MONTANA STATE UNIVERSITY

Limnological studies on Hebgen Lake, Montana
by Danny Bernard Martin

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Botany
Montana State University
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Abstract:
The dynamics of the plankton community in relation to the inorganic chemical and physical environment was studied during the summers of 1964 and 1965, Samples and in situ measurements were taken at five permanent stations on the lake during thirty cruises.

Under average conditions, total visible light was reduced to 1% of surface intensity at a depth of 8.0 meters, while blue, red and green light were extincted to 1% at 2.8, 6.2 and 7.8 meters respectively. Various effects of light on primary productivity and the measurement of community photosynthetic rates have been discussed.

Temperature and conductance in Hebgen Lake are described with respect to both the seasonal and spatial distribution of heat and electrolytes.

The progressive downstream increase in reservoir temperatures is discussed in relation to observed changes in the population densities and birth rates of Daphnia schodleri and D. galeata mendotae. The effects of thermal stratification on the vertical distribution of inorganic nutrients is shown.

Results of the chemical analyses showed Hebgen to be a predominantly sodium bicarbonate lake with relatively low concentrations of potassium, calcium, magnesium, chloride and sulfate. Phosphate was unusually high and it appeared that nitrate might be the most important limiting factor to primary production. Other constituents of the chemical environment discussed are; pH, inorganic carbon, iron, silica and dissolved oxygen.

Standing crops of each taxon in the phytoplankton community were determined by direct count. Lyngbya Birgei and Aphanizomenon flos-aquae reached the highest standing crops, followed in abundance by Anabaena spiroides, Asterionella foraosa, Cryptomonas ovata and Ceratium hirundin-ella. Total algal standing crops ranged from 0.30 to 5.74 mm3/liter. Measurements of chlorophyll were also obtained on each cruise, and values ranged between 1.24 and 4.43 µ g/liter.

Primary productivity was measured by light and dark bottles utilizing both uptake of radioactive carbon and changes in dissolved oxygen. Net photosynthetic rates as measured by C14, ranged from 0.10 to 0.65 g C/m2/ day, and those measured by changes in dissolved oxygen between 0.33 and 2.13 g C/m2/day. Four methods for estimating photosynthetie rates from chlorophyll and light data were employed simultaneously with the light and dark bottle methods, A comparative analysis of all methods used is given.

Standing crops of Daphnia schodleri, D. galeata mendotae, D. pulex, Cyclops bicuspidatus, Diaptomus nudus and D. Ieptopus were obtained. Instantaneous rates of population change, instantaneous birth rates and mortality rates were computed for the two most abundant zooplankters, D, schodleri and D. galeata mendotae. The average productivity for the latter two species was 0.11 g C/m2/day.

221

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by

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TABLE OF CONTENTS

LIST OF TABLES

Page

LIST OF FIGURES

ABSTRACT

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Under average conditions, total visible light was reduced to 1% of surface intensity at a depth of 8.0 meters, while blue, red and green light were extincted to 1% at 2.8, 6.2 and 7.8 meters respectively. Various effects of light on primary productivity and the measurement of community photosynthetic rates have been discussed.

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INTRODUCTION

In 1962, a series of ecological studies was begun on the waters of the upper Madison River in and near Yellowstone National Park. The central and unifying objective of these studies is to determine quantitative and qualitative relationships between the biotic productivity of these waters and certain controlling chemical and physical environmental factors.

Figure 1 shows a map of the waterways, which to date have been included in the studies of the upper Madison River system. Prior to 1964, investigations had been confined to the Firehole, Gibbon, and Madison Rivers above Hebgen Lake. In 1964, the study described in this paper was initiated on Hebgen Lake, and was designed to run concurrently with other research on reaches of the Madison River directly above the lake. The objective was to provide comparative studies of lotic and lentic waters which had the same macroclimate and geochemical history.

Hebgen Lake is an artificial impoundment of the Madison River. The reservoir is formed behind a concrete and earthfill dam, completed in 1915, located 18 miles northwest of West Yellowstone, Montana at lat 44° 51' 50" long 111° 20' 05". The bulk of the lake is contained within Township 12 South, Range 4 East, of Gallatin County, Montana. During the normal, annual high water period (June-July), the lake is approximately 15 miles long, 3 miles wide at the widest point, and has a total surface area of about 20 square miles. During high water, the lake has a maximum depth of about 80 feet (26 meters). Maximum storage capacity of the reservoir is 377,500 acre-feet.

