stoichiometry of suitable equations, but the technical problem of complete transfer of the precipitate from the reaction flask to the filtration apparatus introduces sizeable errors. Further, BaCO\textsubscript{3} tends to form films which adhere to glassware, and being insoluble in water, can not be rinsed free. The second difficulty is the accurate extrapolation to zero thickness. This often is a subjective process, although a line can be fitted to the scatter by a curvilinear least squares formula. A third problem is backscatter, which can result in erroneously high values particularly in very thin samples. This has added significance since it is these samples which approach zero thickness and therefore must be accurate if extrapolation is to be valid. To illustrate this problem, it was found that at densities of less than 0.2g/cm\textsuperscript{2} backscatter became
acute. If the values plotted at these densities were used in extrapolation, a conversion efficiency of 95% was estimated. If these points were ignored, extrapolation indicated 67% conversion. If either of these values were used in calculation of assimilation, the former value would result in a 16% underestimation of the true value (80%) while the latter value would lead to a 20% overestimation. Such subjective and variable interpretation precluded the use of this technique.

Jitts (1957, cited by Goldman, 1961) attempted to resolve the problem of extrapolation by assuming that the self-absorption exhibited by such a series of samples was exponential. Hendler (1959) attempted to treat this relationship as a hyperbolic function. The failure of both these methods is attributed to backscatter at thickness of less than 2mg/cm² (Jitts and Scott, 1961).

A second technique used to determine absolute activity is that of Jitts and Scott (1961). This method employs thin films of carbon-14 labelled plastic which can be counted and then dissolved in a liquid scintillator and the absolute activity determined by comparison with a carbon-14 standard solution. This permits calculation of machine counting efficiency. Knowing the absolute activity of the carbon-14 standard and the counting efficiency, the absolute activity of the unknown can be calculated.

A third and the most precise method for the determination of absolute activity is that of gas analysis
described by Goldman (1961, 1960). This method depends on the conversion of the sample to be analysed to $^{14}$O$_2$ which is then counted by liquid scintillation. The apparatus necessary to perform such an analysis was not available for use in this study.

The determination of the absolute activity of material used in this study was performed by New England Nuclear Corporation, Boston, Massachusetts. An aliquot of our material was liquid scintillated and activity of two samples determined to be 1.59uc/ml. This is approximately 80% of the theoretical value expected if the conversion had been 100% efficient. This value (1.59uc/ml) was used for our absolute activity and as the basis for all calculations of carbon assimilation.

**Determination of Counting Efficiency.** For accurate measurements of primary productivity employing the carbon-14 technique, the counting efficiency of the detection system must be determined using the same counting geometry as that employed in productivity measurements, e.g. phytoplankton filtered on Millipore HA filters (Millipore Corporation, Bedford, Massachusetts).

Jitts (1961) has reviewed standardization procedures and techniques for determining counting efficiency. Jitts and Scott (1961) have suggested the use of carbon-14 labelled plastic films mounted on membrane filters for the estimation of machine efficiency. According to the authors the most important feature of this technique is that the
efficiency of the detection system is determined under conditions closely resembling those used in actual phytoplankton counts. Using this technique, efficiencies of close to 50% were obtained. Using a standard carbon-14 impregnated mylar film, an efficiency of 50% was obtained for the machine used in this study. Because such counting geometry is not identical to nor even approaches that of phytoplankton filtered on membrane filters, it was decided to prepare a series of standards using radioactively-labelled Chlorella pyrenoidosa of known activity and at different cell concentrations.

Two prerequisites necessary for the preparation of such a set of standards are the uniform labelling of the Chlorella culture and the complete assimilation of all the radioactivity added. To achieve the first condition the samples used were taken from the log-growth phase of a stock culture. At this stage it may be assumed that most of the cells are operating at their physiological maximum. To assure complete assimilation of all the radioactivity added, all other carbon sources were reduced by suspending the culture in phosphate buffer at pH 6.0 and enriching the culture medium with a nutrient solution containing trace elements and nitrate.

Three hundred cubic centimeters of buffered Chlorella were prepared with a concentration of approximately $5.7 \times 10^5$ cells per cubic centimeter. Four sterilized serum bottles were filled with buffered culture medium and capped with
air-tight rubber stoppers. To each of the bottles, 0.525μc of Na2C\textsubscript{14}O\textsubscript{3} was added through the rubber stopper with a syringe. The bottles were shaken and placed on aluminum foil under two fifteen-watt, cool-white, fluorescent lamps at a distance of 18 inches. A constant temperature of 25°C was maintained throughout the experiment. One of the four cultures was subsampled at thirty minute intervals for four hours, and then less frequently until the uptake of carbon-14 ceased. These subsamples consisted of a 1 cc aliquot which was suspended in 100cc of distilled water, filtered on a Millipore HA filter, rinsed with 10cc of 10^{-3}M HCL and then with distilled water. The filters were dried at 50°C for one hour, cooled to room temperature and counted. Each sample was counted for a minimum of one thousand counts and the elapsed time printed out. The activities of these subsamples were plotted logarithmically against elapsed time and except for a slight initial lag, a straight line resulted until all the added Na2C\textsubscript{14}O\textsubscript{3} had been utilized. At this time, the activity leveled off and remained constant for over eight hours after which no further subsamples were studied. Within an hour after the rate of incorporation of the added carbon-14 had peaked, the remaining three cultures were subsampled volumetrically and filtered as above. These samples were air dried and counted after 24 hours.

If, as assumed, all algal cells took up equal amounts of radioactive carbon, then one cubic centimeter
of this culture would contain $1.715 \times 10^{14}$ dpm/cc (0.525 uc/68 cc). Samples were chosen to give a counting range of 600-70,000 cpm which is the range I most often encountered in field studies. Further, this sequence of samples gave algal densities ranging from $1.4 \times 10^5$ to $1.4 \times 10^7$ cells/cm$^2$ which cover the ranges observed in most field studies. Figure 4 shows that the relationship between activity and cell density is linear over the range of values studied.

As further check that all the added radioactivity was assimilated, a portion of the culture was brought to a pH of 8.5 and filtered. The filtrate was dried and its activity determined. These data indicated that a maximum of 0.78% and a minimum of 0.26% of the added activity was not assimilated.

Table 1, shows the range and standard deviation of the counting efficiencies determined by the above method. For all calculations of productivity a value of 15% was employed. This value is considerably lower than that reported by Jitts (1961) and for our machine when a mylar C$^{14}$ standard was used. However, I feel it more adequately represents the true counting efficiency for the particular counting geometry employed.

Field Procedure. The generalized field procedure outlined by Goldman (1961) was followed whenever possible. Sampling for all in situ studies was conducted between 0930 and 1000 hours EST with an opaque, two-liter,
Figure 4. The relationship between cell density and radioactivity in a culture of Chlorella pyredinosa after it had assimilated 0.525 uc of Na₂C¹⁴O₃.
<table>
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<th>CC Filtered</th>
<th>Actual CM$^{-1}$</th>
<th>Theoretical CM$^{-1}$</th>
<th>Efficiency</th>
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<td>58,500</td>
<td>428,750</td>
<td>13.65</td>
</tr>
</tbody>
</table>

$\overline{X} = 14.72$

$S_\overline{X} = \pm 0.89$
non-metalic water bottle (G. M. Manufacturing and Instrument Corporation). Samples were collected from the surface, 0.5, 1.5, and 2.5 meters. Each water sample was treated in the following manner. One hundred milliliters of water were placed in each of two sterilized 125 ml pyrex, ground glass stoppered bottles, one of which was clear and the other blackened with tape. A second sample of water was filtered through disks of #25 plankton net placed in a modified membrane filtration apparatus. This procedure removed phytoplankton greater than 60 microns. The resulting filtrate was treated in the same manner as the unfiltered samples. As each sample was collected and treated as described above, it was stored in a light-tight box to reduce light shock until it was incubated. When all the samples had been collected, each bottle was inoculated with one milliliter of Na₂C¹⁴O₃. The dark bottles were capped with aluminum foil to prevent light penetrating into the bottle around the stopper. The samples were then suspended from a float at the same depth from which they were taken.

The float was a square, twenty-eight inches on a side, and constructed of four two inch by six inch boards with a one inch cross piece to which an anchor rope was attached. To avoid shading the incubating bottles, an extension was added which projected three feet beyond the edge of the float. The suspension apparatus consisted of one inch diameter polypropylene rope to which metal dividers
were attached that kept the bottles approximately 18 inches apart. The bottles were fastened to the ends of these dividers by heavy elastics.

After a four hour incubation period, the samples were removed from the water and inoculated with two milliliters of formalin to arrest all metabolic activity. The samples were taken into the laboratory where they were filtered within one hour.

Filtration was accomplished under a partial vacuum using a Millipore filtration apparatus and 47mm diameter Millipore HA membrane filters. The whole water sample was filtered, the retentate rinsed with 10cc of \(10^{-3}\) HCl to remove any absorbed radioactivity. This was followed by a final rinse with 20cc of distilled water. The filters with their radioactive phytoplankton were placed on two-inch diameter stainless steel planchets and stainless steel rings were used as weights to prevent curling of the filters. Samples prepared in this manner were air dried for 24 hours before counting.

The quantity of radioactive carbon assimilated was determined by counting each sample with a thin-window gas-flow, proportional counter (Baird Atomic Corporation). The majority of the samples were counted on a Baird Atomic proportional counter with a Model 135 Scaler-Timer. The remainder were counted on a Baird Atomic, University Series II proportional counter with a general purpose scaler, Model 146, equipped with an automatic planchet changer,
Model 727, and a printing timer, Model 965. Both machines used desiccate gas (90% Argon: 10% Methane). Several samples were counted on both machines as a cross-check. Planchets with their radioactive samples were loaded in the automatic planchet changer, the scaler preset to count 5000 counts, and the elapsed time printed out. These values were converted to counts per minute and then to disintegrations per minute using the value for counting efficiency. The calculation of carbon assimilation uses the equation;

$$\frac{DPM \text{ (Sample)} \times \text{Total Carbon/M}^3}{\text{Absolute Added Activity (DPM)}} \times 1.05$$

which gives the milligrams of carbon assimilated during the period of incubation. A correction of five per cent for isotope discrimination was included in all calculations (Goldman, 1961, Strickland, 1960). Calculations of assimilation were made directly for nanoplankton and total phytoplankton and values for net phytoplankton were obtained by difference.

**Efficiency of the Phytoplankton Community.** The efficiency of the phytoplankton population was determined from the amount of energy available for photosynthesis and the amount of energy actually fixed in photosynthesis. The quantity of utilizable solar radiation available to the algal community was calculated by the procedure described earlier. Since solar radiation is measured in gram calories/cm²/time, it was necessary to convert the quantity of carbon assimilated into a caloric equivalent. In this study the
caloric equivalent of glucose was used. Milligrams of carbon synthesized were converted to calories synthesized using a caloric equivalent of 673,000 calories per mole of glucose (Giese, 1962).

PHYTOPLANKTON

Sampling. Phytoplankton samples were collected from one station at the east end of the reservoir from 0.5, 1.5, and 2.5 meters. Samples were collected with an opaque non-metallic water sampler and preserved in acid Lugol's solution. Preserved, unconcentrated samples were stored in 20 ml vials from which aliquots were taken for qualitative and quantitative analysis.

Identification. Most of the identification and quantitation was performed on preserved samples, although live material was examined whenever possible to assist in identification. When possible, identifications were carried to the species level, particularly for dominants. Several different small flagellates were often very abundant but were difficult to identify in preserved form. The qualitative and quantitative analysis reported here should not be construed as being in any way a definitive analysis of the total phytoplankton community. It is limited to the ability of the experimenter and the inherent problems of identifying preserved material.

Quantitation. The counting technique employed in this study used the inverted microscope and is described
in detail by Lund et al. (1961). Counting was performed at a magnification of 200X on one milliliter of unconcentrated water. Higher magnifications were used only to facilitate identification.

The calculation of cell numbers for colonial and filamentous species was achieved by determining the average cell number for several representative colonies or filaments. This value was then used as a basis for further calculations.
SECTION IV

SEASONAL AND VERTICAL FLUCTUATIONS IN THE PHYSICAL AND CHEMICAL CHARACTERISTICS OF THE OLD DURHAM RESERVOIR

Introduction. Investigation of the physical and chemical properties of this reservoir commenced June 28, 1964. Data was collected intermittently during the summer and terminated October 20, 1964. Collecting resumed March 17, 1965 and continued until January 4, 1966.

Climatic Conditions. Weather conditions were very similar during the summers of 1964 and 1965. Both years were dry with acute drought conditions existing throughout the summer and fall. Rainfall during 1964 and 1965 was approximately 70 and 50 per cent, respectively, of the mean annual rainfall for Durham. The maximum water temperature during 1964 was 29°C on July 28, with epilimnetic water temperatures greater than 26°C from July 7th until August 26th. During the summer of 1965, the maximum water temperature was 26.8°C on August 17th with the temperature of the epilimnion being less than 26°C for most of the summer and frequently less than 24°C. There were no major wind storms (e.g. hurricanes) during either summer. It appears from an analysis of the stratification patterns and field notes that winds of 20-30 mi/hr were adequate to destroy vertical stratification.

Development, Duration, and Destruction of Thermal and Chemical Stratification. The development, duration and
destruction of thermal stratification within this reservoir could only be studied completely during 1965 since no data were available from the spring of 1964. A summarization of the thermal changes occurring during 1965 is represented in Figure 5. The temperature profile of March 17, is characteristic of that which was usually found under the ice. Ice-out occurred around April 8, 1965 and for about one month the water column was thermally homogeneous. Thermocline formation began about May 10, 1965 but the metalimnetic temperature continued to rise as the summer progressed. This gradual warming of the metalimnion resulted from the partial mixing of epilimnetic and metalimnetic water masses.

Stratification continued in varying degrees throughout the summer until fall turnover. It is apparent, however, that this stratification was somewhat unstable and tenuous. The evidence for this conclusion is based on the warming of the metalimnion, and the recurrent partial re-oxygenation of the water at the 2.5 meter level (Figure 6). This is well illustrated by noting the changes occurring between May 26 and July 7, 1965. A further indication of mixing during this time was the elevation of the thermocline from 2.0 meters to 1.0 meter (Figure 5). By September 2, 1965, at 17.8°C a complete mixing of water masses had occurred, marking the fall turnover.

Although this reservoir manifested the classic dimictic circulation pattern common to temperate lakes, one can hardly think of it within the same frame of reference
Figure 5. Patterns of thermal stratification from March 17 to November 6, 1965.
Figure 6. Distribution of CO₂ and O₂ at 2.5 meters during 1965. Oxygen values between May and August show partial re-oxygenation of the metalimnion.
as the larger, deeper lakes. Its stratification was tenuous and there was constant partial mixing of epilimnetic and metalimnetic water masses. There was no true hypolimnion which remained isolated from overlying water for a prolonged period. This partial mixing resulted from wind driven currents, whose effect was accentuated by the reservoir morphometry. Due to the high organic and bacterial content of this reservoir, decomposition proceeded rapidly and anaerobic conditions were readily re-established after partial re-oxygenation. Unless meteorological conditions were favorable, stratification did not persist nor did a sharply delineated thermocline develop.

