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PRIMARY PRODUCTIVITY AND PHYTOPLANKTON COMMUNITY STRUCTURE IN A TEXAS COASTAL COOLING RESERVOIR

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PRIMARY PRODUCTIVITY AND PHYTOPLANKTON COMMUNITY STRUCTURE IN A TEXAS COASTAL COOLING RESERVOIR

by

Margaret Odgen Welch

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

Doctor of Philosophy

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HOUSTON, TEXAS

May, 1980
ABSTRACT

Primary Productivity and Phytoplankton Community Structure
in a Texas Coastal Cooling Reservoir

by

Peggy Welch

Primary productivity was investigated for 24 months in a 404 ha cooling reservoir of a 530 MW electrical generating plant located on the Texas coastal plain. Carbon fixation was estimated in situ at 0.5 meters from the surface and in the laboratory by carbon-14 techniques. For 18 months phytoplankton community structure was analyzed for biomass, density and species diversity.

Increased temperature stimulated the rate of carbon fixation. Average overall carbon fixation for the two-year study for Station 1 was 34 mg m$^{-3}$ hr$^{-1}$ and 24 mg m$^{-3}$ hr$^{-1}$ for Station 2. There was no significant difference between these means but for 66% of the sampling dates, carbon fixation was significantly higher at the heated station than at the control. Four out of seven in situ experiments in which water samples from Station 1 and Station 2 were reversed and incubated at the opposite station indicated that the productivity difference was due to temperature. In laboratory experiments where natural phytoplankton from each station were incubated at different temperatures, the phytoplankton community of each station responded to temperature similarly. However, the difference in primary productivity ($\Delta P$) between stations was not a simple function of the difference in temperature ($\Delta T$) between stations.
Nutrients were low, perhaps due to removal from the water column by the primary producers, but did not appear to be limiting. Values for primary productivity were independent of light intensity and photosynthesis was probably light saturated at the 0.5 m incubation depth.

Community structure was similar at both stations. The phytoplankton at both stations also responded similarly to temperature, increasing in activity up to an optimum range of about 24-28°C and decreasing in activity above 30°C. Community structure changed from greens to bluegreens when the temperature optimum was exceeded.

Peaks of primary productivity occurred in the spring and in the fall and coincided with the occurrence of optimum water temperatures. Hence, it is suggested that temperature was responsible for the seasonal variation in carbon fixation.
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CHAPTER I

INTRODUCTION

PURPOSE

Civilization has developed along ancient or existing waterways, and today urbanization and industrialization develop around available water which must serve many purposes: domestic water supply and sewage disposal, industrial supply and waste disposal, agricultural irrigation, transportation, commercial fishing, and recreation. Industrial utilization primarily includes water for cooling or heat dissipation, as in the electrical generating industry which has become the most important user of cooling water because of the ever-increasing demand for energy by our technological society (Parker and Krenkel, 1970). To predict and manage the effects of artificial thermal additions, an understanding of the biology of high temperature aquatic systems is necessary. This work is directed toward that understanding.

The generation of electrical power in the United States has doubled every six to ten years (Cairns, 1972a). It is estimated that, by the year 2000, production will rise to $2 \times 10^6$ megawatts of electricity resulting in $21 \times 10^{13}$ joules waste heat per day in power plant effluents. Furthermore, when natural water is used for this cooling, it requires approximately one-third the average daily runoff of the United States (Clark, 1969). While the average power plant in the sixties had a capacity of 22 megawatts (Parker and Krenkel, 1970), plants today frequently have a capacity of 600 megawatts, which is considered small for nuclear-powered generating stations. A 1000 MW generating plant re-
quires 23 to 34 m\(^3\) sec\(^{-1}\), and this can be a significant portion of the total flow of rivers, especially during seasonal and low-flow periods.

Most electricity generated in the United States is produced by closed system steam generating plants, in which spent steam is condensed and heat exchanged to cooled water which is released to the environment. The temperature increase of the cooled water, or \(\Delta T\), is a function of the flow rate through the condensers. In the United States \(\Delta T\) is usually 2°C to 10°C (Langford, 1972). This heat is wasted energy in the conversion of potential energy of the fossil fuel to electrical energy; overall efficiency is about 40%. The principle of operation is the same for nuclear-powered generating plants, but the efficiency of conversion is even less, around 33% (Weinberg, 1975).

Industry has several alternate means of dispensing waste heat. The first consists of "once-through" or "run-of-the-river" systems which pump natural waters through condensing units and return them to the waterway where the heat is carried away and dissipated by evaporation. Obviously, this system requires large amounts of water. In the second method, cooling towers cool condenser water evaporatively by air passing through the stream or mist of water. Part of the condenser water is lost to evaporation, and part is collected and reused. A drawback of this system is that the evaporative cooling towers may release moisture into the atmosphere creating corrosive mists, cloud formation, ground fog and ice in the local area. Cooling ponds compose the third alternative. They are open or closed reservoirs which permit condenser water to be released, cooled, and reused. Where land prices permit, cooling ponds and reservoirs are more economically feasible and ecologi-
cally less destructive methods for disposing of waste heat (Roffman, 1974).

Castenholz and Wickstrom (1975) and Patrick (1969) point out that most scientific studies of thermal loading deal with the effects of thermal additions on species or on populations, but that not a great deal is known about the effect at the community level. For the most part, though, the thermal tolerance range and thermal optimum of many species of freshwater algae have been documented (Patrick, 1969; and Foss, 1975). Studies indicate that more species of Cyanophyta grow well above 35°C, and are thermal-tolerant, that the Chlorophyta tend to grow best up to 35°C, and that the diatoms, the Bacillariophyta, succeed below 30°C. Generally, most research shows that the thermal optimum for all species is higher in the laboratory than in natural aquatic systems.

In natural waters, when the thermal optimum for existing species is exceeded, those species are unable to compete for available resources, and the community structure of the system changes. Whether productivity changes under these conditions has not been determined.

**THE UNIFYING IDEA**

How temperature influences productivity in nature is yet to be precisely determined. There are several questions which remain unanswered, such as: What are the controlling factors in temperature and in higher temperature systems? Are other ecological factors, such as solar illumination and nutrient supply, more important than temperature in determining the rate of carbon fixation in natural aquatic systems? Is the structure of the community likely to influence the rate
of carbon fixation in the system? And do organisms, which are adapted to wide temperature ranges, function differently at higher temperatures than at lower temperatures?

The objectives of this study are to measure and to evaluate the effects of increased temperature on phytoplankton community structure and on primary productivity of a cooling reservoir system.

BACKGROUND

**Temperature vs. Productivity in Laboratory Cultures**

Patrick (1969) cites the work of many investigations performed in the laboratory for the purpose of determining the effects of increased temperature on cell growth, photosynthesis and other functions. She points out that many early studies report the maximum temperature for various species of algae to perform those functions. More recent investigations show that optimum temperatures for growth and for photosynthesis are often not the same. They indicate that higher temperatures cause changes in size, dry weight and patterns of growth. Further, research indicates that growth and photosynthetic rate increase to some optimum temperature above which growth and photosynthetic rate are depressed.

Studies of the interaction of light intensity and temperature indicate that, at lower light intensities, temperature increases tend to have little effect on photosynthetic rate, while at higher light intensities temperature increases stimulate the rate of photosynthesis (Golterman, 1975; Steeman-Nielsen and Jørgensen, 1968; and Talling, 1966). Aruga (1965 a and b) shows that the temperature optimum for photosynthesis varies to some extent with environmental temperature under which algae have grown.
Temperature vs. Productivity in Natural Systems

Factors which lead to the variation in biomass, community structure, and productivity are classified as physical (e.g., temperature, light, and turbulence), chemical (both inorganic and organic), and biological (predation, parasitism and competition), many of which are interrelated (Wetzel, 1975).

Riley (1939), with his data from Linsley Pond, analyzed the "inter-related" factors of chlorophyll a, oxygen production, light intensity, temperature, and nutrients. Chlorophyll a and temperature are the only variables in his study which showed statistically significant correlation with primary production at the surface of Linsley Pond.