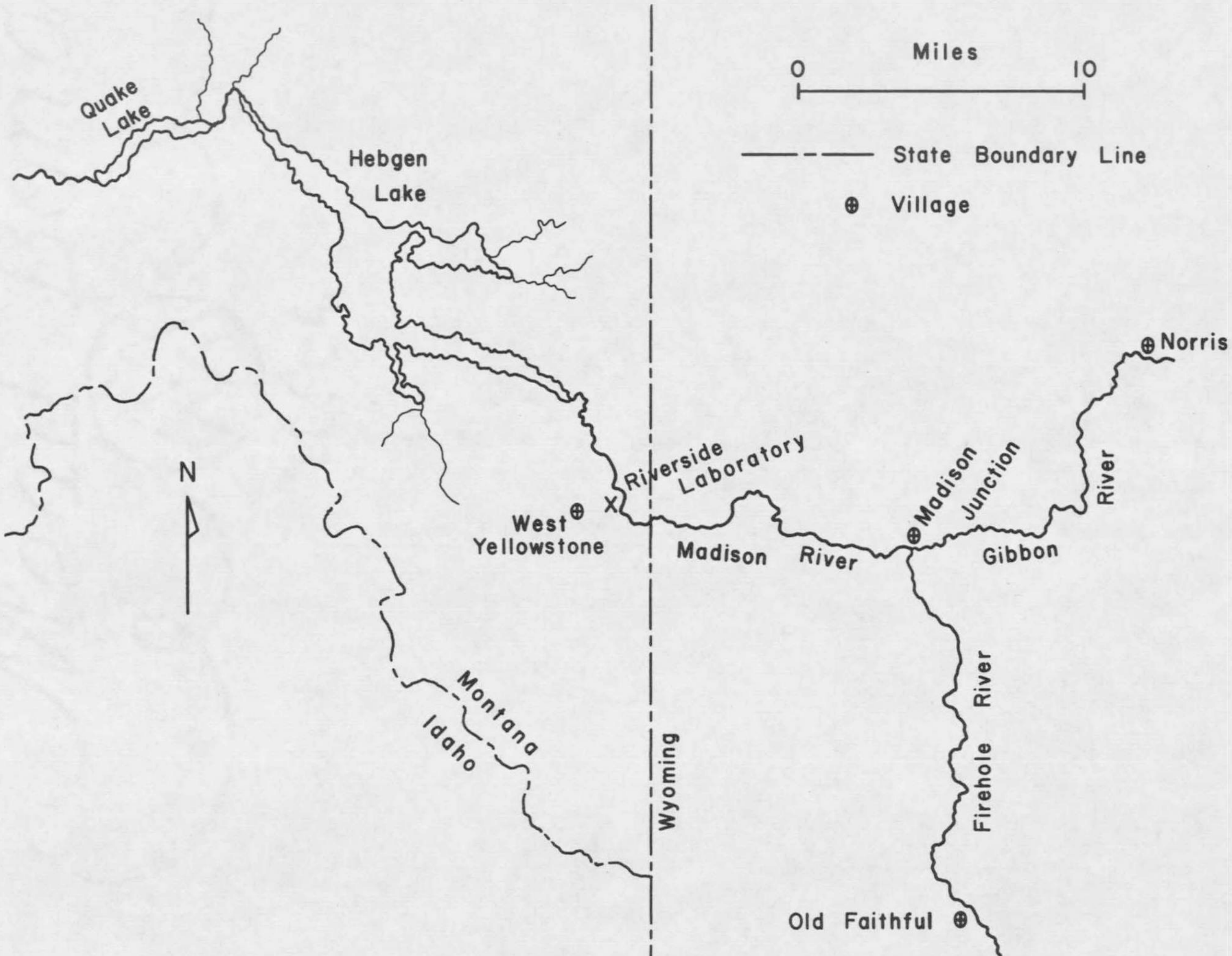

Figure 1. Map of the upper Madison River system and some associated landmarks.

