THE FERTILIZATION OF GREAT CENTRAL LAKE.
I. EFFECT OF PRIMARY PRODUCTION

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ABSTRACT

Commercial fertilizer was added at a rate of 5 tons per week to a lake (51 km^2, mean depth 200 m) over a period of 5 months from May to October 1970. As a result of these additions, surface primary production was increased approximately tenfold while the primary production of the euphotic zone was doubled. The standing stock of primary producers and water clarity were substantially the same as in the previous year when no fertilizer was added. The productive index (mg C/mg Chl *a*/hr) was increased, especially in the immediate area of nutrient enrichment. However, the principal phytoplankton species were very similar at locations near and distant from the area of fertilization. In conclusion, it appears that as a result of adding nutrients at a low but sustained level, primary productivity was increased without substantially changing the nature of the food chain at the primary level of production.

In the Pacific northwest, an earlier study (Nelson and Edmondson, 1955) on the fertilization of a small salmon-producing lake in Alaska showed that the addition of phosphate and nitrate fertilizer increased the production of sockeye salmon (*Oncorhynchus nerka*); in more recent studies by Donaldson et al. (1968), an increase in the production of steelhead trout (*Salmo gairdneri*) was demonstrated in a small lake in the state of Washington. The natural fertilization of lakes from decomposing salmon carcasses has been discussed by Krokhin (1967), who has suggested that the potential deficit from salmon removed by the fishery should be replaced by artificial fertilization. In the report presented here we have carried out a fertilization experiment which differs from the two previous reports (Nelson and Edmondson, 1955; Donaldson et al., 1968) in several respects. These include the size scale of the experiment which was very much larger than any previous experiments, the application of fertilizer as a solution, control of the N:P ratio, and, finally, sustained weekly nutrient additions over a period of 5 months.

Preliminary results of our experiment have been reported (Parsons et al., in press) together with our conclusion that lake production was increased by the addition of fertilizer and that this was achieved without causing a condition of eutrophication. The following account deals specifically with the effect of nutrient enrichment on the primary level of production. Intensive studies on the effect of nutrient additions were carried out during the period May to August 1970 while a more general monitor program has been maintained from 1969 to the present (March 1971). The first sustained nutrient additions were made during the period June to October 1970 and further additions are planned for the next 5 years.

The primary purpose in this study is to increase levels of production in an oligotrophic lake, but not to change the trophic relationships which lead to the production of young sockeye salmon. In this respect the ultimate desideratum of the experiment is to produce larger sockeye smolts at their time of seaward migration; earlier reports have demonstrated that there is a close positive relationship between smolt size and survival (Ruggles, 1965; Johnson, 1965). Since previous studies (Parsons et al., in press) have shown that the migrant smolts from Great Central Lake are small (63 ± 1 mm) and that the primary productivity is very low (ca. 5 g

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C/m^2/year), application of nutrients at a level that would increase primary and secondary production seemed reasonable.

Data used in this presentation have been obtained from Stephens et al. (1969[3]) and Kennedy et al. (1971[4]).

METHODS

ANALYTICAL PROCEDURES

Chlorophyll *a*, nutrients, oxygen, and total CO_2 were all measured as described previously (Strickland and Parsons, 1968); bacteria were enumerated from plate counts after 24 hr incubation at room temperature on Millipore universal medium; major phytoplankton species were enumerated after settling preserved samples; conductivity was measured using a Beckman Solu Bridge (Cedar Grove, N.J.). Primary productivity was measured as the difference in uptake of $^{14}CO_2$ in light and dark bottles; however, on a few days the dark-bottle uptake was exceptionally high and this requires further investigation. For the purpose of this presentation, data have been used only for days when the dark-bottle uptake was less than 20% of the maximum light-bottle uptake.

Radiation was measured with an Epply pyranometer and corrected to give photosynthetically available radiation (PAR) as described previously (Parsons and Anderson, 1970). Light attenuation was routinely measured with a Secchi disc (SD), and an empirical relationship between SD depth (m) and the vertical extinction coefficient was established using a Schüler meter (maximum response at 430 nm). This relationship for light at 430 nm was:

$$K_{10}^{430} = \frac{2.1}{\text{SD depth}}$$

The (total) extinction coefficient for the water column was then found from Jerlov's (1957) light attenuation curves. Mean radiation (I_m) for the water column of depth (d_m) was determined from the expression

$$I_m = \frac{I_0 \left(1 - e^{-kd_m}\right)}{d_m k}$$

where I_0 was the surface radiation and k was the attenuation coefficient for light below the surface meter. The expression was also used to determine the light at various depths in relation to the photosynthetic activity at those depths.