G. Evelyn Hutchinson (1967) (in his inimitable scientific prose) reminds of the difficulties biologists encounter when they attempt to isolate the effects of solar radiation and temperature on the growth of natural phytoplankton. The interaction of light and temperature and the high thermal capacity of the water tends to confound the effects. He points out that the maximum temperature of lakes in the temperate Northern Hemisphere occur in late summer, four to six weeks after the summer solstice. In his discussion of the periodicity of freshwater phytoplankton, he reviews some of the investigations by early limnologists, some experimental studies of the effect of temperature on populations of phytoplankton, and studies in nature on the interaction of light and temperature. Using Lund's (1949) graphical data, Hutchinson estimates the rates of cell division and computes correlation coefficients with light intensity and temperature and concludes that, at the
surface of the lake, temperature is statistically more important than light for rates of cell division. Hutchinson also concludes that, although temperature influences the quantity and composition of the phytoplankton, it is by no means the only important variable.

In an attempt to identify factors influencing productivity, Brylinsky and Mann (1973) use data (from 43 lakes and 12 reservoirs, ranging in location from the tropics to the arctic) collected as part of the International Biological Program. They group 42 variables into four categories: morphological, physical, chemical, and biological. Using correlation and factor analysis to determine the relationship between variables, they show that on a global scale, variables related to solar radiation, such as air temperature, day-length range and visible incident light, have the greatest influence on phytoplankton productivity. They further indicate that variables related to nutrient concentration assume more importance in lakes with a narrower latitudinal range.

Schindler (1978) performed a regression analysis on global data of freshwater phytoplankton production, chlorophyll and phosphorus including some of the sites treated by Brylinsky and Mann (1973). His study is biased toward glacial lakes in north temperate and subarctic regions as nutrient data for the highly productive tropical lakes treated by Brylinsky and Mann were unavailable. He found no significant correlation between net primary productivity and latitude, or between net primary productivity and annual phosphorus input. In lakes with nitrogen to phosphorus input greater than 5:1 (where phosphorus limitation is most likely), he obtained a significant linear correlation ($r=0.59$).
Schindler hypothesized lower latitudes and input of nutrients might be correlated due to higher precipitation, longer periods where the soil in the drainage basin is not frozen, and more efficient soil decomposers at lower latitudes.

In a comparison of phytoplankton production and photosynthetic activity in Lake Victoria, East Africa, and in Windermere, England, Talling (1965) notes that the maximum photosynthetic activity as measured by oxygen evolution (mg O₂ m⁻³ hr⁻¹) occurred during the periods of highest diatom population density as measured by chlorophyll a (mg m⁻³). Although the concentration of chlorophyll a were approximately the same (5-6 mg m⁻³) during the maxima in both lakes, the photosynthetic activity was two and a half times higher in Lake Victoria. He eliminates cell volume as the reason for the higher photosynthetic activity by showing that the approximate estimate of cell volume for Windermere (2.5 mm³ l⁻¹) was more than twice the estimate for Lake Victoria. Pₚₐₓ, the light-saturated photosynthetic rate per unit of population, appeared to be approximately four times higher in Lake Victoria. In short, Talling hypothesizes that the difference in temperature between the tropical and temperate lakes, which was 10-12°C during the diatom maxima, was the major factor in the higher photosynthetic activity. He considers the temperature dependence of light-saturated photosynthesis (Pₚₐₓ) as the most important factor responsible for this.

In a study of the productivity of Lake Lanao, Philippines, Lewis (1974) concludes that temperature is not the primary determining factor in the higher primary productivity usually observed in tropical lakes. Instead, he suggests tropical lakes have higher productivity due to more
rapid nutrient recycling and that the effect of higher temperature is to accelerate the degradation of organic materials and the recycling of nitrogen and phosphorus. Since nutrient limitation in the epilimnion is relieved frequently by mixing associated with tropical storms, he cites the frequent mixing as the single most important factor in the difference in productivity between temperature and tropical lakes.

Lewis also considers two flaws in Talling's theory that higher tropical aquatic productivity may be caused by dependence of photosynthesis on temperature. First, extrapolating the effect of a temperature difference from $Q_{10}$ could overestimate the metabolic rates at the higher temperature. Second, even if higher temperatures are favorable to photosynthesis, this would be unimportant as nutrients and light would limit primary production.

Ichimura (1967) found that the seasonal variation in photosynthetic activity ($P$) vs. light intensity curves for natural coastal phytoplankton populations resulted from variation in water temperature and not from nutrient variation. In more oligotrophic oceanic waters, however, variation in $P$ vs. light intensity was attributed to nutrient variation.

The change or succession of phytoplankton brings about the varying dominance of different algae which differ in such characteristics as factor (nutrients, etc.) requirements, size, surface to volume ratio, specific growth rate, etc. The $P$ vs. light intensity curve varies with the changing dominance of the phytoplankton groups as the curves are different for different species and especially different taxonomic groups (Ryther, 1956).
As natural waters are rarely in a "steady-state" and physical, chemical, and biological factors vary, it seems a single factor rarely might be considered limiting for an extended period of time. In addition, the multiple interaction of at least three factors, light, temperature and nutrients, makes the concept of a "limiting factor" in natural aquatic systems even more difficult to define.

**Temperature vs. Productivity in Man-heated Systems**

The literature on thermal discharges in voluminous. No attempt will be made here to discuss it in detail, as numerous reviews and symposia are available (Krenkel and Parker, 1969; Coutant and Pfuderer, 1973; Gibbons and Sharitz, 1974; Coutant and Talmage, 1975; Esch and McFarlane, 1976; and Talmage and Coutant, 1978 and 1979). Coutant, annually, reviews current literature in the Journal of Water Pollution Control Federation.

Numerous studies on the effect of temperature on specific kinds of organisms, particularly fish, have been made under laboratory conditions (Allen, J.F., 1969). Simmons, Armitage and White (1974) report that heated power plant effluent had no effect on blooms in the Potomac River, but that high concentrations of nutrients from upstream sewage plants were such an important factor that the effect of heat could have been masked. Patrick (1969) notes that, as long as nutrients and light are sufficient, productivity would increase with temperature increase within the thermal tolerance range of the existing algae. When tolerance ranges are exceeded, an alteration in the community structure would occur. Dryer and Benson (1957) report no significant increase in plankton density as a result of thermal discharge into Kentucky Lake.
Trembley (1965) and Hein and Koppen (1979) studied the effects of thermal discharge on algae growing on glass slides. They found those slides from heated water had fewer species and more individuals than the slides from unheated water. When the temperature exceeded 34.5ºC, there was an increase in the Cyanophyta. Foerster, et al. (1974) report that blooms in the Connecticut River correlated well with increased temperature, and they theorize that the mechanism involves an increase in the rate of diffusion across the depletion zone surrounding the algal cell. They also speculate that the shift to blue-green dominance might eliminate some consumers and further alter the community.

Warinner and Brehmer (1966) studied the effect of thermal effluents on a community of marine organisms in a riverine estuary, Yorktown, Virginia, and found an increase in primary production during the winter months and a decrease during the summer months. When the ambient river water was above 15ºC (as it was in the summer) a ΔT of 8ºC depressed production. Above 25ºC, the maximum temperature of the river during this study, a ΔT of 3.5ºC depressed production.

Data on lakes are scarce (Cairns, 1972 b), but the investigators at Savannah River Laboratory in Aiken, South Carolina, have performed numerous studies on Par Pond, a cooling reservoir receiving effluent from a nuclear reactor. Tilly reports on the investigations of phytoplankton and periphyton in Par Pond (1973, 1974; Marshall and Tilly, 1971). Maximum productivity per unit volume of water and productivity per unit area was strongly correlated with increased temperature, but primary productivity per mg chlorophyll a was not. This indicates
that increased density of phytoplankton as measured by chlorophyll a was not responsible for increased rate of photosynthesis.

In Lake Wabamum, Alberta, Canada, increased standing crops of epiphytic and epipelagic algal-communities in an area 8°C above ambient resulted from freedom from ice cover in the winter, permitting light to penetrate the water column and illuminate surfaces all year instead of just during summer (Hickman, 1974; Gallup and Hickman, 1975; and Hickman and Klared, 1975).

It appears that the effect of increased temperature on primary productivity depends primarily on initial environmental temperature. If the environmental temperature is near the upper limits of temperature tolerance, added heat tends to bring about a decrease in the rate of photosynthesis. If ambient temperature is low, as it is in winter, higher temperature tends to increase growth and photosynthesis (Aruga, 1965 a and b; Ichimura, 1967; Steemann-Nielsen and Jørgensen, 1968; Patrick, 1969; and Fogg, 1975).