Throughout an annual cycle, the water level in the reservoir undergoes an average vertical fluctuation of 20 feet (7 meters). This extensive drawdown largely precludes the development of benthic or littoral biotic communities along the margins of the lake. Productivity is therefore limited to the open water or plankton communities.

This report involves the initial limnological investigations carried out on Hebgen Lake. Research was conducted during the summers of 1964 and 1965. The specific relationships considered in this study are diagramed in Figure 2. The approach to this problem was based on the current functional approach to limnetic acquatic ecology. The theoretical aspects of this concept are summarized, relative to the phytoplankton entity, by Findenegg (1965) as follows:

> It is a well known fact that primary production in lakes is controlled by the interaction of many factors which usually are divided into three groups: (1) Physical factors originating directly or indirectly from solar radiation, such as light conditions, temperature, mixing and turbulence by the action of the wind; (2) The content of nutrients in the euphotic zone of the lakes, and (3) the interaction of the organisms present in the plankton community which may promote or hamper the production of certain species.

In the present study, Findenegg's approach has been somewhat extended. First, it was assumed that reciprocal relationships exist between the four entities shown in Figure 2. Events occurring within an individual component effect changes in the other three. Thus, in the community, there emerges an everchanging pattern of cause-and-effect interactions. Discrete events are necessarily studied quantitatively at the level of the individual component, but the results must be interpreted with regard to the entire system. Second, it was considered that relationships between

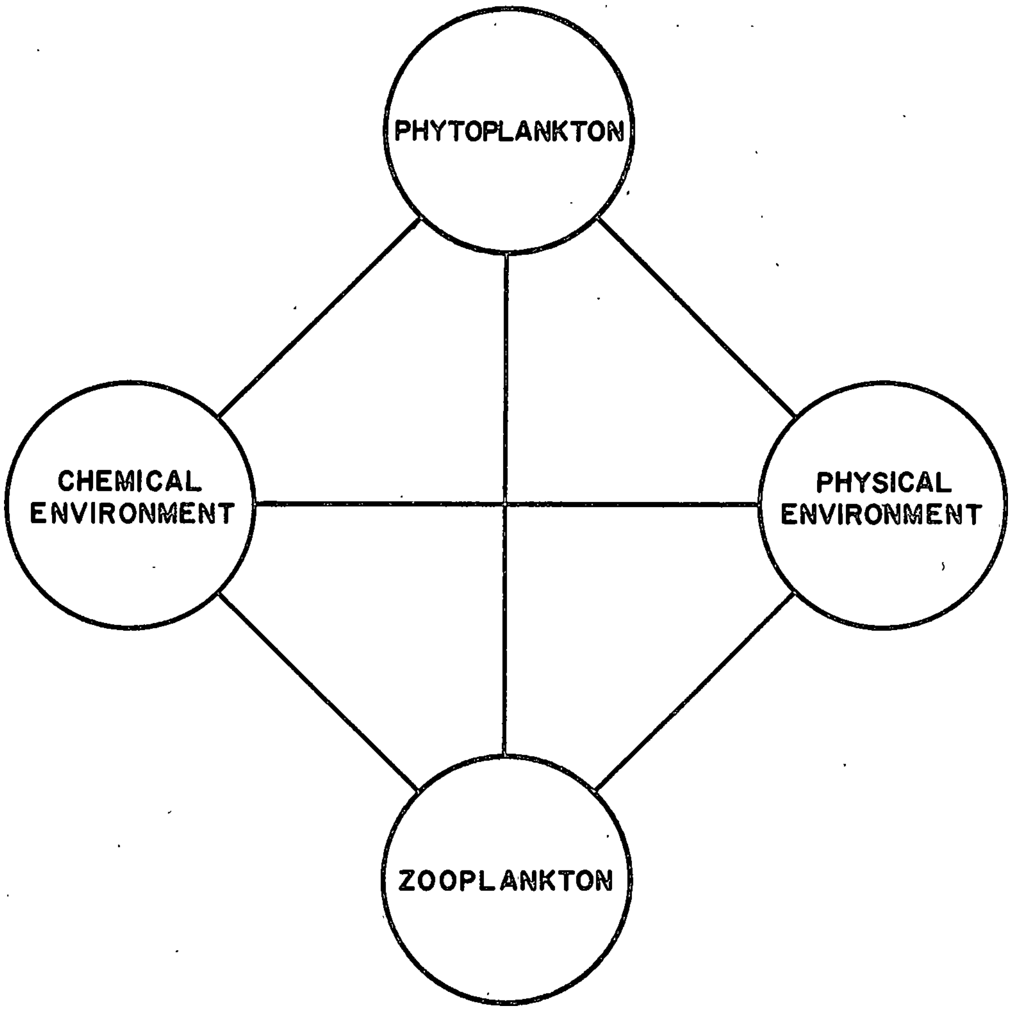

Figure 2. Diagramatic representation of the entities and interrelationships considered in the thesis problem.