NUTRIENT ADDITIONS

The choice of a suitable fertilizer for the waters of Great Central Lake has been discussed previously (Parsons et al., in press). The nutrient addition consisted of a commercial grade of ammonium phosphate and ammonium nitrate which contained trace quantities of other elements essential for plant growth. The mixture is known commercially as 27-14-0 (27% N; 14% P_2O_5; 0% K_2O) and has an N:P ratio of 10:1.

The ammonium nitrate and ammonium phosphate were dissolved separately in 5-ton amounts (total) and the concentrated solutions mixed before distribution. A small quantity of organic material was added to the dissolved inorganic fertilizer at a dilution of 6 liters of fish solubles (obtained from B.C. Packers Ltd.) for every 2 tons of nutrient solution. The dissolved fertilizer was distributed at 10 gal/min (38 liters/min) in the wake of a vessel travelling at approximately 8 knots. The area of nutrient additions is shown in Figure 1, together with sampling stations 1, 2, and 3. Station 1 was sampled during 1969 and 1970, Station 2 was sampled during 1970, and Station 3 was sampled sporadically during 1970 in order to check on the flow of nutrients in a westerly direction; in addition, areal surveys for chlorophyll *a*, transparency, and bacteria were carried out over the whole lake in order to determine within-lake variation.

The area over which nutrients were added represented ca. 3 sq mi (8 km^2) of lake surface; however, from studies on lake circulation it was apparent that the material was transported east

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[3] Stephens, K., R. Neuman, and S. Sheehan. 1969. Chemical and physical limnological observations, Babine Lake, British Columbia, 1963 and 1969, and Great Central Lake, British Columbia, 1969. Fish. Res. Board Can., Manuscr. Rep. 1065: 41-52.

[4] Kennedy, O. D., K. Stephens, R. J. LeBrasseur, T. R. Parsons, and M. Takahashi. 1971. Primary and secondary production data for Great Central Lake, B.C., 1970. Fish. Res. Board Can., Manuscr. Rep. 1127. 379p.

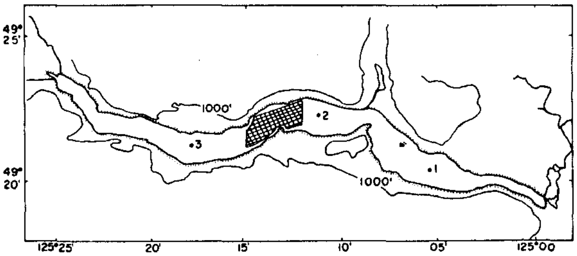

FIGURE 1.—Great Central Lake showing principal sampling stations (1, 2, and 3) and area of nutrient enrichment (crosshatched).

and west at rates of up to 6 miles per day or ca. 10 km/day (Parsons et al., in press). Thus while Station 2 was generally under the most immediate influence of the nutrient additions, Stations 1 and 3 also received an accumulative enrichment. Fertilizer was added at the rate of 5 tons per week from June through to October 1970. During May 1970 approximately 2 tons of fertilizer were added in experiments to determine the rate of mixing and distribution of nutrients in the vessel's wake.

RESULTS

LAKE MORPHOMETRY

Great Central Lake is located on Vancouver Island, B.C., at lat 49°20′ N on an east/west axis between long 125°00′ W and 125°25′ W (Figure 1). It is a long narrow lake (ca. 33 × 1.5 km) with steep sides and a mean depth of 200 m. The yearly mean discharge is approximately 6 × $10^6 m^3$/day with a range from 0.4 × 10^6 to 32 × $10^6 m^3$/day.

TEMPERATURE

The temperature structure at Station 1 is shown in Figure 2. The results are representative for the open waters of the whole lake, and it is apparent that the lake was isothermal during January and February; a thermocline started to form during March and was well established by May. Maximum surface temperature during July was 21.2° C; surface cooling started in September but a thermocline of 10° persisted through October and the lake did not become isothermal until January of the following year.

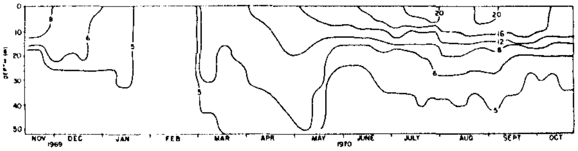

FIGURE 2.—Temperature (°C) stratification at Station 1.

RADIATION

Changes in photosynthetically active radiation (PAR) at the lake surface are shown in Figure 3 together with the mean radiation for the water column 0 to 20 m, calculated on a 24-hr basis.

