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

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.

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A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree

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Approved:

Head, Major Department

Chairman, Examining Committee

Graduate Dean

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.

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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 C^{14}, ranged from 0.10 to 0.65 g C/m^2/day, and those measured by changes in dissolved oxygen between 0.33 and 2.13 g C/m^2/day. Four methods for estimating photosynthetic 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. leptopus* 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/m^2/day.

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.

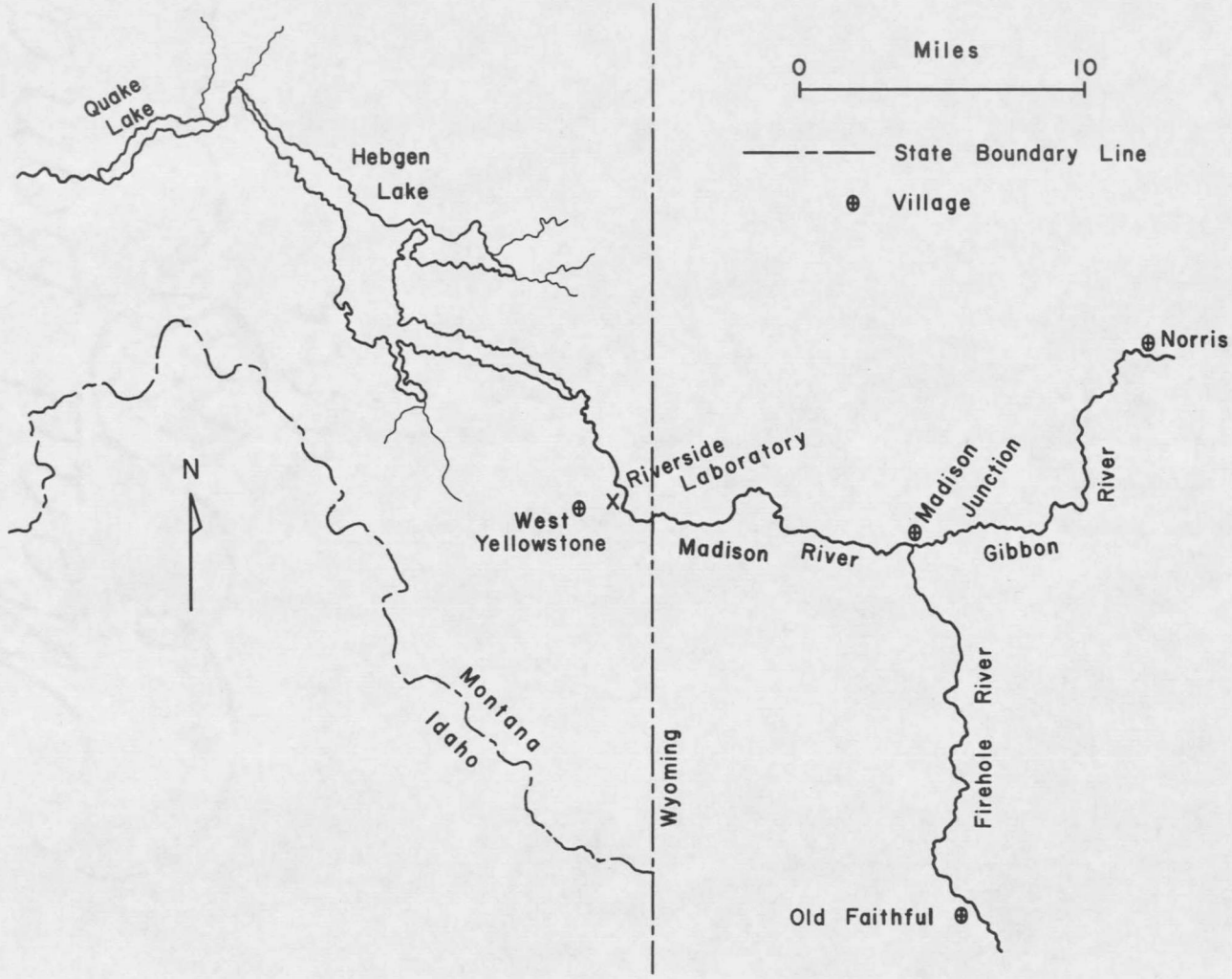

Figure 1. Map of the upper Madison River system and some associated landmarks.

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

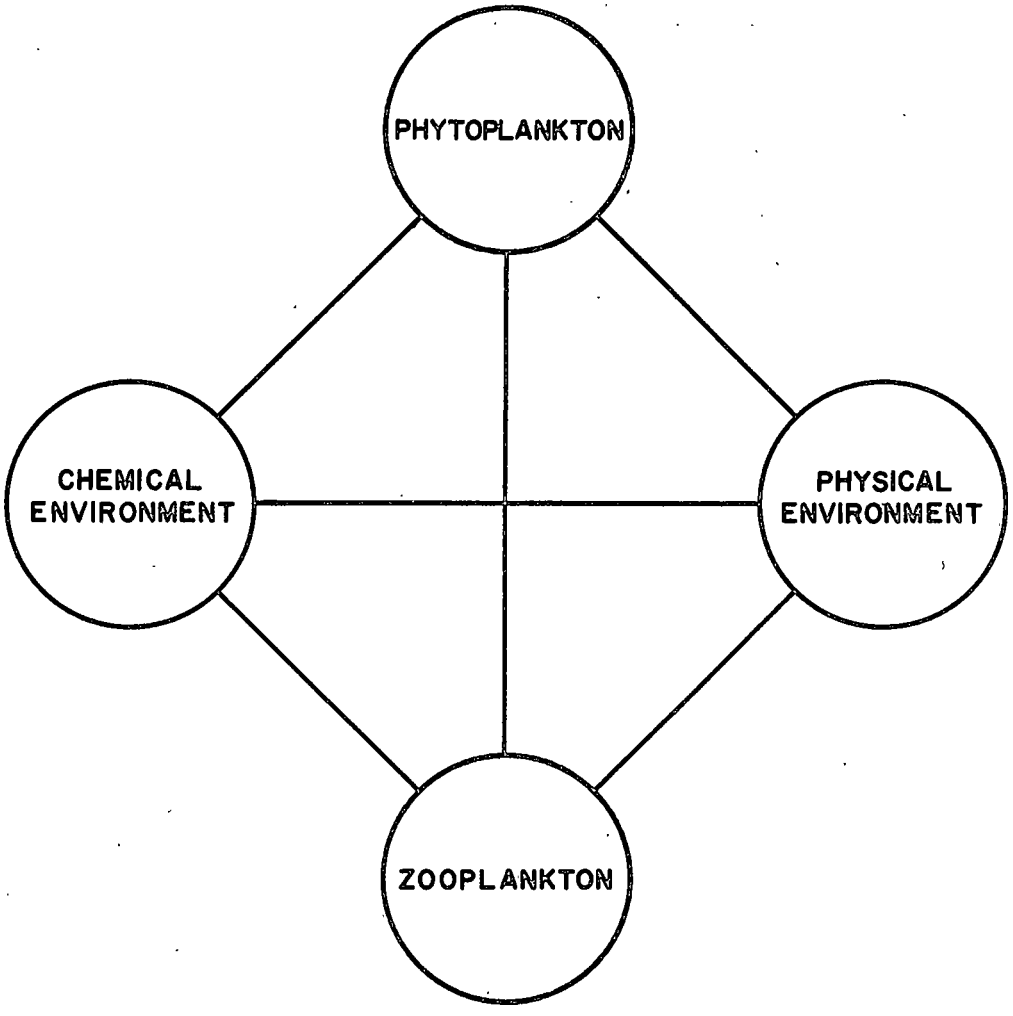

Figure 2. Diagramatic representation of the entities and interrelationships considered in the thesis problem.

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,

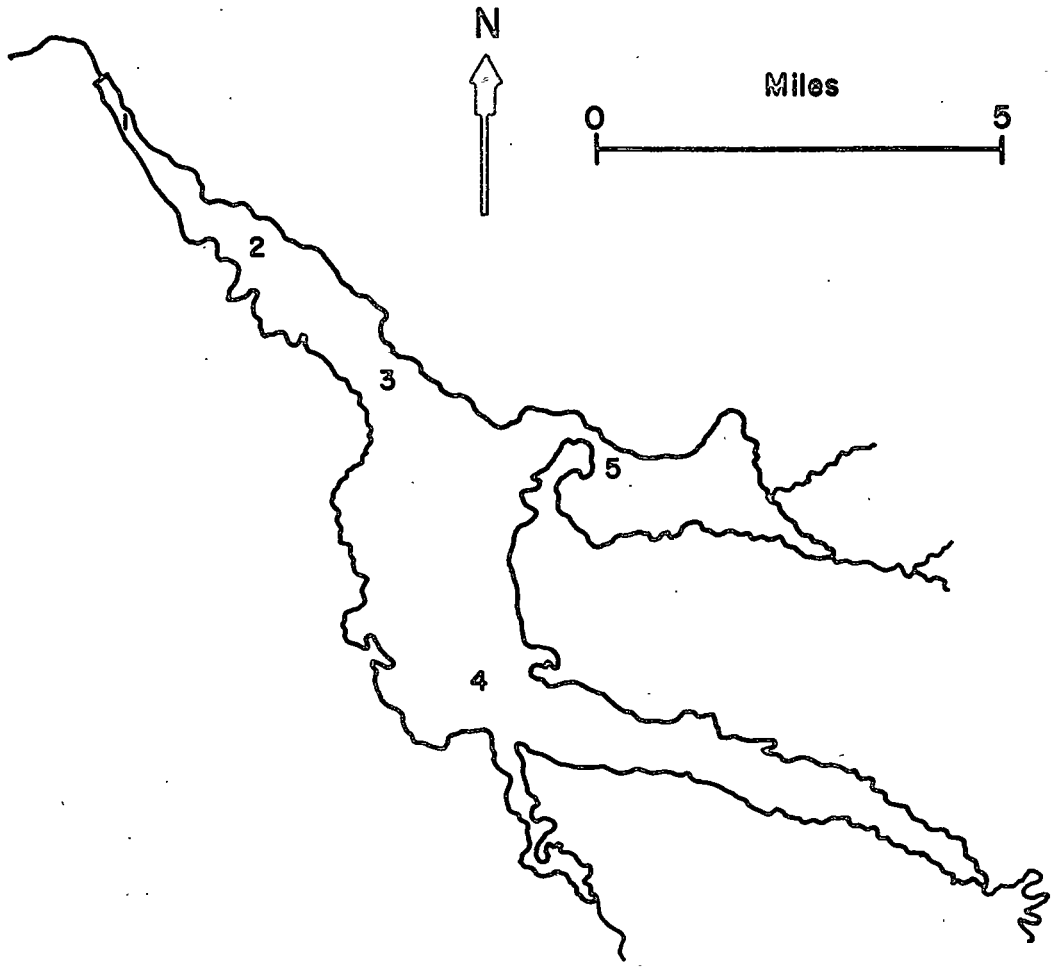

Figure 3. Map of Hebgen Lake showing the location of the five permanent sampling stations.

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

Table I. Total solar radiation at the lake surface (langleys/day), and the mean extinction coefficient of total visible light of each permanent station during 1964.

Cruise Number	Date	Total Solar Radiation	Mean Extinction Coefficient Station 1	Station 2	Station 3	Station 4	Station 5
1	June 24	700	0.58	0.52	0.64	0.59	0.90
2	July 1	657	0.53	0.56	0.62	0.62	0.88
3	July 8	682	0.53	0.57	0.55	0.55	0.80
4	July 15	704	0.53	0.48	0.56	0.56	0.82
5	July 22	694	0.57	0.64	0.59	0.61	0.92
6	July 29	402	0.52	0.58	0.57	0.65	0.98
7	August 5	580	--	--	0.62	--	--
8	August 12	253	--	--	0.60	--	--
9	September 2	206	0.48	0.53	0.54	--	--
10	September 9	562	0.60	0.60	0.59	0.58	1.08
11	September 16	511	0.57	0.60	0.58	0.53	0.84
12	September 23	458	0.69	0.65	0.57	0.57	1.04
AVERAGE			0.56	0.57	0.59	0.58	0.92

the abscissa on a logarithmetic scale and is expressed in relative terms as the percent of corrected surface sunlight. The ordinate axis is the depth of the lake in meters. The three lines on the graph indicate the penetration of total visible light at extinction coefficients of .69, .48, and .58. These three values are the seasonal maximum, minimum and average extinction coefficients when Stations 1, 2, 3, and 4 are considered together.

A number of field and laboratory studies have shown that the compensation point for various phytoplankton organisms is reached at light intensities of about 1% total surface radiation (Verduin, 1964). Therefore, the compensation depth at Stations 1, 2, 3, and 4 would range somewhere between 6.7 and 9.6 meters, with an average of 8.0 meters. By definition, the compensation depth sets the lower limit of the euphotic zone. Hereafter, the term "euphotic zone" will refer to the average euphotic zone, or that layer of water between 0 and 8 meters depth.

Table II gives the average extinction coefficients of total visible light measured on each cruise at Station 3 during 1965. The t-test was used to compare the 1964 and 1965 average transparencies at Station 3. No significant difference was found between the mean extinction coefficients of 1964 and 1965.

Extinction coefficients of light passed by the three colored filters are shown in Table II. On every cruise the light at 450 mμ was much more rapidly absorbed by the water than either red or green. Light at 650 mμ was the next most rapidly attenuated portion of the spectrum, while the penetration of green light nearly paralleled that observed for total

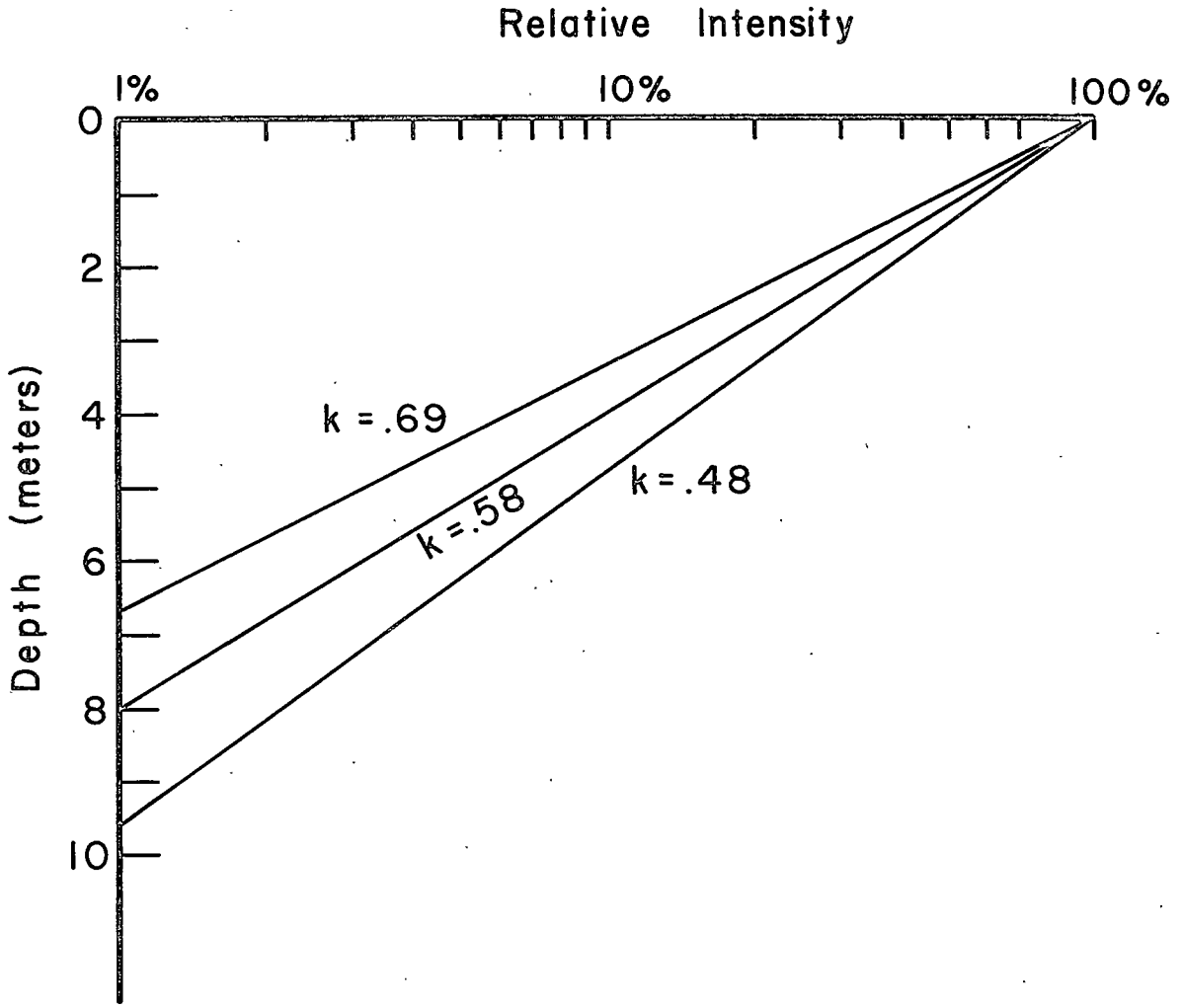

Figure 4. Penetration of total visible light at the maximum, minimum and average extinction coefficients found at Stations 1, 2, 3 and 4.

Table II. Light conditions at Station 3 during 1965. Mean extinction coefficients are for total visible light and light passed by the three colored filters. Total solar radiation at the lake surface is in langleys per day.

Cruise Number	Date	Total Solar Radiation	Mean Extinction Coefficient			
			Blue Filter	Red Filter	Green Filter	Total Light
1	May 30	524	2.06	0.76	0.75	0.67
2	June 6	430	1.92	0.90	0.69	0.82
3	June 17	428	2.09	0.76	0.63	0.64
4	June 24	267	1.68	0.76	0.65	0.68
5	July 1	380	1.59	0.71	0.57	0.62
6	July 8	547	1.44	0.63	0.57	0.52
7	July 15	612	1.36	0.62	0.57	0.56
8	July 22	564	1.54	0.73	0.54	0.68
9	July 29	444	1.48	0.70	0.58	0.60
10	August 5	490	1.82	0.74	0.54	0.49
11	August 12	429	1.60	0.81	0.61	0.63
12	August 19	233	1.24	0.82	0.62	0.60
13	August 26	464	2.04	0.78	0.58	0.56
14	September 2	445	1.28	0.78	0.64	0.62
15	September 9	242	1.42	0.67	0.54	0.57
16	September 16	213	1.66	0.56	0.49	0.53
17	September 23	417	1.66	0.68	0.63	0.59
18	October 2	345	2.17	0.53	0.57	0.48
AVERAGE			1.67	0.71	0.60	0.59

visible light.

Figure 5 shows the average spectral composition of the underwater light at Station 3 during 1965. Under average conditions blue light was reduced to 1% of surface intensity at 2.8 meters, while red light penetrated to 6.2 meters before being reduced to 1%. The 1% level of intensity was reached for green and total light at 7.8 and 7.9 meters respectively.

Ruttner (1963) proposed a system of classifying lakes according to their characteristic transmission values for light of 400, 500, and 600 millimicrons. By this method, Hebgen Lake would be given a code number of 265, since 20, 60, and 50 percent of the light at the 3 wave lengths are transmitted through each successive meter.

Temperature and Conductivity

All profiles of temperature and conductivity are given in the appendix. The various aspects of thermal and conductance conditions considered in this section include: (1) Spatial relations-the vertical or horizontal distribution of heat and electrolytes in the lake at any given instant, (2) Seasonal variation-the events that proceed with time at a given station throughout a season, and (3) Yearly differences-the conditions that grossly characterize one particular summer.

Examination of Table III shows that on any date, there is a progressive decrease in the average euphotic zone temperature from Station 1 to Station 5. The average 1964 temperature profiles for the upper 15 meters of all stations were compared by means of Student's t-test for paired observations. Results of these analyses showed a highly significant

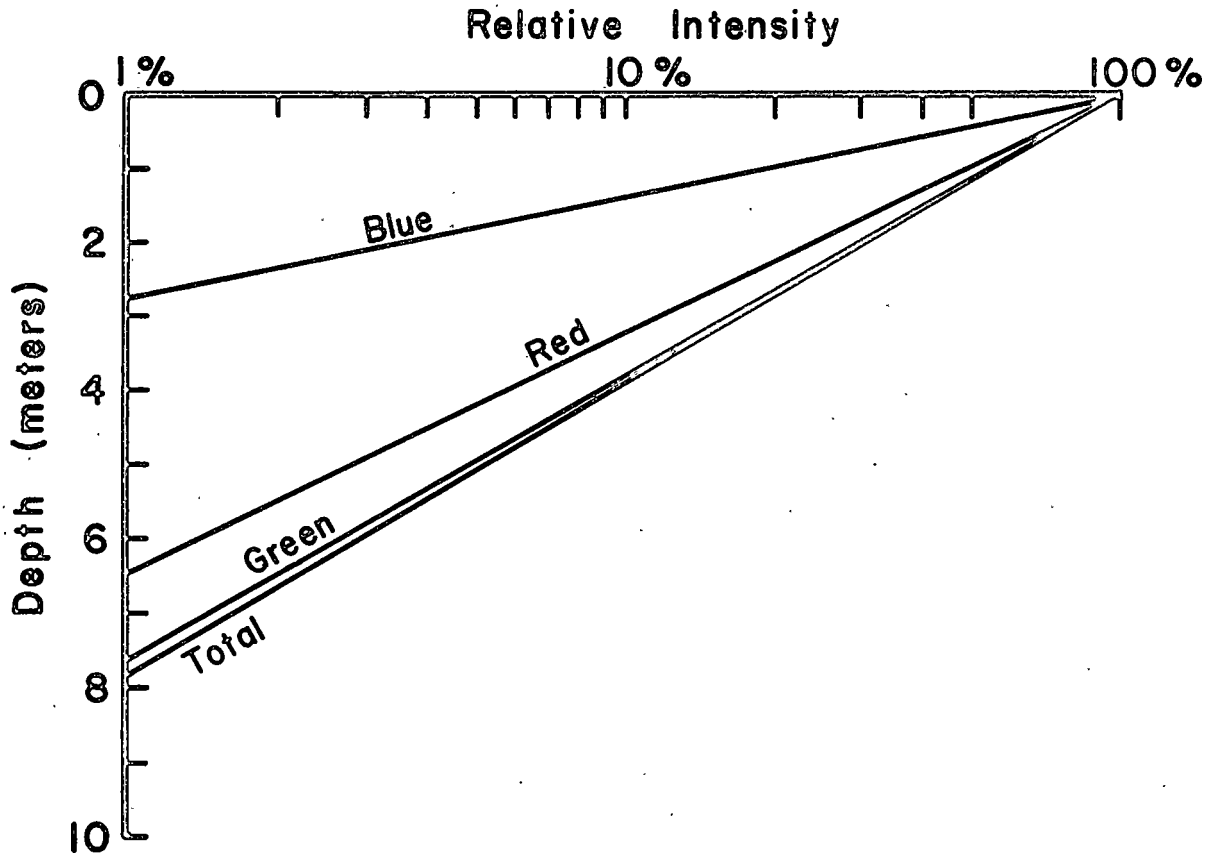

Figure 5. Average spectral composition of light at Station 3 during 1965.

difference between the average profiles for each pair of adjacent stations.

In Table III spatial differences are observed with respect to the average specific conductance at the five stations. In general, there appears to be a progressive increase in the conductivity of the euphotic zone from Station 1 to Station 4. Conductance at Station 5 is markedly less in all cases.