components are not always direct. Events occurring within one entity can be transmitted step-wise, through one or two intervening components, until finally a measurable effect may be manifested in the fourth.

Certain components of the aquatic ecosystem (e.g. decomposers, secondary consumers) have been omitted from this study. Furthermore, each component shown in Figure 2 was not exhaustively treated (e.g. the complete organic and inorganic chemical environment was not quantitatively analyzed).

In this paper, the four major categories shown in Figure 2 have been used to organize the material in the sections of "Methods" and "Results". Interrelationships among the four entities are explored in the "Discussion" section.

METHODS

In this study, all samples and *in situ* measurements were taken during one of thirty cruises on Hebgen Lake. Tables I and II in the "Results" show the dates for each cruise during 1964 and 1965 respectively. When possible, sampling days were spaced at weekly intervals throughout both summers.

Five permanent stations were established on Hebgen during the first cruise of 1964 (see Figure 3). Stations 1, 2 and 3 were located along the lower, main body of the lake. Stations 4 and 5 were located just inside the mouth of the Madison and Grayling Arms respectively.

Light

Permanent records of total solar radiation, incident to the lake surface, were obtained during 1964 and 1965 with an Eppley 50-junction pyranometer and "Rustrak" recorder. These instruments were installed at the Riverside Laboratory, about 20 miles from the outlet of Hebgen Lake (see Figure 1). Daily radiation curves recorded on the "Rustrak" charts were converted to langleys/day by the method given in the Eppley Laboratory Bulletin.

Vertical profiles of light attenuation in the lake were obtained by measuring light intensity at various depths with a submarine photometer. The photometer employs a Weston, Model 856, selenium photocell which is activated by wavelengths of 400 to 700 mμ. Light measured with the selenium photocell is termed "total visible light" and nearly coincides with that portion of the spectrum which is photosynthetically active (Edmondson, 1956). Light intensity was measured at regular depths in the lake,