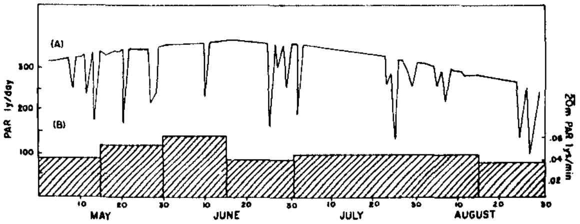

FIGURE 3.—(A) Surface photosynthetically active radiation (PAR) and (B) 15-day mean PAR in the first 20 m.

From the latter results it is apparent that radiation in the water column increased by 50% from the beginning of May until the middle of June; the decrease in radiation during the second part of June was due to a combination of higher extinction coefficients and lower surface radiation. The average radiation remained virtually constant during July and decreased by 20% during the latter half of August.

CHLOROPHYLL *A*

Surface chlorophyll *a* concentrations are presented in Figure 5 in the same way and for the same stations and years as SD data in Figure 4. The two figures have some mirrored similarities;

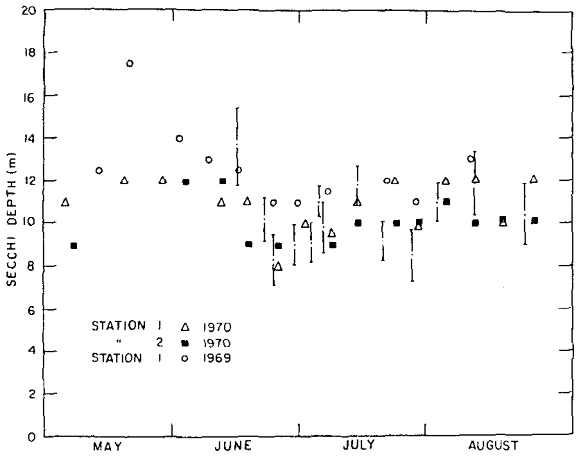

FIGURE 4.—Secchi disc depth at Stations 1 and 2, 1970, and Station 1, 1969. (Mean and standard deviation of values from areal surveys shown as bars.)

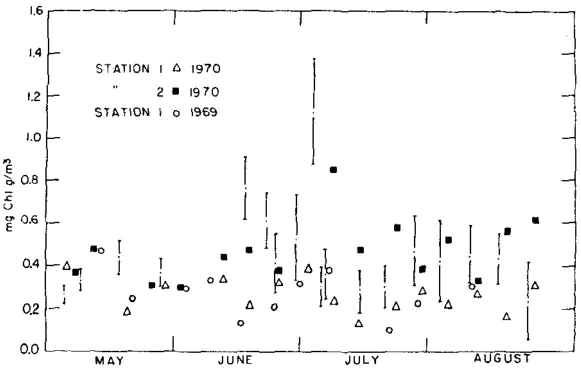

FIGURE 5.—Surface chlorophyll *a* data at Stations 1 and 2, 1970, and Station 1, 1969. (Mean and standard deviation of values from areal surveys shown as bars.)

thus Station 2 chlorophyll *a* values from June to August were generally higher than either Station 1 data for 1969 or 1970; minimum mean SD data (8 to 10 m) occurred between June and July during a maximum in the mean chlorophyll *a* concentration. However, 1969 chlorophyll *a* data at Station 1 do not appear to be significantly different from 1970 chlorophyll *a* data at the same station.

The depth distribution of chlorophyll *a* generally showed a maximum between 10 and 20 m following stratification and nutrient depletion in the surface layers.

pH, CALCIUM, TOTAL CO_2, AND CONDUCTIVITY

pH values were generally between 7.1 and 8.3 with some indication of a seasonal cycle towards higher pH values in summer. Several assays for calcium showed a concentration of 5 mg/liter while specific conductivity was very consistent at 33 μ mhos/cm, except in the immediate vicinity of small streams entering the lake; total carbon dioxide varied over a range from about 2.2 to 4.2 mg C/liter.

OXYGEN

Oxygen profiles to 200 m showed that surface oxygen concentrations were between 80 and 90% saturation during winter and up to 110% saturation during summer. Deepwater oxygen concentrations appeared constant at around 10 mg/liter or about 80% saturation. An oxygen maximum occurred at ca. 20 m during the summer.

NITRATE, AMMONIA, PHOSPHATE, AND SILICATE

Nitrate depth profiles at Station 1 during May to October, 1969 and 1970, are shown in Figure 6. The general form of the two profiles is similar; thus a depletion in the winter level of nitrate (1.0 to 2.0 μg at./liter) becomes apparent towards the end of May and by the end of June about 1 μg at. NO_3N/liter has been removed from the water column, 0 to 10 m. During July and August nitrate in the first 10 to 15 m is close to the limit of detection, but there is a partial return to winter levels during September and October. Some difference in the form of these events is apparent between 1969 and 1970; the utilization of nitrate was more rapid and apparently more complete during 1970; in addition, surface nitrates did not increase in September-October 1970 as they did in 1969.