From the above data, a generalized pattern for the horizontal distribution of heat and electrolytes emerges. Throughout the summer cool, dilute water entered the main body of the lake from the Grayling Creek Arm at Station 5. Grayling Arm water was then mixed with water of warmer temperature and higher conductivity that entered from the Madison River Arm at Station 4. The upper 15 meters of water then underwent significant increases in temperature and decreased in conductivity as it moved downlake past Stations 3, 2, and 1. It should be noted that local upwelling or convergence could alter this general sequence significantly.

Figure 6 shows the thermal regime at Station 3 during the 1964 and 1965 experimental periods. Spring temperatures were warmer during 1965 than on comparable dates in 1964. However, in 1964 greater solar radiation during subsequent periods of time produced more rapid increases in the temperature. Midsummer surface temperatures were greater than 21°C during 1964 while the corresponding high period in 1965 produced surface temperatures of about 19°C. The lake underwent complete thermal mixing in mid-September during both years. The temperature at the onset of fall overturn varied by about 2°C.

Figures 6 and 7 illustrate the more intense degree of thermal

Table III. Average temperature (°C) and specific conductance (K_{25} - in micromhos) of the euphotic zone (0-8 meters) at each permanent station during 1964.

	Station 1		Station 2		Station 3		Station 4		Station 5	
Cruise	°C	K_{25}	°C	K_{25}	°C	K_{25}	°C	K_{25}	°C	K_{25}
1	13.0	259	12.7	259	12.6	233	12.3	249	11.6	132
2	15.8	260	15.0	250	14.6	252	14.9	260	14.5	125
3	18.1	247	17.9	252	17.6	256	17.5	247	17.1	137
4	19.7	244	19.7	247	19.0	252	19.1	259	18.7	202
5	22.6	251	21.7	248	20.9	258	20.6	258	20.7	179
6	22.1	241	21.6	247	21.6	247	21.1	253	21.4	175
7	22.2	230	21.8	230	21.4	256	--	--	--	--
8	20.5	231	20.4	230	20.1	230	19.9	236	19.5	190
9	16.8	--	16.0	--	16.0	--	--	--	14.3	--
10	15.7	244	15.7	245	15.5	246	14.8	259	14.0	213
11	14.5	249	14.5	250	14.5	255	14.1	254	14.0	217
12	13.9	251	13.9	252	13.6	253	13.1	270	12.0	227

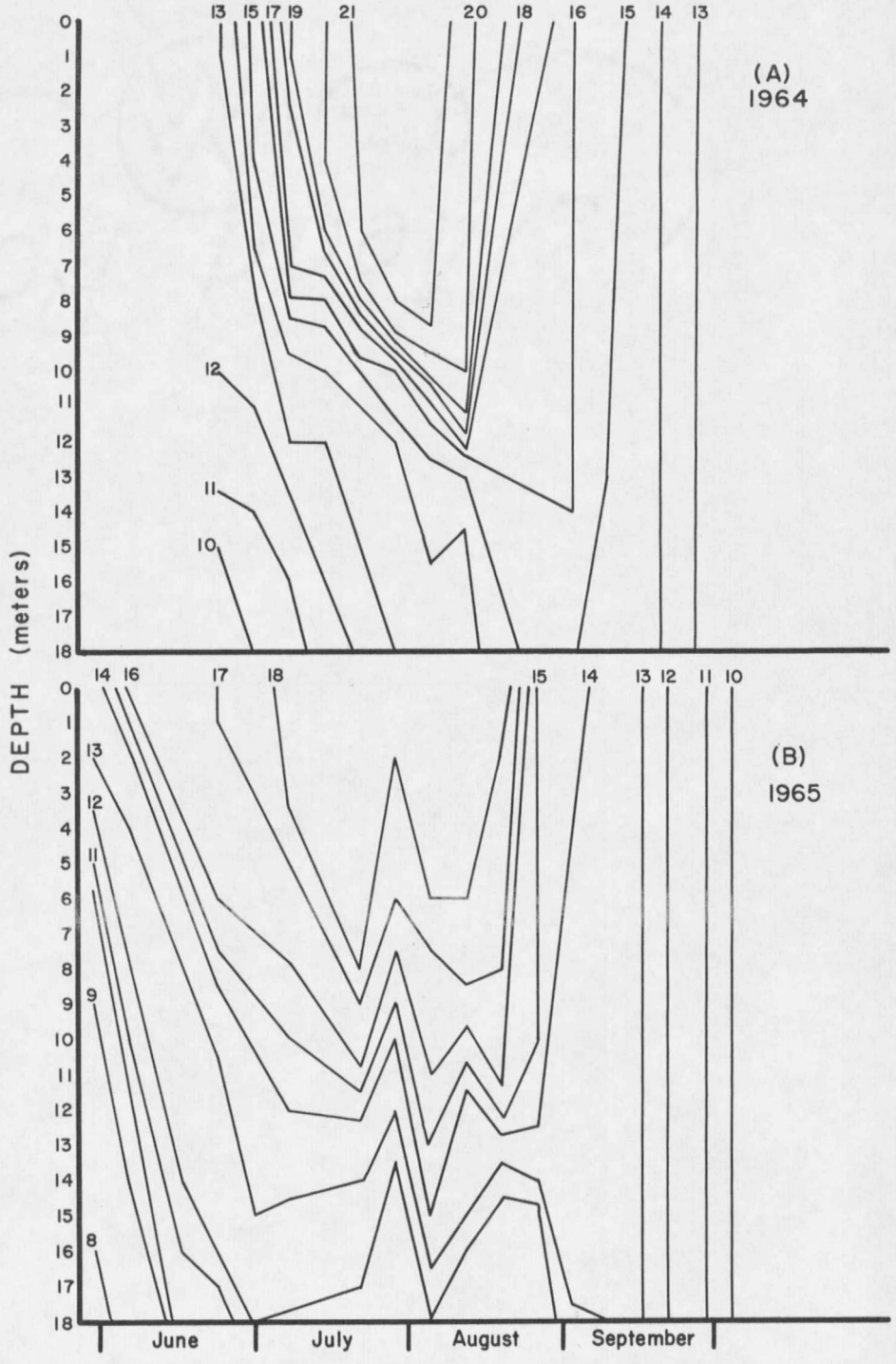

Figure 6. Isotherms at Station 3 during (A) 1964 and (B) 1965.

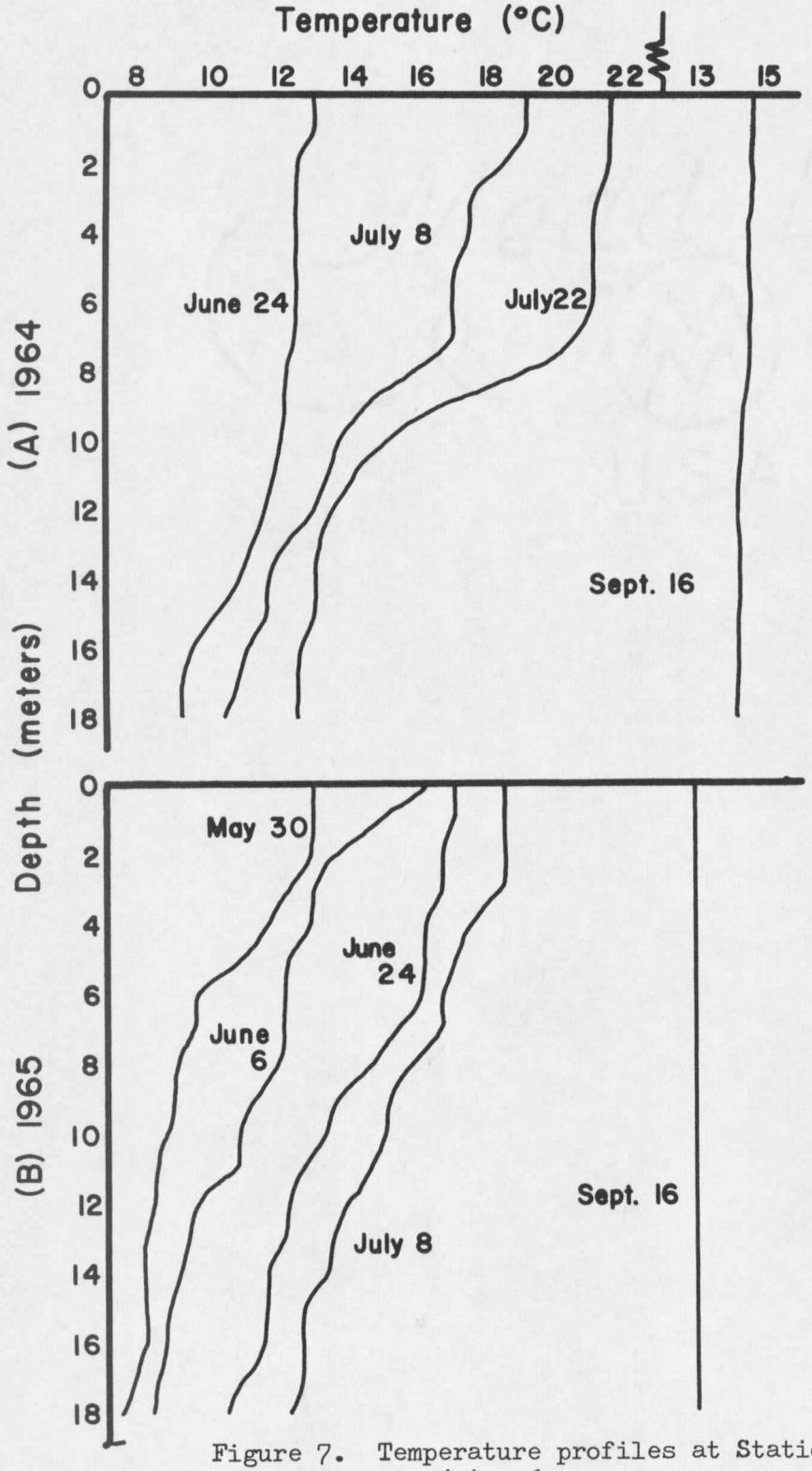

Figure 7. Temperature profiles at Station 3 during (A) 1964 and (B) 1965.

stratification that occurred during 1964. In this year a distinct thermocline formed in mid-July at about 7 meters. As the summer progressed, the metalimnion was driven deeper and reached a maximum of 11 or 12 meters by mid-August. In 1965 a pronounced thermocline never persisted, and Figure 6 (B) shows that more of a uniform thermal gradient existed.

Vertical and seasonal changes in temperature are shown in Figure 7. The effectiveness of Hebgen Lake as a heat trap is well illustrated by the successive temperature profiles. Areas between the profiles represent heat stored over the intervening time period. Because of the constant deep water discharge of cool hypolimnetic water, summer influent temperatures are continually warmer than those of the effluent. Therefore, during the summer Hebgen stores advected heat in addition to heat absorbed from solar radiation. A discussion on the heat budget of reservoirs directly applicable to Hebgen Lake can be found in Wright (1967).

Water Chemistry

Results of the chemical analyses should in part be considered in relation to the geologic formation that comprises the major portion of the upper Madison watershed. Most of the extruded ground water that enters Hebgen Lake via the Madison River or Grayling Creek has been in contact with rhyolite or welded tuff. The similar chemical compositions of these two bedrock formations are shown in Table IV. In Table IV the first column shows the chemical composition of average rhyolite as taken from Daly (1933). Columns 2-7 show the chemical composition of some Yellowstone rhyolite and tuff as determined by Boyd (1961). It can be noted that these formations are primarily compounds of sodium or potassium alumino-

Table IV. Chemical analyses of Yellowstone rhyolites (Boyd, 1961) compared to the average composition of rhyolite (Daly, 1933).

	(1)	(2)	(3)	(4)	(5)	(6)	(7)
SiO_2	72.80	73.15	76.95	76.77	76.78	73.91	67.09
Al_2O_3	13.49	12.13	12.18	11.71	12.09	11.83	13.08
Na_2O	3.38	4.01	2.98	4.01	3.78	3.34	3.97
K_2O	4.46	5.27	5.50	5.10	4.93	5.14	2.75
Fe_2O_3	1.45	1.12	1.07	0.64	0.56	0.92	1.60
CaO	1.20	0.71	0.28	0.49	0.57	0.68	1.89
MgO	0.38	0.13	0.12	0.33	0.10	0.11	0.53
FeO	0.96	0.66	0.26	1.05	0.81	0.66	1.94
TiO_2	0.33	0.14	0.13	0.15	0.08	0.26	0.47
MnO	----	0.04	0.01	0.05	0.02	0.04	0.05
BaO	----	0.08	0.08	0.02	0.00	0.10	0.09
P_2O_5	0.08	0.00	0.07	0.00	0.09	0.00	0.08
ZrO_2	----	0.04	0.03	0.04	0.01	0.04	0.02
H_2O	1.47	2.12	0.30	0.26	0.20	3.05	6.31

(1) Daly's (1933) average rhyolite

(2) Glassy welded tuff; base of Yellowstone tuff; Mt. Everts

(3) Lithoidal welded tuff; Norris Geyser Basin

(4) Obsidian scoria (plateau flow); Reas Pass, Montana

(5) Obsidian (plateau flow); Obsidian Cliff

(6), (7), Perlite (plateau flow); Midway and Upper Geyser Basins

silicates. Taken by weight, calcium and magnesium compounds together usually comprise less than one percent of the total composition.

Concentrations of the four major cations found in Hebgen Lake are shown in Table V. The column headed "0-8," under each ion, is the average euphotic zone concentration. The range of values within the euphotic zone on any given day seldom varied outside the limits of precision for the methods used. The column headed "11, 14, 17" is an average of samples taken from the indicated three depths, and represents conditions in the hypolimnion. In the euphotic zone concentrations of sodium ranged from 1.17 to 1.60 meq/1 with a seasonal average of 1.35. Concentrations of potassium were quite stable throughout the summer, averaging .11 meq/1 in both the euphotic zone and the hypolimnion. The range of concentrations for potassium was .09 to .12 meq/1.

Sodium and potassium are of about equal abundance in Yellowstone rhyolites (see Table IV). The large differences observed in the concentrations of the two ions are due to two factors. First, although the sodium and potassium compounds decompose in the same way, the solubility of sodium is many times greater, leading to a more rapid decomposition of the sodium feldspars. Once both ions are dissolved, sodium takes part in no important precipitation reactions, since nearly all sodium compounds are soluble in water. Several processes tend to selectively remove potassium from solution and return it to the solid phase. Precipitation and adsorption by clays are two means by which this can be accomplished.

The concentration of calcium in the euphotic zone ranged from .19 to .28 meq/1, around a seasonal mean of .23. Concentrations in the hypolimnion

Table V. Concentrations of sodium, calcium, magnesium, and potassium in the euphotic zone (0-8) and in the hypolimnion (11, 14, 17) during 1965.

Cruise	Sodium meq/l		Calcium meq/l		Magnesium meq/l		Potassium meq/l	
	0-8	11,14,17	0-8	11,14,17	0-8	11,14.17	0-8	11,14,17
1	--	--	--	--	--	--	--	--
2	--	--	--	--	--	--	--	--
3	1.24	1.44	0.20	0.23	0.17	0.22	0.10	0.12
4	1.20	1.47	0.19	0.20	0.18	0.19	0.10	0.12
5	1.26	1.42	0.22	0.23	0.17	0.23	0.09	0.10
6	1.36	1.32	0.19	0.20	0.18	0.23	0.10	0.09
7	1.17	1.29	0.19	0.21	0.18	0.21	0.10	0.10
8	1.21	1.27	0.19	0.20	0.12	0.21	0.09	0.09
9	1.31	1.46	0.21	0.21	0.07	0.10	0.10	0.09
10	1.24	1.26	0.26	0.26	0.14	0.15	0.11	0.12
11	1.35	1.31	0.25	0.31	0.15	0.19	0.11	0.12
12	1.41	1.37	0.28	0.33	0.14	0.16	0.12	0.10
13	1.44	1.41	0.26	0.30	0.12	0.14	0.11	0.10
14	1.47	1.41	0.23	0.25	0.14	0.14	0.10	0.10
15	1.44	1.42	0.24	0.24	0.15	0.21	0.11	0.11
16	1.42	1.37	0.26	0.26	0.21	0.23	0.12	0.12
17	1.48	1.47	0.21	0.22	0.18	0.20	0.11	0.12
18	1.60	1.62	0.23	0.24	0.18	0.21	0.11	0.11
AVERAGE	1.35	1.39	0.23	0.24	0.16	0.18	0.11	0.11

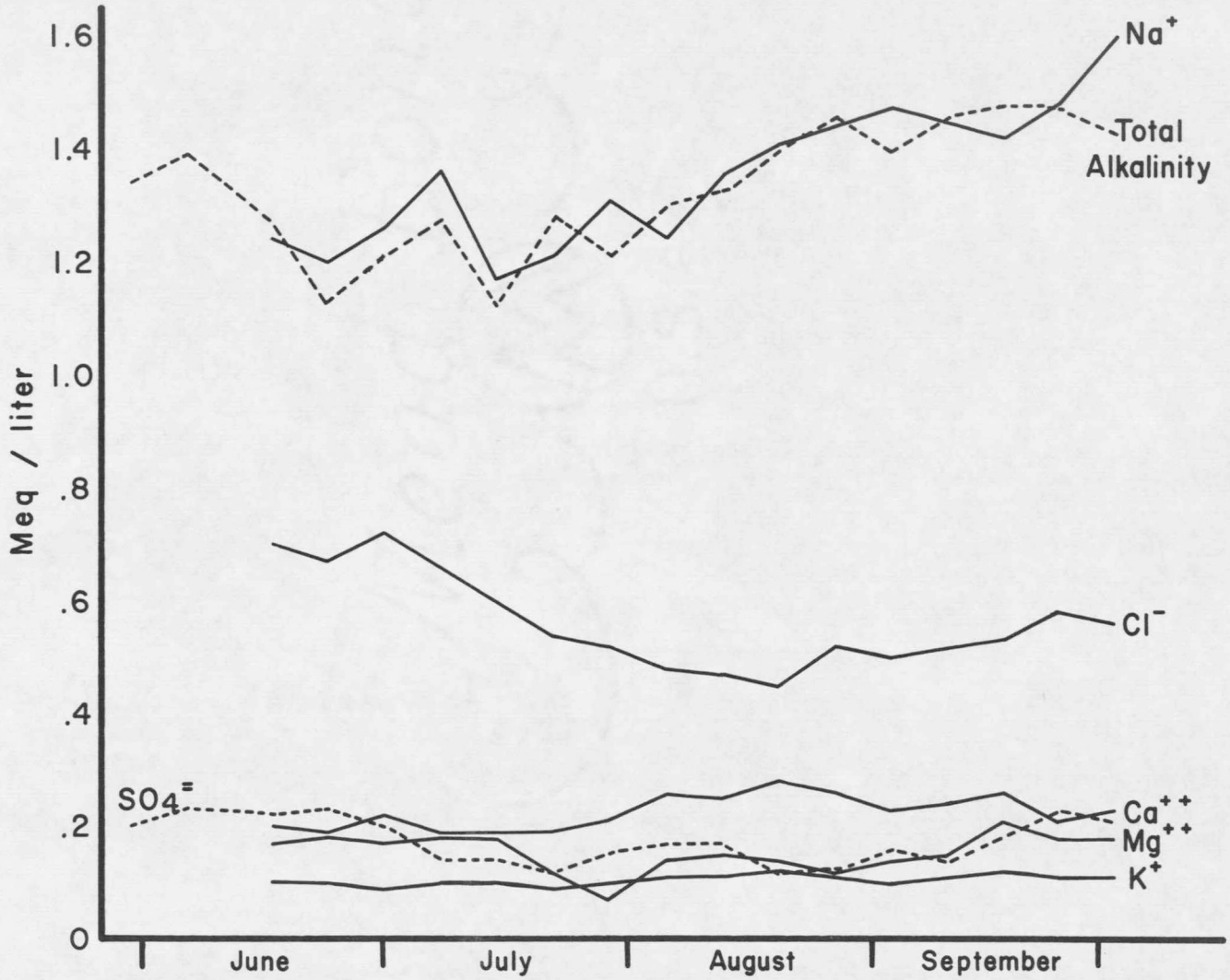

Figure 8. Concentrations of the most abundant cations and anions during 1965.

were consistently slightly higher. Concentrations of magnesium were intermediate to those of calcium and potassium. The relative abundance and seasonal variation with respect to the four predominant cations can be seen in Figure 8.

The most abundant anions in Hebgen Lake were bicarbonate, chloride and sulfate. The total alkalinity, shown in Tables VIII and IX, is largely bicarbonate, since only trace amounts of the carbonate ion exist at the hydrogen ion concentrations found in Hebgen Lake. Concentrations of total alkalinity ranged from 1.12 to 1.48 meq/l in the euphotic zone during 1965. Figure 8 shows that these concentrations nearly coincided with those for sodium over the same period.

Concentrations of chloride and sulfate are shown in Table VI and Figure 8. The seasonal concentration of chloride in the euphotic zone averaged .56 meq/l with a range of .45 to .72. Sulfate concentrations in the euphotic zone fluctuated between .12 and .23 meq/l with an average of .17.

Table VII shows that silica was one of the most abundant constituents found in the water analysis. It will be noted in Table IV, that with the exception of oxygen, silicon is the most abundant element in rhyolite. Crystalline SiO_2, as quartz, is one of the most resistant of all rock minerals to the attack by water. The greater part of dissolved silica in natural waters originates in the chemical breakdown of silicates. In these reactions hydrogen ions replace metallic cations in the silicate lattice. Some of the silicon-oxygen groups of the original mineral are surplus to the new arrangement and these, plus the replaced cations, become available for solution. Silica concentrations in the euphotic zone

Table VI. Concentrations of chloride, sulfate, phosphate and nitrate in the euphotic zone (0-8) and in the hypolimnion (11, 14, 17) during 1965.

Cruise	Chloride meq/l		Sulfate meq/l		Phosphate mg/l		Nitrate µg/l	
	0-8	11,14,17	0-8	11,14,17	0-8	11,14,17	0-8	11,14,17
1	--	--	0.20	0.22	0.39	--	--	--
2	--	--	0.23	0.24	0.19	--	--	--
3	0.70	0.80	0.22	0.23	0.19	0.20	10.8	15.9
4	0.67	0.77	0.23	0.23	0.12	0.16	7.3	9.7
5	0.72	0.73	0.20	0.21	0.08	0.12	2.2	6.9
6	0.66	0.65	0.14	0.14	0.12	0.15	1.2	8.7
7	0.60	0.63	0.14	0.17	0.14	0.16	0.8	15.7
8	0.54	0.61	0.12	0.14	0.11	0.17	6.6	22.7
9	0.52	0.56	0.15	0.16	0.12	0.19	6.2	29.3
10	0.48	0.49	0.17	0.15	0.07	0.19	5.4	52.7
11	0.47	0.43	0.17	0.17	0.14	0.20	4.0	84.0
12	0.45	0.46	0.12	0.12	0.13	0.20	8.0	70.7
13	0.52	0.50	0.12	0.12	0.14	0.17	4.0	57.7
14	0.50	0.49	0.16	0.19	0.16	0.18	5.7	37.3
15	0.52	0.52	0.14	0.15	0.16	0.21	13.0	13.0
16	0.53	0.53	0.18	0.17	0.18	0.20	8.9	9.7
17	0.58	0.57	0.23	0.23	0.20	0.20	11.8	10.7
18	0.56	0.57	0.21	0.23	0.17	0.18	0.5	3.3
AVERAGE	0.56	0.58	0.17	0.18	0.16	0.18	6.0	28.0

Table VII. Concentrations of silica, iron, oxygen, and the specific conductance in the euphotic zone (0-8) and in the hypolimnion (11, 14, 17) during 1965.