Gibbons (1976) presents a model which might represent responses of phytoplankton populations to increasing temperatures (Figure 1). Gibbons hypothesizes that higher temperatures will enhance the "success" of a population up to some optimum temperature. Beyond that, the effect of higher temperatures will negatively affect the population success until such point that the population is eliminated. This model is in agreement with the results of many laboratory studies on the thermal tolerances of species of algae (Patrick, 1969).

Indigenous organisms from subtropical to tropical aquatic systems, adapted to higher environmental temperature, have higher temperature optima and higher temperature tolerance ranges than those organisms
Figure 1: Gibbon's model.
from more temperate environments (Talling, 1961; Patrick, 1969; and Fogg, 1975). In locations where temperature-tolerant species are more important, small temperature increases are not likely to significantly depress productivity during the summer or significantly increase productivity during the winter.

**SCOPE OF STUDY**

There is still controversy among researchers as to what controls primary productivity in aquatic environments at lower latitudes and in thermally altered environments. From the literature, it seems no general correlation of primary productivity to physical or chemical parameter can be made over a large number of different systems, but rather that individual system characterization is required.

This study was designed to determine the effect of temperature on the primary productivity of the natural phytoplankton in an aquatic system of high ambient temperature. In Texas, summer surface water temperatures often have been recorded over 40°C (Drew and Tilton, 1970). The natural phytoplankton community must be adapted to those high temperatures and to temperature ranges of 25°C or 30°C. The investigations of natural phytoplankton productivity in situ allows for species composition change during the seasonal range of temperature.

This study was designed to minimize the confounding environmental factors such as differences in light intensity and differences in community structure. At the same time, the temperature differences between the heated station and the ambient station was maximized.
CHAPTER II

METHODS

DESCRIPTION OF THE STUDY AREA

Lewis Creek Reservoir (Figure 2) is a 404 ha reservoir constructed in 1970 by Gulf States Utilities as a semi-closed system to be used to cool the condenser of a 530 megawatt electrical generating plant. The reservoir was formed by construction of an earthen dam over Lewis Creek, an intermittent stream. The average depth is 5.34 m, the maximum depth, 10.3 m. The elevation of the reservoir is 83 m. It is located in Montgomery County, Texas (latitude 30°26' and longitude 95°32'). The climate is subtropical with mild winters and hot, humid summers. The average daily maximum air temperature in the summer is 35°C and in the winter is 28°C. Rainfall averages 120 cm/year and is well distributed throughout the year (USDA, 1972). The drainage basin is approximately 1000 ha. The area is sparsely populated and the land use of the drainage basin is principally pine timber and livestock range.

Station 1 was located at the outfall of the discharge canal into a small preliminary cooling pond created by construction of a dike across a cove approximately 1 km from the generating plant. The temperature at Station 1 approximated the recorded temperature of the effluent as it left the plant. Station 2 was approximately 2.5 km by water from Station 1 and 15 meters across the dike from the heated station. This juxtaposition of stations permitted almost simultaneous sampling and incubation. The temperature of Station 2 approximated
Figure 2: Approximate bathometry of Lewis Creek Reservoir. Depth in meters.
the recorded temperature of the water at the intake screen.

**SAMPLING**

This study was based on collections made at Stations 1 and 2 from late September, 1976, to September, 1978. In order to minimize the errors inherent in sampling the heterogeneously distributed phytoplankton, one large water sample was taken from surface to 30 cm at each station. Portions of this large sample were used for chemical analysis, primary productivity measurements and phytoplankton cell counts.

**PHYSICOCHEMICAL MEASUREMENTS**

Measurements of temperature, pH, water transparency, solar radiation, and alkalinity were made at each station on each sampling date. Nitrate nitrogen, orthophosphate, and dissolved oxygen measurements were made monthly. Water temperature at the incubation depth of 0.5 m was measured with a mercury thermometer, hydrogen ion concentration with a Corning 130 pH meter in the laboratory, water transparency with a Secchi disk, and instantaneous solar radiation in foot-candles with a Weston Illumination Meter Model 756. Total daily insolation for each sampling date was supplied by Texas A & M Meteorological Center (about 100 km away). The instantaneous light readings taken at the site were correlated with Total Langley's/day using least squares linear regression. The correlation was strong (r = 0.86) and highly significant (Figure 3). Energy available for photosynthesis is in the wavelength range of 400-700 μm and is thought to be about 41% of the total radiation (Vollenweider, 1974). When using barrier layer light meters, such as the Weston 756, it is possible to convert foot-candles or lux units
Figure 3: Daily total Langleys vs. instantaneous light readings.

Equation for the line: \( Y = 41.6x - 100.6 \), \( r = 0.86 \) (\( p < 0.001 \)).
Y = 41.6x - 100.6
r = 0.86  p < 0.001

Figure 3
to photosynthetic available energy using these equations:

\[ 1 \text{ Lux} = 4 \text{ erg/cm}^2\cdot\text{sec} \]
\[ 4.185 \times 10^7 \text{ ergs/cm}^2\cdot\text{sec} = 1 \text{ cal/cm}^2\cdot\text{sec} \]
\[ 1 \text{ gram cal/cm}^2 = 1 \text{ langley} \]

Phenolphthalein and methyl orange alkalinity were measured by titration in the field with 0.02 N sulfuric acid. Duplicate dissolved oxygen samples were fixed by the azide modification of the Winkler method (American Public Health Association, 1971). Total Kjeldahl Nitrogen, NO₃-N, total and dissolved phosphorus were initially analyzed with the Technicon Autoanalyzer, but the levels of these nutrients were below the sensitivity level of the methods. Nitrate nitrogen was measured by the ultra-violet spectrophotometric method (American Public Health Association, 1971) and was read on a Beckman DB-G Grating Spectrophotometer with a Beckman Hydrogen Lamp Power Supply using a 1 cm cuvette. Orthophosphate was measured by the stannous chloride method using a benzene-isobutanol extraction (American Public Health Association, 1971). A ten cm cuvette was used and the color development was read on a Model DK-A Ratio Recording Spectrophotometer. Total CO₂ was calculated from alkalinity titration, pH, temperature and a correction factor. The formula for the correction factor is from Buch (1945) as cited by Vollenweider (1974). Figure 4 is a modification of the graph in Vollenweider (1974) to include temperatures as high as 40°C. These corrections factors are suitable only for waters of very low ionic strength.

**BIOLOGICAL MEASUREMENTS**

Most investigators agree that the Carbon-14 method of estimating
Figure 4: Correction factor to obtain total CO$_2$ from alkalinity.

\[
\frac{a \cdot \Sigma CO}{A'}^2 = \frac{1 + \frac{a_H}{K'_1} + \frac{K'_2}{a_H}}{1 + 2 \frac{K_2}{a_H}}
\]

$K_1$ and $K_2$ = 1st and 2nd equilibrium constants of the CO$_2$-system;

$a_H$ is the hydrogen ion activity found from pH measurements.
growth rate measures approximately net productivity as distinguished from the oxygen evolution method which gives a measure of gross photosynthesis. The Carbon-14 techniques used to estimate primary productivity were modifications of the procedures of Goldman, et al. (1974), and counted by modifications of the liquid scintillation techniques of Schindler, et al. (1974). Immediately after collection of the water samples, the incubation bottles were filled, an ampoule of 1 ml of NaH\textsuperscript{14}CO\textsubscript{3} (5 µCi) was added and the bottles shaken well. The bottles were fastened horizontally to metal racks and incubated at 0.5 meter. To circumvent the problems associated with long incubation periods, incubation time was limited to two hours, always between 10:00 a.m. and 2:00 p.m. After the bottles were removed from the water, they were placed on ice in a light-free box and returned to the laboratory.

The incubation bottles for the experiments were 125 ml bottles. The entire bottle contents were filtered at less than 0.5 atmosphere with a Millipore Filtration Apparatus with a Metricel GA-C filter, 47 mm in diameter, with a 0.45 µm pore size. The funnel and filter were then washed with 50 ml of deionized water (pH of approximately 4.0). The damp filter was placed in scintillation vials, filled with 20 ml of Filter Solv\textsuperscript{TM} Solution. The damp filter dissolved completely in this cocktail in approximately thirty minutes. The vials were counted three times for five minutes each by a Packard Tri-Carb Liquid Scintillation Spectrometer 3000 Series. The counts were corrected for background and the efficiency of the counter was calculated using the Channels ratio method.