Starting from a winter level of 2 μg at. NO_3-N/liter, the total utilization of nitrate in the water column has been determined for the periods February to May, June, and July-August using data shown in Figure 7. The accumulative amount

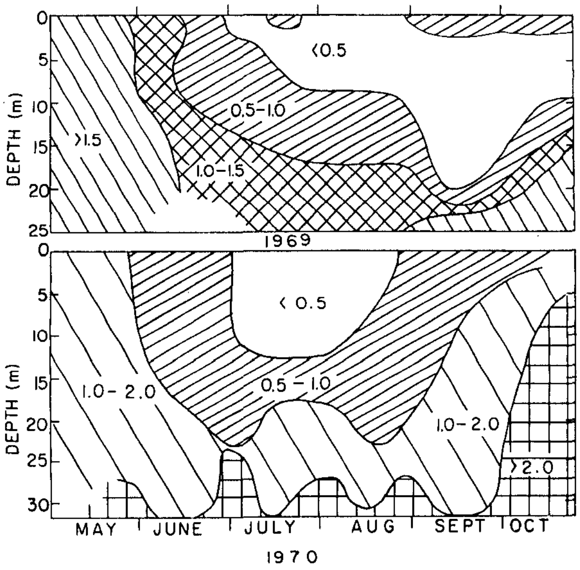

FIGURE 6.—Nitrate (μg at./liter) profiles at Station 1, May to October 1969 and 1970.

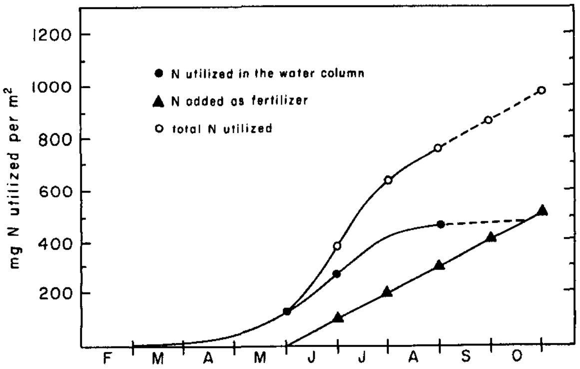

FIGURE 7.—N utilization at Station 1.

of inorganic nitrogen added as fertilizer (expressed per m² for the entire 51 km² lake surface) is also shown; since this was utilized within hours following each addition, the total nitrogen budget is represented as the sum of the natural and added inorganic nitrogen. Some mixing occurred during September and October, and the utilization of inorganic N during this period is shown as an indefinite extrapolation of the nitrogen utilized by the end of August. From these curves and Figure 5 it may be seen that the fertilizer was the principal source of new nitrogen during the period July-August when the lake nitrate was practically exhausted in the euphotic zone.

Ammonia values tended to show sporadic increases during 1970, and at times ammonia may have been the principal inorganic form of nitrogen in the lake, probably through being recycled as excretory products of the zooplankton (Beers, 1962). However, due to analytical difficulties with this radical, further investigation of its seasonal behavior is required, especially with reference to the verification of high values. Phosphate showed similar variations to nitrate although the depletion of phosphate was less regular. Seasonal concentrations ranged from <0.01 to 0.04 μg at. P/liter with about 3% of the values falling in a much higher range of 0.1 to 0.6 μg at./liter. A determination of phosphate utilized and phosphate added (similar to the inorganic N budget shown in Figure 7) was difficult to describe because of the unpredictable occurrence of phosphate throughout the summer; this may have been due to phosphate regeneration. As an overall assessment, however, if a winter level of 0.03 μg at. P/liter were completely utilized in the water column 0 to 30 m, the addition of 100 tons of 27-14-0 would increase the supply of phosphate over the whole lake by a factor of about 450% compared with the increase in the inorganic nitrogen budget of approximately 100% (Figure 7).

From winter to summer, silicate concentrations ranged from about 1.8 to 3.0 mg silica/liter. According to Lund (1965) silicate becomes rate limiting for diatoms at about 0.5 mg/liter, which is considerably lower than the seasonal range for Great Central Lake.