	Silica mg/l		Iron mg/l		Oxygen mg/l		Conductivity micromhos	
Cruise	0-8	11,14,17	0-8	11,14,17	0-8	11,14,17	0-8	11,14,17
1	43	44	--	--	8.54	7.81	253	294
2	45	47	--	--	8.25	7.33	226	279
3	40	45	--	--	7.74	6.85	225	255
4	37	41	0.12	0.12	7.75	6.22	203	241
5	37	40	0.10	0.12	7.45	6.06	205	224
6	38	37	0.12	0.10	7.73	6.02	210	221
7	37	39	0.10	0.10	7.29	5.38	--	--
8	36	36	0.08	0.11	7.34	4.84	205	213
9	36	38	0.09	0.11	7.43	3.96	207	215
10	37	38	0.10	0.11	7.88	3.09	209	217
11	40	38	0.10	0.10	8.14	2.80	218	214
12	40	38	0.05	0.09	8.26	2.58	223	229
13	40	40	0.09	0.11	7.56	5.05	222	230
14	42	41	0.13	0.19	7.12	4.35	227	227
15	43	43	0.11	0.11	7.07	6.16	231	231
16	42	43	0.12	0.12	7.30	6.73	--	--
17	45	45	0.13	0.12	7.73	7.84	--	--
18	43	45	0.11	0.11	7.82	7.80	--	--
AVERAGE	40	41	0.10	0.11	7.69	5.60	219	235

ranged from 36 to 45 mg/l.

The concentration of total iron ranged from .05 to .12 mg/l (see Table VII) in both the euphotic zone and the hypolimnion.

Tables V, VI, and VII show that there was no appreciable accumulation of sodium, calcium, magnesium, potassium, chloride, sulfate, silica or iron in the hypolimnion during thermal stratification. The vertical distribution of each constituent stayed relatively homogeneous as indicated by the similar seasonal averages for each zone.

Table X contains the chemical analysis of water associated with rhyolite formations at several different geographic locations. A comparison of the values in this table with those found in Tables V, VI, and VII shows a remarkable similarity.

Concentrations of oxygen, inorganic carbon and hydrogen ion are shown in Tables VII, VIII, and IX. All of these constituents are highly non-conservative, and large diurnal fluctuations in their concentration were often observed in the euphotic zone. Since all analyses were made on samples collected just before dawn, the weekly values should be comparable. The dissolved oxygen and pH values given would represent daily minimums, while total inorganic carbon should be at a maximum.

Dissolved oxygen in the euphotic zone ranged from 7.07 to 8.54 mg/l during 1965. In 1964, the range was from 6.70 to 8.23 mg/l. Table VII shows that a marked depletion of oxygen occurred in the hypolimnion during the summer stagnation. Concentrations in the hypolimnion decreased steadily from Cruise 1. An average hypolimnetic low of 2.58 mg/l occurred on Cruise 12, shortly before the thermocline started to break down. With

fall overturn, the oxygen supply in the deep water was replenished.

pH in the euphotic zone ranged from 7.89 to 8.85 during 1965. All 1964 pH values were within this range. Tables VIII and IX show that in both years the highest pH occurred in mid-summer.

Total inorganic carbon, taken for both years, ranged from 13.5 - 18.1 mg/l. Spring and summer periods were characterized by fluctuating levels of carbon, never exceeding 17.0 mg/l. With the onset of fall overturn, the epilimnion was enriched, and euphotic zone concentrations were always above 17.0 mg/l.

Concentrations of phosphate are shown in Tables VI and IX. Euphotic zone concentrations were generally high early in the season and again after the onset of fall overturn. There was a noticeable accumulation of phosphate in the hypolimnion with the highest concentrations occurring just prior to the thermal mixing period. In relation to average natural waters, the content of phosphate in Hebgen Lake is quite high.

Nitrate concentrations during 1965 are shown in Table VI. It is noted that nitrate was present in nearly equal amounts, both in the euphotic zone and in the hypolimnion, at the onset of the season. With the progression of thermal stratification, hypolimnetic concentrations increased until at the maximum they are some 20 times greater than those in the euphotic zone. Fall overturn eventually restored vertical homogeneity. Absolute concentrations of nitrate are low, all values being expressed in u grams/liter. However, these values are similar to those reported for many natural waters.

The entire chemical budget of Hebgen Lake can be summarized on the

Table VIII. Total alkalinity, temperature, pH and inorganic carbon in the euphotic zone during 1965.

Cruise	Total Alkalinity meq/l	pH	Carbon mg/l	Temp. °C
1	1.34	8.18	16.3	11.3
2	1.39	8.14	16.9	13.2
3	1.27	7.89	15.7	14.5
4	1.12	8.11	13.5	16.2
5	1.21	8.10	14.8	15.7
6	1.27	8.19	15.2	17.4
7	1.12	8.16	13.6	--
8	1.27	8.29	15.3	17.8
9	1.21	8.42	14.6	17.5
10	1.30	8.67	15.6	18.0
11	1.32	8.85	15.1	18.2
12	1.40	8.78	16.5	17.5
13	1.45	8.50	17.5	15.0
14	1.39	8.56	16.7	16.2
15	1.45	8.41	17.4	14.4
16	1.48	8.41	17.7	12.9
17	1.47	8.35	17.6	11.6
18	1.43	8.38	17.2	10.0
AVERAGE	1.33	8.36	16.0	15.1

Table IX. Total alkalinity, pH, inorganic carbon, oxygen and phosphate in the euphotic zone during 1964.

Cruise	Total Alkalinity meq/l	pH	Inorganic Carbon mg/l	Oxygen mg/l	Phosphate mg/l
1	1.32	8.08	15.8	8.23	0.23
2	1.37	8.12	16.4	7.84	0.14
3	1.30	8.16	15.6	7.54	0.10
4	1.31	7.98	16.4	7.11	0.10
5	1.37	8.31	16.4	6.87	0.25
6	1.39	8.53	16.6	7.23	0.16
7	1.34	8.58	16.0	7.54	0.16
8	1.38	8.59	16.3	7.56	0.15
9	1.47	8.46	17.7	6.70	0.13
10	1.42	8.59	16.9	7.74	0.18
11	1.52	8.49	18.1	7.59	0.18
12	1.44	8.49	17.1	7.44	0.15
AVERAGE	1.39	8.36	16.6	7.45	0.16

Table X. Chemical analyses of water associated with rhyolite formations.

	(1)	(2)	(3)	(4)
Silica (mg/l)	99.0	103.0	60.0	89.0
Sodium (meq/l)	4.35	1.74	1.78	3.68
Calcium (meq/l)	0.12	0.32	0.70	0.26
Magnesium (meq/l)	0.12	0.09	0.62	0.03
Potassium (meq/l)	0.07	--	0.11	0.22
Iron (mg/l)	0.04	0.00	0.01	--
Bicarbonate (meq/l)	1.82	1.26	2.20	1.96
Sulfate (meq/l)	0.62	0.31	0.29	0.40
Chloride (meq/l)	0.28	0.48	0.68	1.52

LOCATION	REFERENCE
(1) Owyhee County, Idaho	Hem, 1959
(2) Sandoval County, New Mexico	Hem, 1959
(3) Harney County, Oregon	Hem, 1959
(4) Madison River near West Yellowstone, Montana	Roeder, 1966

basis of the information presented in this section. Wright (1967) has compared the nutrient regimes of reservoirs and natural lakes; and the generalizations held forth for the former are directly applicable to Hebgen.

During the period of intense biological productivity inorganic nutrients are constantly removed from the epilimnion through photosynthesis. A sizeable fraction of these nutrients then enter the hypolimnion through the sinking of organic matter. In the deep water the elements are again mineralized, but are unable to pass through the thermocline and into the upper layers. This process is illustrated by the previous discussion of nitrate and phosphate.

The surface water discharge of natural lakes continually releases nutrient-poor water downstream. During fall overturn, the nutrients which have been accumulating in the hypolimnion are replaced throughout the water column. By this process natural lakes act as nutrient traps.

In Hebgen, nutrient rich water from the hypolimnion, is constantly being released downstream. This drain on the chemical budget keeps the lake in a steady-state nutrient depletion.

Phytoplankton Standing Crop and Productivity

The plankton flora of Hebgen Lake was not particularly diverse at any time during the 1964 or 1965 experimental periods. Table XI lists all taxa identified from the phytoplankton samples of both years. Those taxa marked with an asterisk in Table XI were rare, being encountered on only a few, isolated occasions.

Table XII gives the average standing crop of the most important algae

Table XI. List of algal taxa identified from phytoplankton samples.

BACILLARIOPHYCEAE

*Achnanthes sp.

*Amphora sp.

Asterionella formosa

*Cocconeis sp.

Cyclotella sp.

Fragilaria crotonensis

*Gomphonema sp.

Melosira granulata

Meridion sp.

Navicula sp.

*Pinnularia sp.

Synedra sp.

CHRYSOPHYCEAE

*Synura uvella

Chrysococcus sp.

CRYPTOPHYCEAE

Rhodomonas lacustris

Cryptomonas ovata

DINOPHYCEAE

Ceratium hirundinella

CHLOROPHYCEAE

Ankistrodesmus falcatus

Chlamydomonas sp.

Chlorella ellipsoidea

Elakatothrix gelatinosa

Gloeocystis sp.

*Kirchneriella sp.

Pediastrum sp.

Pandorina morum

Oocystis sp.

*Scenedesmus sp.

Schroederia setigera

Staurastrum sp.

EUGLENOPHYCEAE

*Trachelomonas sp.

MYXOPHYCEAE

Anabaena spiroides

Aphanizomenon flos-aquae

Table XII. Average standing crop (mm^3/liter) of the principle phytoplankton taxa during 1965.

Cruise	Anabaena spiroides	Aphanizomenon flos aquae	Lyngbya birgei	Cryptomonas ovata	Rhodomonas lacustris	Microplankton	Ceratium hirundinella
1	0.00	0.00	0.00	0.08	0.02	0.02	0.00
2	0.01	0.00	0.00	0.10	0.03	0.03	0.00
3	0.03	0.01	0.00	0.18	0.04	0.05	0.00
4	0.07	0.02	0.00	0.14	0.06	0.05	0.15
5	0.14	0.08	0.00	0.16	0.03	0.02	0.00
6	0.13	0.15	0.00	0.20	0.03	0.02	0.00
7	0.12	0.20	0.00	0.14	0.06	0.04	0.15
8	0.11	0.25	0.00	0.10	0.06	0.05	0.00
9	0.09	0.58	0.33	0.08	0.02	0.06	0.08
10	0.05	1.36	1.66	0.10	0.01	0.05	0.25
11	0.03	1.41	2.72	0.02	0.03	0.06	0.32
12	0.03	2.16	2.96	0.23	0.03	0.05	0.25
13	0.01	0.65	3.74	0.19	0.04	0.04	0.15
14	0.02	0.19	2.30	0.39	0.05	0.06	0.64
15	T	0.10	1.55	0.06	0.01	0.05	0.00
16	0.00	0.24	2.84	0.04	0.01	0.11	0.00
17	0.00	0.41	2.46	0.31	0.03	0.00	0.00
18	0.00	0.44	0.21	0.39	0.06	0.10	0.00

Table XII. (Cont.)

Cruise	Synedra sp.	Asterionella formosa	Fragilaria crotonensis	Melosira granulata	Schroederia setigera	Navicula sp.	Total Standing Crop
1	0.04	0.13	0.01	T	0.00	0.01	0.33
2	0.01	0.05	0.01	0.00	0.00	0.01	0.30
3	T	0.10	0.01	0.00	0.00	0.00	0.44
4	0.00	0.09	0.02	0.00	T	0.00	0.61
5	0.00	0.02	0.01	0.00	0.01	0.00	0.48
6	0.00	0.02	0.01	0.00	0.06	0.00	0.62
7	0.00	0.09	0.04	0.00	0.12	0.00	0.96
8	0.00	0.04	0.06	0.00	0.06	0.00	0.73
9	0.00	0.01	0.04	0.00	0.04	T	1.33
10	0.00	0.00	0.00	0.00	0.01	T	3.49
11	0.00	0.00	0.00	0.00	0.01	T	4.60
12	0.00	0.00	0.00	T	0.03	T	5.74
13	0.00	0.01	0.00	0.00	0.02	T	4.85
14	0.00	0.02	0.00	0.00	0.02	T	3.69
15	T	0.01	0.00	T	0.01	T	1.79
16	T	0.01	0.02	0.01	0.01	T	3.29
17	T	0.01	0.01	0.02	0.00	T	3.36
18	T	0.01	0.03	0.04	0.00	T	1.31

during 1965. This table includes all taxa whose standing crop exceeded .01 mm^3/l at any time during the summer. A "T" for any species indicates that the species was observed on the given date, but that the total cell volume was less than .01 mm^3/l. A zero indicates that no organisms were found. Counts and measurements of Chlamydomonas, Chlorella and Chrysococcus were combined, and their total standing crop appears under the column headed "Microplankton". This was necessary because the distortion of cells, produced by the preservative, made positive identification impossible much of the time. All values in Table XII represent the average standing crop in the euphotic zone.

Table XII shows that during much of the summer various blue-green algae dominated the phytoplankton community. Lyngbya Birgei produced the largest biomass of any species, reaching a density of 3.74 mm^3/l in late August. The only other species which reached a standing crop greater than 1.00 mm^3/l was Aphanizomenon flos-aquae. A pronounced bloom of this species occurred in early and mid-August, producing an observed high of 2.16 mm^3/l.

Anabaena spiroides, Cryptomonas ovata, Creatium hirundinella, Asterionella formosa, Schroederia setigera and the microplankton periodically reached standing crops of between .1 and 1.0 mm^3/l. All other species in Table XII were of limited abundance; their standing crops ranging from between .01 and .1 mm^3/l.

Figure 9 shows the seasonal distribution or succession of certain phytoplankton taxa during 1965. Since large differences exist among the absolute standing drops of the various species, the relative biomass of

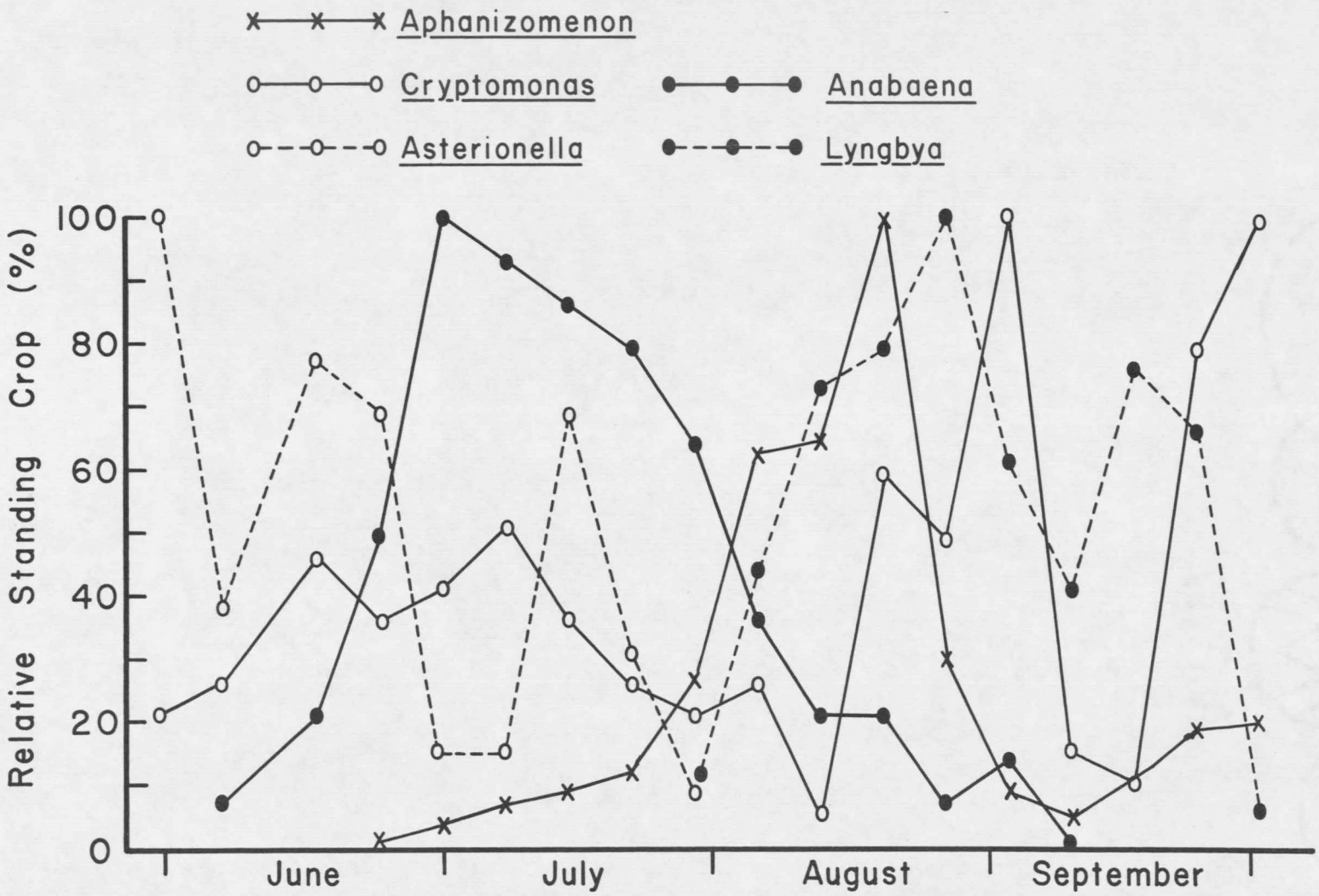

Figure 9. Seasonal standing crops of the five most abundant phytoplankton species during 1965.

each organism is plotted in Figure 9. Relative biomass on any date is the percent of the highest standing crop that that species attained during the summer.

The most important species of the early spring period was Asterionella formosa. The highest standing crop of this organism was observed on May 30, but substantial peaks occurred later on June 17 and July 15. With the demise of the final peak, the abundance remained limited for the duration of the season.

Anabaena spiroides was the next species to reach maximum biomass. From its first appearance on June 6, it reached a peak standing crop of .14 mm^3/l on July 1. A gradual decline in the abundance of this organism followed, until on September 9, its presence was no longer detectable.

The first build up of standing crop, to reach real "bloom" proportions, was that of Aphanizomenon flos-aquae. A gradual increase in the biomass of this species started on about June 17, and continued through the next 8 weeks until the maximum standing crop occurred on August 19. A rather rapid decline, followed by a slight increase, occurred during the rest of the season.

Immediately following the Aphanizomenon peak was the maximum standing crop of Lyngbya Birgei. This organism made its first appearance some five weeks later than Aphanizomenon, but its highest standing crop occurred one week later than Aphanizomenon, on August 26. A two week decline in this organism was followed by another substantial peak on September 16. The latter peak was followed by a rapid decline in standing crop.

There was less of a marked periodicity in the occurrence of

Cryptomonas ovata than in any of the organisms considered in Figure 9. Detectable populations of this organism were present on every date throughout the season. During the season the standing crop ranged from .02 to .39 mm^3/l. A relative standing crop of 100 percent occurred for this organism on September 2 and October 2.

In addition to Cryptomonas, two other constituents of the phytoplankton community occurred with notable consistency. These were Rhodomonas lacustris and the microplankton. The standing crop of the former ranged from .01 to .06 mm^3/l and that of the latter between .02 and .11 mm^3/l. Both factions were present, in these rather limited numbers, during the entire season.

Fragilaria crotonensis and Schroederia setigero maintained small standing crops during parts of the season. Ceratium hirundinella attained rather sporadic peaks, with a maximum of .64 mm^3/l on September 2.

The qualitative aspects of the seasonal periodicity seen in Figure 9 are similar to those found in numerous studies from a wide range of geographic locations. Some of the descriptive literature, pertaining to phytoplankton succession, has been reviewed by Fogg (1965), and Lund (1964 and 1965).

The accumulation of total phytoplankton biomass during 1965 is seen in Figure 10. There was a gradual increase of standing crop from May 30 to about August 1. During this period, the standing crop increased from .33 to 1.33 mm^3/l. From August 1, rapid rates of increase in the standing crop of both Aphanizomenon flos-aquae and Lyngbya Birgei produced the sharp rise and high peak of total biomass on August 19. During this three

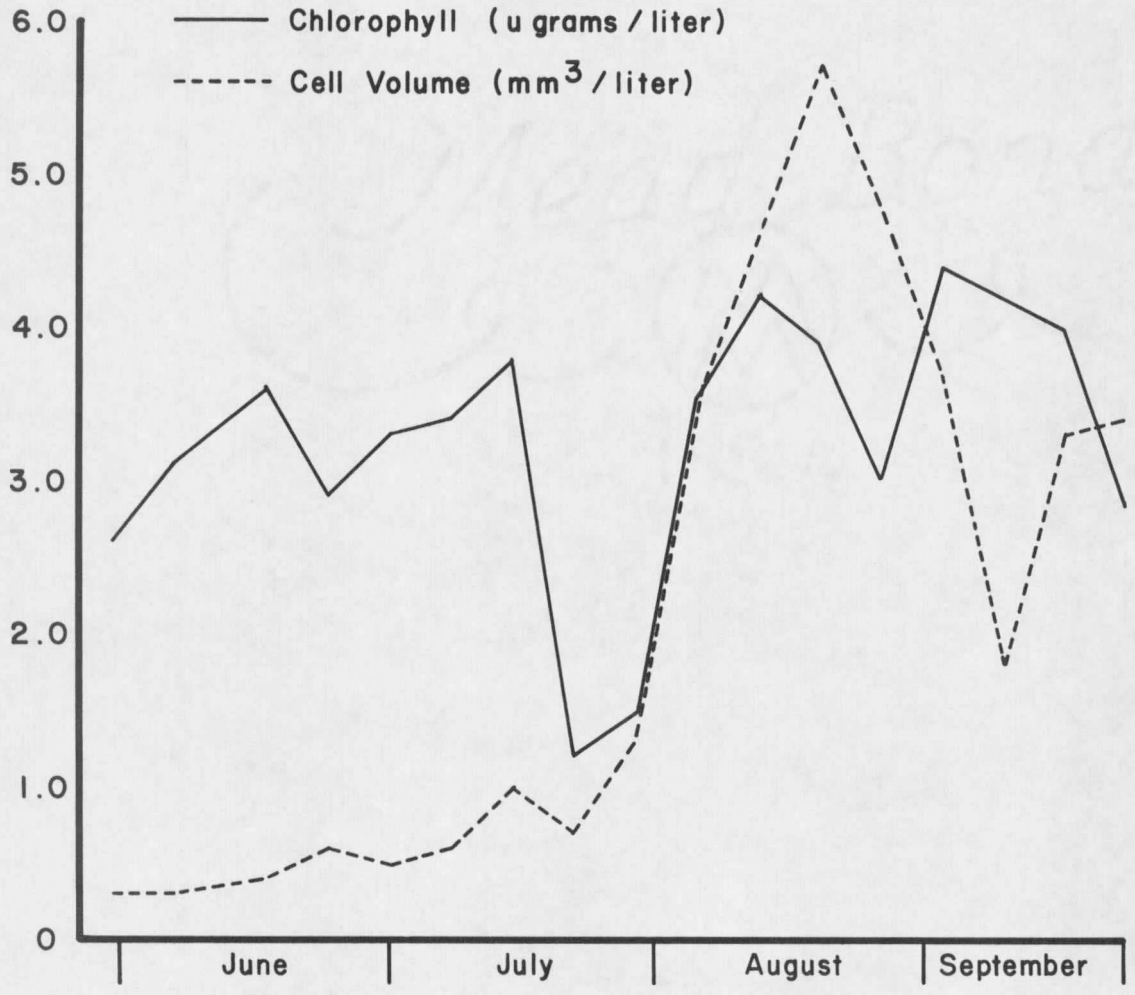

Figure 10. Total phytoplankton standing crop and chlorophyll concentration in the euphotic zone during 1965.

week period, standing crop increased from 1.33 to 5.74 $mm^3/1$. The following three weeks were accompanied by a rapid decline of total standing stock. A substantial rise ended the final two weeks of the study period.