The calculations to determine the amount of CO\textsubscript{2} fixed are from
Goldman, et al. (1974) and are based on this equation:

\[ \frac{\text{C}_{\text{assim.}}}{\text{C}_{\text{avail.}}} = \frac{1^{4}\text{C}_{\text{assim.}}}{1^{4}\text{C}_{\text{avail.}}} \times 1^{2}\text{C}_{\text{avail.}} \times k_{1,2,3} \]

In this equation

\[ 1^{2}\text{C}_{\text{avail.}} = \text{alkalinity in meq} \times \text{pH} \times \text{factor} \times 12 \]

\[ 1^{4}\text{C}_{\text{avail.}} = \text{activity (µCi x efficiency of the counter)} \]

\[ 1^{4}\text{C}_{\text{assim.}} = (\text{counts - background}) \times 1.06^* \]

\[ k_1 = \text{aliquot correction factor (e.g., 250 ml / 100 ml)} \]

\[ k_2 = \text{time correction factor (e.g., 1 hour / 2 hour)} \]

\[ k_3 = \text{dimension factor (mg l}^{-1} \text{ to mg m}^{-3}) \]

* 1.06 is the correction for the isotopic effect of \( 1^{4}\text{C} \) being heavier than \( 1^{2}\text{C} \).

In March, 1977, measurements of numbers and kinds of planktonic organisms were begun by a modification of the method of Edmundson (1974). Twelve liters of the large initial sample were poured through a plankton net of #20 nylon mesh bolting cloth with 68 threads per centimeter. The concentrate was centrifuged at 1500 xg in the laboratory, the supernatant was poured off and the organisms were resuspended in one ml of distilled water. Two drops of this suspension were placed on a slide, covered with a glass cover slip. Five complete strips the width of the slide were counted at 43x magnification. Organisms were identified to
genus (except for the Bacillariophyta).

Because preliminary studies indicated the concentration of nutrients (nitrogen and phosphorus) in Lewis Creek Reservoir might be low, I decided to conduct nutrient enrichment experiments. The objectives were to determine if one or both nutrients might be stimulatory to the natural phytoplankton, and if any interaction between the added heat and some nutrient might have an effect on the productivity of the phytoplankton. Eight nutrient enrichment experiments were conducted to determine the effect of two levels on nitrogen (NaNO₃) and phosphorus (K₂HPO₄) at the two levels of temperature using a factorial design (Ramm and Kern, 1976; Jordan and Bender, 1973). The experimental factorial design was suited to detecting any interactions that might occur between the temperature treatment and the added nutrient treatment. The levels of phosphorus were 0 mg l⁻¹ and 0.8 mg l⁻¹, nitrate-nitrogen. The levels of phosphorus were 0 mg l⁻¹ and 0.4 mg l⁻¹ phosphate-phosphorus.

A series of temperature effects experiments were conducted in which bottles from each station were incubated at both stations. For example, four bottles filled from the 15-liter sample at Station 1 were incubated at Station 1 and at Station 2; and four bottles from Station 2 were incubated at Station 1 and Station 2. This permitted an estimate of the productivity of the same phytoplankton (the population in the fifteen-liter sample) at two levels of temperature; the temperature at Station 1 and the temperature at Station 2.
CHAPTER III

RESULTS

PHYSICAL-CHEMICAL

At Station 1, the maximum temperature was 39°C in August and the minimum temperature was 17°C in January, 1977. The temperature range at Station 2 was 34°C in August, 1977, and 9°C in February, 1978. Temperature at Station 1 was always higher than temperature at Station 2 (Figure 5). To most efficiently cool the condensers during the summer, the power plant operates four pumps with a combined flow rate of 22.6 m³/sec⁻¹. The temperature rise across the condensers was minimized during this time. The smallest difference in temperature (ΔT) between Station 1 and 2 was 0.5°C in May, 1978, when the plant was not in full operation. The next smaller difference was 2°C in October, 1976, and in June, 1977. During the colder months, the differences in temperature were greater. The largest ΔT was 11°C in February, 1978. The flow rate through the power plant during colder weather was 11.3 m³/sec⁻¹. The overall average ΔT was 5.1°C. In the fall and winter, the average ΔT was 6.8°C. In the spring and summer, the average ΔT was 3.6°C.

Secchi disk depth varied seasonally (Figure 6). The transparency of the water decreased during the fall of 1976 and 1977, and a minimum Secchi disk depth of 0.78 meter was measured in April, 1978. During the spring and summer, transparency increased with a maximum Secchi disk depth of 2.3 meters obtained in September, 1977.

The variation of solar radiation was considerable due largely to clouds, despite attempts to sample only on clear, cloudless days. Fig-
Figure 5: Seasonal variation in surface water temperature of Lewis Creek Reservoir at Station 1 (---) and Station 2 (-----).
Figure 6: Seasonal variation in Secchi Disk Depth at Lewis Creek Reservoir.
ure 7 shows solar radiation during the incubation period (Cal cm$^{-2}$ hr$^{-1}$), compared to an estimate for solar radiation expected at 30° latitude.

The underwater light conditions are a function of the local radiation climate and the light attenuation of the water column. Attenuation (extinction) depends on light absorption by solutes and particles and is defined by the vertical extinction coefficient:

$$
\varepsilon = \frac{I}{z_2 - z_1} (\ln I_1 - \ln I_2)
$$

where $z_1$ is depth in meters and $\ln I_z$ is the natural log of the light intensity at that depth (Vollenweider, 1974). In reviewing the findings of numerous authors, Golterman (1975) and Vollenweider (1974) indicate the Secchi disk disappears when about 15% of incident light remains. This varies with local conditions and with observers. The percentage of incident light at the Secchi disk depth was estimated on several occasions by measuring the light intensity at the surface, subsurface, and at meter intervals. During the cooler months, when the water was more turbid, the Secchi disk disappeared where light intensity was approximately 18% of that at the surface. When transparency was greater, light intensity was 14% of surface illumination at the Secchi disk depth. Using 15% of incident light energy as $I_2$ (Secchi disk depth, $z_{SD}$), $\varepsilon$ was calculated for each sampling date. $\varepsilon$ ranged from 0.82 in September, 1978, to 2.43 in April, 1978. Spence, et al. (1971), using a spectroradiometer, measured extinction coefficients ($\varepsilon$) in different Scottish lochs and compared their data with values given by other researchers. They obtained values from 0.55 for a clear calcareous lake to 2.9 for a turbid, eutrophic lake.
Figure 7: Solar radiation (cal cm$^{-2}$ hr$^{-1}$) during incubation of carbon-14 inoculated samples and estimated radiation expected at 30° latitude. Estimated radiation (-----) and measured radiation (------).
Total alkalinity (as CaCO₃) ranged between 100-140 mg l⁻¹ and was the same at both stations. There was no seasonal pattern to the variation. Total alkalinity was due to bicarbonate ions, as phenolphthalein alkalinity was measured only on several occasions. Total hardness ranged between 90-100 mg l⁻¹ as CaCO₃ of which 80% to 90% was contributed by calcium hardness. There was no seasonal variation in pH which ranged between 7.7 and 8.6. These chemical values characterize a moderately hard bicarbonate system (Wetzel, 1975).

Specific conductance ranged between 200 to 450 μmhos cm⁻¹ (25°C). According to Golterman (1971), the amount of dissolved ionic matter in meq l⁻¹ may be estimated by multiplying the conductance in μmhos by 0.01. With the onset of more complete mixing of the water column as evidenced by the decreased water transparency in the fall and winter, an increase in specific conductance might also be expected. This was not the case. There was no seasonal pattern to the variation in specific conductance; the maximum and minimum both occurred in April, 1977.