Examination of dissolved oxygen, carbon dioxide, and temperature distributions during 1964 revealed a pattern similar to that just described for 1965. Though the data are less extensive, they revealed a less pronounced thermal stratification than was found in 1965, with similar recurrent partial re-oxygenation of water at and below the 2.5 meter level. As in 1965, the water temperature below the epilimnion continued to rise throughout the summer. Since on sampling dates when this rise was most pronounced, a partial re-oxygenation of the deeper waters also occurred, one must conclude that vertical mixing of water masses was responsible for metalimnetic warming.

A comparison of the physical and chemical data obtained in this study with that of Smith (1948) is very
interesting. Three things are immediately obvious when one examines his graph (Smith, 1948, p. 15). First, the water level of the reservoir was close to its maximum depth throughout the year, indicating adequate rainfall at this time. A second difference was the cooler metalimnetic temperatures observed in 1947. Smith (1948) reported minimum values of 13°C on August 20 and 27, 1947. For the same dates at the same depth I found values of 18.5°C and 22.0°C. The surface water temperature were within three degrees of each other at this time. In Smith's study, a well defined thermocline existed, while during the two years included in this study, the thermocline was often poorly defined. Smith reported anaerobic conditions below 3.9 meters with an alkalinity of 45 ppm and a free carbon dioxide concentration of 77.5 ppm, which are considerably higher than observations of this author. However, if Smith's data at 2.5 meters are compared with those of 1964 and 1965, the differences are slight. On August 27, the following values for dissolved oxygen and carbon dioxide were recorded at 2.5 meters: 4.0 ppm (1947), 3.7 ppm (1964), and 5.25 ppm (1965) for dissolved oxygen; and 12.5 ppm (1947), 6.0 ppm (1964), and 8.0 ppm (1965) for carbon dioxide. Analysis of thermal stratification and chemical data below 2.5 meters from Smith (1948) indicate the stratification during the summer of 1947 was complete below 3.0 meters. Turnover appeared to have occurred after September 10, 1947 thus
making it later than in 1964 and 1965. Ice formed on the reservoir during the last week of November, 1947 and persisted until approximately April 4, 1948 which coincides closely with this author's observations for 1964-1965. A permanent ice cover did not form until early January 1966.

**Physical and Chemical Conditions Under the Ice.**

Analysis of conditions found under the ice during 1966 compare favorably to data gathered by Smith (1948). The classic thermal stratification was observed in both studies. The concentration of dissolved oxygen gradually decreased at all levels particularly if there was a heavy snow cover. The reduced light penetration resulted in decreased photosynthetic activity and oxygen evolution. The rate of decrease was accelerated near the bottom, as a result of higher temperatures and decomposing organic matter. The dissolved oxygen concentration beneath the ice began to rise before the ice had melted. This is explained by the fact that as the ambient temperature increased, the snow cover melted, increasing the light penetration and the rate of photosynthesis. Another possible source of re-oxygenation could result from tributary inflow. This surface water would be close to 4°C and thus would flow under the colder less dense layers of water and re-oxygenate the deeper water. On March 19, 1947, Smith reported 5.8 and 4.7 ppm of dissolved oxygen from the surface and 3.8 meters respectively. At no time did he report anaerobic
conditions under the ice. On March 17, 1965, 7.85 and 2.20 ppm of dissolved oxygen were found at the surface and 2.5 meters respectively. By April 5, 1965 four days before ice-out, the water temperature had risen from 1.0°C on March 17 to 3.8°C and the oxygen concentration had increased from 7.90 to 13.00 ppm at the surface. It is believed that this increase is primarily the result of increased photosynthetic activity stimulated by greater light penetration. This assumption is substantiated by measurements of primary productivity which manifested a four-fold increase on this date.

**Light Penetration.** Light penetration is one of the most important physical parameters to be considered if one wishes to estimate the efficiency with which the primary producers utilize available solar radiation. Consequently, a thorough record was kept of the percentage of surface radiation penetrating to various depths. This data is summarized for 1965 in Figure 7. Of the factors that affect light penetration, differential phytoplankton density is one of the more important. The effects of changes in plankton densities were more pronounced at the 0.5 and 1.0 meter levels as is evident from the wide fluctuations observed at these levels. A second factor that may markedly effect light penetration is turbidity resulting at spring and fall turnover from the re-suspension of bottom detritus. Increased turbidity need not be confined to periods of
Figure 7. Patterns of light penetration at selected depths during 1965.
complete turnover. Wind acting for a prolonged period at any season would suspend considerable detritus from the littoral areas which could then be circulated throughout the reservoir. Once stratification had been established, and climatic conditions were stable, changes in light penetration became more directly related to plankton densities. The latter can be best illustrated by observing the low per cent transmissions evident during July at 0.5 and 1.5 meters. During July of 1964 and 1965, a bloom of Anabaena planktonica Brunnthaler dominated the plankton community. In July of 1965 only 12.5 per cent of surface light penetrated to 0.5 meters and 9.0 per cent to 1.0 meter. The pronounced decreases in light penetration during May, 1965, and between August 27 and September 2, 1965 can be explained by an increase in turbidity resulting from the spring and fall turnovers respectively.

**pH Determinations.** Changes in pH result primarily from changes in carbon dioxide, dissolved oxygen, and bicarbonate concentrations. Fluctuations in hydrogen ion concentrations occurred, diurnally as a result of variations in photosynthetic and respiratory activity, as the result of vertical stratification of dissolved gases, and seasonally depending on phytoplankton and zooplankton densities. The pH ranged from 9.65 at the surface, during the peak of an Anabaena planktonica bloom, to 5.9 at 2.5 meters during summer stratification. Generally a decrease was evident in
the vertical distribution of pH values during periods of 
stratification, but not at other times. During most of 
the year the pH of the surface waters was between 7.0 and 
8.0 except in the case mentioned above.

**Alkalinity.** Alkalinity was usually restricted to 
bicarbonate alkalinity except on July 14, and July 23, 1965, 
when the pH exceeded 8.3, which resulted in the formation of 
trace amounts of carbonate. Since the bicarbonate content 
of the water is related to the free carbon dioxide 
concentration by the equation:

$$\text{CO}_2 + \text{HOH} \rightleftharpoons \text{H}_2\text{CO}_3 \rightleftharpoons \text{H}^+ + \text{HCO}_3^-$$

one would expect changes in the free carbon dioxide 
concentration to have an effect upon the equilibrium. From 
my observations, it appears that carbon dioxide concentrations 
below 15 ppm resulted in only slight increases in bicarbonate 
alkalinity. As the free carbon dioxide content increased 
above 20 ppm this relationship became more pronounced. On 
July 28, 1964 the free carbon dioxide and bicarbonate 
alkalinity at 2.5 meters were 14.0 and 25.0 ppm respectively. 
On the same date at 3.5 meters, the values were 37.0 and 62.0 
ppm respectively. Smith (1948) reported on July 10, 1947, 
carbon dioxide values of 40.0 and alkalinity of 58.0 ppm 
on the bottom. On August 8, 1947, both the carbon dioxide 
and alkalinity had reached 100.0 ppm. In all cases cited 
above, only minor changes occurred in the pH. If this 
buffer system were not operative, extensive changes in pH
would result. Frequent fluctuations in pH of large amplitude, would have marked effect upon the survival and composition of the plankton community.

**Total Hardness, Calcium, and Magnesium.** Analysis of these factors revealed a remarkably constant picture. Total hardness ranged from 24.00 to 29.00 ppm with a mean of 26.00 ppm. Calcium ranged from 6.6 to 8.0 ppm with a mean of 7.5 ppm. Magnesium ranged from 1.5 to 2.3 ppm and had a mean of 1.7 ppm.

**Conductivity.** Conductivity determinations measure the total quantity of ionic charges present in the water. Changes in the quantity of inorganic ions (e.g. bicarbonate), changes in the quantity of organic molecules derived from bacterial decomposition of organic matter, and varying amounts of organic molecules that are primarily extracellular metabolites derived from rapidly growing algal populations are responsible for changes in conductivity. Except during the time when these processes are operative the conductivity of this reservoir varied only slightly. Changes included under the first two categories listed above occurred under conditions of summer stratification when anaerobic conditions existed. At this time the products of respiration and decomposition, both organic and inorganic, were being liberated into the deeper waters which resulted in an increase in the conductivity. This condition was not very well illustrated by the data collected in this study.
because at 2.5 meters the necessary conditions were not developed well enough. If samples were taken from deeper strata, particularly close to the bottom, more pronounced changes would have been evident. Under the third class of factors influencing conductivity, a very interesting observation was made. Several authors (Fogg and Westlake, 1955, Fogg, 1965, and Gorham et al., 1964,) have reported high concentrations of toxic external metabolites accompanying blooms of blue-green algae. Gorham et al. (1964) characterized the metabolite as a polypeptide, which except at its isoelectric point, would bear either a positive or negative charge. On July 14, 1965 a dense, rapidly-growing surface bloom of *Anabaena planktonica* was present. This population was actually in its log growth phase since almost every cell was in the process of dividing. On this date, the conductivity at the surface and 0.5 meters was the highest observed all year (91.0 Mmhos/cm). No attempt was made to isolate the metabolite and characterize it, but it is felt that it was responsible for the elevated conductivity values noted on this date. The usual values were between 73.0 and 83.0 Mmhos/cm, with a mean of 78.8 Mmhos/cm.

In summary, those chemical factors which are intimately related to metabolic functions show greater or lesser variations depending upon the degree to which the involved water masses are isolated. Further, when buffer systems are involved, variations are easily masked, over a wide range of concentrations, and become pronounced only
under extreme conditions. Most changes can be accounted for by an integrated examination, and analysis of not only the chemical data, but also the dynamics and distribution of phytoplankton and zooplankton populations.
SECTION V

PHYTOPLANKTON STANDING CROP

Introduction. There are several techniques employed for the determination of phytoplankton standing crop. Estimations may be made from cell counts, cell weight, cell volume, cell surface area, oxidation of plant material to CO₂, nitrogen, phosphorous, organic compounds, and pigment analysis. The use of total cell numbers as a basis for estimating standing crop does not take into consideration size differences. High concentrations of small flagellates will provide a different picture than lower numbers of larger organisms, yet their biomass may be identical. This has prompted the use of cell volume as a measure of standing crop, since this accounts for size discrepancies between different groups of phytoplankters. Standing crop, per se, is of less significance than its relationship to productivity. With this relationship in mind, if total cell volume is used as a basis for determinations of standing crop, too much stress will be placed on the large phytoplankton, just as the use of total cell number is likely to cause an over-estimation of the role played by the small-celled species (Paasche, 1960).

Lohmann (1908, cited by Paasche, 1960), working with diatoms, considered plasma volumes, mainly represented by a thin layer of cytoplasm adjacent to the cell wall, as a more
precise measure of standing crop. A further refinement of this idea would be to consider only that part of the cytoplasm containing the chromatophores. The latter should depend upon the total cell surface area (Paashe, 1960). If this is true then the total cell surface area may serve as a fairly good estimate of the volume occupied by the chromatophores and the surrounding cytoplasm, and thus be an adequate measure of the standing crop.

The most satisfactory measure of phytoplankton standing crop, after its separation from detritus, is the oxidation of the plant material back to carbon dioxide from which it originated as a result of photosynthetic reduction (Strickland, 1960). The use of other elements, such as nitrogen and phosphorous, depends on the amounts of these elements in plant cells being constant and capable of accurate determination. The historical development, technical refinements and modifications, and a critical review of techniques for measuring standing crop can be found in Strickland (1960) and Strickland and Parsons (1961), and the reviews cited by them.

**Standing Crop and Pigment Analysis.** One of the most often employed techniques for measuring standing crop is the quantitative estimation of the chlorophyll content of a phytoplankton community. The criticisms of this technique are concerned with the variability of chlorophyll content, the contamination resulting from detrital chlorophyll, and a variety of technical problems associated with its accurate
The recent improvements in extraction, spectrophotometry, and standardization, have resolved most of the technical problems (Parsons and Strickland, 1963). Consequently the most important variables are those contingent upon the physiological condition of the phytoplankton and its relationship to chlorophyll biosynthesis. The physiological condition of a phytoplankton community is closely related to the nutrient conditions in the environment and the age of the cells. Deficiencies in nitrogen, phosphorus, magnesium, and iron result in a marked chlorosis of algal chlorophyll as does senescence (Ryther, 1954, Yentsch and Vaccaro, 1958). As a result, the chlorophyll content of a population may better reflect changes in the functional ability of a phytoplankton population than methods based on cell volume, numbers, or surface area. Conversely, it may more poorly represent changes in the actual standing crop measured as actual biomass. The latter is illustrated by considering the growth and decline of a phytoplankton population. During the log growth phase, the standing crop and chlorophyll content increase rapidly due to an increase in cell numbers and concurrent chlorophyll synthesis. After the population has attained its maximum growth, the biomass will remain high for several days, but functionally the population is static or declining as productivity measurements indicate. That is, new synthesis of organic matter and nutrients are minimal, and physiologically the cells are senescent. The chlorophyll content is also low during this
stage in the growth of an algal population. Since the importance of standing crop depends upon its relationship to organic synthesis, the chlorophyll content can be considered as a sensitive indicator of the functional status of a phytoplankton community under certain conditions. Paasche (1960) found a correlation of 0.74 between cellular surface area and production capacity which is somewhat lower than the correlation coefficients between chlorophyll a and primary productivity determined in this study and by Anderson and Banse (1965). It appears then that the chlorophyll a concentration of a phytoplankton community is the most sensitive indicator of functional standing crop.

**Seasonal Changes in Chlorophyll a Concentration.** The seasonal pattern for chlorophyll a concentration for three depths and for the total water column is illustrated in Figure 8. In general the pattern follows rather closely that discussed for primary productivity. There was a distinct increase in the chlorophyll content under the ice, which reached a maximum on April 5, 1965 shortly before ice-out. This was followed by a steep decline during April, reaching a minimum on May 10, 1965. An increase occurred during late May, which reached a maximum on June 4, 1965, and was followed by a sudden decline on June 11, 1965. This was followed by a continual rise during the latter half of June culminating on July 14, 1965 at the height of the *Anabaena planktonica* bloom. There was a gradual decline until August 4, 1965 when another algal pulse developed which reached its maximum
Figure 8. Seasonal distribution of chlorophyll a concentration (Mg s/m$^3$) for the total water column (m$^2$) and selected depths (1965-1966).
on August 14, 1965. This was followed by a general decline throughout the rest of August and early September. A gradual increase was noted in late September followed by a marked decline during early October. The concentration during November and December appeared to have remained constant until January 4, 1966 when measurements made beneath the ice revealed an almost identical value.

The general pattern at all three depths was quite similar qualitatively but differed quantitatively. The lowest concentrations per cubic meter were observed at 0.5 meters and the highest values were found at 2.5 meters. Analysis of the data collected from a variety of Wisconsin lakes (Manning and Juday, 1941) indicated a gradual increase in the chlorophyll content of the epilimnion with increasing depth. A sharp increase was usually noted at the upper edge of the thermocline as a result of phytoplankton accumulating in this denser water mass. The gradual increase in chlorophyll is the result of settling of the plankton organisms. In a shallow epilimnion as encountered in this reservoir, such a gradual increase was not evident until the thermocline was reached.