Conditions of phytoplankton standing crop and species succession were very similar for the years 1964 and 1965. The same species shown in Figure 9 appeared, became dominant and declined in the sequence shown in Figure 9 and discussed above. Minor variations were found with respect to the dates of these events and the absolute values of standing crop attained. The total standing crop for each cruise during 1964 is shown on Table XV.

Chlorophyll concentrations in the euphotic zone are shown in Tables XV and XVI. These values represent averages of the profiles taken through the euphotic zone. Vertical distribution of the chlorophyll was rarely homogeneous when sampled on any cruise. The dark period immediately preceding the collection of samples was invariably calm, with no wind action on the surface of the lake. This period of reduced turbulence in the epilimnion allowed some degree of micro-stratification to occur in the eplimnion. Non-motile plankton algae would then accumulate in various strata according to their specific gravity, while motile forms might migrate to certain depths. The result would be a seemingly erratic vertical distribution of phytoplankton at the time the samples were collected. Direct cell volume determinations and chlorophyll analyses both showed this to be the case. Thus far, any patterns or direct relations of the vertical distribution of phytoplankton have not been found in this study.

The significance of this complex vertical distribution is somewhat

Table XIII. Primary productivity and respiration as determined with light and dark bottles during 1964.

	(1) TOTAL PRODUCTIVITY			(2)	(3)	(4)
Cruise	C^{14}	Gross O_2	Net O_2	RESPIRATION	NET O_2 / C^{14}	GROSS O_2 / C^{14}
1	--	0.24	0.33	-0.09	--	--
2	--	0.80	0.56	0.24	--	--
3	--	0.40	0.42	-0.02	--	--
4	--	0.65	0.47	0.18	--	--
5	0.32	0.79	0.86	-0.07	2.7	2.5
6	0.35	0.90	1.30	-0.40	3.7	2.6
7	0.65	1.28	0.84	0.44	1.3	2.0
8	0.23	0.45	0.59	-0.14	2.6	2.0
9	0.16	0.26	0.67	-0.41	4.2	1.6
10	0.44	1.10	1.32	-0.22	3.0	2.5
11	0.39	0.85	0.82	0.03	2.1	2.2
12	0.21	0.61	0.53	0.08	2.5	2.9

(1), (2) g C / m^2 / day

(3), (4) Photosynthetic Quotient

Table XIV. Primary productivity and respiration as determined with light and dark bottles during 1965.

	(1) TOTAL PRODUCTIVITY			(2) RESPIRATION	(3) $\frac{\text{NET } O_2}{C^{14}}$	(4) $\frac{\text{GROSS } O_2}{C^{14}}$
Cruise	C^{14}	Gross O_2	Net O_2			
1	0.10	0.44	0.34	0.10	3.4	4.4
2	0.14	0.62	0.51	0.11	3.6	4.4
3	0.26	0.42	0.54	-0.12	2.1	1.6
4	0.22	0.45	0.37	0.08	1.7	2.0
5	0.23	0.58	0.61	-0.03	2.7	2.5
6	0.28	0.70	0.71	-0.01	2.5	2.5
7	0.42	0.84	0.73	0.11	1.7	2.0
8	0.13	0.71	0.67	0.04	5.2	5.5
9	0.12	0.65	0.84	-0.19	7.0	5.4
10	0.42	1.81	1.93	-0.12	4.6	4.3
11	0.40	1.16	1.03	0.13	2.6	2.9
12	0.18	0.75	0.41	0.34	2.3	4.2
13	0.27	1.08	0.92	0.16	3.4	4.0
14	0.45	1.70	2.13	-0.43	4.7	3.8
15	0.39	0.78	0.68	0.10	1.7	2.0
16	0.27	0.40	1.32	-0.92	4.9	1.5
17	0.16	0.34	0.70	-0.36	4.4	2.1
18	--	--	--	--	--	--

(1), (2) g C / m^2 / day

(3), (4) Photosynthetic Quotient

lessened by the normal daytime conditions in Hebgen Lake. During the day strong winds constantly produce large waves on the surface of the lake. This produces turbulence in the epilimnion and reduces the micro-stratification. In short, this mixing produces a more homogeneous vertical distribution of phytoplankton during the period of photosynthetic activity. Average concentrations of chlorophyll presented in Tables XV and XVI are probably representative of conditions throughout the euphotic zone during the period of daytime turbulence.

Yentsch and Ryther (1957) first reported on the diurnal variation found in the chlorophyll content of various marine phytoplankton. Subsequent studies have shown that a diurnal periodicity in the chlorophyll content of natural waters is of widespread occurrence. High and low values often differ by a factor of 2 or 3. On the basis of these studies, the Hebgen Lake samples taken between 0400 and 0600 hours would represent daily low values.

Seasonal fluctuations in the chlorophyll content of the euphotic zone during 1965 are shown in Figure 10. The values ranged between a high of 4.43 ug/l on August 12 and a low of 1.24 ug/l on July 22.

Figure 10 shows the relation between average chlorophyll concentration and average total cell volume in the euphotic zone during 1965. A regression analysis of all simultaneous measurements of chlorophyll and cell volume taken in both years, yielded a correlation coefficient of .46. This value was not statistically significant. The regression coefficient (or slope of the regression line) was .27. A frequency analysis of the chlorophyll/cell volume ratios given in Tables XV and XVI is shown in Figure 11.

This figure shows that ratios of 0.0 - 2.0 were most prevalent. Higher ratios occurred with a uniform limited frequency.

Two explanations present themselves in considering a moor generalized correlation between chlorophyll and cell volume. The first of these would be inherent differences among the predominant species of a community at two different times of year. In Figure 10 it is seen that from May 30 to about July 15 chlorophyll/cell volune ratios are high, ranging from almost 4 to a little over 10. During this time the flora consisted of diatoms, small flagellates, and only one blue-green algae, Anabaena.

With the occurrence of appreciable populations of Aphanizomenon and Lyngbya, ratios decreased sharply to between 1.0 and 2.0. During the peak standing crops of the latter two organisms, ratios dropped to below unity. The more limited evidence of 1964 shows that exactly the same pattern occurred during that year.

An additional note regarding species differences is concerned with differences in the extractions obtained with various organisms. It would appear that the chlorophyll from delicate, fragile cells such as diatoms and flagellates would be easily extracted. The heavy sheath around Lyngbya trichomes and the heavy cell walls often observed in other blue-green algae could make extraction more difficult and often incomplete.

Different physiological conditions of the same species could also account for variations in the chlorophyll/cell volume ratio. Ketchum et al. (1958) have discussed the effects of nitrogen and phosphorus deficiencies on the chlorophyll production of plankton algae. A comparison of the field observations summarized in Figures 9, 10 and Tables XII and

Table XV. Characteristics of the phytoplankton community during 1964.

Cruise	(1) Chlorophyll	(2) Total Cell Volume	(3) Chlorophyll per cell Volume	(4) Maximum Gross O_2 Assimilation Ratio	(5) Maximum C^{14} Assimilation Ratio	(6) F C^{14}
1	2.84	0.85	3.34	2.1	--	--
2	3.36	1.12	3.00	2.7	--	--
3	2.02	0.91	2.22	6.1	--	--
4	2.80	1.66	1.69	7.4	--	--
5	3.22	4.68	0.69	8.7	3.6	0.58
6	3.78	4.10	0.92	8.1	3.2	0.41
7	4.66	5.21	0.89	6.4	3.8	0.53
8	2.92	3.33	0.88	6.4	4.6	0.56
9	2.72	2.18	1.25	2.8	1.4	0.40
10	6.47	3.79	1.71	4.5	1.5	0.39
11	3.57	2.10	1.70	4.0	1.8	0.34
12	2.89	2.53	1.14	3.2	1.2	0.34

(1) μg/liter

(2) mm^3/liter

(3) $\mu g/mm^3$

(4),(5) mg C / mg Chlorophyll / hour

Table XVI. Characteristics of the phytoplankton community during 1965.

Cruise	(1) Chloro-phyll	(2) Chloro-phyll per cell volume	(3) Maximum Gross O_2 Assimilation Ratio	(4) Maximum C^{14} Assimilation Ratio	(5) F C^{14}	(6) pH-CO_2 Productivity
1	2.59	7.85	2.0	0.9	0.23	--
2	3.09	10.30	2.3	1.1	0.27	--
3	3.61	8.20	3.2	2.0	0.34	--
4	2.92	4.79	4.4	2.3	0.31	0.27
5	3.32	6.92	3.0	1.7	0.30	0.30
6	3.35	5.40	5.0	2.2	0.32	0.21
7	3.76	3.92	5.3	3.0	0.30	0.35
8	1.24	1.70	7.8	2.8	0.29	0.21
9	1.53	1.15	8.0	3.7	0.38	0.18
10	3.54	1.01	6.0	2.7	0.22	0.36
11	4.25	0.92	7.8	2.1	0.20	0.45
12	3.90	0.68	7.2	2.9	0.35	0.30
13	3.03	0.62	3.8	1.7	0.24	--
14	4.43	1.20	4.8	1.7	0.20	--
15	4.25	2.37	3.6	1.5	0.29	--
16	3.95	1.20	2.9	1.3	0.22	--
17	2.81	0.84	2.3	1.0	0.29	--
18	--	--	--	--	--	--

(1) ug/liter
(2) ug/mm^3
(3), (4) mg C /mg Chlorophyll / hour
(6) g C / m^2/day

XVI show that physiological variation was probably responsible for differences in chlorophyll/cell volume ratios during the late-season pulse of blue-greens.

Numerous other authors have found poor correlations between chlorophyll concentrations and cell volume. Mullin et al. (1966) found no linear relationship between cell volume and chlorophyll "a" in cultures of marine phytoplankton. Paasche (1960) reported that measurements of cell volume were of limited value in predicting chlorophyll concentrations or primary productivity in the phytoplankton community. Recently, measurements of the total surface area of marine phytoplankton by Mullin et al. (1966) have shown good correlation with other ecologically significant properties of the community.

Results of the light and dark bottle experiments, to determine rates of phytoplankton productivity, are shown in Tables XIII and XIV. Rates of photosynthesis are reported as the total grams carbon assimilated by the phytoplankton community under one square meter of lake surface per day. This value was determined by plotting productivity versus depth and determining the total area under the resulting curve. The "Gross O_2," "Net O_2" and "Respiration" columns refer to those measurements derived from changes in dissolved oxygen. The "C^{14}" column shows the results of the radioactive carbon studies.

Values of gross O_2 and C^{14} productivity have been plotted in Figure 12. This figure shows the degree of relative and absolute agreement obtained by the two methods. From a relative standpoint to the two methods give quite similar results. Both show pronounced peaks of productivity on

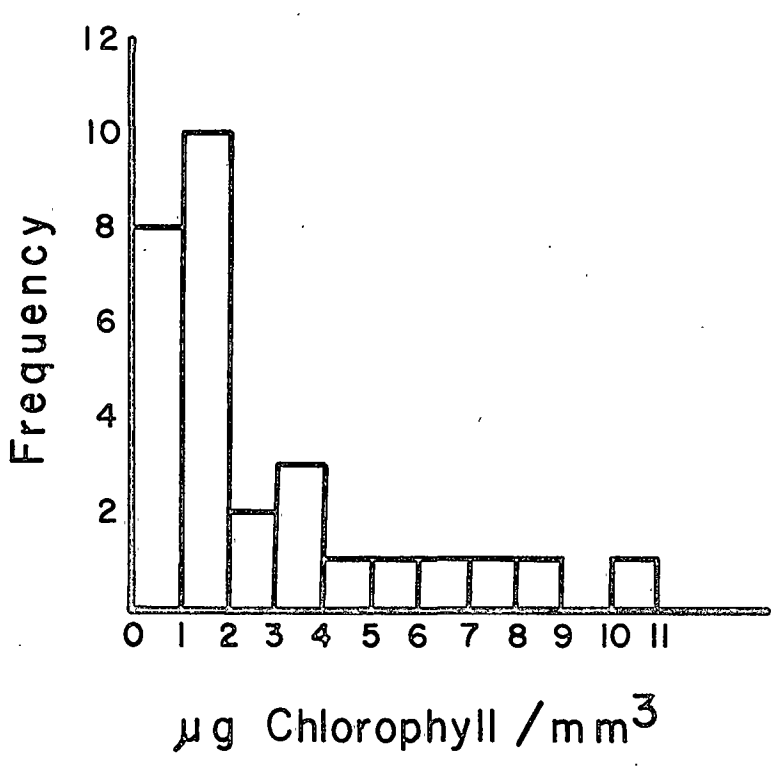

Figure 11. Frequency analysis of chlorophyll/cell volume ratios.

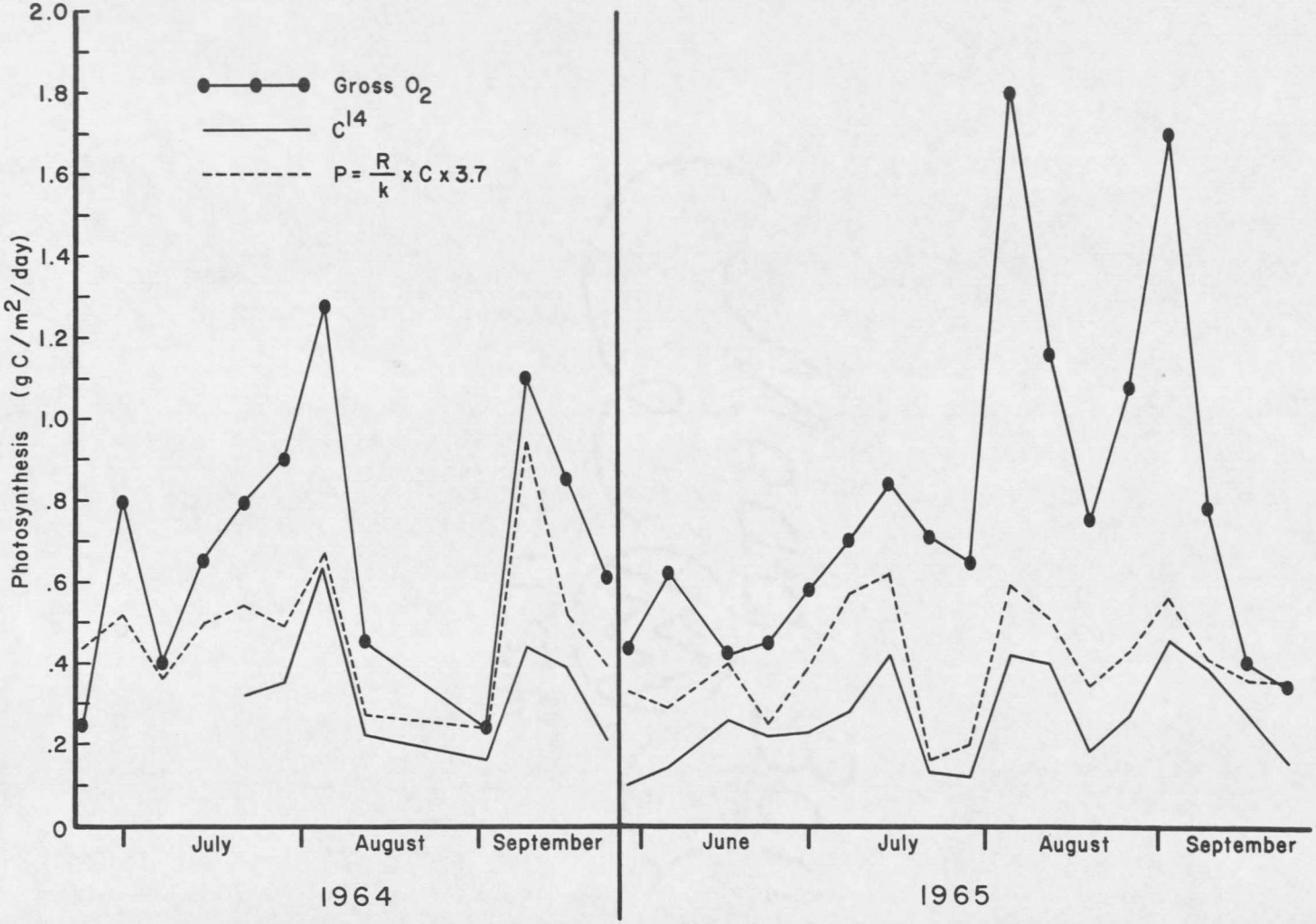

Figure 12. Primary productivity during (A) 1964 and (B) 1965.

August 5 and September 9, 1964 and again on July 15, August 5 and September 2, 1965. The correlation between the two methods during low productivity periods is also good. In short, the overall shapes of the two curves are very similar.

The differences observed in the absolute values of productivity obtained with each method are striking. Values of both net and gross O_2 productivity were, without exception, higher than those obtained with C^{14}. Since great care was taken, throughout both summers, to maintain standardization of methods, it would appear that any error resulting from technique would tend to be a constant value. However, differences in net O_2 and C^{14} measurements vary between a factor of 1.3 and 7.0, while gross O_2 is from 1.5 to 5.5 times greater than C^{14}.

Since a photosynthetic quotient (PQ) of unity was assumed in converting oxygen measurements into units of carbon, columns 3 and 4 in Tables XIII and XIV represent the PQ's for the phytoplankton community during the time of each experiment. Ryther (1956) reviewed a number of experiments, designed to determine the PQ of various planktonic algae, and finally suggested a working value of 1.25. It is obvious that if all values for C^{14} in Figure 12 were multiplied by this number, agreement of the two methods would still be far from close. Therefore it must be concluded that differences between the two methods must either be experimental artifacts or real occurrences in nature.

Eppley and Sloan (1965) performed a number of detailed experiments on the carbon metabolism of various marine phytoplankton. Among their results, they found abnormally high PQ values for several species of

diatoms. Even under carefully controlled experimental conditions, they were unable to detect a possible cause for these high measurements. Thomas (1963) noted a high PQ for phosphorus deficient cultures of Dunaliella primolecta and McAllister et al. (1964) show the same effect for both nitrogen and phosphorus deficient cultures of Skeletonema. Meyers and Cramer (1948) showed that the PQ in Chlorella cultures varied with intensity of illumination.

The PQ values in Tables XIII and XIV were compared to other data taken simultaneously in Hebgen Lake. No adequate correlations were found between these values and nutrients, physical factors or the species composition of the plankton community. It appears that this particular aspect of phytoplankton metabolism needs additional study both in the laboratory and in the field.

Values of community respiration, measured with the dark oxygen bottles, are shown in Tables XIII and XIV. One of the most perplexing aspects of the entire study was the frequent occurrence of increased amounts of dissolved oxygen in the dark bottles at the end of the incubation period. On several occasions, this increase occurred in sufficient amounts to cause the negative respiration values seen in Tables XIII and XIV. This had the further interesting result of making the measured net photosynthesis greater than the gross value. A number of laboratory experiments were undertaken by this author in an attempt to reproduce this phenomenon under controlled conditions. No positive results were obtained. Although it is believed that this dark increase of oxygen is of common occurrence in modern limnological investigations, no literature has been

found relating to the possible cause. The effect of this happening, however, is to place some doubt on the validity of the entire oxygen method.

Table XVI gives the results of the method utilizing in situ changes of CO_2 to estimate primary productivity. It can be seen that the values obtained most nearly coincide with the C^{14} measurements. Better agreement might be obtained if these values were corrected for the physical transport of CO_2 in or out of the euphotic zone. Estimates of eddy diffision, and the subsequent corrections, might be made similar to the method of Wright (1961). In addition, indirect evidence obtained during the collection of the field data, indicated that advection may play an important role in the differential transport of gases past a fixed station. It is suggested that the present method might be improved if an attempt was made to follow discrete water masses throughout a diurnal period.

The relative correlation between chlorophyll and primary productivity can be seen by comparing Figures 10 and 12. Curves for C^{14} and gross O_2 productivity have essentially the same characteristics as the one for chlorophyll. The photosynthetic rates computed by the method of Ryther and Yentsch (1957) are given in Tables XVII and XVIII. This method uses the equation:

$$P = \frac{R}{k} \times C \times 3.7$$

Where P is the productivity in grams carbon per square meter per day, R is a variable, relative rate of photosynthesis--the value of which is fixed by the amount of total solar radiation, k is the extinction

Table XVII. Estimates of primary productivity during 1964 by various methods utilizing chlorophyll and light data.

TOTAL PRODUCTIVITY

g $C/m^2/day$

Cruise	Ryther and Yentsch 1957	Curl and Small 1965	Wright 1959	New Method
1	0.44	--	--	--
2	0.52	--	--	--
3	0.36	--	--	--
4	0.50	--	--	--
5	0.54	0.32	0.63	0.59
6	0.49	0.29	0.48	0.58
7	0.67	0.40	0.83	0.78
8	0.27	0.16	0.69	0.26
9	0.24	0.14	0.15	0.12
10	0.97	0.57	0.35	0.46
11	0.52	0.31	0.21	0.21
12	0.39	0.23	0.11	0.14

Table XVIII. Estimates of primary productivity during 1965 by various methods utilizing chlorophyll and light data.

TOTAL PRODUCTIVITY

g C/m^2/day

Cruise	Ryther and Yentsch 1957	Curl and Small 1965	Wright 1959	New Method
1	0.33	0.20	0.04	0.08
2	0.29	0.17	0.06	0.10
3	0.40	0.25	0.21	0.17
4	0.25	0.15	0.17	0.14
5	0.39	0.23	0.15	0.19
6	0.57	0.34	0.25	0.36
7	0.62	0.37	0.33	0.40
8	0.16	0.10	0.08	0.11
9	0.20	0.12	0.20	0.13
10	0.59	0.35	0.24	0.41
11	0.51	0.30	0.16	0.37
12	0.34	0.20	0.37	0.22
13	0.43	0.26	0.12	0.19
14	0.56	0.33	0.13	0.29
15	0.41	0.25	0.43	0.17
16	0.36	0.21	0.12	0.12
17	0.35	0.21	0.08	0.10
18	--	--	--	--

coefficient of the water column, C is the average chlorophyll concentration, and 3.7 is an average assimilation ratio at light saturation--the units of which are grams Carbon per gram chlorophyll per hour.

Figure 12 shows the values calculated by Ryther and Yentsch's method, plotted with the values for C^{14} and gross O_2 measured productivity. The relative agreement is good in most instances, but it appears that a better fit between this method and either C^{14} or gross O_2 might be obtained by multiplying calculated chlorophyll-light values by a constant factor.

By the authors' admission, the average assimilation ratio of 3.7 was the weakest point in the method. Curl and Small (1965) obtained better comparisons between the chlorophyll-light method and C^{14} measured values by using a locally obtained assimilation ratio.

The assimilation ratio, at the depth of light saturation, was computed for every cruise on Hebgen Lake. Both values of gross O_2 and C^{14} productivity were used. The resultant values are given in Tables XV and XVI. Using the average assimilation ratio, obtained with the C^{14} measurements, the productivity was then calculated using the formula:

$$P = \frac{R}{k} \times C \times 2.2$$

The values obtained with this method are given in Tables XVII and XVIII.

Wright (1959) attempted to replace both constants in the original equation with variables indicative of the local situation. The resultant equation was:

$$P = \frac{4.6}{k} \times F \times T \times C \times R_{opt}$$

Where $\frac{4.6}{k}$ sets the limit of the euphotic zone, F is the ratio of photosynthesis at light saturation to total euphotic zone photosynthesis, T is the number of hours of photosynthesis, C is chlorophyll concentration and R_{opt} is the assimilation ratio at light saturation. Values of F for Hebgen Lake were computed using the C^{14} productivity profiles, and are presented in Tables XV and XVI. Wright's (1959) F values ranged from .34 to .60. F values for Hebgen were between .20 and .58. The productivity computed by this method is shown in Tables XVII and XVIII.