During preliminary studies the spring and summer of 1976, unfiltered surface water samples and samples taken at one meter were subjected to Kjeldahl digestion without the removal of ammonia. No values for nitrate were obtained during the preliminary studies above 0.35 mg l⁻¹ which was the sensitivity limit of the Technicon Autoanalyzer. This same digestion prior to extraction into isobutanol did not yield measurable orthophosphate (<2 μg l⁻¹). In the routine analysis of the undigested samples during the study, phosphorus was always less than 2 μg l⁻¹. Nitrate nitrogen ranged from less than 0.2 mg l⁻¹ to 0.45 mg l⁻¹. Dissolved oxygen was always over 90% of saturation and often over 100% of saturation at both stations (Table I).
TABLE I

Comparison of Lewis Creek Reservoir chemical characteristics with surface water chemistry of nearby reservoirs

<table>
<thead>
<tr>
<th>Lewis Creek Reservoir</th>
<th>Ranges of nearby reservoirs**</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH</td>
<td>7.7-8.5</td>
</tr>
<tr>
<td>Alk</td>
<td>100-140 mg l(^{-1}) as CaCO(_3)</td>
</tr>
<tr>
<td>Orthophosphate</td>
<td>&lt; 2 µg l(^{-1})</td>
</tr>
<tr>
<td>Nitrate nitrogen</td>
<td>&lt; 0.2 mg l(^{-1}) - 0.45 mg l(^{-1})</td>
</tr>
<tr>
<td>Dissolved oxygen</td>
<td>Over 90% saturation</td>
</tr>
<tr>
<td>Conductivity</td>
<td>200-460 µmhos cm(^{-1})</td>
</tr>
<tr>
<td>Hardness</td>
<td>84-119 mg l(^{-1}) as CaCO(_3)</td>
</tr>
</tbody>
</table>

(87-88% calcium hardness)

** Sam Rayburn Reservoir, Livingston Reservoir, Lake Conroe Reservoir.
The Bicarbonate System in Lewis Creek Reservoir

The bicarbonate system of a lake is determined by the geological formations underlying the lake. The watershed runoff modifies the chemical composition of the water. The soil around Lewis Creek Reservoir is primarily a calcareous clay, low in organic matter. The drainage basin is flat, relatively undisturbed, and has little stream dissection (USDA, 1972).

When the pH range of the water is 7.7 to 8.5, the ionic species most available to plants is $\text{HCO}_3^-$. The predominating cation is $\text{Ca}^{++}$ as indicated by the 87% calcium hardness. When the system has about 2 meq L$^{-1}$ alkalinity as $\text{CaCO}_3$, about 50 grams m$^{-3}$ will precipitate when equilibrated with air. Any utilization of free $\text{CO}_2$ or $\text{HCO}_3^-$ tends to further precipitate $\text{CaCO}_3$ (Golterman, 1975). Precipitating $\text{CaCO}_3$ forms a nucleus for chelating io-s, especially phosphorus. This phenomenon could account for the consistently low concentrations of Phosphorus. Adsorption of any $\text{PO}_4^{3-}$ ions onto soil clay particles in the drainage basin probably eliminates loading from intermittent Lewis Creek and the surrounding watershed. Low phosphorus loading might account partially for the low concentrations in the water column.

BIOLOGICAL

Primary Productivity

Primary productivity at Station 1 ranged from 127 mg m$^{-3}$hr$^{-1}$ in September, 1976, to 12 mg m$^{-3}$hr$^{-1}$ in August, 1977. At Station 2, the range of primary productivity measurements was from 76 mg m$^{-3}$hr$^{-1}$ in September, 1976, to 8 mg m$^{-3}$hr$^{-1}$ on four occasions: December, 1976; February, 1977; February, 1978; and July, 1978 (Figure 8a). On April 19,
Figure 8: a) Seasonal variation of carbon-14 fixation at Station 1 (---) and Station 2 (-----).

b) Seasonal variation of photosynthetic efficiency at Station 1 (---) and Station 2 (-----).
\[ \text{mg C}^{14} \text{m}^{-3} \text{hr}^{-1} \]

\[ \text{P/LY} \]

\[ a = \text{STATION 2} > \text{STATION 1} \]

\[ b = \text{STATION 2} = \text{STATION 1} \]

Figure 8a

Figure 8b
and May 1, 1977, primary productivity was significantly higher at Station 2 than at Station 1 (points labelled A). On ten dates labelled B, there was no significant difference between stations in the amount of carbon fixed. On twenty-three of the thirty-five sampling dates, the rate of primary production was significantly higher (p < 0.01) at Station 1. All data was subjected to analysis of variance (Snedecor and Cochran, 1967).

For all the sampling dates, the average rate of carbon fixed at Stations 1 and 2 was 34 mg m\(^{-3}\)hr\(^{-1}\) (SD = 26.4) and 24 mg m\(^{-3}\)hr\(^{-1}\) (SD = 15.6), respectively. However, due to the variability in measurements, the difference between these means was not significant. When productivity values were averaged over each season, rates of fixation were always more at Station 1 than at Station 2. These differences were not statistically significant either.

The first three sampling dates had values which were outside (or just inside at Station 2) the 95% confidence limits of the values obtained. If those dates are considered "outliers" (Snedecor and Cochran, 1967) and omitted from the statistical calculations, the average rate of carbon fixed was 27 mg m\(^{-3}\)hr\(^{-1}\) (SD = 13.3) at Station 1 and 20 mg m\(^{-3}\)hr\(^{-1}\) (SD = 10.1). These means were not statistically different.

Linear regression and stepwise multiple regression analysis showed no correlation of primary productivity and either incident light or light at incubation depth and no non-linear pattern was evident.

Plots of the natural log of primary productivity as a function of temperature for Stations 1 and 2 (Figures 9a and 9b) appear to be curvilinear. If the points are separated at some assumed optimum temp-
Figure 9:  a) Natural log of Carbon-14 fixation vs. temperature at Station 1.

Maximum at 25°C —

Line A: $Y = 2.26 + 0.05 T^O$, $r = 0.29$, $p = 0.16$

Line B: $Y = 6.10 + (-0.09)T^O$, $r = -0.77$, $p = 0.005$

Maximum at 30°C —

Line C: $Y = 1.62 + 0.08 T^O$, $r = 0.57$, $p = 0.005$

Line D: $Y = 4.72 + (-0.03)T^O$, $r = -0.40$, $p = 0.09$

Points within the dotted lines were omitted in the calculations.

b) Natural log of Carbon-14 fixation vs. temperature at Station 2.

Maximum at 25°C —

Line A: $Y = 2.04 + 0.05 T^O$, $r = 0.52$, $p = 0.01$

Line B: $Y = 6.68 + (-0.12)T^O$, $r = -0.73$, $p = 0.002$

Line C: $Y = 2.31 + 0.03 T^O$, $r = 0.45$, $p = 0.01$

Line D: $Y = 8.38 + (-0.17) T^O$, $r = -0.58$, $p = 0.08$

Points within the dotted lines were omitted in the calculations.
erature, two components can be analyzed by the least squares method of linear regression. The Pearson Product-Moment correlation coefficient and the equation for each line are given in the figures. The correlation coefficients are reasonably strong and statistically significant for Stations 1 and 2, reflecting a positive response to increasing temperatures up to 30°C and a negative response above 30°C. In the Figure 9b (ambient T°), the optimum temperatures appear to be in the vicinity of 25°C. In Figure 9a (the heated station), the optimum appears to be closer to 30°C.

As the primary productivity data from Lewis Creek Reservoir appear to fit Gibbons' model (Figure 1), a polynomial regression might better describe the curvilinear relationship using the equation:

\[ Y = a + b_1 (T) + b_2 (T)^2 \]

The equations, correlation coefficients (r) and the coefficient of determination (r²) are shown in Figures 10a and b. The optimum temperatures were calculated from the equations and were estimated to be 25°C for Station 1 and 23°C for Station 2.

It is tempting to hypothesize that the organisms at Station 1 are adapted to higher temperatures. The phytoplankton sampled at Station 1, however, were at ambient temperatures less than 10 minutes before sampling, so it is unlikely that adaptation has taken place. Some incorporation of adapted periphyton which could have been resuspended in the water column could influence the community temperature optimum, but microscopic examination of the phytoplankton organisms never revealed the species of periphyton present in Lewis Creek Reservoir.
Figure 10: Polynomial regressions of the natural log of Carbon-14 fixation for Station 1 (a) and Station 2 (b).

Station 1 —

\[ Y = -85.5 + 9.05 \, T^0 + (-0.17)(T^0)^2 \]

\[ r = 0.56 \]

\[ r^2 = 0.32 \]

\[ n = 32 \]

Station 2 —

\[ Y = -29.25 + 4.88 \, T^0 + (-0.106)(T^0)^2 \]

\[ r = 0.55 \]

\[ r^2 = 0.31 \]

\[ n = 32 \]
Perhaps because primary productivity in Lewis Creek Reservoir is related to temperature as Gibbons (1976) suggests, the difference between Station 1 and Station 2 are not a function of ΔT. As mentioned previously, the ΔT is inversely related to flow rate through the condensers and is generally higher in winter. At this same time, incident radiation and light penetration of the water is less. Figure 11a and b shows a graph of ΔT (the rise in temperature across the condenser) as a function of time and a graph of ΔP (the difference in primary productivity between Stations 1 and 2) also as a function of time. In an attempt to explain the variation in ΔP, a least squares linear regression was performed with ΔT and ΔP as the variables. The Pearson Product-Moment correlation coefficient was 0.07 indicating the magnitude of ΔP is not a function of the magnitude of ΔT.