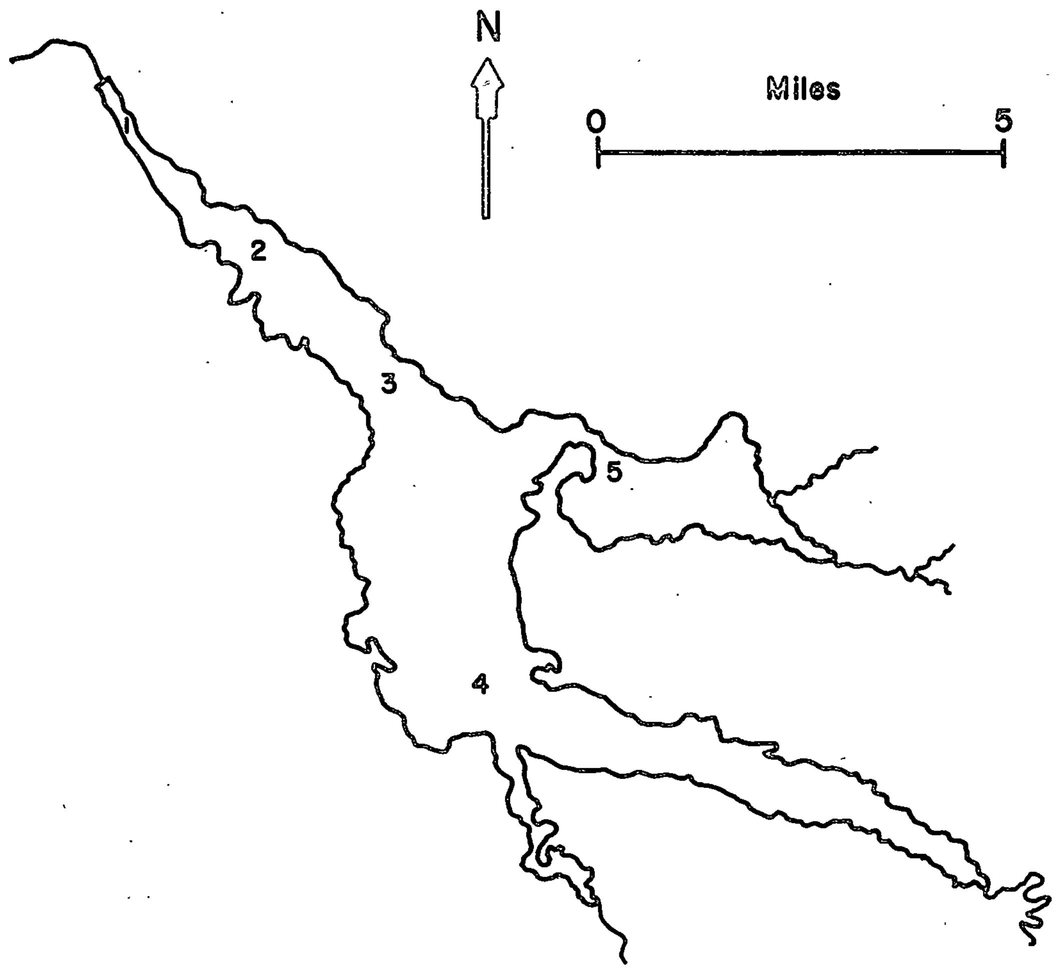

Figure 3. Map of Hebgen Lake showing the location of the five permanent sampling stations.

from the surface to that depth at which the current produced by the photocell was less than 1 microamp.

During 1964, profiles of total visible light were taken at the 5 permanent stations shown in Figure 3. On each cruise, measurements were taken between 0900 and 1500 hours.

In 1965, profiles of total visible light were taken only at Station 3 between 1000 and 1400 hours. In addition, profiles were taken of light passed by the following filters: (a) Blue - Maximum transmission approximately 450 mμ, (b) Green - Max. trans. approx. 550 mμ, and (c) Red - Max. trans. approx. 650 mμ.

The mean "vertical extinction coefficient" (Hutchinson, 1957), and corrected surface reading were computed for each profile by the method of Verdiun (1964).

Temperature and Conductivity

Vertical profiles of temperature and conductivity were taken simultaneously by lowering a platinum electrode with an attached glass bead thermistor into the lake. The electrical resistance across each sensor was measured at one meter intervals from the surface to the bottom of the lake with an Industrial Instruments Conductivity Bridge.

The resistance of the thermistor bead was converted to Centigrade temperature using an experimentally determined calibration curve. Specific conductance at 25° C was computed from the observed resistance of the water according to the method described by American Public Health Association (1965).

Temperature-conductivity profiles were taken at all 5 stations during

1964 and only at Station 3 during 1965.

Water Chemistry

Water for chemical analysis was collected at Station 3 on every cruise during 1964 and 1965. A 3 liter Van Dorn Water Bottle was used to collect samples from the following depths: (a) 1964 - 0, 1½, 3, 4½, 6, 7½ and 9 meters, and (b) 1965 - at 1 meter intervals from the surface to 8 meters and at 11, 14, and 17 (bottom) meters.

Upon collection, two 500 ml aliquots from each depth were immediately filtered through HA "Millipore" filters (pore size - .45 microns) to remove all organisms. About 300 ml of the filtered water was stored in screw-cap polypropylene containers; the remainder was stored in Pyrex glass-stoppered bottles. Storage containers were rinsed with sample prior to filling. Subsequent analyses for each chemical constiuent were run on samples from each depth, resulting in a vertical profile of the chemical environment.

Concentrations of sodium, potassium and calcium were determined with a Beckman DU flame spectrophotometer, following the procedures given in the Bechman Instruction Manual #334-A. Silica, total iron, phosphate, chloride, sulfate, calcium, magnesium and total alkalinity were analyzed using either colorimetric or titrimetric procedures described by American Public Health Association (APHA, 1965). Optical density of the solutions for colorimetric analysis was measured with either a Bausch and Lomb "Spectronic 20" or a Klett-Summerson colorimeter.