BACTERIA

Plate counts of bacterial colonies per 100 ml are shown in Figure 8, together with the range of counts obtained on several days when areal surveys were made. During May, the total number of colonies per 100 ml was generally below the mean value of ca. 9,000 reported by Henrici (1940) for oligotrophic lakes; however, there is

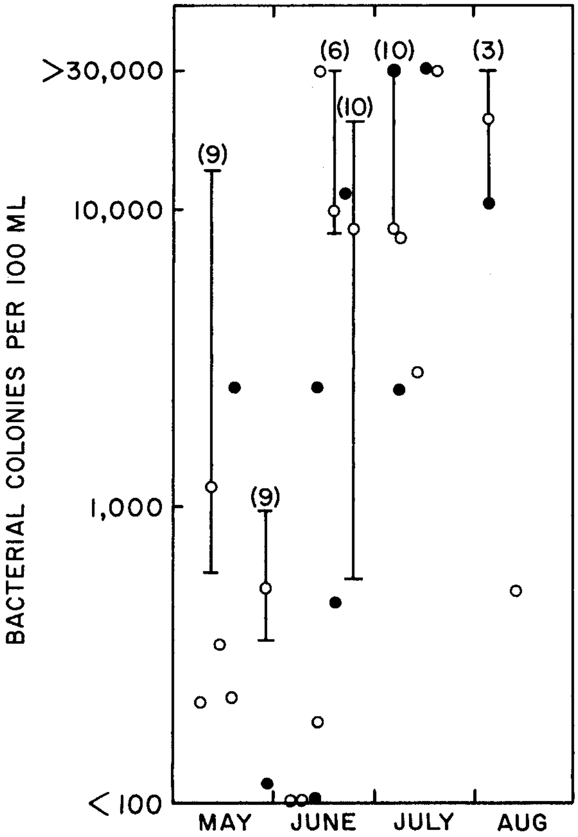

FIGURE 8.—Bacterial colonies per 100 ml surface lake water (○) Station 2; (●) Station 1; (5) number of samples in areal survey and range, I.

some indication in the data that bacterial numbers increased by one or two orders of magnitude during the latter part of June through to August. Summer increases in bacterial flora have been widely observed in lakes (e.g., Snow and Fred, 1926; Nauwerck, 1963), and while nutrient level could have affected this increase (e.g., see Bosset, 1965), we have no previous data on which to judge the effect.

PHYTOPLANKTON SPECIES

Principal phytoplankton species from surface samples at Station 1 and 2 during 1970 are shown in Figure 9 on a relative scale. From these results it is apparent that the predominant algae during May and early June were *Dinobryon, Rhizosolenia,* and *Nitzschia.* During June and July *Gymnodinium, Cyclotella,* and the euglenoid *Phacus* reached maximum numbers but tended to decline by August. Predominant algae of late summer and autumn were the chlorophyte *Nannochloris* and the cyanophyte *Chroococcus.* Second maxima in *Dinobryon, Rhizosolenia,* and *Cyclotella* occurred during the winter together with a maximum in *Tabellaria.*

Two studies (May and June) on the depth distribution of the principal species showed that maxima in *Rhizosolenia, Tabellaria,* and *Phacus* were found at the bottom of the thermocline (ca. 20 m); *Cyclotella* and *Gymnodinium* maxima occurred at the top of the thermocline (ca. 10 m) while *Nannochloris, Dinobryon, Nitzschia,* and *Chroococcus* showed maxima within the top 0 to 10 m.

PRIMARY PRODUCTION

Surface primary production values at Station 1 during 1969 and 1970 and at Station 2 during 1970 are shown in Figure 10; the mean and coefficient of variation of surface primary production for the months of June to August are also shown on each figure. The total average primary production in the water column 0 to 30 m at Stations 1 and 2 during 1970 was approximately 12 g C/m^2/year compared with approximately 6 g C/m^2/year at Station 1 during 1969.

Primary production per unit of chlorophyll *a* at different depths for Station 1, 1969 and 1970, and Station 2, 1970, are shown plotted against the light intensity at the same depths in Figure 11. A considerable amount of scatter is apparent in the data which is partly due to differences in environmental factors as well as to the lack of precision in attempting to establish photosynthesis versus light intensity relationships on the basis of ecological rather than experimental data. Polynomial curves were fitted to each set of data using an IBM computer. The shape of these curves is consistent with *P* vs. *I* relationships obtained by physiologists under experimental laboratory conditions and differences in asymptotic values reflect differences in the nutrient supply (Ichimura and Aruga, 1964).