The relationship between the assimilation ratio at light saturation and total solar radiation is shown in Figure 13. It is seen that over the entire range of field light conditions, the ratio is independent of the amount of sunlight falling on the lake surface. The other most likely physical factor to affect the maximum assimilation ratio would be temperature. In Figure 14 the log of the assimilation ratio at light saturation is plotted against the average temperature in the euphotic zone. A rather clear cut linear relationship is observed, with the ratios obtained by both gross O_2 and C^{14} measurements. The lines, which are eye-fitted to the points, give the photosynthetic mechanism an approximate Q_{10} of 4.4. This is somewhat higher than the Q_{10} of 3.2 obtained by Williams and Murdock (1966) in similar field investigations.

The relationships observed between temperature and assimilation ratios were used to modify the original method of Ryther and Yentsch (1957). The formula used was:

$$P = \frac{R}{k} \times C \times A_T$$

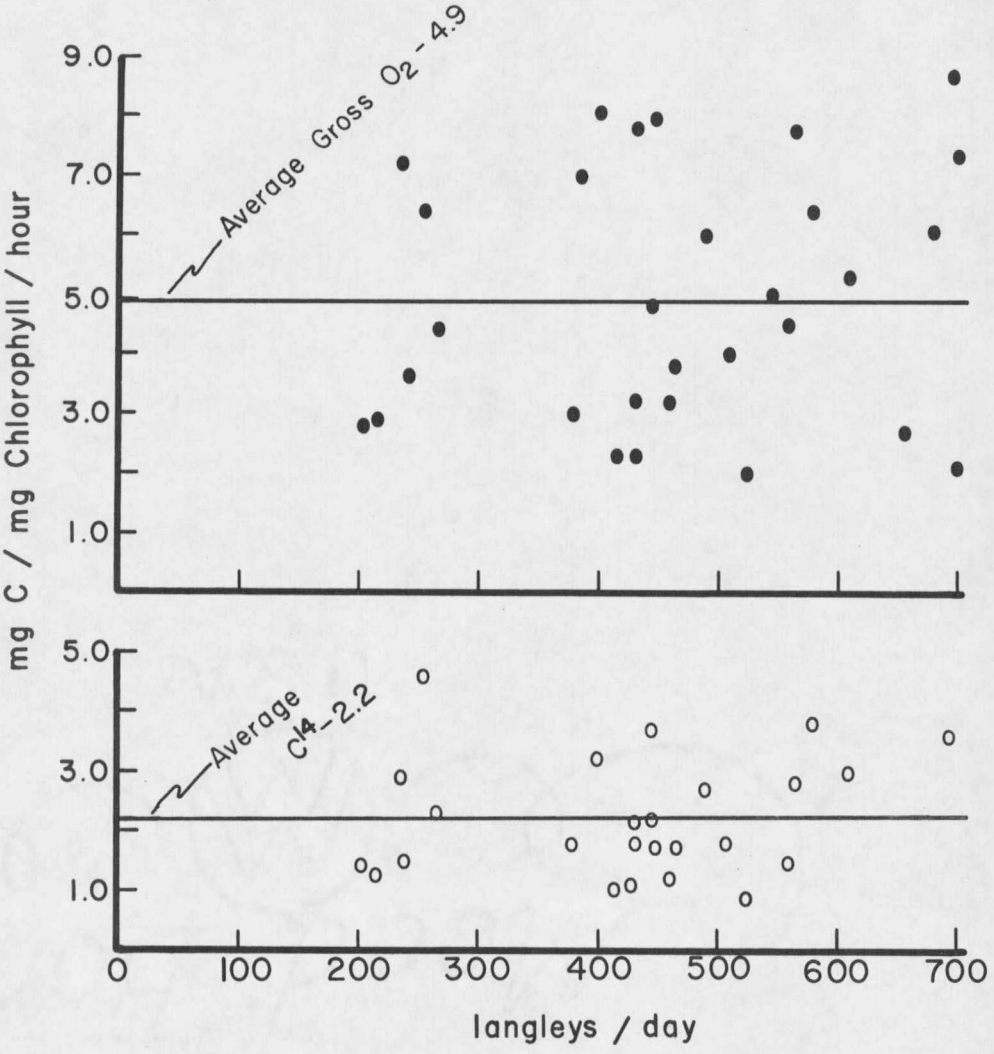

Figure 13. Assimilation ratios at light saturation as a function of total solar radiation.

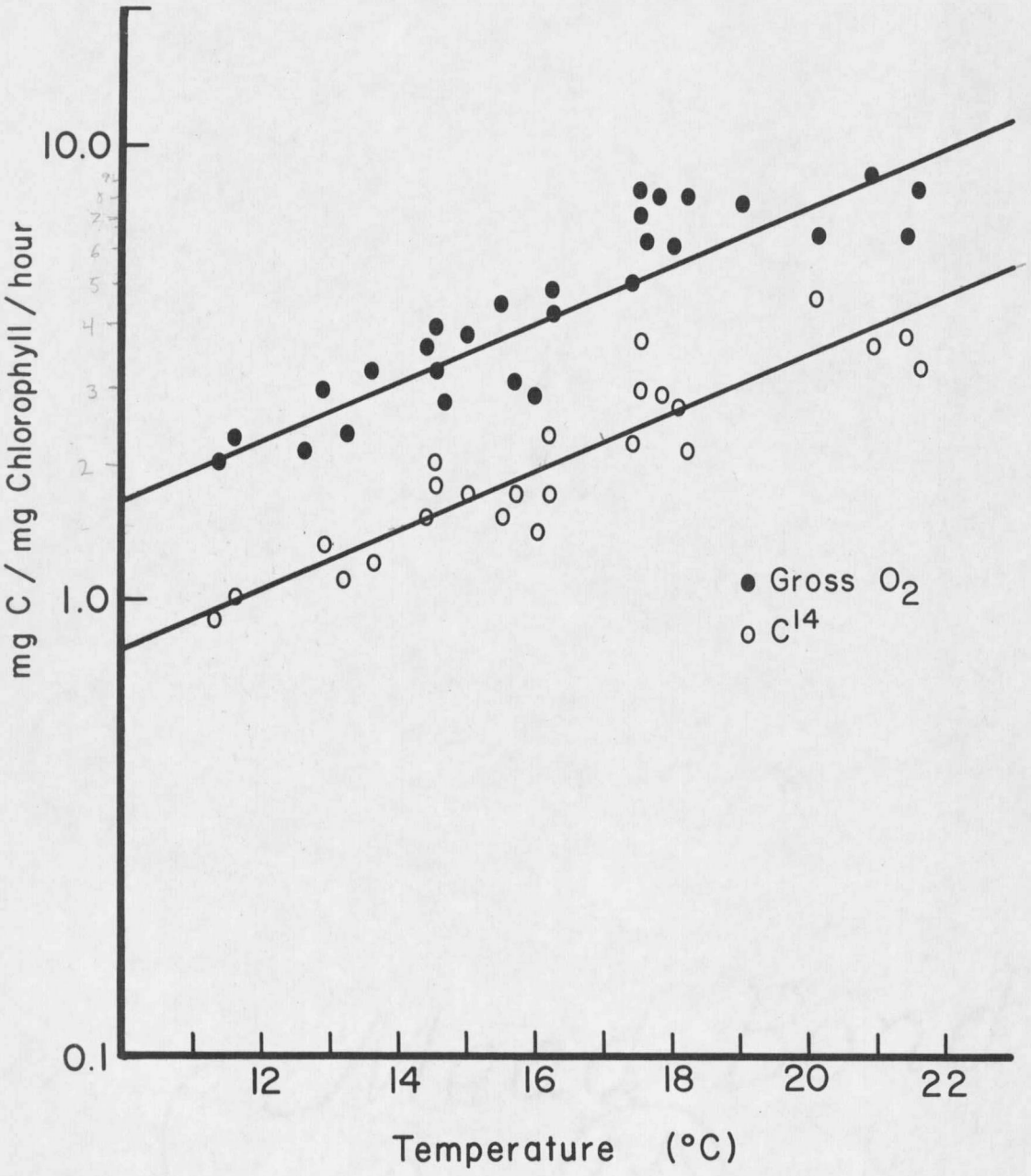

Figure 14. Assimilation ratios at light saturation (on a logarithmetic scale) as a function of the temperature of the euphotic zone.

Where all variables are the same as in the original equation except A_T.

A_T (the temperature-dependent assimilation ratio) is found in Figure 14 at the intersection of the line through the points and the average temperature of the euphotic zone on the particular day.

A comparative analysis of the four chlorophyll-light methods is summarized in Figure 15. A regression line between C_{14}-measured photosynthesis and each method of calculation was computed from the data in Tables XIII, XIV, XVII and XVIII. The dotted line on each axis represents the perfect 1:1 correlation. In each small figure, b indicates the slope of the regression line and r is the correlation coefficient.

The two methods (A and B) which utilized the constant assimilation ratios gave the poorest fit with respect to the perfect line. This merely indicates that in nature there is enough variation from the average condition to seriously limit the accuracy which can ever be obtained by such methods. Methods C and D yielded regression lines that best fit the desired 1:1 situation. This was to be expected, since both methods used data which more nearly represented the populations under consideration.

It would appear that methods C and D represent an approach in the right direction. In Wright's (1959) method the major improvement was to take into account seasonal variation in the vertical productivity profiles. This is synonymous with saying that differences in the species composition of the phytoplankton community are being considered. The new method in this paper introduces a variable assimilation ratio based on knowledge of the euphotic zone temperature. In the future, it would seem desirable to further refine these methods with information based on the concentration

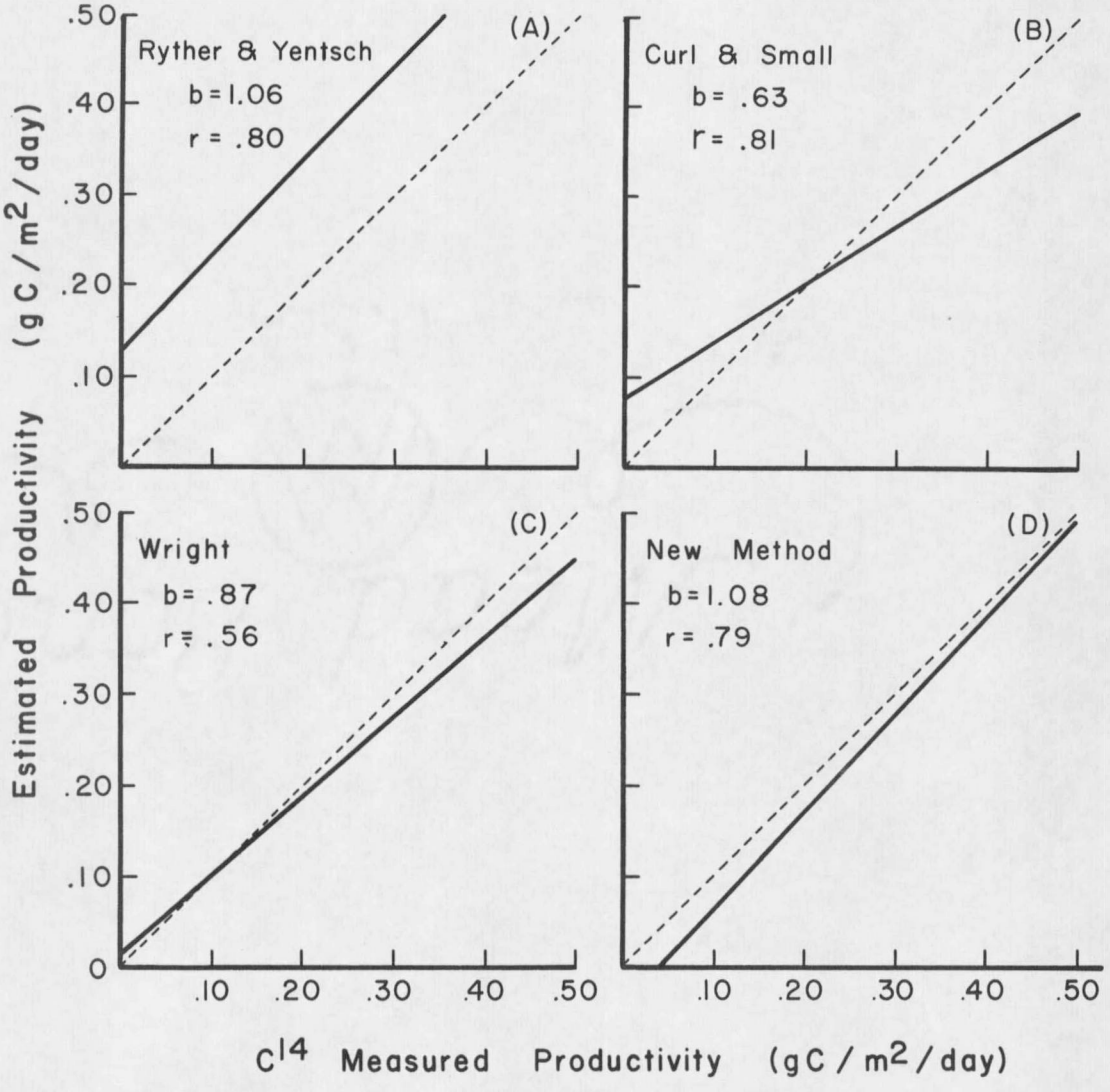

Figure 15. A comparative analysis of four methods for estimating primary productivity.

of nutrients and/or other environmental factors.

Zooplankton Standing Crop and Productivity

Table XIX shows the standing crop of the six major zooplankton species found at each station during 1964. Population densities are reported as the number of individuals per square meter of lake surface. Values at each station have been weighted to compensate for differences in the depths of the water.

The most abundant zooplankters at every station were Daphnia schodleri and D. galeata mendotae. Populations of D. pulex were usually too low to permit adequate sampling.

Among the copepods encountered, Diaptomus nudus reached the highest standing crops at every station. Diaptomus leptopus and Cyclops bicuspidatus thomasi maintained limited populations at every station throughout most of the season.

Figures 16 to 20 show the seasonal distributions of Daphnia schodleri and D. galeata at the five stations during 1964. A pronounced peak, early in the season, was observed in the D. schodleri populations at all stations. The magnitude of this spring maximum varied between 1.1×10^6 organisms per square meter at Station 4 and 7.0×10^4 per square meter at Station 5. Stations 12, 2, and 3 were all similar with respect to the size of this spring peak, reaching highs of between 5.0×10^5 and 7.0×10^5 D. schodleri per square meter. The date of the spring maximum varied from June 24 at Station 2 to July 15 at Station 5. Following the spring peak, populations of D. schodleri characteristically declined to lower mid-season densities at all five stations. Toward the end of the experimental period, there was

Table XIX. Population densities of the six principle zooplankton species at each station during 1964.

STATION 1

number / m^2 x 10^4

Cruise	*Daphnia schodleri*	*Daphnia galeata*	*Daphnia pulex*	*Cyclops bicuspidatus*	*Diaptomus nudus*	*Diaptomus leptopus*
1	17.8	0.0	0.2	0.4	0.0	0.2
2	21.6	3.6	0.4	2.0	0.2	0.4
3	13.0	0.4	0.0	0.8	0.2	0.2
4	29.2	2.0	0.2	1.2	2.4	1.2
5	27.4	1.8	0.2	2.2	6.8	4.2
6	32.2	3.2	2.2	3.0	3.4	2.6
7	14.4	2.4	0.0	3.2	0.8	1.6
8	13.6	6.2	0.0	1.4	1.4	0.2
9	37.2	37.6	0.2	0.6	2.6	1.0
10	31.8	21.4	0.6	0.4	5.8	0.6
11	9.0	3.6	0.0	0.2	0.6	0.2
12	4.0	2.8	0.2	0.0	0.4	0.2

Table XIX (cont.)

STATION 2

number / m^2 x 10^4

Cruise	Daphnia schodleri	Daphnia galeata	Daphnia pulex	Cyclops bicuspidatus	Diaptomus nudus	Diaptomus leptopus
1	68.7	0.7	0.1	2.0	0.7	0.1
2	24.8	0.0	2.5	0.4	0.1	0.3
3	35.7	8.5	0.0	5.3	0.4	0.4
4	34.2	1.1	0.8	1.8	2.4	0.4
5	11.9	0.4	0.1	1.0	2.7	1.0
6	18.2	2.0	0.0	1.3	2.4	1.4
7	21.7	23.1	0.1	2.5	0.8	2.1
8	8.0	5.0	0.1	0.8	0.6	0.4
9	31.4	20.7	0.0	0.3	1.1	0.3
10	32.8	25.8	0.0	0.1	5.0	0.1
11	9.4	5.3	0.0	0.1	0.4	0.1
12	11.3	3.6	0.1	0.0	1.0	0.1

Table XIX (cont.)

STATION 3

number / $m^2 \times 10^4$

Cruise	Daphnia schodleri	Daphnia galeata	Daphnia pulex	Cyclops bicuspidatus	Diaptomus nudus	Diaptomus leptopus
1	17.8	0.0	0.0	1.4	0.2	0.2
2	23.1	0.0	1.0	0.8	0.2	0.2
3	60.0	3.9	0.0	4.2	1.4	0.3
4	--	--	--	--	--	--
5	9.2	2.6	0.0	1.4	3.2	2.0
6	14.1	2.2	0.0	1.0	1.2	1.5
7	10.2	14.3	0.3	2.7	1.7	2.6
8	6.5	10.4	0.0	0.7	1.0	1.0
9	10.7	26.2	0.0	0.3	0.2	1.0
10	25.8	41.6	0.0	0.3	3.2	0.3
11	14.1	7.8	1.7	0.2	1.7	0.2
12	28.9	14.3	0.2	0.0	2.6	1.0

Table XIX (cont.)

STATION 4

number / m^2 x 10^4

Cruise	Daphnia schodleri	Daphnia galeata	Daphnia pulex	Cyclops bicuspidatus	Diaptomus nudus	Diaptomus leptopus
1	40.1	2.2	0.0	0.8	1.1	0.8
2	84.9	3.9	1.8	0.1	0.5	0.3
3	110.3	3.5	0.0	0.8	0.7	0.3
4	9.2	1.9	0.3	0.1	0.0	0.1
5	9.7	1.1	0.1	0.3	1.2	0.1
6	9.9	7.2	0.0	4.2	5.1	1.6
7	--	--	--	--	--	--
8	13.4	21.9	0.1	1.9	1.9	1.1
9	--	--	--	--	--	--
10	9.3	13.2	1.4	0.1	0.4	0.1
11	7.8	31.7	0.1	0.1	2.4	0.3
12	46.6	16.9	0.0	0.1	2.3	1.1

Table XIX (cont.)

STATION 5

number / m^2 x 10^4

Cruise	Daphnia schodleri	Daphnia galeata	Daphnia pulex	Cyclops bicuspidatus	Diaptomus nudus	Diaptomus leptopus
1	1.3	0.8	0.0	0.2	0.0	0.1
2	0.2	0.2	0.0	0.1	0.0	0.0
3	2.9	2.2	0.0	0.4	0.1	0.1
4	7.3	3.1	0.0	0.2	1.4	0.8
5	2.2	15.2	0.0	0.2	0.6	0.8
6	2.0	5.5	0.0	0.8	0.2	0.4
7	--	--	--	--	--	--
8	2.5	10.2	0.1	2.1	1.8	0.4
9	12.8	34.2	2.9	0.6	4.8	2.4
10	4.1	54.6	0.0	0.1	3.9	1.0
11	6.6	36.4	0.0	0.0	0.9	0.3
12	5.5	11.2	0.0	0.1	1.2	0.4

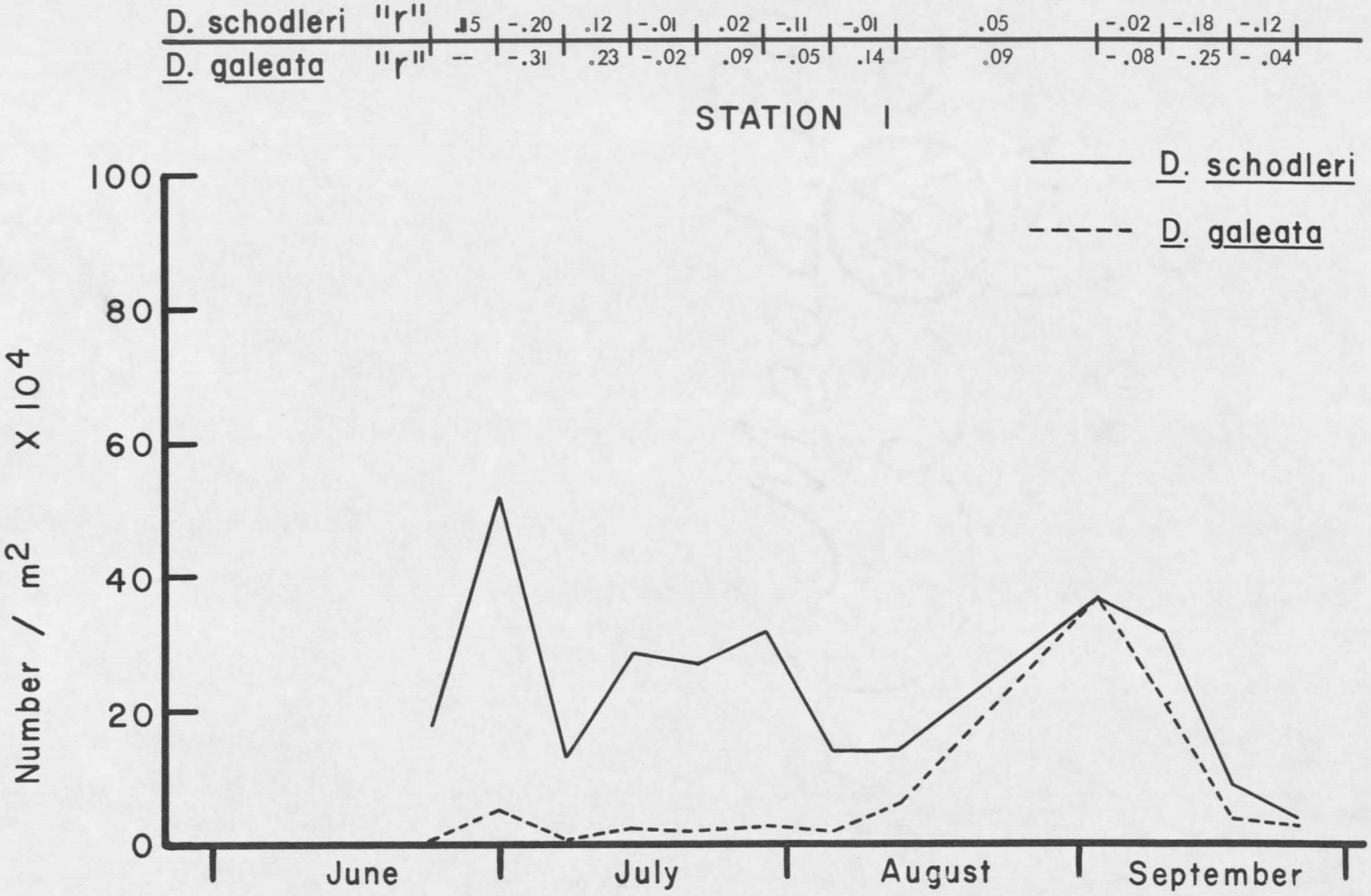

Figure 16. Standing crop and instantaneous rate of population change of Daphnia schodleri and D. galeata mendotae at Station 1 during 1964.