**Community Structure**

**Density:**

The numbers of organisms were generally of the same magnitude at both stations and were significantly correlated (Figure 12a) \( r = 0.76, p < 0.0001 \), but were often slightly higher at Station 2. There was a peak in numbers of organisms at both stations in April, 1977, and again in June, 1977. In the spring, both stations were dominated by diatoms, except in early March, 1977, the dominant organism at Station 1 was *Tetraedon regulare*, a small green alga. In April, 1978, both stations were dominated by *Tetraedon regulare*. In July, 1977, the dominant organisms at both stations were diatoms. On the remainder of the sampling dates, the dominant organism was *Anabaena filospaqua*, a large blue-green algae. The smallest numbers of organisms were found in July and August, 1977.
Figure 11: Seasonal variation of a) the difference in temperature, $\Delta T^O$, between Stations 1 and 2, and of 
b) the difference in primary productivity, $\Delta P$, between Stations 1 and 2.
Figure 12:  
a) Seasonal variation of the density (natural log of 
cells x $10^4$ per liter) of phytoplankton at Station 
1 (-----) and Station 2 (------).

b) Seasonal variation of the biomass (mg freshweight per 
$m^3$) at Station 1 (-----) and Station 2 (------).
The most frequently found species of phytoplankton are listed in Table II with the estimated volume.

A similarity in community structure at Stations 1 and 2 is evident when the relative abundance of the different groups of phytoplankton at both stations is compared (Figure 13a and b). The differences are: diatoms were not present in August at Station 2, and green algae were infrequent in August at Station 1. A few Euglenophyta and Chrysophyta (others) were present at both stations, mostly in the spring.

The density at both stations were negatively correlated with temperature (Figure 14a) \( r = -0.41, p < 0.01 \).

**Biomass:**

In this study, cell volume was estimated from measurements of algal cells in \( \mu^3 \) and expressed as \( 10^6 \mu^3 \) liter\(^{-1} \) which is equal to \( \mu g \) liter\(^{-1} \) which is assumed to mg m\(^{-3} \) if the specific gravity of the algae is 1 (Berman and Pollenger, 1974). Figure 12b shows the variation of the natural log of biomass with time for Stations 1 and 2. Biomass (12b) and density (12a) vary over time in a similar fashion. The peak of biomass in the spring is not as pronounced as the peak of numbers, indicating a predominance of smaller kinds of organisms in the spring. Density was correlated with biomass (Figure 14b) \( r = 0.58, p < 0.001 \).

During April, 1977, biomass at both stations was dominated by *Pediastrum duplex*, a large colonial green alga. In April, 1978, biomass at both stations was dominated by *Closterium* sp., a large desmid. On the remainder of the sampling dates, the biomass was dominated for *Anabaena* sp., a relatively larger blue-green filamentous alga. Fig-
<table>
<thead>
<tr>
<th>Organism</th>
<th>Biovolume per cell $\mu^3$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Chlorophyta</strong></td>
<td></td>
</tr>
<tr>
<td>Tetraedon regulare</td>
<td>2121</td>
</tr>
<tr>
<td>Podiastrum simplex</td>
<td>10537</td>
</tr>
<tr>
<td>Scenedesmus quadricauda</td>
<td>1000</td>
</tr>
<tr>
<td>Chlorella sp.</td>
<td>200</td>
</tr>
<tr>
<td>Cosmarium sp.</td>
<td>3000</td>
</tr>
<tr>
<td>Tetraedon muticum</td>
<td>40</td>
</tr>
<tr>
<td>Staurastrum margaritaceum</td>
<td>2145</td>
</tr>
<tr>
<td>S. alternaris</td>
<td>1617</td>
</tr>
<tr>
<td>S. gracile</td>
<td>410</td>
</tr>
<tr>
<td>Codastrum microsporum</td>
<td>3000</td>
</tr>
<tr>
<td><strong>Bacillariophyta</strong></td>
<td></td>
</tr>
<tr>
<td>Synedra acres</td>
<td>3511</td>
</tr>
<tr>
<td>S. ulva</td>
<td>5000</td>
</tr>
<tr>
<td>Acanthes sp.</td>
<td>1640</td>
</tr>
<tr>
<td>Navicula sp.</td>
<td>300</td>
</tr>
<tr>
<td><strong>Cyanophyta</strong></td>
<td></td>
</tr>
<tr>
<td>Anabaena flosaquae</td>
<td>200</td>
</tr>
<tr>
<td>Oscillatoria rubescens</td>
<td>30,000/filament</td>
</tr>
<tr>
<td><strong>Chrysophyta</strong></td>
<td></td>
</tr>
<tr>
<td>Dinobryon styselatcum</td>
<td>800</td>
</tr>
</tbody>
</table>
Figure 13: Seasonal variation of the relative abundance of the density of phytoplankton organisms: a) at Station 1, and b) at Station 2.
Figure 14:  

a) Linear regression of density of phytoplankton on temperature (both Stations).

b) Linear regression of density of phytoplankton on biomass (both Stations).
Figure 14

14a

$Y = 11.9 + (-0.26)X$, $r = -0.41$, $p < 0.001$

14b

$Y = 2.98 + 0.002X$, $r = 0.58$, $p < 0.001$
ures 15a and b show the relative abundance of the different groups of organisms for Stations 1 and 2. These figures are similar, again indicating that community composition was similar at both stations. However, in February and March, 1978, Ulothrix sp., a filamentous green alga, and some larger pennate diatoms dominated the biomass at Station 2 while Anabaena sp. dominated the biomass at Station 1. In addition, the diatoms at Station 1 were very small organisms.

Activity Coefficient:

Activity coefficient (P/B) productivity divided by biomass) (Findenegg, 1971) in Lewis Creek Reservoir varied between 0.003 and 0.64 mg C assimilated hour⁻¹ mg⁻¹ biomass (Figure 16a). The highest values were obtained in the spring when the phytoplankton was dominated by diatoms and green algae. The lowest values were obtained in June and December, 1977, when Anabaena sp. dominated in terms of both density and biovolume of the phytoplankton. This agrees with results obtained by other investigators (Kalff, 1972; Berman and Pollenger, 1974) who showed that smaller species are more metabolically active, probably due to a higher surface to volume ratio.

When production rate per unit area or unit volume is divided by some measure of population density per unit area or volume, the ratio is termed mean specific rate (Talling, 1969), activity coefficient (Findenegg, 1971), relative assimilation rate (Elster, 1965), or bioactivity (Ohle, 1956). There has not been standardization of methods used for computing this ratio. Some investigators have used chlorophyll a per unit volume, others have used dry weight or estimated biovolume after the method of Nauwerek (1963) as a measure of population.
Figure 15: Seasonal variation of the relative abundance of the biomass of the phytoplankton organisms: a) at Station 1, and b) at Station 2.
Figure 16:  a) Seasonal variation of activity coefficient (P/B) at both stations: Station 1 (- - - -); and Station 2 (- - - -).

b) Seasonal variation of primary productivity (Carbon-14 fixation) at both stations: Station 1 (- - - -); and Station 2 (- - - -).
density. More recently, investigators have chosen to express standing crop as g C m$^{-3}$ assuming wet weight or biovolume is 10% carbon (Strickland, 1960; Goldman, et al., 1968; Lewis, 1974; Berman and Pollen, 1974).

A comparison of temporal variation in the activity coefficient (Figure 16a) and $\text{C}^{14}$ assimilation rate (Figure 16b) shows that effect of additional heat at Station 1 is evident in both graphs. For eighteen out of twenty-two sampling dates, the activity coefficient was higher at Station 1 than at Station 2.