Analysis of variance performed on the chlorophyll a concentrations (Table 2) in the Old Durham Reservoir at 0.5, 1.5, and 2.5 meters indicate there was no difference between the total chlorophyll a concentrations at 0.5 and 1.5 meters but there was a significant difference between those at 0.5 and 1.5 meters compared with that at 2.5 meters. Such
<table>
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<th>Per Cent</th>
<th>Nannoplankton</th>
<th>Per Cent</th>
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<td>0.50-71.28</td>
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a marked difference is most certainly the result of the algal populations settling and accumulating in deeper, denser water.

**Net Plankton and Nannoplankton Chlorophyll a Concentrations.** On several dates, the chlorophyll a content of net phytoplankton and nannoplankton were measured (Figure 9). These graphs show the seasonal contribution of each component as a percent of the total chlorophyll a. Figure 9 indicates that the greatest contributions of net phytoplankton occurred during the spring and early summer with nannoplankton dominating during the fall. An increased reoccurrence of net phytoplankton was observed during October, November, and January. Analysis of the seasonal distribution of these components indicates that at 0.5 meters the contribution of net phytoplankton is slight and highly variable. Unlike the analysis based on total water column, this analysis lacked the definite pattern evident in the former. The mean value for net phytoplankton at 0.5 meters was 17% of the total with nannoplankton accounting for 83%. The lack of net phytoplankton at this depth may simply be the result of its sinking into deeper water, particularly in the absence of currents adequate for mixing of the epilimnion. This would be reflected in an increase in the percent contribution of this component to the total chlorophyll a with increasing depth. This is illustrated in Table 2. At 1.5 and 2.5 meters a very distinct pattern of net phytoplankton existed as compared to that at 0.5 meters. In addition, there was a definite increase in the percent
Figure 9. Seasonal contribution of netplankton and nannoplankton chlorophyll a to the total chlorophyll a for the total water column ($M^2$) and selected depths.
contribution of this component to the total chlorophyll a with increasing depth. This is illustrated in Table 2. At 1.5 and 2.5 meters a very distinct pattern of net phytoplankton existed as compared to that at 0.5 meters. In addition, there was a definite increase in the per cent contribution to the total chlorophyll a with increasing depth (Table 2).

Riley (1940) in his study of Linsley Pond found a mean chlorophyll concentration of 13.58 mgs/M^3. Manning and Juday (1941) in their studies of Wisconsin lakes found a wide range of values depending upon the type of lake. Scaffold Lake which most closely resembles the Old Reservoir morphometrically, had chlorophyll concentrations ranging from 35-225 mgs/M^3 which are in the same range of those reported here.

**Diurnal Variations in Chlorophyll a Concentration.**

On June 16 and July 27, 1965 diurnal studies of productivity, oxygen, and chlorophyll a were performed in addition to the regular sampling schedule.

In 1957, Doty and Oguri determined that there existed a daily photosynthetic capacity of planktonic algae under constant illumination. Yentsch and Ryther (1957) investigated the relationship between the diurnal in situ fluctuations in the chlorophyll a content of phytoplankton and their photosynthetic capacity when exposed to constant illumination. They determined that the highest concentrations of chlorophyll a occurred during early morning and late
afternoon with lowest values at mid-day and mid-night. In the study of the Old Reservoir, phytoplankton populations were not confined to carboys as in the above study, but single samples were taken from the same location in the reservoir at four hour intervals from 0600 hours to 1800 hours at the surface and 0.5 meter depths. Since only single samples were taken without any attempt to account for possible horizontal heterogeneity of the phytoplankton populations, the results are not intended to be conclusive. In spite of the sampling inadequacies, a definite diurnal fluctuation was evident on both dates at the depths chosen (Table 3). Such diurnal fluctuations can be directly related to fluctuations in light intensity. At high light intensity, such as that encountered in surface waters during mid-summer, the chlorophyll within the cell may undergo photo-oxidation, or show the adaptive behavior postulated by Odum et al. (1959) for surface phytoplankton communities. Since this adaptive behavior is closely related to light intensity, the alternation of low and high light intensities throughout the day would be expected to produce reciprocal diurnal fluctuations in chlorophyll concentration.
<table>
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<td>Surface</td>
</tr>
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<tr>
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</tr>
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</tr>
<tr>
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</tr>
<tr>
<td>9.28</td>
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</tbody>
</table>

**TABLE 3**

**DIURNAL VARIATION IN CHLOROPHYLL A CONCENTRATION (MGS/M³)**
SECTION VI

PRIMARY PRODUCTIVITY

Introduction. Primary productivity can be defined as the rate at which energy is fixed and stored by the photosynthetic or chemosynthetic activity of producer organisms (e.g. green plants, chemosynthetic bacteria) (Odum, 1959). Since all organisms require energy, in the form of food, for the maintenance of metabolic functions, growth, and reproduction, the primary producers form the most important trophic level in terms of energy fixation and storage. It is upon them that all the other trophic levels in an ecosystem must depend for their energy. An accurate measurement of the energy entering an ecosystem is therefore essential to the complete analysis of the community's metabolism.

Primary productivity must be further divided into net primary productivity and gross primary productivity. All organisms require energy for the maintenance of their general metabolic functions. The primary producers, even while photosynthetically fixing energy are also using energy for the support of their own metabolic activity. The total energy involved in both photosynthesis and respiration during a period of time is termed gross primary productivity (Odum, 1959). Net primary productivity is the rate of storage of energy in excess of that used for respiration.
In undertaking the study of primary productivity, it is essential that one know which of these aspects is being measured by the technique employed. Further, depending upon what information is desired, the investigator can choose the technique which best satisfies his experimental design.

The most important question that confronted early workers using the carbon-14 technique was what exactly was it measuring; gross productivity, net productivity, or something else? Steemann-Nielsen (1952) asserted that the technique measured gross photosynthesis minus a small correction for the respiration of recently-labeled carbon. During experiments of short duration (four hours) this correction amounted to approximately four per cent. Ryther (1954) in studying cultures of Dunaliella euchlora at different stages in their growth curves and under nitrogen and phosphorous deficiencies, found that the P:R ratio varied from 10:1 under optimum growth conditions to 1:1 under conditions of complete nutrient deficiency. In all cases the uptake of C-14 corresponded closely with the oxygen produced in excess of respiration, that is, net production was apparently being measured. In studies performed in a large-volume plastic sphere (Antia et al., 1963) the authors stated that in the coastal waters studied, during a diatom bloom, the C-14 method measured the net production of particulate matter, whereas the oxygen method measures the gross total production of organic matter. In 1964, Menzel
and Varraro developed a technique which permitted the direct measurement of carbon uptake and loss by unicellular algae in culture. Ryther and Menzel (1965) using this technique in conjunction with C-14 studies, concluded that the C-14 method gives a reliable measure of the amount of carbon that was fixed during photosynthesis and retained by the algae. They made no attempt to account for the carbon that was fixed and lost. Nevertheless, if large amounts were excreted, it must have been newly-labelled products of photosynthesis otherwise there would not have been such close agreement between the two methods. It would appear then that the carbon-14 technique is measuring net primary productivity. This places an immediate restriction upon it as a tool for the study of community metabolism since it can not be used to study respiration as can the oxygen technique. Further one can not arbitrarily assume a certain constant correction for respiration rate as has been proposed (Steeman-Nielsen, 1952) since nutrient conditions, light conditions particularly near the compensation point, and stage in life-history are all acting to modify this constant. However, since it is only the net productivity that is available to higher trophic levels, it is this value which is often most significant ecologically. One must keep the distinction between the oxygen and C-14 techniques in mind when comparing literature values. In this study the productivity values reflect the net primary productivity and must be viewed as such.

Regional Limnological Studies. Unfortunately, there are very few extensive and systematic limnological studies
of New England lakes and ponds. There are only two published reports involving primary productivity. Most of the reported limnological studies involve the investigation of Connecticut lakes and ponds, particularly Linsley Pond. Under the impetus and direction of G. E. Hutchinson and his staff at Yale, this pond is probably the most intensively investigated lake in New England. Seasonal studies of phytoplankton population dynamics were performed by Riley (1939, 1940) and Hutchinson (1944), paleolimnological and biostratonomic studies by Deevey (1939, 1942), studies on the role of vitamins and lake metabolism (Hutchinson, 1943, Hutchinson and Setlow, 1946, Benoit, 1957, Hutchinson, 1941), phosphorous metabolism (Hutchinson, 1941), studies on the natural occurring isotopes of carbon (Oana and Deevey, 1960, and Deevey and Stuiver, 1964) are a sampling of the diverse types of investigations performed on Linsley Pond as well as other Connecticut lakes. An extensive review of the work performed on New England limnology can be found in Frey's Limnology of North America (1963).

Comprehensive limnological investigations of New Hampshire's lakes and ponds are lacking and except for a survey of the State's major watersheds edited by E. E. Hoover (1937, 1938) and H. E. Warfel (1939), no systematized studies have been reported. Even the latter study, though extensive in scope, provided little useful information on the trophic structure or seasonal phytoplankton and zooplankton population dynamics. With the present emphasis on water
conservation, more information is being collected by state agencies which should result in a more complete limnological picture of this region.

Studies on the primary productivity of New England lakes are limited to two published reports. Riley (1940) studied the seasonal productivity of Linsley Pond but due to technical problems associated with his use of the light and dark bottle oxygen technique his data seem unreliable (Manning and Juday, 1941). A second study (Rupp and DeRoche, 1965) involved the correlation of primary productivity, measured by the carbon-14 technique, with the standing crop of fish populations in three Maine lakes. Productivity measurements in this study were restricted to a few samples during mid-summer and have limited comparative value.

Classification of the Old Durham Reservoir.
Measurements of primary productivity commenced on March 17, 1965 and continued uninterrupted until November, 1965.

The average net primary productivity per M² per day from March to November is 549.18 mgs carbon. If this value were used to calculate the total productivity per year, a value of approximately 150 gms of carbon per M² results. This calculation is actually for only nine months, since during the remaining three months ice covers this reservoir and productivity is very low. This value is similar to those found by Jonasson and Mathiesen (1959) for Esrom Sø (135 gms/M²/year) and Furesø (160 gms/M²/year) in their studies on the primary productivity of two Danish eutrophic
lakes. The production of 150 gms C/M²/year is much lower than the very shallow eutrophic lakes of Denmark which produce in excess of 500 gms C/M²/year, but is considerably higher than the oligotrophic Lunzer Untersee of Austria (40 gms C/M²/year). In comparing the value obtained in this study (549.18 mgs C/M²/day) with those obtained for some eutrophic lakes in the United States one finds that Borax Lake, California, a shallow, hard water lake, has an annual mean productivity of 249.3 mgs C/M²/day (Wetzel, 1964), while Clear Lake, California, a large, shallow, eutrophic lake studied by Goldman and Wetzel (1963) had an annual mean productivity of 437.8 mgs C/M²/day. If placed in Rodhe's (1958) classification of lake types, the old Durham Reservoir would fall into the eutrophic range of the spectrum, whether classification is based on the productivity per M² or M³.

**Seasonal Patterns of Primary Productivity.** The classical seasonal pattern for primary productivity of temperate lakes includes a spring maximum shortly after ice-out, a prolonged period of low productivity during the summer, followed by a second period of high productivity in the autumn after nutrient regeneration of the epilimnion from fall turnover (Ruttner, 1953).

Examination of the seasonal trends of primary productivity reported in the literature indicate that only the spring pulse in productivity is a fairly reliable occurrence. Rodhe (1958) stated that the amount of organic matter produced by the spring maximum on Lake Erken
is nearly constant from year to year. Jonasson and Mathiesen (1959) indicated that Danish lakes may be ice-bound or not, and this may cause the presence or absence of a spring maximum. After the initial spring maximum, the pattern for the rest of the year appears variable. In his studies on Lake Erken, Rodhe et al. (1958) indicated the extent of seasonal pattern variation during the years 1954 and 1955. The former had a much lower spring pulse than the latter, and manifested rather high and widely fluctuating values during the summer and fall. The latter displayed a low productivity during the summer with a definite increase during the fall after turnover. Borax Lake exhibited a definite spring pulse followed by a decline in June with a sudden resurgence in productivity during July and August (Wetzel, 1964). Goldman and Wetzel (1963) working in Clear Lake found a spring maximum followed by a slight decline in June. This was followed by an elevated sustained productivity through the summer with an extremely high pulse (2442 mgs C/m²/day) occurring in October which the author attributed to a bloom of Aphanizomenon ovalisporum Forti. In general, the more eutrophic bodies of water will display a definite spring pulse in productivity, but generally have a high constant productivity throughout the summer and early fall. The latter is often punctuated with unialgal blooms primarily of cyanophycean character. The seasonal productivity pattern of oligotrophic lakes includes both a spring and fall maximum with a sustained period during the summer of low
productivity (Rodhe et al. 1958).

Examination of Figure 10 reveals a pattern for the Old Reservoir that is characteristic of eutrophic lakes. Productivity had already begun to rise during late March and early April in spite of an extensive ice cover. The productivity reached a peak and leveled off at 185 mgs C/m²/day on April 5, 1965 and remained about the same during the ice free period from April 8, 1965 to April 21, 1965. A slight decline in productivity occurred during early May, followed by a gradual but pronounced increase in late May and early June, 1965. Carbon fixation gradually decreased during June, possibly the result of nutrient depletion, and reached a low on June 23, 1965. During the first two weeks of July, the primary productivity of this reservoir experienced its greatest increase (5400 mgs C/m²/day) which was attributable to a bloom of Anabaena planktonica. This bloom was succeeded in August by a Coelosphaerium Nagelianum-Microcystis aeruginosa association which persisted throughout August and September and exhibited a very high sustained productivity. There is the possibility that another peak in productivity occurred early in October, but if so, it was missed in the sampling schedule. During October and November, the productivity dropped precipitously. By January it had fallen to less than 1 mg C/m²/day and on February 7, 1966 primary productivity was non-detectable. It is interesting to note that an increase in productivity was already in progress under the ice just prior to its thawing. In study
Figure 10. The seasonal pattern of primary productivity in the Old Durham Reservoir (1965-1966).
of Lake Erken (Rodhe et al., 1958) the productivity started to rise under the ice and continued shortly afterwards until it reached a peak. Whereas, in this study, the productivity declined after ice-out and did not start to rise until more than three weeks later. The phytoplankton community responsible for this delayed pulse was dominated by Asterionella formosa Hassal which is often involved in spring pulses of temperate lakes (Lund, 1961). Therefore this delayed pulse can probably be called the spring pulse for this reservoir. A possible explanation for the delay may be attributed to the high turbidity evident after ice-out and its effect on light penetration. A second explanation may involve changes in the phytoplankton communities from those responsible for the increase occurring under the ice to that responsible for the spring pulse (Asterionella).

Vertical Distribution of Primary Productivity.
Seasonal patterns of primary productivity when represented for the total water column obscure the more interesting changes that occur within the water column. These vertical profiles (Figure 11) of productivity often provide interesting and supplemental data on the functional attributes of observed phytoplankton population dynamics.