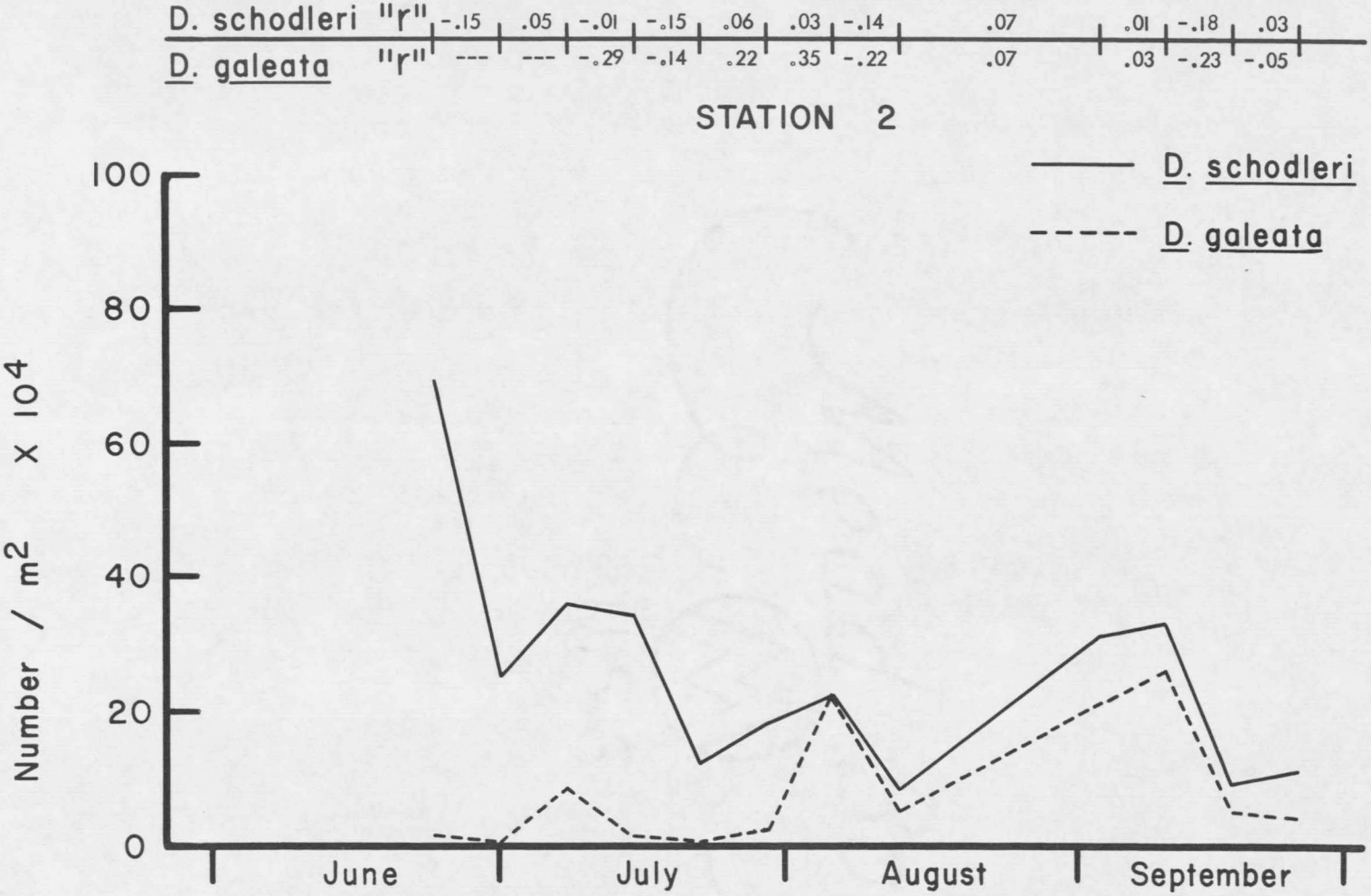

Figure 17. Standing crop and instantaneous rate of population change of Daphnia schodleri and D. galeata mendotae at Station 2 during 1964.

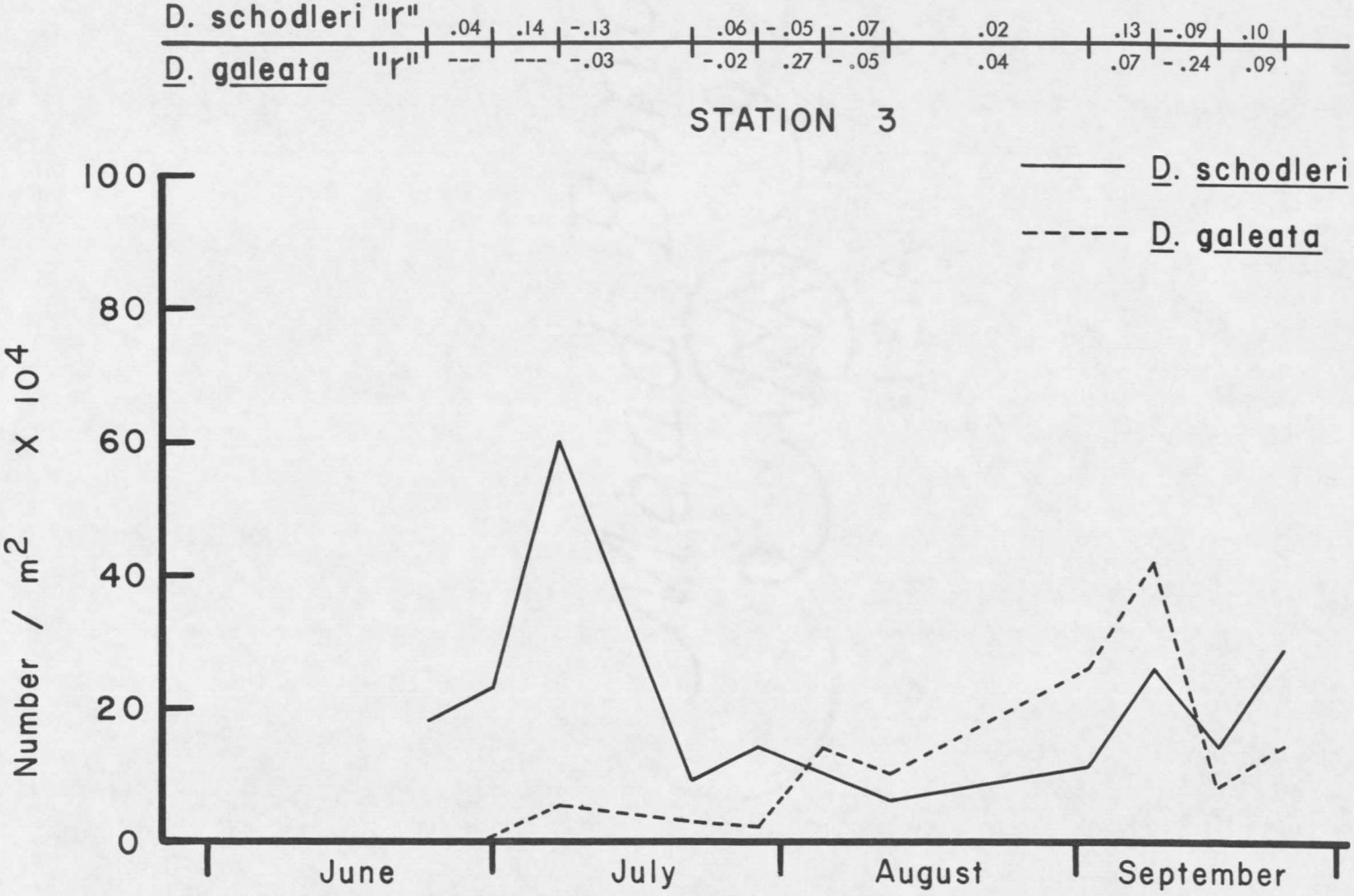

Figure 18. Standing crop and instantaneous rate of population change of Daphnia schodleri and D. galeata mendotae at Station 3 during 1964.

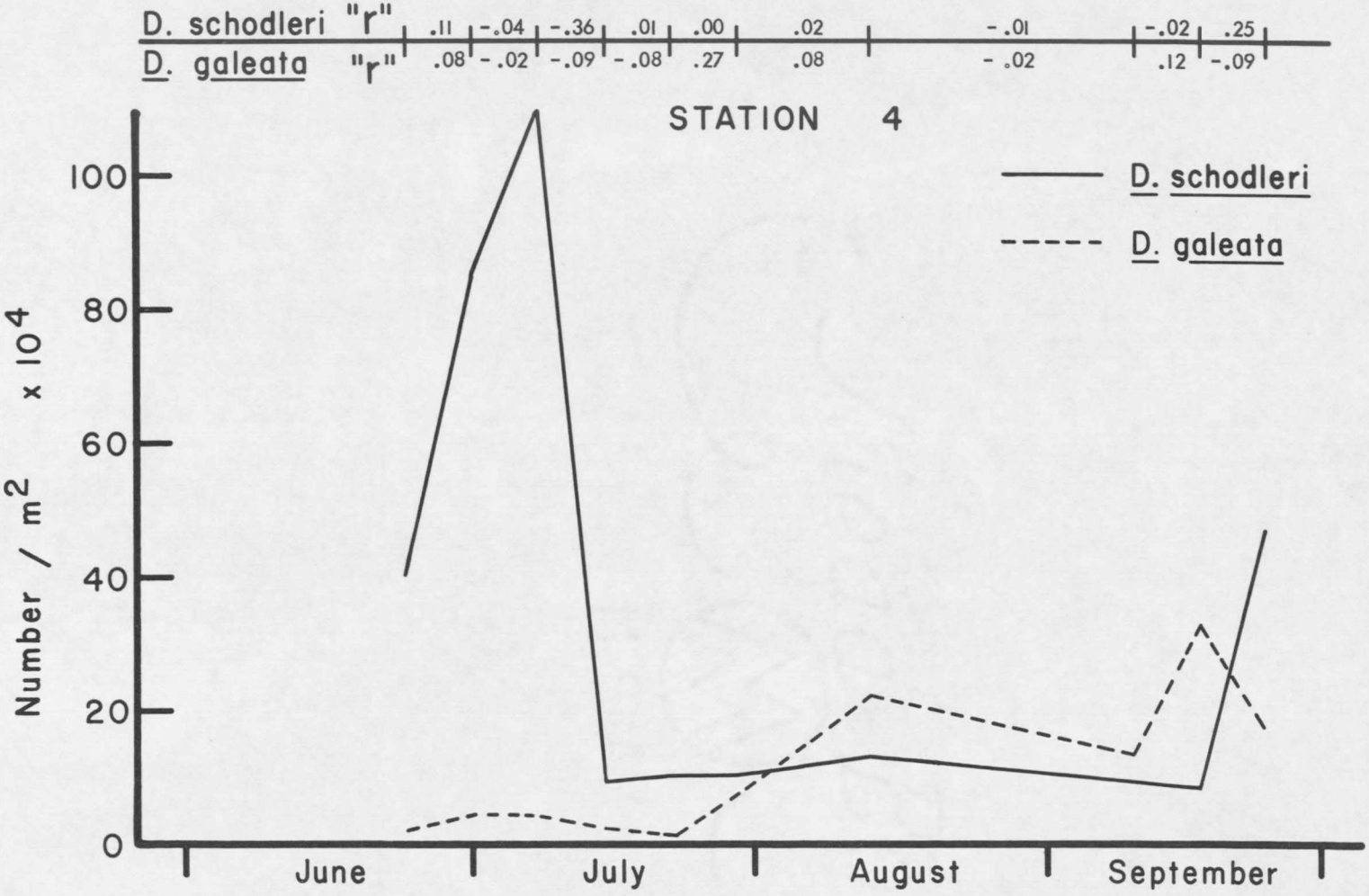

Figure 19. Standing crop and instantaneous rate of population change of Daphnia schodleri and D. galeata mendotae at Station 4 during 1964.

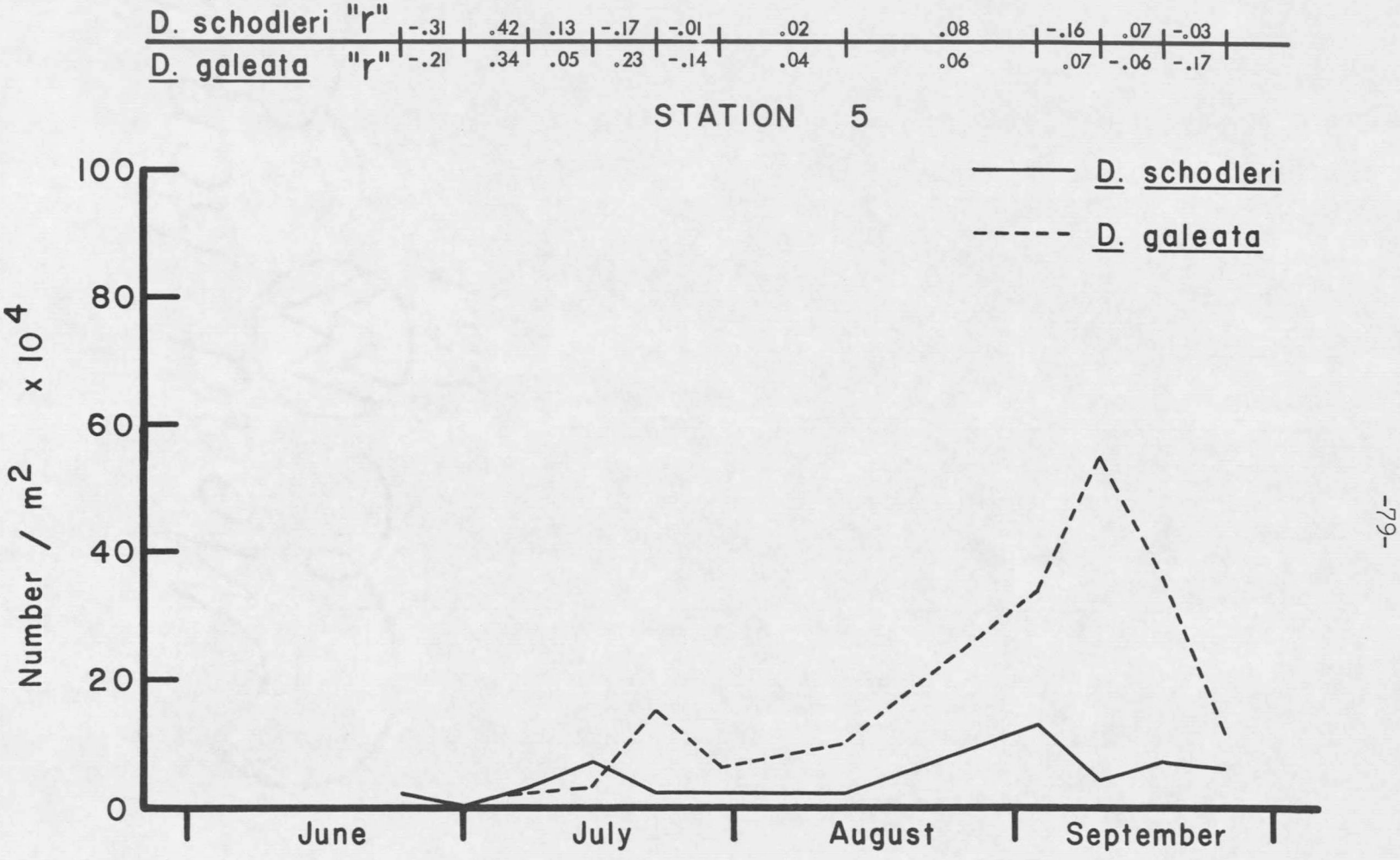

Figure 20. Standing crop and instantaneous rate of population change of Daphnia schodleri and D. galeata mendotae at Station 5 during 1964.

a second, usually less pronounced peak in numbers of D. schodleri.

At Station 1, D. schodleri was clearly the dominant cladoceran. Populations of D. galeate remained small until, in early September, a noticeable peak in the numbers of this organism occurred.

At the second station, there was a marked increase in the prominence of D. galeata relative to Station 1. In addition to the early autumn pulse, there were pronounced peaks of D. galeata in July and August. D. schodleri however, still maintained higher populations throughout the season.

Station 3 was the furthest down-lake station at which populations of D. galeata clearly exceeded those of D. schodleri during parts of the season. The September pulse of D. galeata resulted in numbers greater than those of D. schodleri, and the mid-season period was also characterized by higher numbers of the former.

Relative numbers of the two cladocerans at Station 4 remained about the same as those at Station 3. The higher numbers of D. galeata were observed during August and on into mid-September.

At Station 5, D. galeata had clearly replaced D. schodleri as the dominant cladoceran throughout most of the season.

A comparison of Tables XIX and XX and Figures 18 and 21 show that zooplankton populations were very similar at Station 3 throughout both 1964 and 1965. The peak populations of Daphnia schodleri occurred on the same dates in 1964 and 1965, namely July 8 and September 9. In both years, D. galeata replaced D. schodleri as the most abundant cladoceran on about August 5. The highdst standing crop of D. galeata occurred on September

Table XX. Population densities of the six principle zooplankton species at Station 3 during 1965.

number / m^2 x 10^4

Cruise	*Daphnia schodleri*	*Daphnia galeata*	*Daphnia pulex*	*Cyclops bicuspidatus*	*Diaptomus nudus*	*Diaptomus leptopus*
1	0.5	0.3	0.2	0.1	0.0	0.0
2	0.7	0.2	0.2	0.1	0.0	0.0
3	16.7	1.9	1.2	4.8	1.4	0.8
4	20.2	2.2	0.5	1.8	0.2	0.4
5	17.5	2.0	0.2	0.5	0.4	0.6
6	75.6	8.7	1.0	5.0	1.1	0.6
7	19.2	5.3	0.0	1.1	0.5	1.3
8	16.5	6.6	0.2	1.9	1.9	2.9
9	7.0	4.1	0.2	0.8	2.0	2.6
10	16.0	9.9	0.0	2.7	2.9	5.1
11	13.3	20.4	0.0	1.2	3.8	3.0
12	6.1	13.1	0.0	0.3	3.9	1.1
13	11.4	19.0	0.1	0.5	1.9	0.2
14	16.7	18.4	0.0	0.4	1.3	0.4
15	34.8	39.6	0.0	0.5	8.1	0.0
16	25.5	7.3	0.0	0.7	7.9	1.0
17	11.2	18.4	0.0	0.3	2.1	0.3
18	18.7	12.1	0.7	0.2	1.9	0.2

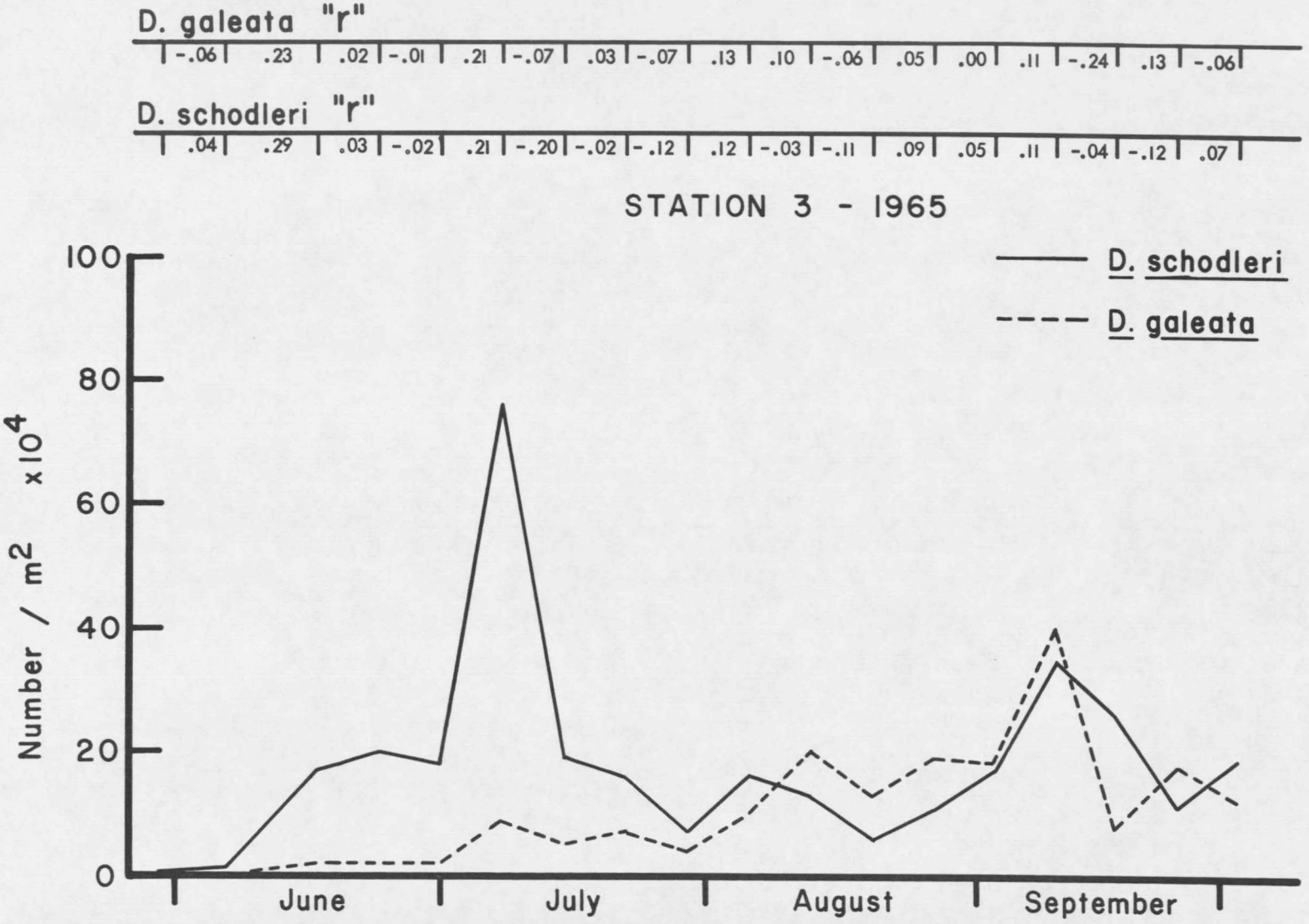

Figure 21. Standing crop and instantaneous rate of population change of Daphnia schodleri and D. galeata mendotae at Station 3 during 1965.

9 in 1964 and 1965. In addition to similarities in the shapes of the curves for the two years, the absolute values for population densities are also about the same.

Certain population statistics were calculated for Daphnia schodleri and Daphnia galeata for 1964 and 1965. The finite birth rate (B) of each species was computed for each weekly sample using the relationship:

$$B = \frac{E}{D\ N_o}$$

E, the number of eggs per square meter of lake surface, was calculated for each species from the direct egg counts. Loose eggs in each sample were prorated to the individual species on the basis of the number of attached eggs counted on each species. D, the duration of the reproductive instars, was taken from the data reported by Hall (1964). The temperatures used in obtaining a value for D were those shown in Table III. N_o was the population density of the species at the time of sampling as shown in Tables XIX and XX.

The instantaneous birth rate (b) was calculated from the relationship:

$$e^b = 1 + B$$

Where e is the base of natural logarithms and B is the finite birth rate.

The instantaneous rate of population change (r) was computed for each interval of time between samples using:

$$N_t = N_o\ e^{rt}$$

where N_o equals the initial population and N_t is the population after time t.

With b and r known, the mortality rate (d) was computed with the

formula:

$$d = b - r$$

The instantaneous rates of population change are shown for D. schodleri and D. galeata in Figures 16 to 20. Positive "r" values indicate a net increase in the populations during the time interval shown while negative values indicate a net decrease. It is noted that over certain periods there is a similar increase or decrease in populations of both species, (i.e., r values for each species have a like positive or negative sign). It is assumed that during these periods overall conditions are more unselective, and tend to cause a mutual rise or decline in the populations of both species. During other time intervals, the signs for the two species are opposite. This would indicate that during these periods factors were operative which selectively inhibited one species and enhanced the growth rate of the other species. The variation in the distribution of positive and negative "r" values and the range in absolute values of r encountered, point up the complexity of the dynamics within the zooplankton community.