Hydrogen ion concentration was determined with a Beckman expanded scale pH meter. The pH meter used was thermally compensated and was standardized with two buffers (to bracket the range of pH encountered) before each use.

Nitrate determinations were made according to the method of Mullin and Riley as described by Barnes (1962). Total inorganic carbon was computed from pH, temperature and total alkalinity, using the formulae derived by Saunders et al. (1962).

Total alkalinity, nitrate, phosphate and pH determinations were made within 3-6 hours after field collection; all other analyses were run within 48 hours.

The method used for dissolved oxygen was the Alsterberg modification of the Winkler technique (APHA, 1965). Samples for the determination of dissolved oxygen were drawn carefully from the Van Dorn Water Bottle into separate 300 ml Pyrex, glass-stoppered bottles. The unfiltered samples were "fixed" immediately upon collection, and titrations were made from 2-6 hours later.

Total alkalinity, pH, phosphate, dissolved oxygen and inorganic carbon determinations were made during 1964. All analyses referred to in this section were made during 1965.

Phytoplankton Standing Crop and Productivity

Vertical profiles of phytoplankton standing crop were obtained at Station 3 for each cruise during 1964 and 1965. The total cell volume per unit volume of water (mm^3/liter) was determined for each taxon in the phytoplankton community as follows: (1) A 125 ml sample of lake water was taken from the Van Dorn Water Bottle at each sampling depth, and preserved with about 5 drops of Lugol's acetic acid solution. (2) Later, in the laboratory, the phytoplankton were uniformly resuspended in the solution, and a 10 ml settling chamber was filled with the phytoplankton sample. (3) After 24 hours, the sediment was examined with an inverted microscope. Morphological units (cells, trichomes, colonies etc.) representing each taxon were counted and their linear dimensions measured with a Whipple micrometer disk. (4) By assuming an appropriate geometrical shape, the average cell volume per morphological unit was computed. A series of ratios involving sample volume, magnification and number of fields counted were used to compute cell volume per liter. Lund et al. (1958) have discussed the various aspects of the procedure described above along with the statistical validity of direct count methods.

Identification of the phytoplankton organisms was carried out to the species level where possible; but in several cases, only generic designations have been made. Smith (1960) and Prescott (1951) contain descriptions of all phytoplankters included in this report.

Vertical profiles of chlorophyll "a" concentration were taken at Station 3 for each cruise in 1964 and 1965. Five milliliters of 90% acetone were used to extract pigments from the phytoplankton which were concentrated on replicate "Millipore" filters during the procedure of collecting water for chemical analysis. Extraction was carried out in the dark for 24 hours at 0-10 ^{o}C. After extraction, the solutions were centrifuged and the optical density of each supernatant solution was determined. Absorbance values determined on the Beckman, Model DU spectrophotometer were converted to chlorophyll "a" per liter following the method of Richards and Thompson (1952). The methods of Wright (1959) and

Odum et al. (1958) utilizing the Klett-Summerson and Bausch and Lomb spectrophotometers respectively were also used. On several occasions, the three above mentioned methods were applied simultaneously in order to maintain standardization of techniques.

Two types of light and dark bottle experiments were used to obtain profiles of primary productivity at Station 3. Two clear and two darkened bottles were filled with lake water from each of the following depths: (a) 1964 - 0, 1½, 3, 4½, 6, 7½, and 9 meters, and (b) 1965 - 0, 1, 2, 3, 4, 5, 6, 7, and 8 meters. These samples were taken from the Van Dorn Water Bottle along with the samples for chemical and chlorophyll "a" analysis. One light and one dark bottle from each depth was inoculated with 10 microcuries of $NaC^{14}HO_3$. The other set of light-dark bottles was used to determine changes in dissolved oxygen that occurred during the subsequent incubation period. Light and dark bottles were filled between 0400 and 0600 hours, suspended in the lake at the depths from which the samples were taken, and removed from the lake 12 hours later. Upon removal, the bottles for dissolved oxygen analysis were immediately "fixed," and titrations were performed 1-3 hours later. Differences between the initial oxygen concentration of the water and concentrations in the light and dark bottles were used to estimate community respiration along with gross and net photosynthesis. A photosynthetic quotient of one (1.00) was used to convert oxygen concentrations to units of carbon. Samples for C^{14} analysis were filtered through "Millipore" filters. After the filters were dried, they were dissolved in 2 ml methanol. This solution was added to 15 ml of toluene-base scintillation fluid. Activity of the C^{14} from each filter was measured by standard procedures on a Nuclear Chicago liquid scintillation counter. Photosynthetically assimilated C^{14} was determined by subtracting the activity of each dark bottle from its corresponding light bottle as suggested by McAllister (1961). The relationships described by Ryther (1956) were used to compute primary productivity at each depth.