Species diversity:

Margalef (1965) points out that primary production is generally mathematically and biologically a function of the structure of the community. Biotic diversity has been used to describe the structure of an ecological community (Patten, 1962; Sager and Hasler, 1969; Fogg, 1975). I calculated the species diversity at each station on each sampling date. Using the formula of Shannon (1948) based on information theory:

$$\text{Diversity (H')} = \sum_{i=1}^{S} p_i \ln p_i$$

where $p_i$ is the proportion of the total population of individuals $(N)$ belonging to the $i$th species $(n_i)$ or $n_i/N$. Species diversity (Figure 17a) was highest (2.440) in January and lowest in July and August (0.397). This is in contrast to studies on other more northern lakes (Moss, 1973; Lund, 1964) where species diversity was higher in the summer and lower in winter and early spring. However, as Patrick (1969) pointed out, diversity decreases with increasing temperature after some
Figure 17: a) Seasonal variation in species diversity at both stations. Station 1 (———); Station 2 (———).

b) Linear regression of species diversity on temperature.
critical tolerance range for the community.

A least squares linear regression was performed on the data (Figure 17b). The correlation was negative and relatively strong (-0.69, p 0.001). To determine if there was a relationship between community structure as described by species diversity and primary production, the two were plotted against each other. No pattern was evident.

EXPERIMENTS

Temperature Effect Experiments in the Field

On seven sampling dates, temperature effect experiments reversing the incubation bottles from each station (e.g., incubating samples from Station 1 at Station 2, etc.) were performed (Figure 18a). On three of the sampling dates (November 10, February 27, and May 19) there were no statistically significant differences in the amount of carbon fixed in samples from Stations 1 and 2, or as a result of reversing the samples. On the other four dates, the samples incubated at the original stations and the reversed samples did show statistically significant differences. Samples from Station 1 (the heated station) incubated at Station 2 showed lower carbon fixation than those samples from Station 1. Those samples from Station 2 which were incubated at Station 1 (at a higher temperature) showed higher carbon fixation than those from Station 2 incubated at Station 2. The activity coefficient reflected a similar response (Figure 18b).

In March and April, when the volume, numbers, and kinds of organisms in the samples were estimated, 91% of the individuals in March and 98% of the individuals in April were contributed by small Chlorophyta (200 μ³) and Bacillophyta. In June, 55% of the numbers of organisms
Figure 18: a) Results of in situ temperature effect experiments. H-H = Station 1 samples incubated at Station 1; H-C = Station 1 samples incubated at Station 2; C-C = Station 2 samples incubated at Station 2; C-H = Station 2 samples incubated at Station 1. Dates underlined = no significant difference between samples.

b) Activity coefficients of same experiments.
were *Anabaena* sp. (80000 µ³). Findenegg (1965), in stressing the importance of qualitative phytoplankton counts, discussed the inverse correlation frequently found between the quantity of algal biomass and the production per unit of fresh weight (activity coefficient). He attributes this phenomenon to several factors, the most important being the higher metabolisms of the smaller planktonic organisms. The dominance of smaller organisms in March and April could account for the higher activity coefficients at both stations, as compared to those in June. Temperature, however, must account for the difference between Station 1 and Station 2 samples in the amount of carbon fixed on each date.

**Temperature Effect Experiments in the Laboratory**

In December, 1977, January and February, 1978, a series of experiments were performed *in situ* and in the laboratory in a constant light (1200 foot-candles) and constant temperature growth chamber. Samples were incubated as usual at the station of origin and additional samples were incubated at various temperatures in the laboratory. In the laboratory at the same temperature, there was no significant difference in the rate of primary production between water samples from Stations 1 and 2 (Figure 19).

Analysis of variance showed that nutrient enrichment had no effect on primary productivity in any of the eight experiments. It is possible that the levels of nutrients were insufficient to stimulate the organisms. However, levels of nutrient spikes were within the ranges of the concentrations of nitrogen and phosphorus in three synthetic culture media for algae and typical eutrophic freshwater (Fogg, 1975) and should have been high enough to stimulate a photosynthetic response
Figure 19: Results of carbon-14 experiments in situ and at different temperatures in the laboratory for samples from Stations 1 and 2.
if those nutrients were limiting. The two-hour incubation of the spiked bottles could coincide with the characteristic lag phase of microorganisms grown in culture (Peterson, et al., 1974; Schelske, et al., 1974). Other studies have allowed for this lag period and previously spiked large enclosed samples (Jordan and Bender, 1973) to permit uptake of the nutrients before sampling for rates of carbon fixation. Some have added nutrients to the incubation bottles, but have incubated for a longer period (Powers, et al., 1972). A final possibility is that the nutrient enrichment experiments were conducted at light intensities at or above that of light saturation of photosynthesis. Under these circumstances, it would be difficult to assess the effect of nutrient enrichment (Ganf, 1975).
CHAPTER IV

DISCUSSION AND CONCLUSIONS

COMPARISONS WITH OTHER LAKES

Comparisons of primary productivity of other systems are difficult because most investigators report data as mg C m\(^{-2}\) which varies not only with the trophic state but with the thickness of the euphotic zone. Comparison of Lewis Creek Reservoir phytoplankton productivity with other warm water aquatic systems is presented in Table III. Average ambient mg C m\(^{-3}\) hr\(^{-1}\) (Station 2) for Lewis Creek Reservoir was multiplied by the average depth and by 10 hours as an estimate of the average number of hours in which solar radiation is sufficient for carbon fixation to estimate mg C m\(^{-2}\)day\(^{-1}\).

Characterization of the trophic state of lakes has been the subject of numerous studies using many different parameters. One of the more recent investigations (Carlson, 1977) developed a numerical Trophic State Index, TSI, on a scale of 0 to 100 using any of several parameters, one of which is Secchi disk transparency. Based on Carlson's TSI, Lewis Creek Reservoir falls in the middle of the scale or mesotrophic. According to Wetzel (1975), mesotrophic type lakes have the ranges of primary productivity of the phytoplankton and other characteristics presented in Table IV. Values either measured or estimated for Lewis Creek Reservoir are presented for comparison. Apparently, Lewis Creek Reservoir could be considered mesotrophic by these criteria.

The assumption of such classifications based on phytoplankton
### TABLE III

Comparison of Values for LCR with Other Warm Water Systems

<table>
<thead>
<tr>
<th>Lake</th>
<th>Location</th>
<th>mg C m$^{-2}$day$^{-1}$</th>
<th>mg C m$^{-3}$hr$^{-1}$</th>
<th>Investigator</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lanao</td>
<td>8°N124°E</td>
<td>0.1700</td>
<td>31.9$^*$</td>
<td>Lewis, 1974</td>
<td>Low nutrients. Extreme nitrogen depletion.</td>
</tr>
<tr>
<td>Tradinghouse Creek Reservoir</td>
<td>31°34'N 96°57'W</td>
<td>0.2060</td>
<td>69.0$^*$</td>
<td>Lind, 1975</td>
<td>No nutrient data.</td>
</tr>
<tr>
<td>Waco Reservoir</td>
<td>31°34'N 97°13'W</td>
<td>0.8570</td>
<td>39.0$^*$</td>
<td>Kimmel and Lind, 1972</td>
<td>Phosphorous limited. Very turbid.</td>
</tr>
<tr>
<td>LCR</td>
<td>30°26'N 95°32'W</td>
<td>0.1280$^*$</td>
<td>24.0</td>
<td>This study.</td>
<td></td>
</tr>
</tbody>
</table>

$^*$ Estimated from data given.
TABLE IV

General Range of Primary Productivity and Related Characteristics of Mesotrophic Lakes and Lewis Creek Reservoir

<table>
<thead>
<tr>
<th>Trophic type</th>
<th>Mean Phytoplankton biomass (mg C/m²/day)</th>
<th>Light Extinction coefficient</th>
<th>PO₄-P (μg l⁻¹)</th>
<th>NO₃-N (μg l⁻¹)</th>
<th>Inorganic solids (mg l⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mesotrophy</td>
<td>250-1000</td>
<td>100-300</td>
<td>0.1 - 2.0</td>
<td>10-30</td>
<td>500-1100</td>
</tr>
<tr>
<td>LCR</td>
<td>1280</td>
<td>77-5500</td>
<td>0.82 - 2.43</td>
<td>&lt;2-40</td>
<td>450-1000</td>
</tr>
</tbody>
</table>
productivity is that other sources of primary production are small compared to phytoplankton production. Soon after this study was begun, it became obvious a large macrophytic population dominated the extensive littoral zone in Lewis Creek Reservoir, a large periphyton community existed on all submerged surfaces and larger benthic algae developed extensive mats. Although this study was not designed to characterize Lewis Creek Reservoir, any further study to do so would have to center on the benthic algae and macrophytic productivity.