Assuming that planktonic algae within the epilimnion are evenly distributed, one can postulate two basic types of curves to represent the vertical distribution of primary productivity. On a bright sunny day the rate of photosynthesis will increase with depth to an optimum
Figure 11. Vertical distribution of primary productivity for the total phytoplankton populations.
Day 21-IX-1965

Grams C/m³/day

Day 2-IX-1965

Day 15-X-1965

Day 16-XI-1965

Day 21-IX-1965

Day 28-IX-1965

on of primary
the total
ations.
light level and then gradually decline with increasing depth. On an overcast day the light optimum will be at the surface with a continually declining curve with increasing depth. Both these basic types are represented in Figure 11. The uneven distribution of algae within the epilimnion, however, will cause distortions in these curves. The concentration of *Anabaena planktonica* within the top meter of water is an example of such distortion and the effect it has on a productivity profile (Figure 11, 14-VII-65). Another example of curve distortion resulting from differential algal densities is the curves 4-VIII-65 and 12-VIII-65. Both these curves resulted from extremely high densities of *Coelosphaerium Nagelianum* at 1.5 and 2.5 meters. The densities of this alga at 2.5 meters were fifty to one hundred times greater than at 0.5 meters. Therefore, although the light intensity at these depths was greatly reduced the productivity was high simply as a result of such high algal densities. In addition to *Coelosphaerium Nagelianum*, many small flagellates (*Cryptomonas erosa* and *Chroomonas* sp.) were also present.

If a visual comparison of the curves in their proper sequences is made, a pattern seems to be evident which gives some insight into the successional changes occurring. The profiles representing static, non-actively producing populations are exemplified by the dates, 17-111-65 and 10-V-65. Profiles which are slightly convex, 21-IV-65 and 23-VI-65, are indicative of declining populations.
Phytoplankton populations that are actively assimilating carbon often are represented by curves showing a pronounced increase in productivity in the upper 1.5 meters of water (5-IV-65, 4-VI-65, 11-VI-65, 7-VII-65, and 14-VII-65). Generally if a sequence from a non-actively producing population to an actively-producing population is followed, there appears to be at first, a slight increase in production at all depths, succeeded by a marked differential increase in productivity in the upper meter or meter and one-half of water. This is primarily the result of the differential availability of light necessary for photosynthesis. This is supplemented by higher temperatures and leads to differential phytoplankton densities which further accentuate productivity. Occasionally the productivity at the surface is somewhat less than that at 0.5 meters. This may be the result of two factors; a differential phytoplankton density which seems unlikely in a well agitated epilimnion, and from the photo-oxidation of chlorophyll at high light intensities (Goldman et al., 1963).

The annual mean productivity for each depth is summarized in Table 4. Comparing the depths for total productivity, there is a relatively small difference between the surface and half meter values but much greater differences between 0.5 and 1.5 meters and between 1.5 and 2.5 meters. When the original data, from which this table was constructed, were subjected to an analysis of variance, no significant difference was found between the surface and
<table>
<thead>
<tr>
<th></th>
<th>Total Plankton</th>
<th>Net Plankton</th>
<th>% of Total</th>
<th>Nannoplankton</th>
<th>% of Total</th>
</tr>
</thead>
<tbody>
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<td>129.30</td>
<td>33.82</td>
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</tr>
<tr>
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<td>49.83</td>
<td>171.51</td>
<td>50.17</td>
</tr>
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<td>35.48</td>
<td>93.91</td>
<td>64.52</td>
</tr>
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<td>47.16</td>
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<tr>
<td>M^2</td>
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<td>236.56</td>
<td>35.70</td>
<td>312.53</td>
<td>64.30</td>
</tr>
</tbody>
</table>
0.5 meter productivities. The differences between 0.5 and 1.5 meters and between 1.5 and 2.5 meters were highly significant ($P=0.001$). The plankton populations and the environmental factors responsible for productivity at the surface and 0.5 meters were uniform, otherwise significant differences would have resulted. The differences noted in the deeper layers are primarily the result of the rapid attenuation of solar radiation below one meter.

**Summer Nutrient Regeneration.** Active photosynthesis requires that several parameters be satisfied. In addition to adequate supplies of carbon and energy, sufficient quantities of nutrients and vitamins, are necessary. During the summer, when the epilimnion is essentially isolated from nutrient regeneration operative in the metalimnion, this reservoir manifested a very high sustained productivity. Essential nutrients would appear to be removed from circulation and unavailable for the growth of successive epilimnetic phytoplankton populations. Both light and carbon were present in adequate amounts in the epilimnion at all times, except under the ice when the former is a limiting factor.

At least two supplementary explanations may be promulgated to account for the high summer productivity, and the nutrient regeneration necessary to sustain it.

Nutrient replenishment of the epilimnion resulted primarily from bacterial decomposition and nutrient regeneration occurring in the shallow sections of the
reservoir. A considerable portion of this reservoir is very shallow with a high mud surface to volume ratio. This area \((75 \times 10^3 \text{ m}^2)\) is primarily within the 0-2.0 meter contour level. Considerable decomposition and nutrient regeneration occurred in the shallow northwesterly portion of the reservoir. The dissemination of these nutrients was facilitated by the prevailing northwesterly winds and the narrowness of the reservoir basin.

A second explanation involves the characteristics of the phytoplankton communities themselves. The dominant phytoplankters during the summer are cyanophycean, of which several species have the ability to fix atmospheric nitrogen (Fogg, 1956, Hutchinson, 1957), thus excluding this important nutrient as a limiting factor. Further, the requirements of the cyanophyceans for phosphate are lower than for other groups of phytoplankton (Hutchinson, 1944). *Anabaena planktonica* was the first cyanophycean to attain dominance, and was responsible for the highest productivity values observed during this study. Though it is not known whether this particular species fixes nitrogen, other members of this genus do (Hutchinson, 1957 p.847, Fogg, 1956, Dugdale and Dugdale, 1962). Consequently large quantities of nitrogen were probably fixed, with the subsequent release of nitrogenous metabolic products into the water during growth (Hutchinson, 1944, and Dugdale and Dugdale, 1962). The growth of such a population would provide a substratum for bacterial decomposition which would result in the release
of nitrogenous metabolic products into the water during growth (Hutchinson, 1944, and Dugdale and Dugdale, 1962). The growth of such a population would provide a substratum for bacterial decomposition which would result in the release of considerable quantities of nutrients. Since *Anabaena* accumulates at or near the surface, the resulting nutrients would remain in the epilimnion and not be lost to the metalimnion, thus keeping them available for successive phytoplankton populations. The second dominant cyanophycean association was comprised of *Coelosphaerium Naegelianum* Unger and *Microcystis aeruginosa* Kuetzing; emend. Elenkin. It is not known whether either of these two species are capable of nitrogen fixation. Assuming they cannot, the nutrients resulting from the metabolism and decomposition of the *Anabaena* bloom would be expected to provide a favorable nutrient environment for their initial development. Their continued development would be contingent upon further nutrient replenishment which in this situation probably resulted from fall turnover on September 2, 1965. A slight increase in productivity was noted at this time. Thus there are at least two possible explanations that might account for the high summer productivity. The quantitative analysis of each of these and other factors may provide considerable insight into the pattern of nutrient metabolism, regeneration and renewal in small lakes during summer stratification.
Seasonal Contribution of Netplankton and Nannoplankton to the Primary Productivity in the Old Durham Reservoir. The seasonal changes in the per cent of total productivity contributed by nannoplankton and netplankton are illustrated in Figure 12. Prior to ice-out, the net phytoplankton dominated the plankton community and was responsible for 60 to 80% of the total productivity. From May 22 to June 23, 1965, the nannoplankton was responsible for 65% to 85% of the total productivity. Productivity during July was dominated by net phytoplankton (82%) primarily *Anabaena planktonica*. This was succeeded by a *Coelosphaerum-Microcystis* community which appeared to be both netplankters and the dominants during this time, on the basis of qualitative analysis. The distribution of productivity indicated, however, that the nannoplankton accounted for 78% of the total productivity during August. There was a slight increase in net phytoplankton productivity late in September followed by a marked increase in nannoplankton productivity during October with a resurgence of net phytoplankton productivity in November.

Examination of data from Lake Erken (Rodhe et al., 1958) reveals that the high values for nannoplankton production during spring and early summer were due to the small centric diatom *Stephanodiscus pusillus*. The spring diatom pulse evident in this reservoir was due to the much larger pennate diatom, *Astrionella formosa* which is usually retained by #25 plankton netting. Rodhe et al.
Figure 12. The per cent contribution of netplankton and nannoplankton to the total productivity during 1965.
(1958) reported the highest values for net phytoplankton production in July, August, and September when blue-green algae were dominant. A similar pattern was observed in this reservoir except that the peak for net plankton production was reached in July rather than in August as it was in Lake Erken.

The data for Lake Erken indicate that the average annual contribution of the net phytoplankton to the total productivity was 15-25% while that of the nannoplankton was 75-85%. Verduin (1956) stated that 35% of the total productivity of Lake Erie is attributable to netplankton and 65% to nannoplankton. The mean values determined for the total water column in this study were 35.7% for the net phytoplankton and 64.3% for the nannoplankton. Thus in all of these lakes phytoplankton populations less than 60 microns are responsible for most of the productivity throughout the year.

Verduin's data from western Lake Erie (1956, Table II) indicate that the maximum values for nannoplankton production occurred during late summer and autumn when it accounted for 93% to 100% of the total production. The contribution of the components appeared equal during winter with net phytoplankton production dominant in the spring (61%) and early summer (59%).

The construction of a generalized pattern for the seasonal contribution of net phytoplankton and nannoplankton from the above studies is possible. The value of such a
generalization is limited since there is considerable variation between the phytoplankton communities in these lakes as well as yearly variations within the same lake. In eutrophic lakes that characteristically have cyanophycean blooms, the contribution of the net phytoplankton is highest during July and August, with the nannoplankton dominating during spring and fall. The relative importance of each component during the winter varies, being approximately equal in this reservoir and Lake Erie, but in favor of the nannoplankton in Lake Erken.

As mentioned earlier several other authors have also investigated the relative contributions of ultraplankton and netplankton, but arbitrarily selected 0.45 to 10 microns and those forms greater than 10 microns as their size categories. Wetzel (1964) indicated that during the summer months most photosynthetic activity resulted from forms greater than 10 microns while the significance of the ultraplankton increased and became dominant in the winter months. Similar findings were reported for other eutrophic waters (Lund, 1961, Goldman and Wetzel, 1963). This relationship of size to seasonal variation in environmental conditions has been related to the inherent advantages of reduced surface area to volume ratios during periods when light and nutrients are limiting (Rodhe et al., 1958). The shift of phytoplankton populations to smaller forms more suited to a changing, more restrictive environment appears to be a common mode of adaptation among fresh-water forms (Wetzel, 1964). Another possible
explanation for this seasonal size shift is the possibility of a change of dominance from autotrophic to heterotrophic productivity. Confirmation of this hypothesis has been obtained using carbon-14 labelled organic compounds (Parsons and Strickland, 1962, Wright and Hobbie, 1965).

**Vertical Distribution of Net Phytoplankton and Nannoplankton Productivity.** In addition to examining the seasonal changes of net phytoplankton and nannoplankton productivity, it seemed desirable, especially in such a shallow lake, to investigate this same relationship vertically within the water column. Previous studies involved only one depth in the epilimnion or the data was pooled thus making comparative analysis impossible. The vertical distributions of netplankton and nannoplankton productivity on each sampling date are represented in Figure 13. Examination of these curves is very instructive, showing not only which component of the phytoplankton population is responsible for the productivity, but also the role of these components with increasing depth. One interesting sequence is that involving the development of the net phytoplankton bloom of *Anabaena* *planktonica*. This sequence commences with the graph 30-VI-65 and terminates with 27-VII-65. At the beginning of this bloom, the relative contributions of netplankton and nannoplankton to the total productivity are similar at each depth. On 7-VII-65 the nannoplankton production remained constant but a marked increase occurred in the net phytoplankton production within
Figure 13. Vertical distributions of netplankton productivity and nannoplankton productivity. Netplankton (solid line); Nannoplankton (dashed line).
the top meter of water. By 14-VII-65, the net phytoplankton production had reached a peak with evidence that the nannoplankton productivity was also starting to increase. The latter resulted from considerable fragmentation of *Anabaena* trichomes which passed through the plankton net. As the *Anabaena* population became senescent, more fragmentation occurred which accounted for the continued increase in nannoplankton production on 21-VII-65. By this time, however, the total productivity had decreased to approximately 33% of its peak value. Another interesting sequence is that described previously for the month of August.

Examining the components on a percentage basis for each depth (Table 4), reveals that on an annual basis, nannoplankton production always exceeded netplankton production. The surface and 1.5 meter depths displayed very similar percentages while the contributions of each component was essentially equal at 0.5 meters. The greatest divergence was observed at 2.5 meters where the annual mean productivity of the nannoplankton exceeded 75% of the total productivity at this depth. At this depth light penetration was poorest, often with less than five per cent of the incident radiation reaching it. Further, this area was in the metalimnion, often devoid of oxygen, and had a high concentration of carbon dioxide. During stratification the plankton communities were characterized by many small flagellates such as *Chroomonas* sp. and *Cryptomonas eros* which are known to be heterotrophic (Wright, 1964). In
addition to these, dinoflagellates (*Ceratium hirundinella* (O.F. Mueller) dujardini and *Glenodinium* sp.), a diverse group of euglenoids (*E. polymorpha* Dangeard, *E. acus* Ehrenberg, *Phacus orbicularis* Huebner) and several species of *Trachelomonas* (especially *T. volvocina* Ehrenberg), all contributed to the plankton communities occupying this stratum. Under certain conditions these flagellates were extremely abundant and were probably responsible for much of the observed productivity at this depth. Since the conditions at this depth appear to be more favorable for heterotrophic rather than autotrophic metabolism, a study of this factor may be illuminating.
SECTION VII

PRIMARY PRODUCTIVITY AND CHLOROPHYLL A CONCENTRATION

Introduction. Since chlorophyll a is the primary photosynthetic catalyst, there should be a functional relationship between its concentration and the rate of photosynthesis. Further, at and below light saturation, at a given temperature, the rate of photosynthesis should be linear with respect to both chlorophyll concentration and light intensity. The elucidation of this relationship has been the object of considerable research both in culture (Emerson, 1929, Emerson et al., 1940, cited by Strickland, 1960) and in natural phytoplankton populations (Manning and Juday, 1941, Edmondson, 1955, Ryther, 1956, Ryther and Yentsch, 1957, Odum et al., 1959, Strickland, 1960, Wright, 1959, Verduin, 1956, Cassie, 1963, and Anderson and Banse, 1965). In general, it appears that a definite functional relationship exists, but the extent of the relationship varies considerably. This variation has been attributed to fluctuations in temperature, nutrients, and light conditions. In addition, there has been no standardization of the methods for measuring chlorophyll concentration or the rate of photosynthesis in these studies. Thus it would appear that no simple equation can be formulated to relate chlorophyll concentration and light data to primary
productivity (Strickland, 1960). Saunders et al. (1962) categorically reject the use of chlorophyll concentration as an estimate of standing crop or metabolic density in any refined analysis of photosynthesis in natural waters. Not all workers share this view, and several have found a rather high statistical correlation between primary production and chlorophyll concentration (Edmondson, 1955, Ryther, 1956, Wright, 1959, Anderson and Banse, 1965, and Cassie, 1963). As most of this work has been performed either in the open ocean or in large freshwater lakes, it seemed worthwhile to investigate this relationship in a shallow eutrophic lake.