On several occasions during 1965, an attempt was made to follow *in situ* changes in the CO_2 concentration of the euphotic zone. Profiles of pH, temperature and total alkalinity were taken during the day at 3 hour intervals, starting before sunrise and continuing until after dark. Preliminary investigations on the relationship between pH and CO_2 were made on Hebgen water samples using the method of Beyers *et al.* (1963). Curves derived empirically by this method were nearly equivalent with those calculated from the equations of Saunders *et al.* (1962. Net change in the CO_2 concentration at each sampling depth was determined graphically by plotting CO_2 concentration against time of day.

The method of Ryther and Yentsch (1957) was used to estimate primary productivity at Station 3. This method assumes an average ratio between chlorophyll and productivity at light saturation and requires additional data on: (1) The average chlorophyll concentration of the euphotic zone, (2) total solar radiation, and (3) the extinction coefficient of the water column. Various authors such as Curl and Small (1965) and Ichimura *et al.* (1962) have modified this original method by substituting assimilation ratios of the local populations, obtained with light and dark bottle experiments. Other investigators (Wright, 1959 and Williams and Murdock, 1966) have incorporated additional information into the formulae. A comparative analysis of several light-chlorophyll methods, using data from Hebgen Lake, will be included in the next section.

Zooplankton Standing Crop and Population Dynamics

Zooplankton samples were collected from all 5 permanent stations during 1964, and at Station 3 in 1965. Oblique tows, from the bottom of the lake to the surface, were made with a Clarke-Bumpus plankton sampler, using a #10 net. Collections were preserved in the field with 95% ethanol.

In the laboratory, the total volume of each sample was measured. Upon uniformly suspending the organisms in the sample, 1 ml aliquots were removed and placed in a Sedgewick-Rafter counting cell. A 30X binocular microscope, equipped with a Whipple micrometer disk, was used to count and measure each zooplankter in the aliquot. The number of eggs per aliquot, and the clutch size of egg bearing individuals were also counted. Successive 1 ml aliquots from the same sample were examined until 100 individuals of the most common species had been counted and measured. From the above data, the population density of each species (number/liter) was determined for each sample. Specific parameters of the populations such as instantaneous birth rate, death rate and rate of increase were estimated using the methods described by Edmondson (1960), Hall (1964) and Wright (1965). A more complete description of the calculations and assumptions involved in computing population statistics will appear in the following section, using data from the Hebgen samples.

RESULTS

Light

The total solar radiation received on each sampling day during 1964 and 1965 is given in Tables I and II. Values for the two summers ranged from 206 to 704 langleys per day. Examination of values for comparable calendar dates in 1964 and 1965 points up two facts regarding seasonal weather patterns during the two summers. First, throughout the 1964 sampling period, Hebgen Lake received more solar energy than was received during the same period in 1965. Second, the random distribution of high and low values of total radiation reflects the frequent, although erratic occurrence of rain storms and heavily overcast skies in the Upper Madison Canyon.

Table I gives the average extinction coefficient of total visible light at each sampling station for the 1964 cruises. It is noted that Stations 1, 2, 3, and 4 appear to be quite similar with respect to transparence, while at Station 5 light is consistently attenuated at a much greater rate. A t-test, preceeded by the standard F-test, was used to compare the average extinction coefficients of the five stations. Between 120 and 150 degrees of freedom were available for each test between each of the 10 possible pairs of stations. The statistical analysis showed no significant difference in the average transparency conditions among Stations 1, 2, 3, and 4. A highly significant difference was found when Station 5 was compared with each of the other four stations.

A summary of underwater light conditions at Stations 1, 2, 3, and 4 during 1964 is presented in Figure 4. Light intensity is plotted along