THE EFFECT OF ADDED HEAT ON PRIMARY PRODUCTIVITY

One of the objectives of this study was to evaluate the effects of increased temperature on phytoplankton primary productivity. The results of this study indicate increased temperature increased the rate of production of the phytoplankton in Lewis Creek Reservoir. For 66% of the sampling dates, carbon fixation was significantly higher at the heated station. The temperature effect experiments in which water samples were reversed, also indicated temperature affected carbon fixation.

This conclusion is further supported by the laboratory experiments in which water samples from each station were incubated in the constant light and constant temperature chamber. Although carbon fixation was significantly different at each station in situ, the phytoplankton community of each station responded similarly to the same temperature in the laboratory.

The difference in primary productivity was greater in the fall and winter as evidenced by greater ΔPs. This effect was not a simple function of greater ΔTs, however, as these two variables were not sig-
nificantly correlated.

The rate of primary productivity was higher at Station 1 than at Station 2 even though the data indicates the phytoplankton community was the same as species composition, density, and biomass were similar at the two stations.

Lind (1974) observed increased rates of photosynthesis in a similar study in Tradinghouse Creek Reservoir, McLennan County, Texas. Heat stimulated photosynthesis up to about 40°C in Tradinghouse Creek Reservoir.

Lind also observed a phenomenon he called a "heat-cold" shock when samples from the heated station incubated at the unheated station had lower rates of photosynthesis than samples from the unheated station incubated at the unheated station. This "heat-cold" shock was not observed in my experiments, possibly because ATs were generally lower than those in Tradinghouse Creek Reservoir.

**FACTORS AFFECTING ANNUAL VARIATION OF PRIMARY PRODUCTIVITY**

**Nutrients**

Productivity appears to peak in the spring and in the fall in Lewis Creek Reservoir. This is in agreement with classical phytoplankton productivity literature (based on studies of more northern lakes). Classically, these increases are attributed to more complete mixing of the mineralized nutrients from the hypolimnion and, in the spring, to increase solar radiation and freedom from ice cover.

With a generally well-mixed system such as Lewis Creek Reservoir, nutrient availability and nutrient depletion are probably not responsible for the annual variation in carbon fixation.
Lewis Creek Reservoir is well mixed by the prevailing southeast-erly winds during most of the year and by occasional, strong north-westerly winds in the winter. The density differential of the hot-test water in August and September (the calmest months) flowing over ambient water might create an isolated epilimnion. Then fall mixing might provide the pulse of nutrients to stimulate the peak in produc-tion activity. Although this mixing was not reflected in the chemis-try of the water, transparency decreases during fall are consistent with the hypothesis that some stratification occurred.

Data from Lewis Creek Reservoir indicate low nutrient concentra-tions in the water column, but in spite of this, productivity values averaged about 25 mg C m⁻³ hr⁻¹ (0.13 gm C m⁻² day⁻¹). How was this possible? In April, 1978, and July, 1978, measurements of 40-50 µg l⁻¹ PO₄-P and 1 mg l⁻¹ NO₃-N were obtained in bottom water samples. Apparently, algal activity removed the nutrients from the water column as it was supplied by mixing. This concurs with conclusions of Lewis (1974) in the studies on Lake Lanao that nutrient concentrations were very low because of rapid phytoplankton uptake. Fogg (1975) suggests that the concentration measured in the water represent the balance between the supply of nutrients and the nutrients which are consumed, hence when algal activity is high, nutrient concentration may be low. As he points out, the level at which a nutrient becomes limiting varies with the level of other environmental factors, for instance, light intensity. Fogg (1975), discussing the growth rate of algae in relation to phosphate concentration, describes studies which found maximum growth rates at phosphate concentration less than 20 µg l⁻¹.
Chara spp., which forms dense mats in the littoral zones of Lewis Creek Reservoir, is one such organism listed. Many blue-green algae, by way of their gas-vacuole bouyancy control mechanisms, descend at night to phosphate richer waters at the bottom and rise to the lighted and nutrient depleted waters in the morning.

**Light**

Statistical analysis indicated seasonal variation in primary productivity was not accounted for by light intensity variation. The rates of photosynthesis obtained in these studies probably represent light-saturated photosynthesis ($P_{\text{max}}$) most of the year. This was indicated by preliminary studies of carbon fixation with depth in the water column. $P_{\text{max}}$ is independent of light intensity (Golterman, 1975; Steemann-Nielsen and Jørgensen, 1968; and Talling, 1966).

At latitudes lower than those where most classical primary productivity studies have been performed, annual variation in solar radiation is not so pronounced. A spring increase in solar radiation certainly occurs at the latitude of Lewis Creek Reservoir (30° N latitude) and could partially account for the minor peaks in primary production. The examination of photosynthetic efficiency also indicated, however, that primary production appeared to be independent of light intensity.

**Temperature**

Temperature is the primary factor responsible for the seasonal variation of primary productivity. Water temperatures (Figure 5) reached the estimated optimum temperatures for the Lewis Creek Reservoir phytoplankton (Figures 9 and 10) in the spring and in the fall at
approximately the same time productivity of the phytoplankton appeared to peak (Figure 8a). Summer temperatures were above 30°C which clearly depressed carbon fixation (Figures 9 and 10).

My data suggest that Talling (1965) is correct in considering temperature the primary factor influencing higher productivity observed in tropical waters. His reasoning, that the temperature dependence of $P_{\text{max}}$ (light-saturated photosynthesis) is the mechanism, may be incorrect, however. It may be that phytoplankton communities are functioning at optimum temperatures as is the case in the spring and fall in subtropical Lewis Creek Reservoir.

**Community Structure**

Associated with increased production in the spring was a change in community composition of the phytoplankton. A predominance of smaller kinds of algae, diatoms and small green algae, occurred in March and April of each year. The highest values for the activity coefficient which reflects metabolic activity also occurred in March and April of each year. This agrees with results obtained by other investigators (Kalf, 1972; Berman and Pollinger, 1974) who showed that smaller species are more metabolically active, probably due to a higher surface-to-volume ratio. Here, we may have an advantage to those organisms which can divide faster to utilize available nutrient more quickly. Those species which can tolerate temperatures above the community optimum have an advantage. In most aquatic systems, these are members of the Cyanophyta. A decrease in the species diversity encountered in the summer was due to the dominance of blue-green algae. The changes in community structure are what one might predict
from the temperature optimum and from studies which have been made on phytoplankton temperature optimum (Cairns, 1956; Trembley, 1965; Patrick, 1971 and 1974).

Even though more temperature tolerant species were dominant in the summer productivity did not continue to increase. Additional heat did not significantly depress productivity further, however, contrary to other studies (Warinner and Brehmer, 1956; Patrick, 1969; and Lind, 1974). This may have been due to higher optimum temperatures for the natural phytoplankton in Lewis Creek Reservoir and to smaller ΔTs in the summer.

It seems the role temperature plays in primary productivity at lower latitudes is somewhat more than that affecting "light-saturated" rate of photosynthesis. It is evident from the literature and from this study that aquatic systems in tropical and subtropical latitudes function differently than do those at higher latitudes. More studies characterizing aquatic primary productivity at lower latitudes are needed to better define global primary productivity and to resolve the questions still in the literature (Talling, 1966; Brylinsky and Mann, 1973; Lewis, 1974; and Schindler, 1978).

CONCLUSIONS

1. For 66% of the sampling dates, carbon fixation was significantly higher at the heated station.

2. Four out of seven in situ experiments, in which water samples were reversed, indicated temperature affected carbon fixation.

3. In laboratory experiments incubating the natural phytoplankton from each station at different temperatures, the phytoplankton commun-
ity of each station responded similarly to temperatures in the laboratory.

4. The difference in primary productivity between stations, ΔP, was not a simple function of the difference in temperature between stations, ΔT.

5. Peaks in seasonal variation of primary productivity occurred in the spring and the fall and coincided with the occurrence of the estimated optimum water temperatures.

6. Nutrients were low due to removal from the water column by the primary producers, but did not appear to be limiting.

7. Values for primary productivity were independent of light intensity.

8. The community structure was similar at both stations. The organisms responded similarly to temperature. The community structure changed when the temperature optimum was exceeded.
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