**Primary Productivity and Chlorophyll a Concentration.**

To investigate this relationship, simultaneous determinations of chlorophyll a concentration and primary productivity were performed. As only three to five samples were collected each month, no statistically valid results could be obtained by grouping data by month, temperature, or phytoplankton communities. This may not be as much of a disadvantage as first thought, because Edmondson (1955) and Ryther (1956) both concluded that their observed correlations between chlorophyll a and primary productivity were independent of changes in species composition. Therefore, light penetration, temperature, and nutrient concentration were the main variables operative.

Chlorophyll a only was chosen for this study because it is the primary pigment involved in the
photosynthetic mechanism, it can be measured with greatest accuracy, and it is common to all phytoplankton species. Some of the best correlations have been found with chlorophyll a (Anderson and Banse, 1965) or with chlorophyll a and carotene (Cassie, 1963, Wright, 1964, Yentsch, 1962, McAllister et al., 1961).

The results of the correlations determined in this study are summarized in Table 5. The best correlations were found in the upper meter of water where the plankton populations were well mixed, and the light intensity within the optimal intensity and spectral range for photosynthesis. With increasing depth, light conditions became marginal, the water column became stratified at 2.5 meters accompanied by oxygen depletion, H₂S formation, and pH changes. These factors appeared particularly detrimental to phytoplankton as evidenced by the poor correlations found at this depth for total phytoplankton and net phytoplankton. Closer examination of these data revealed that most of the variation resulted from the net phytoplankton. It was the latter which gave the poorest correlation at 2.5 meters (r=0.196). A possible explanation for this is that the net phytoplankton as classified in this study (>60 microns) tend to settle rapidly into deeper water. Evidence for this assumption is that there were significant differences in net phytoplankton chlorophyll a concentrations at 0.5 and 1.5 meters. There were no differences when nannoplankton or total plankton chlorophyll a were analysed. The rapid
<table>
<thead>
<tr>
<th>Depth</th>
<th>Total Phytoplankton</th>
<th>Net Phytoplankton</th>
<th>Nanoplankton</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5M</td>
<td>( Y = 11.56X - 62.79 )</td>
<td>( Y = 50.32X - 67.25 )</td>
<td>( Y = 6.03X - 11.34 )</td>
</tr>
<tr>
<td></td>
<td>( r^2 = 0.682 )</td>
<td>( r^2 = 0.656 )</td>
<td>( r^2 = 0.752 )</td>
</tr>
<tr>
<td></td>
<td>( r = 0.835 )</td>
<td>( r = 0.809 )</td>
<td>( r = 0.887 )</td>
</tr>
<tr>
<td></td>
<td>( P = 0.001 )</td>
<td>( P = 0.001 )</td>
<td>( P = 0.001 )</td>
</tr>
<tr>
<td>1.5M</td>
<td>( Y = 2.09X + 27.43 )</td>
<td>( Y = 1.76X - 13.21 )</td>
<td>( Y = 2.50X + 4.86 )</td>
</tr>
<tr>
<td></td>
<td>( r^2 = 0.275 )</td>
<td>( r^2 = 0.162 )</td>
<td>( r^2 = 0.417 )</td>
</tr>
<tr>
<td></td>
<td>( r = 0.524 )</td>
<td>( r = 0.402 )</td>
<td>( r = 0.646 )</td>
</tr>
<tr>
<td></td>
<td>( P = 0.020 )</td>
<td>( P = 0.100 )</td>
<td>( P = 0.010 )</td>
</tr>
<tr>
<td>2.5M</td>
<td>( Y = 0.88X - 0.71 )</td>
<td>( Y = -0.12X + 9.69 )</td>
<td>( Y = 1.58X - 18.92 )</td>
</tr>
<tr>
<td></td>
<td>( r^2 = 0.239 )</td>
<td>( r^2 = 0.038 )</td>
<td>( r^2 = 0.639 )</td>
</tr>
<tr>
<td></td>
<td>( r = 0.483 )</td>
<td>( r = 0.196 )</td>
<td>( r = 0.799 )</td>
</tr>
<tr>
<td></td>
<td>( P = 0.050 )</td>
<td>( P = 0.500 )</td>
<td>( P = 0.001 )</td>
</tr>
</tbody>
</table>
settling of the net phytoplankton into deeper water, and into conditions for which they were not adapted, would account for the poor correlation found at this depth. The nannoplankton communities dominant in the deeper waters were mostly flagellates (Pyrrophyta, cryptomonads, and Euglenophyta) that appeared to be well suited to the conditions at these depths. Thus a better correlation was found between their chlorophyll a content and primary productivity. The improved relationship evident with the nannoplankton would offset some of the poor correlation found for the net phytoplankton, resulting in an intermediate correlation when the total plankton population was considered.

The correlation coefficients found in this study agree consistently with those of other workers. Taking the correlation coefficient \((r=0.835)\) for total plankton at 0.5 meters as being representative of optimal conditions, close agreement is found with Edmondson (1955, \(r=0.860\)), Anderson and Banse (1965, \(r=0.591-0.928\)), Cassie (1963, \(r=0.788\)), and Wright (1959, \(r=0.910\)). Fifteen species investigated by Ryther (1956) showed a linear relationship between chlorophyll a concentration (up to 0.04 mg/l) and photosynthesis at constant light intensity.

From the data presented above, one can conclude that in a well mixed epilimnion, under optimal light intensities, there exists a statistically significant correlation between chlorophyll a concentration and primary productivity. At low light intensities, within the thermocline and
hypolimnion much poorer correlations may be expected. The physiological sensitivity of the phytoplankton community to its environmental conditions appears to be accurately manifested in its chlorophyll a concentration. It does not seem unreasonable therefore to consider it as an adequate measure of functional standing crop under the above defined conditions. No better correlations have been found using cell volume (Wright, 1959, Verduin, 1957) or cell surface area (Paasche, 1960). When the amount of work involved in the latter techniques is considered, the ease with which chlorophyll a is determined renders this technique even more attractive.
SECTION VIII

ASSIMILATION COEFFICIENT

Introduction. Having determined the existence of a statistically significant relationship between chlorophyll a concentration and the rate of photosynthesis, the next problems are to quantify this relationship and to investigate the effects of such environmental variables as light intensity and temperature. Unfortunately, the data from the literature do not suggest any simple relationship between environmental factors, chlorophyll concentration, and assimilation (Odum et al., 1959, Strickland, 1960). The most important reason for this is that chlorophyll containing systems show considerable adaptation to environmental conditions. It is certain aspects of this adaptive behavior that will be discussed below as it is manifested in changes in the assimilation coefficient.

Assimilation Coefficient. Assimilation coefficient may be defined as the amount of carbon synthesized per unit of chlorophyll a per unit of time, preferably at a standard illumination. Literature values are presented for a variety of algal species, temperatures, nutrient concentrations and illuminations. The range of such values is between 1.0 and 10.0 mgs C/mg chlorophyll a/hour at 0.1 ly/min. of illumination (Strickland, 1960). Extensive tabular reviews of much of the work on assimilation
coefficients can be found in Strickland (1960) and Odum et al. (1959).

In this study, assimilation coefficients were determined for total plankton, net phytoplankton and nannoplankton at 0.5, 1.5, and 2.5 meters. The results of these determinations are found in Figures 14 and 15. The assimilation coefficient for the total plankton showed considerable variation both with season and depth. At 0.5 meters, which represents approximately optimal illumination (0.1-0.2 ly/min) for most of the year, the range is 0.09 to 5.5 with a mean of 1.9. The values at 1.5 meters are generally lower except for one day (September 7, 1965). The range at this depth is 0.02 to 1.8 with a mean of 0.76. The range of values at 2.5 meters is zero to 0.63 with a mean of 0.18. The mean for the total euphotic zone is 0.965 mgs C/mg chlorophyll a/hour. Thus there is a definite decrease in assimilation coefficient with increasing depth which parallels a decrease in light intensity and an increase in chlorophyll a concentration (Table 6). The vertical distributions of the assimilation coefficients and light are almost linear when plotted logarithmically. When the assimilation coefficients were plotted logarithmically with chlorophyll a concentration, a similar relationship was found (Figures 16 and 17).

Table 7 shows the relationship between the average optimum assimilation coefficient, the average temperature at 0.5 meters, and the extinction coefficient between the
Figure 14. Seasonal patterns of assimilation coefficients for the total phytoplankton population.
Figure 15. Seasonal patterns of assimilation coefficients for total plankton (- - - - -), netplankton (o---o), and nannoplankton (+--+-) for the total water column (m^2).
<table>
<thead>
<tr>
<th>Depth</th>
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<th>Chlorophyll a Concentration</th>
<th>Light Trans. Percent</th>
</tr>
</thead>
<tbody>
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<tr>
<td><strong>Total Phytoplankton</strong></td>
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<tr>
<td>M²</td>
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<tr>
<td><strong>Net Phytoplankton</strong></td>
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<td></td>
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<td>10.36</td>
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<td>1.613</td>
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<tr>
<td>M²</td>
<td>3.438</td>
<td>7.31</td>
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<tr>
<td><strong>Nannoplankton</strong></td>
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<td>0.5M</td>
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<td>17.05</td>
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<td>0.704</td>
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<td>0.192</td>
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<tr>
<td>M²</td>
<td>0.732</td>
<td>21.64</td>
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</table>
Figure 16. The relationship between assimilation coefficient and light transmission for total plankton, netplankton, and nannoplankton.
Figure 17. The relationship between assimilation coefficient and chlorophyll a concentration for total plankton, netplankton and nannoplankton.
<table>
<thead>
<tr>
<th>MONTH</th>
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<th>TEMPERATURE °C</th>
<th>EXTINCTION COEFFICIENT</th>
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<td>March</td>
<td>0.229</td>
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<td>0.264</td>
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</tr>
<tr>
<td>May</td>
<td>1.105</td>
<td>18.25</td>
<td>3.41</td>
</tr>
<tr>
<td>June</td>
<td>2.361</td>
<td>22.60</td>
<td>2.41</td>
</tr>
<tr>
<td>July</td>
<td>3.732</td>
<td>24.40</td>
<td>2.51</td>
</tr>
<tr>
<td>August</td>
<td>1.822</td>
<td>23.80</td>
<td>1.72</td>
</tr>
<tr>
<td>September</td>
<td>1.732</td>
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<td>October</td>
<td>1.295</td>
<td>10.60</td>
<td>1.83</td>
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</tbody>
</table>
surface and 0.5 meters for each month. There is no observable relationship between assimilation coefficient and extinction coefficient. The relationship between assimilation coefficient and temperature is at least positively correlated but not describable in a linear manner. Wright (1959) observed similar relationships which were not easily defined.

Odum et al. (1959) postulated four types of chlorophyll adaptations to light intensity by producer systems. The phytoplankton distributions characteristic of this reservoir would fall into their category exemplified by a stratified community. In this type of community, there is an increase in chlorophyll concentration with depth. Part of the increase in chlorophyll content in this reservoir is the result of differential phytoplankton densities resulting from settling and entrapment of algae in the metalimnion. In addition there is probably an adaptive relationship operative.

Phillips and Myers (1954), Sargent (1940), Gessner (1955, cited by Odum et al., 1959) found that light-adapted cells had less chlorophyll per cell than shade-adapted cells. The explanation for these observations is that the rate of chlorophyll biosynthesis appears to be inversely related to light intensity. Detrimental effects appear at and above 0.5 ly/min (Strickland, 1958) or 0.2 ly/min (Talling, 1961, cited by Goldman et al., 1963). The actual mechanisms involved are discussed by Goldman et al. (1963) and the
adaptive significance by Odum et al. (1959). They stated
that successfully surviving photosynthetic systems have a
mechanism whereby they can alter the concentration of their
energy gathering mechanism (e.g. chlorophyll concentration)
in order to adapt to the rate of energy influx (solar
radiation) so as to develop maximum power output of the
entire population throughout the euphotic zone. For the
optimum functioning of the input-output system postulated
by Odum et al. (1959), less chlorophyll will be needed at
high light intensities and more at lower light intensities.
The decreased chlorophyll concentrations in the well-lighted
surface waters permit more light to penetrate to deeper
water where it can be used. As the amount of available light
energy decreases with depth, more chlorophyll is needed to
capture enough light energy to maintain an optimum input-
output adjustment. At decreased light intensities, the need
to synthesize more chlorophyll exists which also requires
energy. This decreases the net amount of carbon produced
by the cell and as a result the assimilation coefficient
decreases. A further example of this adaptive behavior,
other than the vertical distribution discussed above, is
the diurnal changes that might occur. As the light intensity
increases throughout the morning and early afternoon, one
would expect a decrease in chlorophyll a content. If this
were adaptive and not the result of light injury, the rate
of primary production should increase or at least remain
constant. This coupled with a decrease in chlorophyll a
adaptive significance by Odum et al. (1959). They stated that successfully surviving photosynthetic systems have a mechanism whereby they can alter the concentration of their energy gathering mechanism (e.g. chlorophyll concentration) in order to adapt to the rate of energy influx (solar radiation) so as to develop maximum power output of the entire population throughout the euphotic zone. For the optimum functioning of the input-output system postulated by Odum et al. (1959), less chlorophyll will be needed at high light intensities and more at lower light intensities. The decreased chlorophyll concentrations in the well-lighted surface waters permit more light to penetrate to deeper water where it can be used. As the amount of available light energy decreases with depth, more chlorophyll is needed to capture enough light energy to maintain an optimum input-output adjustment. At decreased light intensities, the need to synthesize more chlorophyll exists which also requires energy. This decreases the net amount of carbon produced by the cell and as a result the assimilation coefficient decreases. A further example of this adaptive behavior, other than the vertical distribution discussed above, is the diurnal changes that might occur. As the light intensity increases throughout the morning and early afternoon, one would expect a decrease in chlorophyll a content. If this were adaptive and not the result of light injury, the rate of primary production should increase or at least remain constant. This coupled with a decrease in chlorophyll a
would result in an increase in the assimilation coefficient. When the diurnal data for June 16, and July 27, 1965 were analyzed, Odum's hypothesis was confirmed (Table 8).

The system described above permits the most efficient use of available light energy. When the whole euphotic zone was considered, Ichimura (1958), (cited by Odum et al., 1959) found an increase in the assimilation coefficient as the total chlorophyll increased. A similar relationship was noted in this study when the mean assimilation coefficient /M² was compared to the mean chlorophyll a concentration /M². Wright (1959) on the other hand, found that both euphotic zone photosynthesis and optimal photosynthesis decreased with increasing chlorophyll concentration. In this study, if the optimal rate of photosynthesis is taken as that at 0.5 meters (34% of the incident radiation) and compared with standing crop at the same depth, an inconclusive relationship is observed, although it appears that there is a decrease in optimal photosynthesis with increase in standing crop.