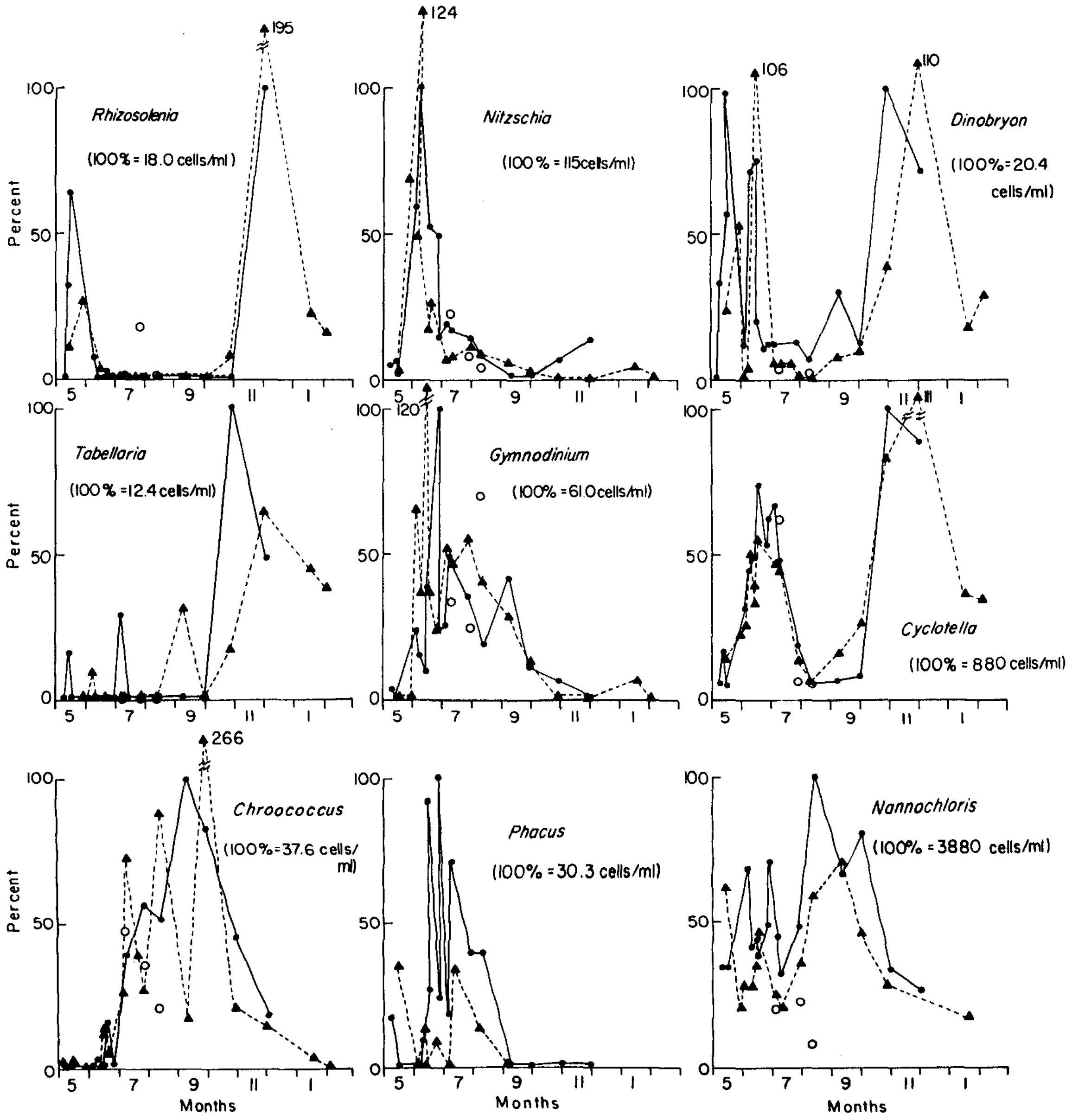

FIGURE 9.—Principal phytoplankton species at Station 1 (●), Station 2 (▲), Station 3 (○) during 1970.