Figure 22 shows the instantaneous birth rates of D. schodleri and D. galeata at the five stations during 1964. In general, peaks in the birth rate precede peaks in population density by about one or two weeks. It should be noted however, that high birth rates are not always immediately followed by high population densities.

At all stations in Figure 22, curves for D. schodleri, run throughout the entire summer, and are characterized by two or three pronounced peaks. The dates of each peak vary with respect to different stations,

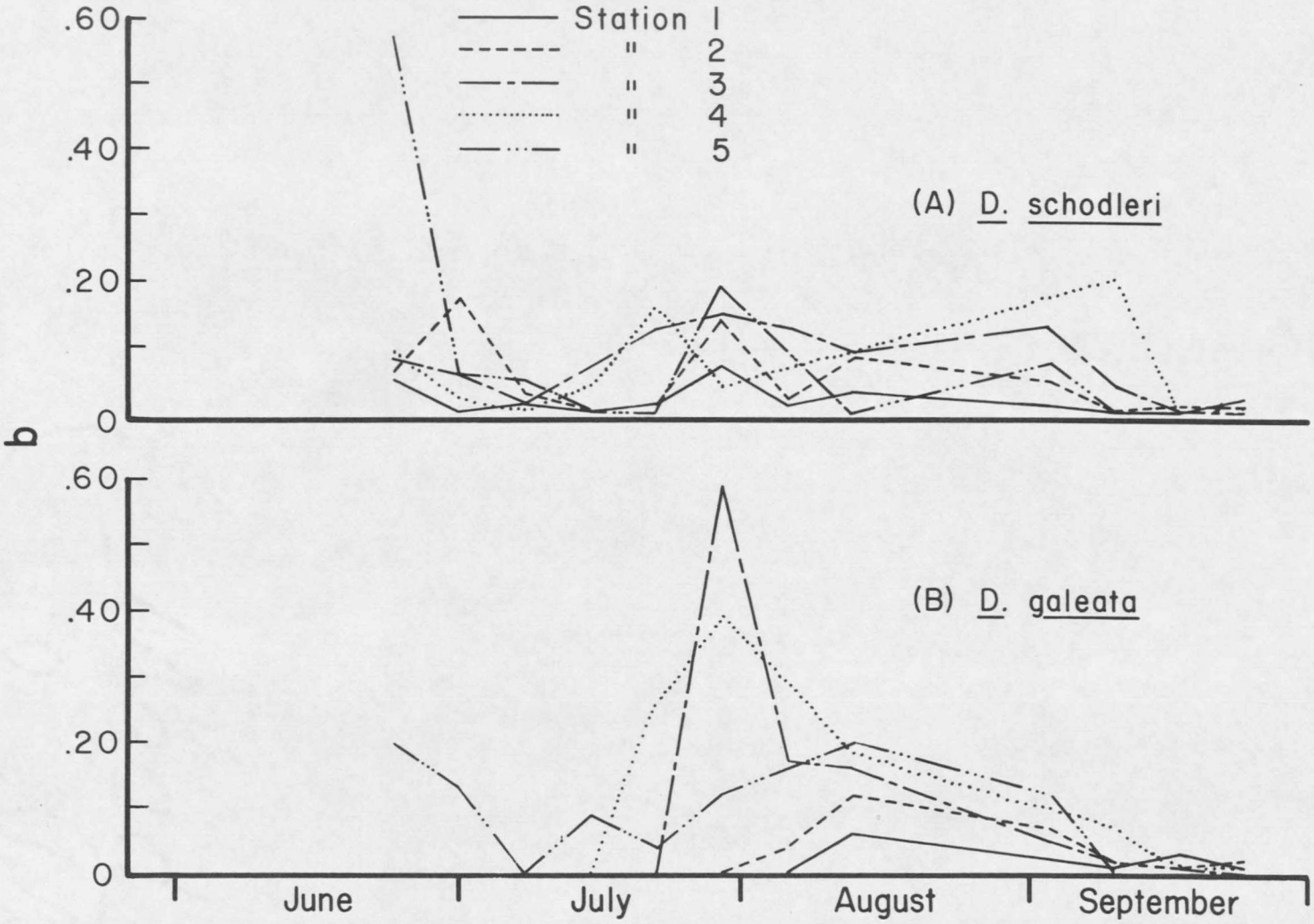

Figure 22. Instantaneous birth rates of (A) Daphnia schodleri and (B) D. galeata mendotae at the five stations during 1964.

but the general pattern is for one early summer peak, one mid-summer peak, and one peak early in September. It is noted that the early summer peaks and September peaks usually give rise to substantial D. schodleri populations, while the mid-summer peaks in b, result in less marked changes in the population.

Birth rates of D. galeata showed a definite pattern with respect to the five permanent stations. At Station 5, there was a substantial birth rate throughout most of the season. At Station 4, a birth rate was not detected until July 22, and at Stations 3, 2, and 1, birth rates stayed below detectable limits until July 29, August 5, and August 12 respectively. The areas under each of the five curves for the five stations, show that the birth rates of D. galeata became progressively higher from Station 1 through Station 5. This differential birth rate at the five stations coincides with the progressive increase in population density noted earlier at the five stations.

Mortality rates of D. schodleri and D. galeata are shown in Table XXI for Station 3 during 1965. The frequent occurrence of negative mortality rates indicates that on these same dates, birth rates were probably underestimated. One of the main problems encountered in the processing of zooplankton samples and data was the occurrence of large numbers of loose eggs in the preserved samples. Often times large numbers of loose Daphnia eggs had to be assigned to one species or the other on the basis of relatively small counts of attached eggs. This could have easily led to errors in the estimation of the finite birth rate. These errors could not be avoided; however, it is admitted that some estimates of b in this study

Table XXI. Instantaneous birth rates (b) and mortality rates (d) of Daphnia schodleri and Daphnia galeata at Station 3 during 1965.

	Daphnia schodleri			Daphnia galeata		
Cruise	Eggs per Liter	b	d	Eggs per Liter	b	d
1	0.24	0.10	0.06	0.00	0.00	0.06
2	0.48	0.18	-0.11	0.00	0.00	-0.23
3	2.39	0.05	0.02	1.77	0.32	0.30
4	5.31	0.12	0.14	0.00	0.00	0.01
5	1.09	0.03	-0.18	0.00	0.00	-0.21
6	2.21	0.02	0.22	0.00	0.00	0.07
7	0.63	0.02	0.04	0.00	0.00	-0.03
8	1.63	0.06	0.18	1.63	0.13	0.20
9	0.46	0.04	-0.08	3.00	0.35	0.22
10	2.48	0.09	0.12	6.11	0.30	0.20
11	1.03	0.04	0.15	3.36	0.09	0.15
12	0.70	0.06	-0.03	0.00	0.00	-0.05
13	1.03	0.03	-0.02	2.46	0.05	0.05
14	1.11	0.03	-0.08	1.72	0.04	-0.07
15	2.83	0.03	0.07	2.83	0.02	0.26
16	0.33	0.00	0.12	0.00	0.00	-0.13
17	0.18	0.00	-0.07	0.26	0.00	0.06
18	2.04	0.02	--	1.16	0.02	--

are perhaps unrealistic.

An estimation of D. schodleri and D. galeata productiveity was made for 1965, using the method described by Wright (1965). On the basis of the length-frequency analyses, made on each weekly sample, it was estimated that the average biomass of D. schodleri was 1.11 g C/m^2 and that of D. galeata was .69 g C/m^2. The average birth rates of the two were .05 and .07 respectively. The average turnover rate of 20 days for D. schodleri yielded an average productivity of .06 g C/m^2/day. The turnover rate of 14 days for D. galeata gave an average productivity of .05 g C/m^2/day. Total net productivity of the two species would then equal .11 g C/m^2/day. This agrees with Wright's (1965) estimate for the same two species in Canyon Ferry Reservoir of .15 g C/m^2/day.

DISCUSSION

Certain relationships between total solar radiation and primary productivity have been discussed in the previous section. That sunlight is the most important limiting factor in the plankton community has been expressed by Ryther (1956) for the marine environment and by Edmondson (1956) in reference to inland lakes. In considering local, short term situations however, it must be concluded that total radiation is only one of several factors interacting to determine phytoplankton productivity. Under the range of field conditions encountered during both summers on Hebgen Lake, no correlation was found between total community photosynthesis and total sunlight. A comparison of Tables I and II with Tables XIII and XIV show that factors other than light must certainly be operative in determining primary productivity; while a consideration of the predictive value of the chlorophyll-light methods shows that the size and physiological state of the standing crop is one such factor of at least equal importance.

The direct effect of light, as it penetrates the water, is to increase the standing crop of phytoplankton. As the concentration of algal cells in the water increases, light penetration decreases, so that the phytoplankton becomes self-shading. Inverse correlations between plankton density and light penetration have often been described, but in the field it is usually difficult to establish the direct casual relationships, due to the unknown effects of detritus and other non-algal forms of turbidity. Talling (1960a) however, has reported a clear case of self-shading in a field population of Asterionella. In Hebgen, extinction coefficients could not be correlated with phytoplankton standing crops. The significantly

higher attenuation of light at Station 5 was associated with the constant higher turbidity present at that station. This turbidity was a result of the shallow depth of the station and the action of wind-induced turbulence on the bottom.

Aside from the quantity of light available to the phytoplankton community certain workers have concerned themselves with the spectral composition of underwater light. Rhode (1965) studied the quality of underwater light in relation to C^{14} measured photosynthesis in 12 European lakes. Six of these lakes had the same blue-red-green ascending order of light penetration that characterized Hebgen. The other six had various other combinations of underwater light quality. Results of the studies showed that below the depth of light saturation, photosynthesis was proportional to the most penetrating component, regardless of its wave length characteristic. Attempts to correlate the extinction coefficients of blue, red, and green light in Hebgen, with the total standing crop of phytoplankton gave negative results. Nevertheless, on a theoretical basis significant correlations between light quality and standing crop, and perhaps even the species composition of the standing crop, should at times be possible. The conditions for such correlations would include a minimum of detritus and other suspended material and more elaborate instrumentation.

Perhaps the most important relationship shown between the physical and chemical environments in Hebgen Lake was the effect of thermal stratification on the vertical distribution of dissolved inorganic substances. The data for 1965 revealed a strong clinograde oxygen curve near the end of the summer stagnation period. During this same period, there was a

large accumulation of nitrate, and a lesser build up of phosphate, in the hypolimnion. The distribution of biologically less important nutrients seemed to be little affected by the summer stratification; however, examination of the conductivity profiles shows a marked accumulation of total electrolytes in the hypolimnion. Since it was noted earlier that a less pronounced thermocline was present in 1965 than in 1964, it is reasonable to assume that thermally induced chemical stratification would have been greater during 1964.

The net depletion of non-conservative nutrients from the epilimnion, that occurs during thermal stratification, has several effects in the phytoplankton community. Of special interest in Hebgen Lake, is the concentration of nitrate in the euphotic zone. A comparison of Tables VI and XVI, shows that a strong inverse relationship exists between nitrate concentrations and the phytoplankton standing crop-expressed in terms of chlorophyll content.

The effects of nitrate deficiency on the cholorphyll "a" content of phytoplankton cells has been reviewed by Ketchum (1954) and further reported by Ketchum et al. (1958). The low concentrations of nitrate observed in Hebgen Lake, coupled with the inverse correlation between this nutrient and chlorophyll, has led to the conclusion that nitrate may often be limiting to the phytoplankton standing crop.

Silicates and phosphates are also biologically important nutrients, and in many natural waters their concentrations are often limiting (Hutchinson, 1957; Fogg, 1965). The extended studies of Lund et al. (1963) would place the limiting concentration of silica at about .5 mg/l

for increased growth of diatoms such as Asterionella. It is seen from Table VII that concentrations of this nutrient in Hebgen are consistently one order of magnitude above this limiting value. A large quantity of work, some of which is summarized in Mackenthun (1965) shows that phosphate concentrations in Hebgen Lake are also several times higher than any reported as limiting to phytoplankton productivity.

Little information is available concerning the carbon dioxide requirements of phytoplankton. Certain workers such as Wright (1960) have found evidence of carbon dioxide limitations during periods of phytoplankton blooms, while others (Talling, 1960b) found little reduction of the nutrient in relation to natural rates of photosynthesis. The general tendency in Hebgen Lake for pH to increase and inorganic carbon to decrease during the height of the summer phytoplankton standing crop indicates the correlation between phytoplankton biomass and CO_2, even though the latter may not become actually limiting.

The significance of the various other elements, considered in the present study, with respect to phytoplankton productivity can be found in Lewin (1962). In general it can be stated that the concentrations of these nutrients in Hebgen Lake are sufficiently high so as to be considered not limiting.

Nutrient concentrations not only effect total primary productivity, but also the species composition of the phytoplankton community. The seasonal succession of phytoplankton cannot be entirely related to the concentration of a single inorganic nutrient nor to any combination of nutrients. It has been shown, however, that the occurrence of diatoms

usually coincides with the higher levels of inorganic nutrients present early in the season. The position of blue-greens in the successional pattern is usually accompanied by low levels of nitrate-nitrogen and/or high phosphate/nitrate ratios.

Temperature is undoubtedly a direct as well as indirect causative factor in phytoplankton succession. Different species may predominate at different times because of the interaction between prevailing temperature and other environmental factors. The limitations of temperature per se in controlling species periodicity is seed in a comparison of the years 1964 and 1965. Although Figure 6 shows many differences in the thermal regimes of 1964 and 1965, the succession of algal species in both years was essentially the same. If temperature were a dominant controlling factor, a shift in species composition should follow the onset of fall overturn, since it is seen in Figure 6 that euphotic zone temperatures drop sharply at this time. During both 1964 and 1965, the fall period of thermal mixing was accompanied by increased growth of the same blue-green algae that were predominant throughout the warmest periods.

Some of the recent research on algal succession has been reviewed by Fogg (1965). Many of the important factors connected with this phenomenon, such as the organic chemical environment, the production of growth-inhibiting substances and the concentrations of certain trace nutrients, have not been included in this study. The well defined periodicity of certain phytoplankton species in Hebgen Lake would provide an excellent opportunity for further research.

The steady depletion of nutrients from the epilimnion during the

summer leaves two alternatives in maintaining sufficient quantities in the euphotic zone for continued algae growth. Either nutrients must be added from external sources or the nutrients present must be rapidly recycled. In the case of nitrogen, large quantities are often added to the euphotic zone by nitrogen-fixing bacteria and blue-green algae. The importance of nitrogen fixation, in the overall nitrogen metabolism of fresh waters has been stressed by Dugdale and Dugdale (1962). In quantitative studies of nitrogen fixation in Lake Mendota, Goering and Neess (1964) observed a rate of 14.8 u grams of nitrogen fixed per liter in 24 hours. This amounted to more than the total nitrate-nitrogen observed in the euphotic zone of Hebgen Lake on any cruise during the 1965 experimental season.

Most workers have agreed that various species of Anabaena are the principle nitrogen fixers in the phytoplankton community. If this is the case, it could be expected that limited amounts of nitrogen would be fixed in Hebgen Lake from late spring until early autumn (see Figure 9). Other authors (Sawyer and Ferullo, 1961; Krauss, 1958) have reported the fixation of nitrogen by Aphanizomenon and members of various families of blue-greens, of one of which Lyngbya is a member. If these latter two genera can be implicated in the nitrogen-fixation occurring in Hebgen Lake it is obvious that the overall importance of nitrate-nitrogen as a limiting factor would be greatly changed.

The role of zooplankton as agents for phosphate regeneration has been studied extensively. Recent work by Barlow and Bishop (1965) showed that Daphnia liberated about 80% of the assimilated phosphorus back into the epilimnion of Cayuga Lake during the period of strong thermal stratifica-

tion. Pomeroy et al. (1963) have found turnover times for total phosphorus to be as low as eight days in coastal waters during summer. The effects of increased temperature on the metabolism of the zooplankton would tend to accelerate the recycling process during the most critical periods.

One of the effects of temperature on primary productivity was noted in one of the methods of estimating photosynthesis from chlorophyll and light data. The concentration of nutrients in the euphotic zone will also effect the predictive value of such methods. If a large standing crop is present in an environment where one or more nutrients are limiting, productivity will probably be over estimated. The productivity of a small standing crop, present in a nutrient-rich medium, will undoubtedly be greater than that estimated from its chlorophyll concentration. The controlling effects of the nutrient supply on the assimilation ratio has been demonstrated by Holmes (1958) and McAllister, Shah and Strickland (1964). While there are many unknown variables to contend with in the chlorophyll-light methods, some of the measurable factors may also become sources of error. The measurements of chlorophyll and the physical data are of great importance in these methods. For example, a change in extinction coefficient from .55 to .56 at 400 langleys per day results in a 4% difference in calculated production.

It is difficult to explain the differences observed between the C^{14} and dissolved O_2 methods of measuring primary productivity. The empirical evidence first presented by Ryther (1954), and repeatedly confirmed in subsequent studies, shows that the C^{14} method often approximates net photosynthesis. From a theoretical standpoint, the light and dark bottle

O_2 method would underestimate net photosynthesis due to the consumption of oxygen by non-autotrophic organisms such as bacteria and zooplankton. Recently, a large amount of literature has appeared on the excretion of various organic metabolites of phytoplankton in almost every phase of growth and under a wide variety of environmental conditions. Underestimates of total assimilated carbon might result from the excretion of C^{14} labeled organics back into the medium.

The correlation between total phytoplankton standing crop and zooplankton population density, as seen in Figures 10 and 21, is not particularly high. This is to be expected if consideration is made for the species composition of the phytoplankton community. Certain workers (c f. Wright, 1965) have found good correlations between reproductive rates of various zooplankton species and the phytoplankton standing crop. However, others (Edmondson et al., 1962 and Edmondson, 1965) show more pronounced relationships between zooplankton and the microplankton portion of the standing crop.

Tappa (1965) has shown a high degree of food selectivity in various species of Daphnia. On the basis of this and other studies it would appear that Cryptomonas, Rhodomonas, Asterionella and the microplankton would consistute the most important food species in Hebgen Lake. The zooplanton food value of such organisms as Lyngbya, Anaboena, and Aphanizomenon, which often comprise the bulk of the phytoplankton standing crop, is questionable.

If the biomass of the three major blue-green algae are in fact scarcely utilized by zooplankton populations, then their standing crops

must be entirely limited by the chemical and physical environment. The standing crops of the smaller planktonic algae must be primarily limited by zooplankton grazing pressure. The following hypothetical illustration of Harvey (1945) shows the magnitude of effect of zooplankton utilization. "If an initial population of 100 cells per liter undergoes six successive cycles of division, the final population would be 6400 cells per liter. If, however, one cell in every 10 is eaten in the intervals between divisions, the population will only reach 3400 cells per liter, although only 413 cells have been eaten."

The work of Rhode et al. (1958) has shown that rates of productivity among various species in the phytoplankton community are seldom proportional to their biomass or standing crops. Photosynthesis in the "nanoplankton" is consistently much higher than the "netplankton" on a weight or volume basis. In most cases the total contribution of the larger forms is no more than 10-20%. The high rates of productivity observed in the microplankters is attributed to the large surface area-volume ratio.

If it is true that the smaller organisms possess an inherently greater capacity for biomass productivity, then the outcome of their competition with the larger forms, in the absence of zooplankton grazing, would be obvious. However, selective predation, of the organisms with the competitive advantage allows both types of organisms to coexist in what appears to be an undiversified habitat. Further support of this hypothesis is seen by the seasonal distribution of the two classes of organisms in Hebgen Lake. Cryptomonas, Rhodomonas and the microplankton all maintain substantial populations throughout the season under a wide range

of environmental conditions. The larger forms such as Anabaena, Aphanizomenon and Lyngbya however, are restricted to what is evidently a rather specialized set of environmental conditions.

One of the most interesting features of the zooplankton data concerns the spatial distribution of Daphnia schodleri and D. galeata. The progressive importance of D. galeata, both with respect to standing crop and rates of reproduction, coincides with a significant decrease in the temperatures at Stations 1 through 5. On the basis of a simple temperature regulated relationship, one would conclude that D. galeata was favored by the cooler prevailing temperatures at Station 5 and that D. schodleri was able to dominate at Stations 1 and 2 because of the warmer temperatures. Stations 3 and 4 would represent the intermediate temperatures at which first one organism, and then the other, dominated during different times of the season. These conclusions would be in general agreement with the findings of Brooks (1946), Hall (1964), McNaught and Hasler (1964) and Wright (1965) who all found that peak populations and/or high birth rates in D. galeata were associated with low temperatures.

If temperature was the primary regulatory factor operative at the five stations, then the same sequence should repeat itself at each station during the seasonal temperature cycle. It is noted in Figures 16 through 22 that this is not the case. In the spring when temperatures are low, D. schodleri is dominant at all stations. When D. galeata is able to replace D. schodleri, it is later in the season when water temperatures are at a maximum. Examination of Figure 22 also shows that the birth rates of D. galeata were most significant during the periods of highest temperatures

at all stations. These findings on the seasonal distribution of D. schodleri and D. galeata are diametrically opposed to the results of the authors cited in the preceding paragraph.

Two conclusions on the distribution and dynamics of Daphnia in Hebgen Lake have been reached. First, it is suggested that temperature alone does not regulate the birth rates and subsequent standing crops of D. schodleri and D. galeata, and second that the perhaps unique situation found in Hebgen Lake would offer a good opportunity for further study on the ecology of these two species.

APPENDIX

Table XXII. Temperature (°C) profiles at Station 3 during 1965.

Depth	Cruise 1	Cruise 2	Cruise 3	Cruise 4	Cruise 5	Cruise 6
0	12.9	16.2	14.6	17.0	17.4	18.4
1	12.9	15.0	14.6	17.0	17.0	18.4
2	12.9	13.5	14.6	16.6	15.8	18.4
3	12.2	12.9	14.6	16.6	15.8	18.4
4	11.6	12.9	14.6	16.1	15.4	17.4
5	10.9	12.2	14.6	16.1	15.0	17.0
6	9.6	12.2	14.2	16.1	15.0	16.6
7	9.6	12.2	14.2	15.4	15.0	16.6
8	9.0	11.9	14.2	14.6	15.0	15.8
9	9.0	11.2	14.2	13.5	15.0	15.0
10	8.7	10.8	13.3	13.3	15.0	15.0
11	8.4	10.8	12.6	12.6	15.0	14.6
12	8.4	9.5	12.2	12.2	14.2	13.9
13	8.1	9.3	11.9	12.2	14.2	13.5
14	8.1	9.0	11.9	11.6	13.5	13.3
15	8.1	8.7	11.6	11.6	12.9	12.6
16	8.1	8.7	10.8	11.6	12.2	12.6
17	7.8	8.4	10.5	10.9		12.6
18	7.5	8.4	10.5			12.2

Table XXII. (cont.)

Depth	Cruise 7	Cruise 8	Cruise 9	Cruise 10	Cruise 11	Cruise 12
0	--	17.4	19.6	18.4	18.8	19.2
1	--	17.9	18.4	18.4	18.8	18.8
2	--	17.9	17.9	18.4	18.8	17.4
3	--	17.9	17.4	18.4	18.4	17.0
4	--	17.9	17.4	18.4	18.4	17.0
5	--	17.9	17.4	18.4	17.9	17.0
6	--	17.9	17.0	17.9	17.9	17.0
7	--	17.9	16.2	17.4	17.4	17.0
8	--	17.9	15.8	16.6	17.4	17.0
9	--	17.0	15.0	16.6	16.6	16.6
10	--	16.6	13.9	16.6	15.8	16.6
11	--	15.8	13.2	16.1	14.6	16.2
12	--	14.2	12.9	15.8	13.5	15.4
13	--	13.5	12.2	15.0	13.2	13.5
14	--	12.9	11.6	14.6	12.9	12.2
15	--	12.2	11.6	13.9	12.9	11.6
16	--	12.2		13.2	11.9	11.6
17	--	11.9		12.6	11.2	10.9
18	--	11.6		12.2		9.9

Table XXII. (cont.)