In addition to variations in light intensity, other environmental factors have an effect upon the adaptive behavior of the chlorophyll-photosynthesis system. As temperature increases, the rates of reactions and recycling of materials increases, thus, less materials are needed for the same flux of energy because the materials are re-used more often. Such a situation appears to be limited to a population which does not show a substantial increase.
### TABLE 8

**DIURNAL VARIATION IN ASSIMILATION COEFFICIENTS, PRIMARY PRODUCTION, AND CHLOROPHYLL A CONCENTRATION**

<table>
<thead>
<tr>
<th>TIME</th>
<th>PRIMARY PRODUCTION</th>
<th>CHLOROPHYLL A CONCENTRATION</th>
<th>ASSIMILATION COEFFICIENT</th>
</tr>
</thead>
<tbody>
<tr>
<td>June 16, 1965</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0600</td>
<td>50.50</td>
<td>6.90</td>
<td>1.83</td>
</tr>
<tr>
<td>1000</td>
<td>85.00</td>
<td>4.00</td>
<td>5.30</td>
</tr>
<tr>
<td>1400</td>
<td>105.00</td>
<td>9.25</td>
<td>2.84</td>
</tr>
<tr>
<td>1800</td>
<td>21.30</td>
<td>14.14</td>
<td>0.37</td>
</tr>
<tr>
<td>July 27, 1965</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0600</td>
<td>87.60</td>
<td>12.50</td>
<td>1.73</td>
</tr>
<tr>
<td>1000</td>
<td>354.00</td>
<td>11.80</td>
<td>7.45</td>
</tr>
<tr>
<td>1400</td>
<td>279.00</td>
<td>8.60</td>
<td>8.15</td>
</tr>
<tr>
<td>1800</td>
<td>9.65</td>
<td>12.00</td>
<td>2.00</td>
</tr>
</tbody>
</table>
Consequently, at higher temperatures, less chlorophyll may be needed at any instant because of the greater possible turnover rate. Thus, there may be a slight increase in assimilation number with higher temperatures (Rabinowitch, 1956, Myers and Katz, 1955, cited by Odum et al., 1959).

Another consideration is cell size. Metabolism and diffusion vary as the one-third power of the linear thickness of the tissue (Odum, 1956). In small cells with more chemical respiratory turnover per gram, more chlorophyll per gram is necessary to maintain the proper input-output optimum than in large cells. Working with Chlorella ellipsoida, Tamiya et al. (1953) found that the smaller cells had more chlorophyll per gram than did larger cells. If increases in chlorophyll concentration in smaller cells were not offset by their higher net productivity, larger cells with less chlorophyll might have greater assimilation coefficients. I am not aware of any experiments which relate to this problem. However, when the assimilation coefficients for the net phytoplankton and nannoplankton are compared (Figure 15), the net phytoplankton had consistently greater assimilation coefficients and lower chlorophyll concentrations. However, the extremely high assimilation coefficients of the former raise the question of possible technical error.

There are, therefore, several factors which can markedly modify assimilation coefficients. As a result, there is no universal value that can be used to predict
productivity from chlorophyll concentration. Ryther and Yentsch (1957) postulated a mean assimilation value of 3.7 for oceanic waters which was closely approximated by Wright (1959) for a fresh-water lake. It must be kept in mind that these are optimal values. In natural populations this value varies by an order of magnitude (Wright, 1959, Strickland, 1960). Cassie (1963) reported that a value of 4.8 would introduce less bias than the 3.7 proposed by Ryther and Yentsch. These values are considerably higher than that found in this study (1.958).
SECTION IX

EFFICIENCY OF THE PLANKTONIC PRIMARY PRODUCERS

Introduction. The ultimate source of energy for the maintenance of biological activity is the sun. Only a small fraction, however, of the incident solar radiation is fixed by photosynthetic organisms and converted into organic matter which can be utilized for the growth and reproduction of the primary producers themselves and as an energy source for all non-photosynthetic organisms (Odum, 1959). Because the primary producers form the connecting link between solar energy and organic synthesis, the amount of energy that has been fixed by the photosynthetic organisms in the net production of organic matter will ultimately limit the number of non-photosynthetic organisms that can exist at higher trophic levels. Since, in the transfer of energy from one trophic level to another, entropy increases, a thermodynamic limit is established on the amount of energy flowing within a community. Therefore it is of interest to determine how efficient the phytoplankton community is in its utilization of available solar energy.

Research into the mass culture of algae for food sources, have demonstrated that under rigidly controlled conditions of light, temperature, and nutrient replenishment, efficiencies of 20 to 50 per cent can be achieved (Tamiya, 1957).
As will be evident from the following discussion, there is considerable discrepancy between the values cited above and those obtained from the study of natural photosynthetic communities. In the latter the efficiency of the primary producers rarely exceeds one or two per cent. The efficiencies in natural communities would be expected to vary widely depending on seasonal changes in temperature, light species composition of the plankton community, and available nutrients. This would result in wide fluctuations in the energy flow within an ecosystem throughout the year. Since in the reservoir investigated in this study, the planktonic primary producers were the most important source of energy in the ecosystem, a seasonal study of their efficiency was performed.

**Seasonal Efficiency of the Primary Producers.** The efficiency of the primary producing community is defined as the ratio of energy fixed photosynthetically per unit time to the quantity of photosynthetically utilizable energy per unit time. Any factor that changes either of the above variables will obviously alter the efficiency of the community.

The efficiency under a thick ice cover with several inches of snow cover was quite low as evidenced by the value for March 17, 1965. A pronounced increase in efficiency was detected on April 5, 1965 although the ice cover still persisted. The light penetration had increased from that recorded on March 17 (Table 9),
### TABLE 9

**RELATIONSHIP BETWEEN EFFICIENCY AND USEABLE LIGHT - 1965**

<table>
<thead>
<tr>
<th>Date</th>
<th>Gm·cal/M²/Day $\times 10^4$</th>
<th>Efficiency</th>
</tr>
</thead>
<tbody>
<tr>
<td>17-III</td>
<td>31.70</td>
<td>0.108</td>
</tr>
<tr>
<td>5-IV</td>
<td>53.90</td>
<td>0.610</td>
</tr>
<tr>
<td>21-IV</td>
<td>181.00</td>
<td>0.214</td>
</tr>
<tr>
<td>10-V</td>
<td>158.60</td>
<td>0.172</td>
</tr>
<tr>
<td>22-V</td>
<td>181.00</td>
<td>0.330</td>
</tr>
<tr>
<td>26-V</td>
<td>223.50</td>
<td>0.244</td>
</tr>
<tr>
<td>11-VI</td>
<td>215.00</td>
<td>0.535</td>
</tr>
<tr>
<td>16-VI</td>
<td>264.20</td>
<td>0.317</td>
</tr>
<tr>
<td>23-VI</td>
<td>225.00</td>
<td>0.304</td>
</tr>
<tr>
<td>30-VI</td>
<td>93.00</td>
<td>0.690</td>
</tr>
<tr>
<td>7-VII</td>
<td>228.50</td>
<td>0.989</td>
</tr>
<tr>
<td>14-VIII</td>
<td>235.50</td>
<td>3.630</td>
</tr>
<tr>
<td>21-VII</td>
<td>255.00</td>
<td>0.824</td>
</tr>
<tr>
<td>4-VIII</td>
<td>232.00</td>
<td>0.864</td>
</tr>
<tr>
<td>12-VIII</td>
<td>265.00</td>
<td>0.709</td>
</tr>
<tr>
<td>24-VIII</td>
<td>283.00</td>
<td>0.351</td>
</tr>
<tr>
<td>2-IX</td>
<td>255.00</td>
<td>0.605</td>
</tr>
<tr>
<td>16-IX</td>
<td>208.50</td>
<td>0.447</td>
</tr>
<tr>
<td>21-IX</td>
<td>163.20</td>
<td>0.390</td>
</tr>
<tr>
<td>23-IX</td>
<td>164.50</td>
<td>0.707</td>
</tr>
<tr>
<td>15-X</td>
<td>162.25</td>
<td>0.073</td>
</tr>
<tr>
<td>9-XI</td>
<td>97.50</td>
<td>0.049</td>
</tr>
</tbody>
</table>
resulting in a definite increase in production within the produced conditions of near light saturation for the phytoplankton community which resulted in an increase in efficiency. After ice-out, the productivity on April 21, 1965 was almost identical to that found under the ice on April 5, 1965 but its distribution within the water column was more uniform because of the greater light penetration. The efficiency on April 21, 1965 was only one-third of that found on April 5, 1965 which indicates that although there was a tripling of the available light energy (Table 9) after ice-out, most of it was not used. We can generalize that whenever the available light is at or near the saturation level, photosynthesis is most efficient providing other factors are equitable. All solar radiation above the saturation value is wasted photosynthetically. Therefore, light intensities above saturation, but below the level that produce light injury are non-limiting and changes in phytoplankton productivity are dependent on other factors. We find then, that the changes in efficiency after ice-out are closely related to the total productivity (Figure 18). Although the total quantity of incident solar radiation increased during spring and summer, these increases were less significant than the changes in the rates of energy fixation by the phytoplankton.

The range of efficiencies noted in this study were 0.067% to 5.95% with an annual mean of 0.50%. Table 10 is a summary of the mean efficiencies for the total water
TABLE 10
MEAN MONTHLY PHYTOPLANKTON EFFICIENCIES

<table>
<thead>
<tr>
<th>Month</th>
<th>M²</th>
<th>S</th>
<th>0.5</th>
<th>1.5</th>
<th>2.5</th>
</tr>
</thead>
<tbody>
<tr>
<td>March</td>
<td>0.108</td>
<td>0.107</td>
<td>0.164</td>
<td>0.052</td>
<td>---</td>
</tr>
<tr>
<td>April</td>
<td>0.299</td>
<td>0.157</td>
<td>0.548</td>
<td>0.400</td>
<td>0.090</td>
</tr>
<tr>
<td>May</td>
<td>0.184</td>
<td>0.092</td>
<td>0.269</td>
<td>0.343</td>
<td>0.131</td>
</tr>
<tr>
<td>June</td>
<td>0.512</td>
<td>0.178</td>
<td>0.501</td>
<td>0.650</td>
<td>0.720</td>
</tr>
<tr>
<td>July</td>
<td>1.565</td>
<td>0.580</td>
<td>1.678</td>
<td>2.201</td>
<td>1.800</td>
</tr>
<tr>
<td>August</td>
<td>1.320</td>
<td>0.124</td>
<td>0.361</td>
<td>0.809</td>
<td>3.930</td>
</tr>
<tr>
<td>September</td>
<td>0.423</td>
<td>0.157</td>
<td>0.336</td>
<td>0.693</td>
<td>0.507</td>
</tr>
<tr>
<td>October</td>
<td>0.064</td>
<td>0.035</td>
<td>0.069</td>
<td>0.083</td>
<td>0.067</td>
</tr>
<tr>
<td>November</td>
<td>0.038</td>
<td>0.017</td>
<td>0.045</td>
<td>0.053</td>
<td>---</td>
</tr>
<tr>
<td>( \bar{X} )</td>
<td>0.504</td>
<td>0.161</td>
<td>0.442</td>
<td>0.588</td>
<td>1.030</td>
</tr>
</tbody>
</table>
column and the individual depths studied. The efficiencies for the total water column (m²) increased throughout the spring reaching a maximum in July and gradually declining after that. The efficiencies were lowest at the surface and increased with depth (decreasing light intensity) with maximum efficiencies occurring at 1.5 and 2.5 meters. This pattern is in agreement with that postulated for a stratified community (Odum et al., 1959). Approximate illumination at these depths was 1,200 and 400 foot-candles respectively, which are near the optimum for some algae (Ryther, 1956b). Because the above efficiencies resulted from measurements of net primary productivity, their ecological significance is enhanced, since it is the net organic synthesis that is available for use by organisms at higher trophic levels.

Previous estimates of primary producer efficiencies involved a variety of techniques and types of primary producers. Transeau (1926) performed one of the pioneer studies on the accumulation of energy by plants when he constructed the energy budget of a cornfield. He determined that a corn plant utilizes about 1.6% of the energy reaching it. He assumed that only 20% of the total radiation was used in photosynthesis, thus the corrected efficiency was 8%. The photosynthetically active portion of the electromagnetic spectrum comprises approximately 50% of the total radiation incident to the earth's surface. Transeau's value recalculated on this basis results in an actual efficiency of 3.2%. This efficiency represents the efficiency
only during the growing season whereas the following study performed on the primary producers of Lake Mendota included the entire year (Juday, 1940). Juday calculated the net efficiency as being 0.4% assuming an average turnover of the phytoplankton every two weeks. He recalculated the efficiency to be 0.91%, assuming a weekly turnover time. Lindeman (1942) determined the progressive efficiencies of three trophic levels in Cedar Bog Lake and recalculated the efficiencies of the four trophic levels of Juday in Lake Mendota. The efficiency of the primary producers in Lake Mendota, a eutrophic lake, was 0.41% while that of Cedar Bog Lake, a senescent bog, was only 0.10% annually. It must be noted that neither of these studies included a correction for the photosynthetically active range of the spectrum. Hutchinson (cited by Frey, 1963) recalculating Riley's (1940) data from Linsley Pond, estimated an efficiency of 0.112% based on gross productivity measurements. Riley's (1940) measurements of primary productivity seem unreliable however, due to the excessively long incubation periods employed. In another study, Riley (1944) estimated the efficiency of the oceans at 0.18% based on total incident radiation. Rodhe (1958) in a 23 month study of Lake Erken, reported an uncorrected efficiency of 0.12%. Finally, Odum (1957) in his study of the trophic structure of Silver Springs found an annual net efficiency corrected for the photosynthetically active portion of the spectrum of 5.0%. This is the highest value for a natural community yet reported.
The values cited above and those found in this study are very similar when one consider the diverse methods employed in their determination. The range for natural aquatic communities appears to be between 0.10% and 5.0% with most values near 0.50%.
SECTION X

PHYTOPLANKTON POPULATION DYNAMICS

Introduction. This section describes a comprehensive investigation of the vertical and seasonal phytoplankton communities of the eutrophic Old Durham Reservoir. The description and quantitation of these algal associations is useful and informative both in their own right, and as an interpretive aid for other observed phenomena. Attempts were made to discover the ecological significance of the vertical distribution patterns. In addition, the successional phytoplankton communities described in this study are compared with other selected floristic studies. No attempt was made to compare comprehensively the literature in this field.

Seasonal Changes in Phytoplankton Density. The seasonal changes in phytoplankton density for the three depths sampled are illustrated in Figure 19. During March and early April, a distinct density stratification was evident under the ice, but this stratification was destroyed during spring turnover. Thus on April 21, 1965, the phytoplankton densities at all levels were similar. The phytoplankton population densities showed little change during May and early June. After June 15, 1965 there was a marked rise in population density culminating on July 14 with a bloom of Anabaena planktonica Brunnthaler. This
Figure 19  Seasonal changes in the phytoplankton density at 0.5, 1.5, and 2.5 meters.
resulted in cell densities of 450,000 cells/cc at 0.5 and 1.5 meters and 150,000 cells/cc at 2.5 meters. During late July and early August, a gradual decline in the density of *Anabaena* occurred in the upper waters as the bloom became senescent. The anomalous increase in phytoplankton density evident at 2.5 meters on August 12, 1965 was the result of an extremely high concentration of *Coelosphaerium Nagelianum* whose numbers returned to a concentration similar to that found at other depths on August 24, 1965. This anomaly may possibly be explained by a marked heterogeneity in the plankton distribution at this sample location. Throughout the duration of August, September, and early October, a gradual decline in phytoplankton density occurred at all depths. A single sample taken under the ice on January 4, 1966 revealed a slight vertical density stratification with a distinct species stratification. The distribution on this date represents surface, 0.5, and 1.5 meter depths.