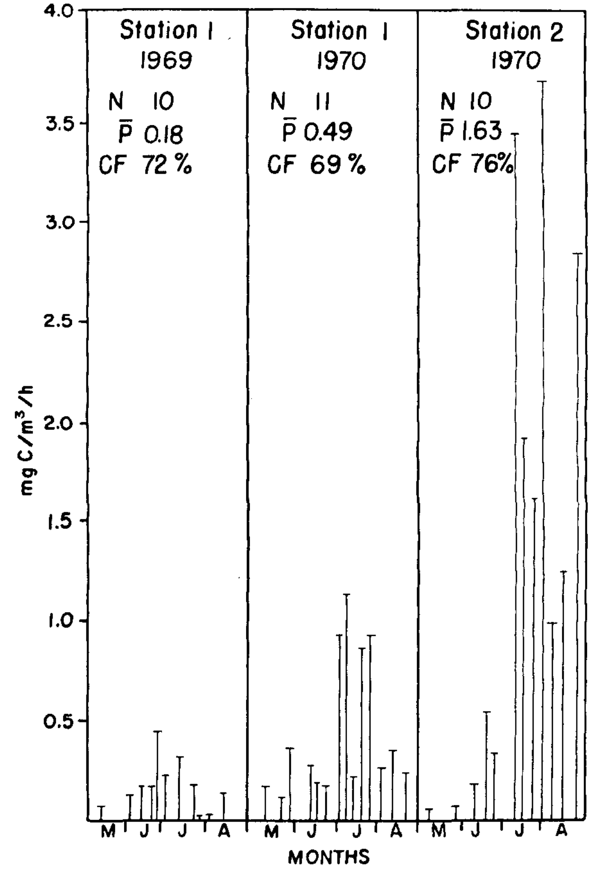

FIGURE 10.—Surface primary production, May to August. (N = number of samples, $\bar{P}$ = mean surface production, and CF = coefficient of variation—all values for the period, June to August.)

However the degree of scatter in the ecological data requires some expression of confidence limits. At Station 1 (1969), which was located at a considerable distance from the area of fertilization, 95% confidence limits for the asymptotic value of 1.03 mg C/mg Chl *a*/hr were 0.84 and 1.22; for 1970 at the same station the 95% confidence limits for the asymptotic value of 1.55

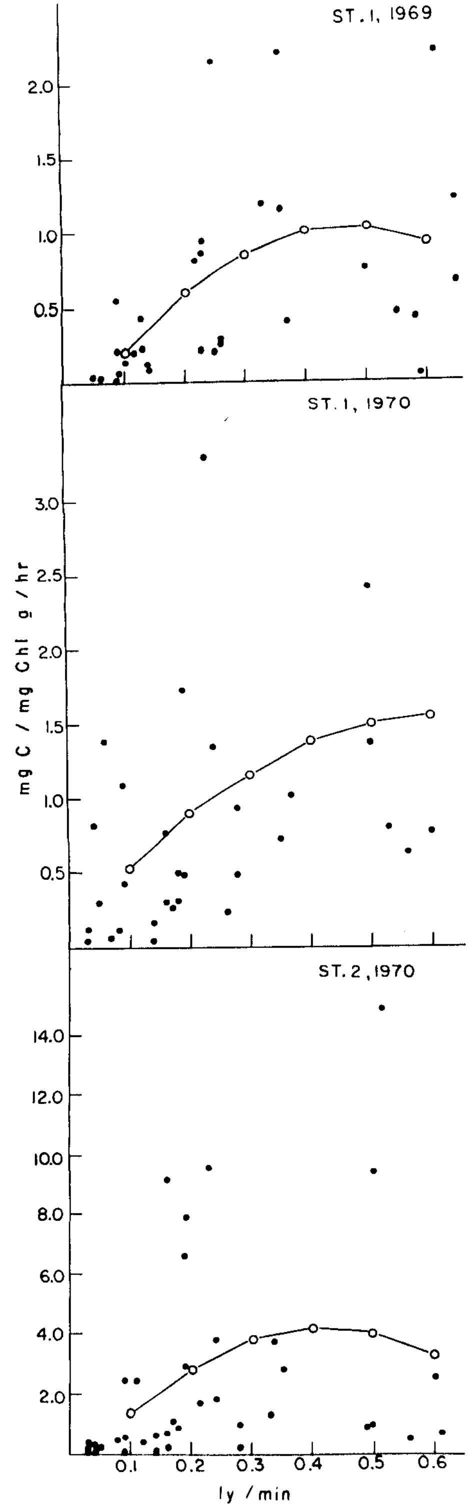

FIGURE 11.—Productivity indices plotted against light intensity at Station 1, 1969 and 1970, and Station 2, 1970 (○——○ computed best fitting polynomial curve).

mg C/mg Chl *a*/hr were 1.12 and 1.98. At Station 2 in 1970, however, the scatter of points is so great that 95% confidence limits become very large. The probable reason for this is that the station was sometimes in the area to which nutrients were first added, and sometimes the movement of water containing freshly added nutrients was away from Station 2 (Figure 1). If in fact it is assumed that there were only two alternatives in such a narrow lake (i.e., movement of nutrients towards or away from Station 2) then the 50% confidence limits for the asymptotic value of 4.17 mg C/mg Chl *a*/hr were 2.26 and 6.07.