Depth	Cruise 13	Cruise 14	Cruise 15	Cruise 16	Cruise 17	Cruise 18
0	15.0	16.6	14.6	12.9	11.6	12.2
1	15.0	16.6	14.6	12.9	11.6	10.2
2	15.0	16.6	14.6	12.9	11.6	9.9
3	15.0	16.2	14.6	12.9	11.6	9.6
4	15.0	16.2	14.6	12.9	11.6	9.6
5	15.0	16.2	14.2	12.9	11.6	9.6
6	15.0	15.8	14.2	12.9	11.6	9.6
7	15.0	15.8	14.2	12.9	11.6	9.6
8	15.0	15.8	14.2	12.9	11.6	9.6
9	15.0	15.8	14.2	12.9	11.6	9.6
10	15.0	15.8	14.2	12.9	11.6	9.6
11	14.6	15.8	14.2	12.9	11.6	9.6
12	14.6	15.8	14.2	12.9	11.6	9.6
13	13.2	15.8	14.2	12.9	11.6	9.6
14	12.9	15.0	14.2	12.9	11.6	9.6
15	11.6	15.0	14.2	12.9	11.2	9.6
16	10.5	14.6	13.5	12.9	10.9	9.6
17		13.5	13.2	12.9		9.6
18		12.6	12.9	12.9		9.6

Table XXIII. Specific conductance (micromhos) profiles at Station 3 during 1965.

Depth	Cruise 1	Cruise 2	Cruise 3	Cruise 4	Cruise 5	Cruise 6
0	229	211	212	215	215	210
1	229	217	226	215	214	203
2	229	218	226	216	211	210
3	241	191	226	209	204	210
4	260	208	226	204	198	211
5	263	245	226	204	200	207
6	275	247	229	189	200	216
7	272	247	227	193	202	212
8	277	247	223	185	202	212
9	277	256	218	201	202	203
10	279	259	223	209	200	207
11	287	259	243	223	210	205
12	289	278	249	237	219	212
13	294	279	251	237	218	216
14	294	282	253	245	220	223
15	300	287	258	247	236	234
16	300	287	268	247	241	234
17	305	295	270	256		236
18	305	300	270	256		241

Table XXIII (cont.)

Depth	Cruise 7	Cruise 8	Cruise 9	Cruise 10	Cruise 11	Cruise 12
0	--	205	210	210	218	218
1	--	205	207	212	218	218
2	--	205	207	212	216	223
3	--	205	208	212	218	225
4	--	205	208	210	218	227
5	--	205	206	210	218	225
6	--	205	208	209	218	225
7	--	205	199	211	219	225
8	--	205	211	191	215	223
9	--	210	211	209	214	225
10	--	205	209	209	209	225
11	--	206	208	208	207	225
12	--	208	210	209	211	218
13	--	211	214	211	212	229
14	--	214	217	214	213	217
15	--	218	220	218	213	220
16	--	219		222	219	222
17	--	220		229	223	228
18	--	226		239		240

Table XXIII (cont.)

Depth	Cruise 13	Cruise 14	Cruise 15	Cruise 16	Cruise 17	Cruise 18
0	220	227	230	--	--	--
1	220	227	230	--	--	--
2	222	227	230	--	--	--
3	222	227	230	--	--	--
4	222	227	231	--	--	--
5	222	227	231	--	--	--
6	222	227	231	--	--	--
7	222	227	231	--	--	--
8	224	227	231	--	--	--
9	224	225	231	--	--	--
10	224	225	231	--	--	--
11	226	227	231	--	--	--
12	224	227	231	--	--	--
13	216	227	231	--	--	--
14	218	228	231	--	--	--
15	219	228	225	--	--	--
16	246	224	223	--	--	--
17		225	231	--	--	--
18		232	234	--	--	--

Table XXIV. Profiles of temperature (°C) and specific conductance (K_{25}) at Station 1 during 1964. Conductance expresses as micromhos.

	Cruise 1		Cruise 2		Cruise 3		Cruise 4	
Depth	°C	K_{25}	°C	K_{25}	°C	K_{25}	°C	K_{25}
0	14.6	257	16.7	266	18.5	244	19.7	251
1	14.6	257	16.7	258	18.5	249	19.7	241
2	14.4	258	16.7	258	18.5	239	19.7	243
3	14.3	263	16.3	258	18.5	241	19.7	238
4	13.0	264	15.8	256	18.5	249	19.7	243
5	12.0	259	15.3	255	18.0	252	19.7	249
6	11.5	263	15.1	254	17.9	247	19.7	249
7	11.5	253	14.8	268	17.6	252	19.7	243
8	11.5	253	14.6	267	17.2	242	19.7	243
9	11.5	282	13.5	268	17.0	256	19.1	255
10	11.5	268	12.5	279	16.0	248	17.7	263
11	11.5	263	11.1	273	14.0	256	15.3	275
12	11.1	273	11.0	277	13.0	263	14.0	278
13	11.0	261	11.0	261	12.5	261	12.9	269
14	10.8	268	10.5	295	12.1	254	12.5	271
15	10.5	265	10.4	281	12.1	254	12.0	293
16	10.2	283	10.2	283	11.5	276	12.0	272
17	10.2	277	9.5	313	11.2	287	11.9	279
18	9.1	295	9.0	318	10.4	309	11.5	294
19	9.0	298	8.8	309	9.9	321	10.9	308
20	8.5	301	8.7	324	9.6	320	10.6	311
21	8.0	316	8.5	329	9.6	303	10.6	311
22	8.0	316	8.2	352	9.6	323	10.6	311
23	8.0	316	8.2	352	9.6	323		
24	8.0	323						

Table XXIV (cont.)

	Cruise 5		Cruise 6		Cruise 7		Cruise 8	
Depth	°C	K_{25}	°C	K_{25}	°C	K_{25}	°C	K_{25}
0	22.5	248	22.1	244	21.5	229	20.5	233
1	22.5	254	22.1	252	22.0	231	20.5	234
2	22.5	260	22.1	259	22.2	230	20.5	231
3	23.0	254	22.1	236	22.2	230	20.5	230
4	23.0	257	22.1	236	22.4	229	20.5	229
5	23.0	254	22.1	236	22.2	230	20.5	229
6	23.0	240	22.1	236	22.5	229	20.5	231
7	22.5	248	22.1	233	22.4	229	20.5	233
8	21.5	244	22.1	239	22.0	231	20.5	229
9	19.8	245	21.0	256	21.4	227	20.5	232
10	17.0	250	19.5	247	20.6	228	20.0	231
11	16.0	251	17.5	247	20.0	230	19.8	230
12	14.6	254	16.0	246	16.6	235	17.2	239
13	14.0	261	15.0	254	15.5	237	16.9	234
14	13.4	263	14.0	269	14.5	241	16.1	236
15	12.9	269	13.6	272	13.7	248	15.0	240
16	12.9	269	13.4	265	13.3	251	13.5	249
17	12.5	269	13.0	363	13.1	252	13.0	252
18	12.3	267	12.8	272	12.7	265	12.8	254
19	11.6	275	12.0	278	12.7	286	12.5	261
20	11.0	285	11.6	287	12.5	289	12.0	264
21	10.8	293	11.0	291	12.0	297	11.6	267
22	10.8	340	11.0	338	12.0	311	11.5	294
23	10.8	344						
24	10.8	348						

Table XXIV (cont.)

	Cruise 9		Cruise 10		Cruise 11		Cruise 12	
Depth	°C	K_{25}	°C	K_{25}	°C	K_{25}	°C	K_{25}
0	16.8	--	15.7	242	14.5	248	13.9	251
1	16.8	--	15.7	243	14.5	248	13.9	251
2	16.8	--	15.7	244	14.5	248	13.9	251
3	16.8	--	15.7	244	14.5	250	13.9	251
4	16.8	--	15.7	244	14.5	250	13.9	251
5	16.8	--	15.7	245	14.5	248	13.9	251
6	16.8	--	15.7	243	14.5	250	13.9	251
7	16.8	--	15.7	244	14.5	249	13.9	251
8	16.8	--	15.7	243	14.5	249	13.9	251
9	16.8	--	15.7	244	14.5	250	13.9	251
10	16.8	--	15.7	245	14.5	248	13.9	251
11	16.8	--	15.5	246	14.5	250	13.9	251
12	16.8	--	15.0	248	14.5	250	13.9	251
13	16.8	--	15.0	248	14.5	250	13.9	251
14	16.8	--	15.0	247	14.4	251	13.9	251
15	16.8	--	14.5	251	14.4	249	13.8	253
16	16.8	--	14.0	256	14.4	251	13.8	253
17	16.5	--	12.6	265	14.4	249	13.8	262
18	14.9	--	12.2	268	14.1	255	13.8	257
19	12.6	--	12.0	270	13.4	260	13.8	258
20	12.6	--	12.0	270	12.9	263	13.8	263
21	11.6	--	11.5	270	12.4	296	13.6	301
22	11.5	--	11.5	291	12.4	296	13.6	301
23		--	11.5	291				
24								

Table XXV. Profiles of temperature (°C) and specific conductance (K_{25}) at Station 2 during 1964. Conductance expressed as micromhos.

	Cruise 1		Cruise 2		Cruise 3		Cruise 4	
Depth	°C	K_{25}	°C	K_{25}	°C	K_{25}	°C	K_{25}
0	14.2	249	16.5	262	19.0	243	20.1	244
1	14.2	255	16.2	248	19.0	244	20.1	240
2	14.2	255	15.9	250	18.8	243	20.1	246
3	13.3	261	15.0	251	18.5	247	20.1	244
4	12.5	261	14.7	246	17.9	250	20.1	244
5	12.1	264	14.5	254	17.2	258	20.1	244
6	11.9	260	14.5	242	17.2	263	19.6	249
7	11.2	270	14.2	259	16.7	269	19.4	253
8	10.6	259	13.2	240	16.5	251	17.8	259
9	10.7	261	12.5	253	15.0	249	16.2	263
10	10.7	266	11.9	265	13.4	265	15.1	270
11	10.7	274	11.5	246	12.7	270	14.2	274
12	10.1	273	11.5	253	12.2	273	13.4	286
13	10.0	287	11.5	253	11.8	258	12.8	287
14			11.0	266	11.5	273	12.4	275
15			11.0	266	11.5	307	12.0	293
16					11.2	290	12.0	293
17					11.0	291	12.0	296
18					10.5	295	11.5	297
19					10.1	315	11.1	307
20					10.1	315		

Table XXV.(cont.)

	Cruise 5		Cruise 6		Cruise 7		Cruise 8	
Depth	°C	K_{25}	°C	K_{25}	°C	K_{25}	°C	K_{25}
0	22.0	250	21.4	245	21.8	232	20.5	228
1	22.5	248	21.4	254	22.0	231	20.5	230
2	22.2	249	21.4	254	21.9	232	20.5	230
3	22.2	249	21.4	251	21.9	232	20.5	226
4	22.2	249	22.1	241	21.8	231	20.5	230
5	22.2	252	22.1	244	21.8	231	20.5	231
6	22.2	255	22.1	250	21.8	227	20.3	232
7	20.6	231	21.6	244	22.0	226	20.3	230
8	19.6	247	21.3	240	21.2	230	20.0	234
9	17.5	247	20.9	242	20.8	228	20.0	234
10	15.5	254	18.0	255	20.0	231	19.6	236
11	15.0	249	16.5	259	17.2	236	19.0	236
12	14.0	269	15.2	253	15.6	239	18.0	238
13	14.0	269	13.2	267	15.0	240	18.0	238
14					14.0	247		
15					13.9	245		
16					13.2	250		
17					13.1	254		
18					13.0	247		
19					13.0	260		
20					13.0	260		

Table XXV (cont.)

	Cruise 9		Cruise 10		Cruise 11		Cruise 12	
Depth	°C	K_{25}	°C	K_{25}	°C	K_{25}	°C	K_{25}
0	16.0	--	15.7	244	14.7	249	13.9	250
1	16.0	--	15.7	245	14.6	251	13.9	251
2	16.0	--	15.7	244	14.6	249	13.9	251
3	16.0	--	15.7	245	14.5	250	13.9	251
4	16.0	--	15.7	245	14.5	251	13.9	254
5	16.0	--	15.7	245	14.5	250	13.9	251
6	16.0	--	15.7	245	14.5	249	13.8	252
7	16.0	--	15.7	245	14.5	250	13.8	252
8	16.0	--	15.7	245	14.5	250	13.8	252
9	16.0	--	15.7	245	14.5	250	13.8	252
10	16.0	--	15.7	245	14.5	250	13.8	252
11	16.0	--	15.7	248	14.5	253	13.8	252
12	16.0	--	15.5	249	14.5	251	13.8	252
13	16.0	--	15.3	247	14.3	256	13.8	252
14	16.0	--	15.2	248	14.3	259	13.8	252
15	16.0	--	15.2	253	14.3	259	13.7	253
16	16.0	--					13.5	254
17							13.5	254
18							13.5	254
19							13.5	276
20							13.5	276

Table XXVI. Profiles of temperature (°C) and specific conductance (K_{25}) at Station 3 during 1964. Conductance expressed as micromhos.

	Cruise 1		Cruise 2		Cruise 3		Cruise 4	
Depth	°C	K_{25}	°C	K_{25}	°C	K_{25}	°C	K_{25}
0	13.0	240	15.5	252	19.1	265	19.9	248
1	13.0	236	15.5	253	19.1	258	19.9	248
2	12.5	237	15.0	254	18.4	245	19.9	248
3	12.5	230	15.0	248	17.5	255	19.9	248
4	12.5	237	14.9	242	17.5	237	19.9	248
5	12.5	236	14.5	259	17.1	250	19.5	250
6	12.5	236	14.3	255	17.0	264	18.9	256
7	12.5	226	13.5	247	17.0	264	17.5	258
8	12.2	225	12.8	261	15.8	263	16.0	267
9	12.1	227	12.5	253	14.5	258	14.6	274
10	12.0	234	12.2	244	13.7	274	13.9	279
11	11.8	236	12.0	250	13.4	274	13.4	280
12	11.5	242	11.5	251	13.0	282	12.9	283
13	11.2	253	11.5	253	12.2	273	12.5	283
14	10.8	265	11.0	277	11.7	277	12.1	299
15	10.0	276	10.6	280	11.7	286	12.0	293
16	9.5	290	10.6	264	11.0	288	12.0	287
17	9.2	313	10.6	269	10.8	290	11.6	320
18	9.2	306	10.0	300	10.4	306	11.6	328
19	9.0	357	9.5	313	10.1	308	11.6	328
20			9.5	313	10.1	315		

Table XXVI (cont.)

	Cruise 5		Cruise 6		Cruise 7		Cruise 8	
Depth	°C	K_{25}	°C	K_{25}	°C	K_{25}	°C	K_{25}
0	21.5	262	21.7	250	20.9	256	20.0	230
1	21.5	262	21.7	250	21.0	250	20.2	228
2	21.5	265	21.7	253	21.3	257	20.2	231
3	21.1	255	21.7	245	21.4	263	20.2	231
4	21.0	256	21.7	245	21.5	262	20.2	230
5	21.0	265	21.7	236	21.7	261	20.1	232
6	21.0	259	21.7	260	21.7	252	20.0	231
7	20.5	256	21.7	239	21.7	252	20.0	230
8	19.1	244	21.0	242	21.7	252	20.0	228
9	16.5	241	19.8	243	20.7	251	20.0	236
10	15.0	249	16.0	256	19.4	250	20.0	235
11	14.0	256	15.4	252	16.8	252	19.5	237
12	13.5	267	14.1	266	15.2	253	17.6	238
13	13.0	263	13.8	265	14.8	261	15.0	243
14	13.0	263	13.7	258	14.6	262	14.4	246
15	13.0	250	13.2	275	14.5	253	13.5	249
16	12.5	271	13.2	267	13.5	259	13.2	256
17	12.5	266	13.0	263	13.0	265	13.2	251
18	12.5	266	13.0	263	12.9	266	12.2	260
19	12.0	329	12.6	279				
20	12.0	246	12.6	332				

Table XXVI (cont.)

	Cruise 9		Cruise 10		Cruise 11		Cruise 12	
Depth	°C	K_{25}	°C	K_{25}	°C	K_{25}	°C	K_{25}
0	16.0	--	15.5	246	14.6	253	13.6	251
1	16.0	--	15.6	246	14.6	253	13.6	251
2	16.0	--	15.6	245	14.6	253	13.6	254
3	16.0	--	15.6	245	14.6	254	13.6	254
4	16.0	--	15.6	245	14.5	258	13.6	254
5	16.0	--	15.5	246	14.5	258	13.6	254
6	16.0	--	15.5	246	14.5	259	13.6	254
7	16.0	--	15.5	246	14.5	256	13.6	254
8	16.0	--	15.5	246	14.5	250	13.6	254
9	16.0	--	15.5	246	14.3	251	13.6	254
10	16.0	--	15.5	246	14.3	250	13.6	254
11	16.0	--	15.5	246	14.2	252	13.6	254
12	16.0	--	15.4	248	14.2	250	13.6	254
13	16.0	--	15.0	252	14.2	250	13.6	256
14	16.0	--	14.8	251	14.2	250	13.6	255
15	16.0	--	14.4	258	14.2	250	13.6	256
16	16.0	--	14.2	260	14.1	251	13.5	255
17	15.8	--	13.7	260	14.1	269	13.5	255
18	15.6	--	13.7	264	14.1	277	13.5	282
19	15.6	--	13.5	312			13.5	291
20	15.4	--						

Table XXVII. Profiles of temperature (°C) and specific conductance (K_{25}) at Station 4 during 1964. Conductance expressed as micromhos.

	Cruise 1		Cruise 2		Cruise 3		Cruise 4	
Depth	°C	K_{25}	°C	K_{25}	°C	K_{25}	°C	K_{25}
0	14.0	255	16.5	273	18.5	259	20.6	274
1	13.5	254	15.5	262	18.5	255	20.6	274
2	13.0	248	15.0	265	18.2	257	20.6	271
3	12.5	249	15.0	254	18.0	244	20.0	268
4	12.5	249	14.9	254	17.5	255	19.2	251
5	11.5	246	14.7	255	17.1	267	19.0	252
6	11.4	242	14.7	255	16.9	274	18.2	251
7	11.2	242	14.5	257	16.5	256	17.1	235
8	11.2	257	13.5	266	16.1	248	16.5	253
9	11.2	255	13.1	262	15.5	257	16.2	250
10	11.2	257	12.5	263	13.1	285	15.5	257
11	11.2	262	12.1	251	12.7	247	14.9	263
12	11.0	256	11.5	270	12.2	265	13.5	285
13	10.5	272	11.0	274	11.5	268	13.2	287
14	--	280	10.5	281	11.5	270	12.6	292
15	--	280	10.5	281	11.5	273	12.6	288
16							12.6	288

Table XXVII (cont.)

	Cruise 5		Cruise 6		Cruise 7		Cruise 8	
Depth	°C	K_{25}	°C	K_{25}	°C	K_{25}	°C	K_{25}
0	22.0	266	21.5	260	--	--	20.0	236
1	22.0	256	21.5	254	--	--	20.0	234
2	21.0	272	21.5	254	--	--	20.0	234
3	20.5	275	21.5	260	--	--	20.0	234
4	20.5	250	21.5	254	--	--	20.0	234
5	20.5	247	21.5	260	--	--	20.0	236
6	20.5	250	21.0	250	--	--	20.0	236
7	20.0	250	20.5	244	--	--	19.6	238
8	18.5	255	19.4	237	--	--	19.6	238
9	17.5	242	17.7	239	--	--	19.5	239
10	17.0	243	16.9	238	--	--	19.2	236
11	16.0	243	15.5	246	--	--	17.5	230
12	15.4	252	14.5	253	--	--	16.5	236
13	15.0	271	13.6	259	--	--	15.4	242
14	14.5	253	13.6	254	--	--	15.0	240
15	14.0	269	13.6	259	--	--	15.0	245
16	14.0	269			--	--	15.0	249

Table XXVII (cont.)

	Cruise 9		Cruise 10		Cruise 11		Cruise 12	
Depth	°C	K_{25}	°C	K_{25}	°C	K_{25}	°C	K_{25}
0	--	--	15.0	257	14.7	254	13.2	267
1	--	--	15.0	258	14.5	254	13.2	269
2	--	--	15.0	257	14.0	256	13.2	269
3	--	--	15.0	257	14.0	254	13.2	269
4	--	--	14.6	260	14.0	254	13.1	270
5	--	--	14.6	260	14.0	254	13.1	272
6	--	--	14.6	260	14.0	254	13.1	272
7	--	--	14.6	260	14.0	254	13.1	272
8	--	--	14.6	260	14.0	254	13.1	272
9	--	--	14.6	260	13.7	256	13.0	272
10	--	--	14.6	260	13.6	258	13.0	271
11	--	--	14.6	260	13.5	263	13.0	271
12	--	--	14.6	262	13.5	266	13.0	272
13	--	--	14.6	278	13.5	277	13.0	272
14	--	--	14.5	291	13.5	277	13.0	275
15	--	--	14.0	291	13.5	283	13.0	275
16	--	--	14.0					

Table XXVIII. Profiles of temperature (°C) and specific conductance (K_{25}) at Station 5 during 1964. Conductance expressed as micromhos.

	Cruise 1		Cruise 2		Cruise 3		Cruise 4	
Depth	°C	K_{25}	°C	K_{25}	°C	K_{25}	°C	K_{25}
0	16.4	121	18.9	114	21.5	126	21.8	211
1	13.0	131	17.5	117	19.0	134	21.6	204
2	12.8	132	17.0	108	18.5	127	21.6	202
3	12.5	133	17.0	119	17.4	124	21.6	199
4	11.5	137	15.2	165	16.8	239	20.5	176
5	10.2	113	13.1	--	16.0	162	19.7	207
6	9.6	144	12.5	--	15.6	145	18.1	214
7	9.5	144						
8								

Table XXVIII (cont.)

	Cruise 5		Cruise 6		Cruise 7		Cruise 8	
Depth	°C	K_{25}	°C	K_{25}	°C	K_{25}	°C	K_{25}
0	22.5	126	22.5	221	--	--	21.0	222
1	22.5	140	22.5	236	--	--	20.8	223
2	21.6	195	22.5	221	--	--	20.0	166
3	21.5	215	22.5	210	--	--	20.0	166
4	21.5	215	22.5	168	--	--	20.0	171
5	21.2	180	21.5	149	--	--	19.0	--
6	21.0	181	20.5	147	--	--	17.0	--
7			19.4	113	--	--		
8			19.4	113	--	--		

Table XXVIII (cont.)

	Cruise 9		Cruise 10		Cruise 11		Cruise 12	
Depth	°C	K_{25}	°C	K_{25}	°C	K_{25}	°C	K_{25}
0	14.5	--	15.4	242	15.2	226	13.0	245
1	14.5	--	15.1	243	15.2	225	12.9	244
2	14.5	--	14.5	220	14.5	222	12.0	225
3	14.5	--	13.8	206	14.0	220	12.0	200
4	14.5	--	13.8	203	14.0	216	11.9	211
5	14.5	--	13.5	202	13.6	216	11.9	218
6	13.0	--	13.5	199	13.5	209	11.6	223
7			13.5	204	13.5	211	11.6	227
8			13.5	202	13.5	212		

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