**Seasonal and Vertical Changes in Phytoplankton Composition.** The data for this analysis were organized by population density and by the number of species. In the first method, each major phytoplankton group was assessed as a percentage of the total population (Figure 20). A similar procedure was employed using the number of species in each major group rather than population density (Figure 21).

The plankton communities under the ice were dominated by the Pyrrophyta with the subdominants being the Chlorophyta
Figure 20. Seasonal changes in the major phytoplankton groups, based on their contribution to the total population density during 1965 and 1966.
and Chrysophyta. After ice-out during April and May, the plankton communities were primarily dominated by the Chrysophyta and Chlorophyta with a distinct decline in the Pyrrophyta and Euglenophyta. Although early June was similar to May, the gradual development of the summer Cyanophyta was evident during the latter half of this month with concurrent decreases in the Chlorophyta and Chrysophyta. July was dominated essentially by the Cyanophyta with only token representation of the other major groups. Basically the same pattern persisted through August and September, but with changes in the species composition. In October, a decline in the Cyanophyta was evident with indications of the return of the Chlorophyta and Chrysophyta. By November the Chrysophyta dominated the plankton almost entirely, and this situation was still evident on January 4, 1966. The seasonal distribution patterns for 1.5 and 2.5 meters are basically similar to that discussed for 0.5 meters and need not be discussed in detail. There are however, certain differences that are worthy of mention.

The first notable difference relates to the distribution of the Euglenophyta. This group showed a distinct increase in importance at 2.5 meters, often accounting for 20% to 40% of the total plankton at this depth from March to mid-June. A second difference is the marked stratification of the Cyanophyta during late June and early July and the presence of the Pyrrophyta at 2.5 meters during this period. The unusual pattern occurring on August 12,
1965 has already been discussed. There is little difference in the vertical distribution patterns after August 30, 1965 since the water at this time was thermally unstratified and subject to continued mixing. The pattern under the ice revealed an increase in importance of the Chlorophyta with depth as well as distinct species stratification which will be discussed later.

In comparing the patterns discussed above with those where the number of species is used (Figure 21), an obviously different picture emerges. The basic seasonal patterns that are so evident when population densities are compared, are nonexistent when the data is organized in this manner. In general, less variation is found both seasonally and with depth. This approach more closely represents changes in species diversity. It is interesting to note that most of the major groups are well represented at all times, particularly the Chlorophyta.

**Phytoplankton Communities.** The species composition of the phytoplankton communities will be described for each depth and seasonally, emphasizing the dominant and subdominant associations. A summarization of this data is in Table 11.

The first natural temporal grouping involved the communities present under the ice. The dominant phytoplankter in these samples at 0.5 meters was the dinoflagellate *Glenodinium pulvisculus* (Ehrenberg) Stein which accounted for 50% of the population density. Primary
Figure 21. Seasonal changes in the major phytoplankton groups based on their contribution to the total number of species present during 1965 and 1966.
### TABLE 11

**SEASONAL AND VERTICAL DISTRIBUTION OF DOMINANT SPECIES**

<table>
<thead>
<tr>
<th>DATE</th>
<th>0.5M</th>
<th>1.5M</th>
<th>2.5M</th>
</tr>
</thead>
<tbody>
<tr>
<td>30-III-1965</td>
<td><em>Gloeodinium pulviscillum</em></td>
<td><em>Gloeodinium pulviscillum</em></td>
<td><em>Gloeodinium pulviscillum</em></td>
</tr>
<tr>
<td></td>
<td><em>Syrma uvelia</em></td>
<td><em>Syrma uvelia</em></td>
<td><em>Syrma uvelia</em></td>
</tr>
<tr>
<td>5-IV-1965</td>
<td><em>Gloeodinium pulviscillum</em></td>
<td><em>Gloeodinium pulviscillum</em></td>
<td><em>Gloeodinium pulviscillum</em></td>
</tr>
<tr>
<td></td>
<td><em>Syrma uvelia</em></td>
<td><em>Syrma uvelia</em></td>
<td><em>Syrma uvelia</em></td>
</tr>
<tr>
<td>21-IV-1965</td>
<td><em>Dinobryon tertulorium</em></td>
<td><em>Ancistradenus foliatus</em></td>
<td><em>Ancistradenus foliatus</em></td>
</tr>
<tr>
<td>8-V-1965</td>
<td><em>Syrma uvelia</em></td>
<td><em>Syrma uvelia</em></td>
<td><em>Syrma uvelia</em></td>
</tr>
<tr>
<td>19-V-1965</td>
<td><em>Dinobryon tertulorium</em></td>
<td><em>Dinobryon tertulorium</em></td>
<td><em>Dinobryon tertulorium</em></td>
</tr>
<tr>
<td>11-VI-1965</td>
<td><em>Antierinella formosa</em></td>
<td><em>Antierinella formosa</em></td>
<td><em>Antierinella formosa</em></td>
</tr>
<tr>
<td>16-VI-1965</td>
<td><em>Antierinella formosa</em></td>
<td><em>Antierinella formosa</em></td>
<td><em>Antierinella formosa</em></td>
</tr>
<tr>
<td>23-VI-1965</td>
<td><em>Antierinella formosa</em></td>
<td><em>Antierinella formosa</em></td>
<td><em>Antierinella formosa</em></td>
</tr>
<tr>
<td>30-VI-1965</td>
<td><em>Anabaena plantidentia</em></td>
<td><em>Anabaena plantidentia</em></td>
<td><em>Anabaena plantidentia</em></td>
</tr>
<tr>
<td>7-VII-1965</td>
<td><em>Anabaena plantidentia</em></td>
<td><em>Anabaena plantidentia</em></td>
<td><em>Anabaena plantidentia</em></td>
</tr>
<tr>
<td>14-VII-1965</td>
<td><em>Anabaena plantidentia</em></td>
<td><em>Anabaena plantidentia</em></td>
<td><em>Anabaena plantidentia</em></td>
</tr>
<tr>
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<tr>
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<tr>
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<tr>
<td>15-X-1965</td>
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<td><em>Krioderia alpina</em></td>
<td><em>Krioderia alpina</em></td>
</tr>
<tr>
<td>9-XI-1965</td>
<td><em>Dinobryon tertulorium</em></td>
<td><em>Dinobryon tertulorium</em></td>
<td><em>Dinobryon tertulorium</em></td>
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<tr>
<td></td>
<td>SURFACE</td>
<td>0.5M</td>
<td>1.5M</td>
</tr>
<tr>
<td>4-I-1966</td>
<td><em>Dinobryon sociale</em></td>
<td><em>Syneura acus</em></td>
<td><em>Syneura acus</em></td>
</tr>
</tbody>
</table>

The second natural grouping of phytoplankton communities developed following ice-out, and persisted until June. During this period the communities were dominated by the Chrysophyta and Chlorophyta. The primary associates were *Dinobryon sertularia* and *Synura uvella* with *Asterionella formosa* (Hassal) developing in May. The dominant Chlorophyta during this period were *Ankistrodesmus falcatus* and *Scenedesmus quadricauda* (Turpin). The Pyrrophyta were still represented by *Glenodinium pulvisculus* with lesser numbers of *Ceratium hirundinella* (O. F. Muell) Dujardin, and *Gymnodinium* Penard. The Euglenophyta were mainly represented by *Trachelomonas volvocina* with traces of *T. hipsida* (Perty) Stein, *Phacus orbicularis* Huebner, *Euglena acus*, and *Euglena polymorpha* Dangeard. The month of June may be considered a transitional period for remnants of earlier communities persisted, but there were indications of the development of the dominant summer cyanophycean communities. The Old Reservoir still contained a chrysophycean-chlorophycean community during the earlier half of June. However, the dominant chrysophycean alga was the diatom *Asterionella formosa*. The Chlorophyta were represented primarily by *Ankistrodesmus falcatus* with subordinate species being
Scenedesmus quadricauda, *Pediastrum duplex* Meyen, *P. tetras* (Ehrenberg) Ralfs, and *P. obtusum* Lucks. The Euglenophyta displayed, as mentioned before, a definite preference for the deeper waters. As a result, the communities at this depth often had several species in this group. The dominant member was *Trachelomonas volvocina* in association with *T. hipsidei*, *T. similis* Stokes, *Phacus orbicularis*, *P. longicauda* (Ehrenberg) Dujardin, *Euglena acus*, and *Euglena polymorpha*. During June the Pyrrophyta were still represented by *Ceratium hirundinella* and *Glenodinium* sp. During the latter half of June there were indications that the Cyanophyta were beginning to develop, and on June 30, 1965 *Anabaena* planktonica comprised 46% of the total cell density at 0.5 meters and 39% at 1.5 meters.

On July 7, 1965 there was a marked change in the character of the phytoplankton community. The surface community was primarily represented by *Anabaena* planktonica (50%) with the Chlorophyta as subdominants. The latter consisted primarily of *Schroederia setigera* (Schroeder) Lemmermann with lesser amounts of *Scenedesmus quadricauda*, *Pediastrum tetras*, *P. obtusum*, and *Coelastrum recticulatum* (Dang) Senn. The Chrysophyta were represented primarily by *Asterionella formosa* with traces of *Dinobryon sertularia*. The Pyrrophyta were represented by *Ceratium hirundinella*. This dinoflagellate showed a distinct vertical distribution pattern having a density of 30, 50, and 632 cells/cc at 0.5, 1.5 and 2.5 meters respectively. The Euglenophyta
showed a similar distribution having 20, 110, and 178 cells/cc with increasing depth. This group was dominated by *Trachelomonas volvocina* with the subordinates being the same as those in June. The conditions on July 14 were very similar to those described for July 7, except that a marked stratification of *Anabaena planktonica* had developed. Cell densities for this species were 28,000, 16,500 and 1,000 cells/cc at the three depths sampled. In addition to the taxa mentioned above, a group of small flagellates was evident also during this month. These flagellates are classified as Cryptomonads, and were represented by two species, *Cryptomonas erosa* (Ehrenberg) and *Chroomonas sp.* which were often moderately abundant at the deeper depths. The pattern discussed above persisted for most of July with minor variations. As the month of July ended, the bloom of *Anabaena planktonica* had become senescent and was succeeded by another community.

The community during August was dominated, as in July, by the Cyanophyta. However, there was a change in the species comprising this community. The dominant Cyanophyta were *Coelosphaerium Nagelianum* Unger and *Microcystis aeruginosa* which displayed a vertical distribution somewhat similar to *Anabaena planktonica*. A second pronounced change occurred in the decline of *Ceratium hirundinella* and the appearance of *Glenodinium quadricens* (Stein) Schiller as the dominant dinoflagellate in the deeper waters. The Chrysophyta were represented only by a few individuals of
Asterionella formosa, and Tabellaria sp.. The cryptomonads and Chlorophyta were well represented. The latter were represented primarily by Ankistrodesmus falcatus, Kirchneriella lunaris (Kirchner), Tetraedron minimum (A. Braun) Hansgirg, Scenedesmus quadricauda, Pediastrum duplex, Pandorina morum (Muell.) Bory, and Staurastrum leptocladium Nordstedt. The species of Euglenophyta were numerous. The dominant was Trachelomonas volvocina with moderate abundance of Phacus orbicularis. The remaining associates were Euglena acus, E. polymorpha, Trachelomonas hipsida var. coronata Lemmermann, T. acanthostoma, (Stokes) Deflandre, T. similis, and T. lecustris DrezePolski. In addition to the Coelosphaerium-Microcystis community the latter half of August witnessed the development of another blue-green algae identified as Anabaena Felisii (Meneghini) Barnet and Flahault. This species was quite abundant (5,000-10,000 cells/cc) and at times exceeded Microcystis in total cell density.

September was characterized by a general continuation of the pattern described for August, but with the complete replacement of Microcystis aeruginosa by Anabaena Felisii as the co-dominant with Coelosphaerium Nagelianum. This basic pattern persisted throughout the month of September.

October populations demonstrated a further decline in the importance of the Cyanophyta whose representation was completely dominated by Anabaena Felisii. Trachelomonas volvocina was the dominant Euglenophyta with T. similis,
T. acanthostoma, T. hipsida, and Phacus orbicularis being occasional components. There was a slight increase in the importance of the Chrysophyta, represented particularly by Dinobryon sociale Ehrenberg, D. sertularia, Asterionella formosa, and Tabellaria fenestrata (Lyngbye) Kuetzing. The cryptomonads were represented by Cryptomonas erosa and Chroomonas sp.. The Chlorophyta were quite important (23%) in October, with Kirchneriella lunaris being dominant. The important chlorophycean associates were Scenedesmus quadricauda, Crucigenia tetrapedia, (Kirchner) West and West, Pediastrum duplex, Kirchneriella obesa (W. West) Schmidle, and Coelastrum recticulatum. There was no significant distributional differences with depth since the water column during this period was unstratified. The communities present during October may be considered transitional between summer cyanophycean-dominated communities and chrysophycean-dominated fall communities.

The phytoplankton community of November was composed of typically cold water species. The Chrysophyta contribute 96% of the total density, 93% (7950 cells/cc) of which was Dinobryon sertularia mixed with equal amounts of Asterionella formosa and Synedra acus Kuetzing. In addition, a few cells of Dinobryon divergens Imhof and Tabellaria fenestrata were also present. The Euglenophyta were represented by Trachelomonas lacustris. The Cryptomonads comprised only 1.4% of the total plankton density. The Chlorophyta dominated the plankton in terms of the number of species (11) but
contributed only 230 cells/cc or 3.0%. The species present were *Kirchneriella lunaris*, *Scenedesmus quadricauda*, *Ankistrodesmus falcatus*, *Micractinium pusillum* Presenius, *Characium limneticum* Lemmermann, *Golenkina radiata* Chodat, *Pediastrum obtusum*, *Tetraedron minimum*, *Schroederia setigera*, *Scenedesmus incrassatulus* Bohlin, and *Lagerheimia ciliata* (Lag.) Chodat. Still present in the sample from 1.5 meters were two filaments of *Anabaena Fellsii*.

The final collection was taken January 4, 1966 under 36 cm of ice. The plankton at all depths was dominated by the Chrysophyta, but a definite species stratification was evident. The sample taken at the water surface just below the ice was dominated by *Dinobryon sociale* (6080 cells/cc) and *Chrysococcus* sp. (2224 cells/cc) with lesser numbers of *Synura uvella* (320 cells/cc), *Dinobryon sertularia* (200 cells/cc), *Asterionella formosa* and *Synedra acus* at 20 cells/cc. At 0.5 meters the dominant chrysophycean was *Synedra acus* (1538 cells/cc) with *Dinobryon sociale* (258 cells/cc), *Asterionella formosa* (148 cells/cc), *Mallomonas* sp. (124 cells/cc), *Chrysococcus* sp. (50 cells/cc), and *Dinobryon sertularia* (20 cells/cc) as associates. A similar distribution of chrysophytes was found at 1.5 meters. The chlorophyta were distributed evenly at all depths with *Ankistrodesmus falcatus* being dominant and *Schroederia setigera*, *Golenkina radiata*, *Scenedesmus quadricauda*, and *Pandorina morum* as occasionals. The Euglenophyta showed minor vertical stratification at this time. *Trachelomonas*
volvocina was the dominant, with cell densities of 6, 103, 136 at the surface, 0.5, and 1.5 meters respectively. 
Euglena acus on the other hand showed a density distribution of 2, 1, and 0 cells/cc with increasing depth. The other two associates were Trachelomonas hipsida and T. lacustris.