DISCUSSION

The principal purpose of this report is to establish the effect of inorganic nutrient enrichment on the primary production of Great Central Lake. From data in Figure 10 it is quite apparent that primary productivity was increased in surface samples during 1970 compared with 1969, both at Station 1 and particularly at Station 2, which was very close to the area of repeated enrichment. However, while the effect of nutrient enrichment was apparent to the extent of a tenfold increase in surface primary productivity, the integrated productivity for the water column only showed an approximate doubling in primary productivity during the first 3 months of nutrient enrichment (see Parsons et al., in press, for primary production depth profiles). This result is in keeping with the fact that the total inorganic nitrogen addition to the lake (Figure 7) was only sufficient to approximately double the natural reservoir of inorganic nitrogen in the upper 10 m, based on winter nitrate levels. However, it does not take into account nitrogen fixation by the blue-green alga, *Chroococcus*, which may have taken arvantage of the increased supply of phosphate to become one of the predominant summer plankters.

The question is, whether some factor other than fertilization could have accounted for the increased primary productivity? Firstly, it is apparent that since the largest increase in primary productivity occurred at the surface, it cannot be argued that the increased primary productivity was due to greater enrichment of the water column from the hypolimnion, especially in view of the high degree of stratification (Figure 3) and apparent nitrate depletion in the epilimnion (Figure 6). It might be argued that the increased productivity was due to an increase in standing stock of primary producers and increased radiation. Data in Figure 5 indicate that the standing stock of primary producers at Station 2 was generally higher than at Station 1 during 1969, although the effect is within a 95% probability of being due to within-lake variations in standing stock of chlorophyll *a*. However, in order to examine this question in more detail, primary productivity data for Stations 1 and 2 in 1970 and Station 1 in 1969 have been expressed as the production per unit chlorophyll *a* and plotted against the calculated light intensity at various depths (Figure 11). This presentation of data has been used by Ichimura and Aruga (1964) to compare the productivity of oligotrophic, mesotrophic, and eutrophic lakes under conditions of different standing stocks of primary producers, light conditions, and photosynthesis. From their findings it was concluded that oligotrophic lakes had a productive index of between 0.1 and 1.0 mg C/mg Chl *a*/hr, which is very similar to the range of values computed from the data in Figure 11 for Station 1 during 1969. The computed range for Station 1 during 1970 was appreciably higher, however, and enters the classification for mesotrophic lakes which have a photosynthetic index of up to 2 mg C/mg Chl *a*/hr; finally the asymptotic value (4.17) from Station 2 in 1970 is within Ichimura's and Aruga's (1964) range for eutrophic lakes, which the authors report as having photosynthetic indices of up to 6 mg C/mg Chl *a*/hr. Since the only basis for this classification is the effect of nutrient enrichment in enhancing the photosynthetic response, it may be concluded that our observed increase in primary productivity was determined by the artificial addition of fertilizer.

Secondary effects of nutrient enrichment may also have influenced the primary formation of particulate material through a heterotrophic cycle. Unfortunately, our evidence for this is not substantial and rests mainly on the increase in bacterial numbers (Figure 8) and the fact that very high dark uptake of ^{14}C-bicarbonate (up to 50% of the light bottle uptake) were encountered during the summer at some stations following fertilization. We are at present not sure of the accuracy of this result, however, and it will be reinvestigated during 1971. Nauwerck (1963) has concluded that the heterotrophic formation of particulate material is a principal mechanism for supplying food to particle feeders in some lakes and one might expect this mechanism to be enhanced by the additional availability of nitrogen and phosphorus.

The most interesting aspect of changes in the species composition of the principal primary producers is that in spite of differences in surface primary productivity at Stations 1 and 2 during 1970 (Figure 10) the relative abundance of principal species at these two stations (and on several occasions at Station 3) was substantially the same (Figure 9). This was important because it was intended that there should be no change in the species composition of organisms leading up the food chain to young salmon, but only an increase in their productivity. In addition, the occurrence of the *Cyclotella-Chroococcus* association is characteristic of oligotrophic lakes (Hutchinson, 1967) which indicates that the general classification of the lake (based on species association) had not been changed by fertilization. However, some eutrophic species of phytoplankton, such as *Ceratium, Peridinium,* and *Scenedesmus*, were also observed as minor constituents of the plankton, especially during the summer.

In conclusion, it appears that the fertilization of Great Central Lake resulted in an increased primary production but did not substantially change the standing stock of primary producers, water clarity, or the principal phytoplankton species at locations near and distant from the site of nutrient enrichment. The effect of zooplankton on the primary producers was essentially to suppress the increase in standing stock of phytoplankton while the standing stock of zooplankton itself increased by almost an order of magnitude. Zooplankton growth and distribution are described in the second paper in this series (LeBrasseur and Kennedy, 1972).

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