Of the many possible studies to which this data may be compared, a study of the seasonal changes in the phytoplankton communities of Pymatuning Reservoir, Pennsylvania, seemed most pertinent (Hartman and Graffius, 1960). Five basic communities were described with more possible if species changes were included. Briefly, a winter community consisted primarily of diatoms with a subordinate assemblage of Chlorophyta. An interesting departure from this basic pattern was the appearance of large numbers of dinoflagellates in late winter which parallels the situation described for the Old Durham Reservoir. Hartman and Graffius (1960), reported the true spring community was composed of unicellular and colonial greens, but it lasted for only two weeks from mid-May to early June. The presence of such a community in the study reported here developed shortly after ice-out and reached a peak in early May. The summer community of Pymatuning Reservoir was dominated by the Cyanophyta which lasted from early June through August. Within this time there was succession of species similar to that noted in this study. The fall community in Pymatuning Reservoir was transitional, with decreasing dominance of the Cyanophyta, a temporary dominance of greens and finally the
development of the diatoms which were to dominate the winter populations. This community persisted from September to mid-November. In the Old Durham Reservoir, the Cyanophyta persisted as dominants throughout September with a decline evident in October. This was immediately succeeded in November, not by the Chlorophyta, but by the Chrysophyta. The latter persisted under the ice during January.

The two reservoirs described above are basically similar in their successional phytoplankton community patterns. The patterns described are those characteristic of eutrophic lakes, particularly, the dominance of summer cyanophycean communities. A similar pattern was described for Linsley Pond (Hutchinson, 1944) with an excellent description of the physico-chemical conditions as they related to species succession.

The problem of using algae as indicators of lake types has been reviewed by Rawson (1956a) and Brook (1965). Rawson questions whether there are actually any reliable indicators of oligotrophic conditions. With this in mind, it might appear superfluous to describe the seasonal phytoplankton communities of an oligotrophic lake. There are, however, enough differences between the phytoplankton communities characteristic of oligotrophic and eutrophic lakes to warrant a brief comparison.

Rawson (1956b) made a comprehensive study of the seasonal net plankton population dynamics of oligotrophic Great Slave Lake, Canada. Of the 160 species of algae
identified, two diatoms, *Melosira islandica* Ehrenberg and *Asterionella formosa* were dominant, the blue-green algae were few with the chrysophycean *Dinobryon* being numerous. From a seven year average of dominant phytoplankton communities, the following seasonal succession pattern emerged. The dominant phytoplankter after ice-out was *Melosira* which reached a maximum density in early July. This rapidly declined during late July and leveled off during August, but still was more abundant than any of the other species. *Asterionella* showed a gradual rise throughout the summer, and became the dominant plankter during September. *Dinobryon* had its maximum density during July, and fluctuated throughout the summer, and, except on one occasion, never exceeded *Asterionella*. From this brief summary, it is evident that this lake was dominated at all times by the Chrysophyta though other groups were present. There is no successional pattern as characterized the eutrophic lakes.

Between the two extreme types discussed above, one finds an infinite number of intermediate types which reflect the intricate and complex relationships between morphometry, biotic, physico-chemical, and climatic factors. The involvement of these factors makes it difficult to relate trophic structure to algal composition except for the more extreme cases.

In summary, there were eight different phytoplankton communities evident between March 1965 and January 1966
based on the dominant species associations. If only major ecological groups were considered, four or possibly five communities could be discerned in the Old Durham Reservoir. In addition to the seasonal pattern of succession, there were several interesting vertical patterns of distribution discussed. These relationships were the result of the differential distribution of environmental factors which resulted in the establishment of conditions that more suitably satisfied the optimal ecological requirements of particular species of phytoplankton. The various flagellated euglenoids showed a marked preference for deeper water with diminished light intensity and environmental conditions often associated with heterotrophic nutrition. The Cyanophyta showed maximum early development in the surface water since they tended to float as a result of pseudovacuole formation. Further these species appeared to be quite tolerant of high light intensities that would be detrimental to other species. The cryptomonads are small flagellates with known heterotrophic tendencies (Wright, 1964) which characteristically occupy the deeper strata during the summer, and are often numerous under the ice. The Chrysophyta are usually considered cold water forms that dominate the spring and fall plankton communities (Rodhe, et al., 1958). Thus the physiological requirements of the algae dictate which species will develop in response to successive environmental changes both temporally and vertically. The importance of vertical distribution is magnified in this lake by its
particular morphometry and the extension of the euphotic zone into the metalimnion.
SECTION XI

SUMMARY

The Old Durham Reservoir is a shallow eutrophic body of water with an area of four hectares and a maximum volume of 81,000 cubic meters. About 82 per cent of this volume is contained within the upper two meters of depth. Such morphometric characteristics coupled with the reservoir's orientation parallel to the prevailing northwesterly winds have a marked influence on the physical, chemical, and biological properties of this lake.

Analysis of the physical and chemical characteristics of this reservoir revealed unstable thermal and chemical summer stratification patterns. Although anaerobic conditions persisted below 2.5 meters for most of the summer, there were several instances of partial re-oxygenation of the metalimnion. Light penetration was affected by phytoplankton density and suspended detritus, the latter being particularly important during spring and fall turnover.

Chlorophyll a concentration was employed as a measure of phytoplankton standing crop. Seasonal and vertical distribution patterns were investigated for total phytoplankton, net phytoplankton, and nannoplankton. Generally there was a gradual increase in chlorophyll a concentration with increasing depth, with a marked increase
in the thermocline (2.5 meters). This was the result of settling and entrapment of algae, particularly net phytoplankton. Chlorophyll \( a \) concentrations for total phytoplankton ranged from 4.50 to 135.00 mgs/m\(^3\) with an annual mean of 28.95 mgs/m\(^3\). Net phytoplankton and nannoplankton contributed 24 and 76 per cent of the total chlorophyll respectively. The contribution of net phytoplankton to the total chlorophyll \( a \) concentration increased with depth as a result of settling. The mean chlorophyll \( a \) concentration for the total water column was 86.85 mgs/m\(^2\). Two diurnal, in situ studies of chlorophyll \( a \) concentrations are also reported.

Primary productivity was measured seasonally and vertically for total phytoplankton, net phytoplankton, and nannoplankton using the C-14 technique. Maximum productivity was achieved during a bloom of \textit{Anabaena planktonica} on July 14, 1965 when 5,400 mgs C/m\(^2\)/day were synthesized. The mean productivity for the total plankton population was 549.17 mgs C/m\(^2\)/day. Net phytoplankton contributed 35.7 per cent (236.56 mgs C/m\(^2\)/day), and nannoplankton 64.3 per cent (312.58 mgs C/m\(^2\)/day) to the total productivity. The contribution of net phytoplankton to the total productivity decreased with increasing depth while that of nannoplankton increased with depth. Net phytoplankton dominated the productivity during early spring, during the first two weeks in July, and under the ice in January. The importance of nutrient regeneration during summer stratification was
discussed as it related to morphometry and nitrogen fixation by summer cyanophycean populations.

The relationship between primary productivity and chlorophyll a concentration was studied statistically. High correlations were found for epilimnetic populations with poorer correlations for metalimnetic populations. Net phytoplankton which settled readily into deeper waters gave the poorest correlations (r=0.196). Nannoplankton populations within the metalimnion gave moderately good correlations (r=0.79) which indicated that these populations were better adapted to these conditions than the net phytoplankton that settled out and became entrapped there.

Seasonal and vertical assimilation coefficients were calculated for total phytoplankton, net phytoplankton, and nannoplankton. The optimal assimilation coefficient was 1.9 mgs C/mg chlorophyll a/hour with a range of 0.09 to 5.50. The annual mean for the total euphotic zone was 0.96 mgs C/mg chlorophyll a/hour. Assimilation coefficients decreased with increasing depth, decreased logarithmically with decreasing light intensity, and increased logarithmically with decreasing chlorophyll a concentration. No definable relationship was observed between mean monthly assimilation coefficients and mean monthly temperatures or extinction coefficients. Net phytoplankton had consistently higher assimilation coefficients than nannoplankton. The relationship of assimilation coefficient to these variables was discussed using the models of adaptive behavior of
chlorophyll postulated by Odum et al. (1959). As a further confirmation of this hypothesis, the diurnal variations in assimilation coefficients were studied.

The efficiency of the primary producing communities was closely related to light intensity when the latter was below the saturation level (e.g. under the ice). After ice-out, when the light intensity was well above saturation for most of the euphotic zone, the patterns for efficiency more closely paralleled primary productivity. Phytoplankton efficiencies ranged from 0.07 to 5.95 per cent with an annual mean for the total euphotic zone of 0.50 per cent. Generally efficiency increased with depth, primarily because light intensity decreased faster than productivity.

Phytoplankton population dynamics were studied qualitatively, seasonally, and vertically within the water column. Seasonal changes in phytoplankton density showed a gradual rise throughout spring, culminating in a bloom of *Anabaena planktonica* on July 14, 1965, with gradually declining populations after that. Eight basic successional phytoplankton communities were identified during the year. These communities were defined on the basis of the dominant species present. However, examination of Table 11 indicates that many more might be included since there were often different dominant phytoplankters observed at different depths, particularly below the thermocline. Several of these vertical distribution patterns were discussed and certain ecological implications
were considered.
LITERATURE CITED


APPENDIX A

Table A  A list of the algal species identified from the Old Durham Reservoir during the course of this study.
### TABLE A

#### CYANOPHYTA

- *Anabaena planktonica* Brünthaler
- *Anabaena felisii* (Benqhiini) Bornet and Flahault
- *Coelosphaerium Nagelianum* Unger
- *Microcystis aeruginosa* Kuetzing: emend. Elenkin
- *Chroococcus limneticus* Lemmermann
- *Anphanothece* sp.
- *Gleocapsa* sp.
- *Oscillatoria* sp.

#### EUGLENOPHYTA

- *Euglena polymorpha* Dangeard
- *Euglena acus* Ehrenberg
- *Euglena oxyuris* Schmarda
- *Phacus orbicularis* Kuebner
- *Phacus longicauda* (Ehrenberg) Dujardin
- *Phacus tortus* (Lemmermann) Skvortzow
- *Phacus Nordstedtii* Lemmermann
- *Trachelomonas volvocina* Ehrenberg
- *Trachelomonas hirsuta* (Perty) Stein
- *Trachelomonas h. var. coronata* Lemmermann
- *Trachelomonas robusta* Swirenko
- *Trachelomonas similis* Stokes
- *Trachelomonas armata* (Ehrenberg) Stein
- *Trachelomonas lacustris* Drozepolski
- *Trachelomonas acanthostoma* (Stokes) Deflandre

#### PYRROPHYTA

- *Ceratium hirundinella* (O.F. Muell.) Dujardin
- *Glenodinium quadricens* (Stein) Schiller
- *Feridinium* sp.
- *Glenodinium Gymnodinium* Penard
- *Glenodinium pulvisculus* (Ehrenberg) Stein

#### CHRYSOPHYTA

- *Asterionella formosa* Hassal
- *Synedra acus* Kuetzing
- *Tabellaria fenestrata* (Lyngbye) Kuetzing
- *Meridion circulare* (Greville) C.A. Agardh
- *Fragilaria* sp.
- *Navicula* sp.
- *Nitzchia* sp.
- *Dinobryon sertularia* Ehrenberg
- *Dinobryon sociale* Ehrenberg
- *Dinobryon divergens* Imhof
- *Mallomonas* sp.
- *Synura uvella* Ehrenberg
CRYPTOMONADALES

Cryptomonas eosa Ehrenberg
Chroomonas sp.

CHLOROPHYTA

Gonium sociale (Dujardin) Warming
Pandorina morum (Mueller) Bory
Eudorina elegans Ehrenberg
Picodorina sp.
Volvox globator Linnaeus
Chlorella vulgaris Seyerinck
Dictyosphaerium pulchellum Wood
Micractinium pusillum Fresenius
Golenkina radiata Chodat
Golenkina paucispina West and West
Ankistrodesmus falcatus (Corda) Ralfs
Ankistrodesmus f. var. mirabilis (West and West) G.S. West
Lagerheimia ciliata (Lagerheim) Chodat
Schroederia setigera (Schroeder) Lemmermann
Kirchneriella lunaris (Kirchner) Moebius
Kirchneriella obesa (W. West) Schmidt
Westella botryoides (W. West) de Wildemann
Tetraedron gracile Reinsch
Tetraedron limneticum Borge
Tetraedron regulare Kuetzing
Tetraedron constrictum G.M. Smith
Tetraedron trigonum (Naegeli) Hansgirg
Tetraedron lobulatum var. polyfurcatum G.M. Smith
Gloeocystis ampla (Kuetzing) Lagerheim
Characium limneticum Lemmermann
Scenedesmus quadricauda (Turpin) de Brebisson
Scenedesmus incrassatus Bohlin
Scenedesmus denticulatus Lagerheim
Scenedesmus bijuga (Turpin) Lagerheim
Crucigenia tetrapedia (Kirchner) West and West
Pediastrum duplex Heyen
Pediastrum tetras (Ehrenberg) Ralfs
Pediastrum obtusum Lucks
Cloelastrum reticulatum (Dangeard) Senn
Cloelastrum microporum Naegeli
Closterionsis longissima Lemmermann
Gonyostoma semen (Ehrenberg) Diesing
Staurastrum gracile Ralfsii
Staurastrum leptocladium Nordstedt
Staurastrum pulchellum Brebisson
Cosmarium sp.
Closterium sp.
Regression and correlation program for the equation $Y = Ax + B$.

Language = Load and Go
READ 78, M  
DO 93 K = 1, M  
READ 77, N  
ZN = N  
SUMX = 0.0  
SUMX2 = 0.0  
SUMY = 0.0  
SUMY2 = 0.0  
SUMXY = 0.0  
DO 83 I = 1, N  
READ 76, X,Y  
SUMX = SUMX + X  
SUMX2 = SUMX2 + X*X  
SUMY = SUMY + Y  
SUMY2 = SUMY2 + Y*Y  
83 SUMXY = SUMXY + X*Y  
A = (SUMXY - (SUMX*SUMY)/ZN)/(SUMX2 - (SUMX*SUMX)/ZN)  
B = SUMY/ZN - (A*SUMX)/ZN  
G = SUMXY - (SUMX*SUMY)/ZN  
H = SQRTF ((SUMX2 - (SUMX**2)/ZN)*(SUMY2 - (SUMY**2)/ZN))  
R = G/H  
R2 = R * R  
T = R * SQRTF ((ZN - 2.)/(1. - R2))  
93 PRINT 75, B,A,R,T,R2  
STOP  
END