Hydrobiologia vol. 45, 1, pag. 45—63, 1974

Phytoplankton Productivity in Findley Lake

by

GEORGE R. HENDREY* & EUGENE B. WELCH**

ABSTRACT

Findley Lake is a dimictic, oligotrophic, subalpine lake located in the western Cascade Mountains, Washington. The lake is snow covered for most of the year so that the growing season was 3.5 months in 1971 and 4.5 months in 1972. Rapid melt of the lake's snow cover in summer allowed the sudden development of a phytoplankton productivity maximum (as measured by the ^{14}C tracer method) of 86 mg m^{-2} hr^{-1} and a peak of 48 mg chlorophyll *a* per m^1 within two weeks of surface clearing in 1972, followed by a rapid decline of productivity and biomass. Annual production (between 10 October, 1971 and 21 October, 1972) was 36 g/m^2 in the 27.5 m water column. Autotrophic carbon assimilation during the snow-covered period was insignificant. The total production for the lake in 1972 was 530 kg carbon.

The concentration of available nitrogen (NO_2 + NO_3 + NH_3 as N) at 15 m ranged from 12 to 76 mg/m^3 while PO_4-P ranged from 0.5 to 8.3 mg/m^3. *In vitro* nutrient enrichment experiments with natural phytoplankton communities from the lake indicated that while N and P together were growth limiting, P alone produced a growth response while N alone did not.

Contributions to production from net-, nanno-, and ultraplankton were determined by fractional filtration of ^{14}C-labeled phytoplankton samples. The nannoplankton, dominated by diatoms, accounted for 58% to 94% of productivity.

INTRODUCTION

Artificial eutrophication of lakes, causing increased plant growth, appears to have been the invariable outcome of man's settlement or development of any lake drainage basin. The recently acquired public awareness of this situation has led to an increased interest in predicting the results of watershed development on lake ecosystems. In order to obtain a better understanding of ecosystem interactions and improve the accuracy of predicting effects of eutrophication, detailed models of ecosystems are being prepared. It is hoped that

* Current address: Norwegian Institute for Water Research Blindern, Oslo 3, Norway.

** Department of Civil Engineering University of Washington, Seattle.

these models will become useful tools to assist in the management of our natural resources.

A comprehensive, integrated study of the interactions between aquatic and terrestrial components within a unit watershed of the Coniferous Forest Biome is being carried out under the auspices of the International Biological Program at Findley Lake, Washington. In order to obtain realistic estimates of parameters to be used in modeling the watershed, detailed descriptions of the system's components must be made. This investigation has been concerned with the primary production of the phytoplankton in Findley Lake and the relationship between production, nutrient concentration, and light availability.

Findley lake environment

Findley Lake is a subalpine cirque lake located in the western Casdace Mountains, 18 km southwest of Snoqualmie Pass. The watershed basin was carved by glaciation at least 15,000 years ago, and has an area of 2.6 km². Surrounding ridge crests attain elevations of over 1447 m, so the cirque walls are rather steep, with several prominent talus slopes and avalanche scars. The lake surface is 9.02 ha (Wolcott, 1965) and the maximum depth is 27.5 m. The lake has two relatively deep basins (Figs. 1 and 2). One is adjacent to a meadow, with a depth of 15 m; the other with a depth of 27.5 m, is a continuation of a talus slope beneath cliffs on the western side of the lake. The average depth of the lake is 7.3 m. There are numerous temporary inflow streams from snowmelt on the hillsides around the lake, while the outlet is through a single stream, Findley Creek, at the northwest corner.

The nearest high-elevation meteorological station is located at Stampede Pass (elevation 1196 m). Here the mean annual tempera-

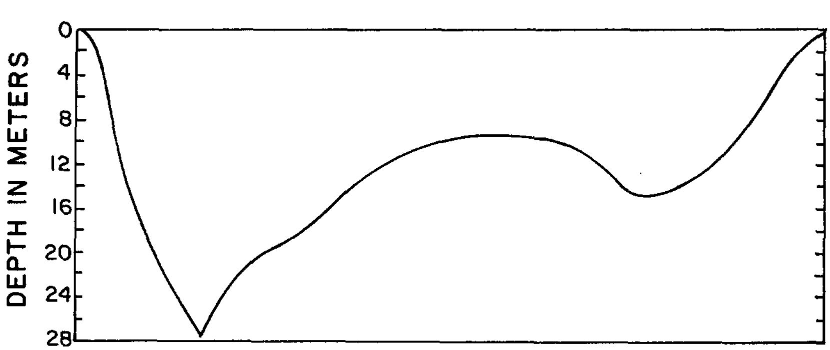

Fig. 1. An east-west cross section of Findley Lake showing the bottom profile.

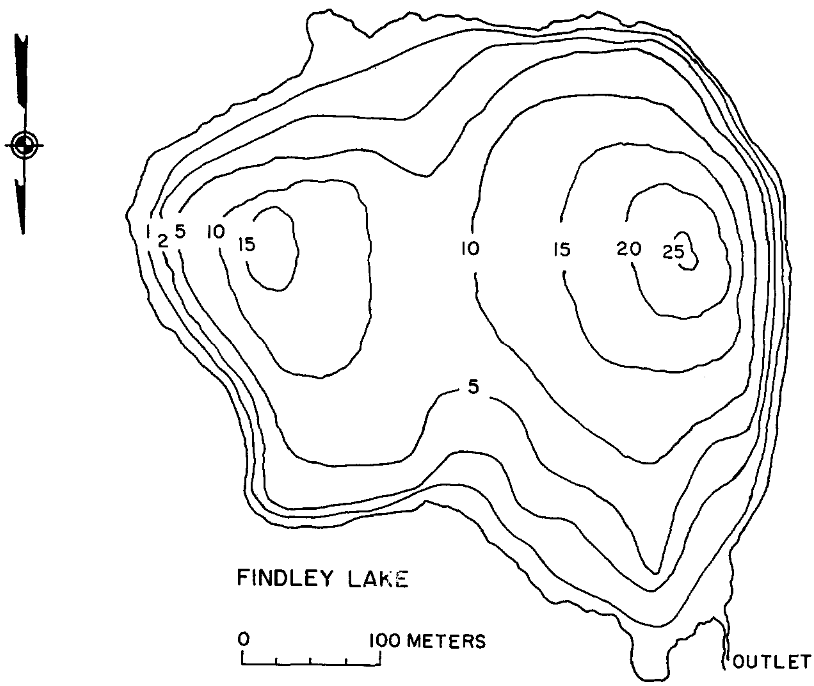

Fig. 2. Topography of Findley Lake with depth in meters. (Courtesy of PAUL R. OLSEN).

ture is 3.4°C with January the coldest month and July the warmest. Mean precipitation is 234 cm. In the winters of 1971 and 1972, record-breaking snow accumulations occurred in the Cascades. At Findley Lake the maximum snow accumulation in 1972 was approximately 4 m. The Findley cirque opens to the north so that the ridge crests around the rest of the lake cause considerable shading in the early morning and late afternoon, and for most of the day in the winter.

METHODS

Primary productivity of phytoplankton was determined by the ^{14}C carbon assimilation method described by STRICKLAND & PARSONS (1968). Two light bottles and a dark bottle (Pyrex, 125 ml volume) were suspended from a chain at 5 m intervals through the water column to 25 m. Each bottle received a measured 100 ml of lake water from each incubation depth and was inoculated with 0.5 ml of a solution of $NaH_2{}^{14}CO_3$ with a specific activity of 22.25 μCi/ml, or 11.02 μCi per bottle. After an incubation period of 3 to 4 hours, the bottles were recovered and injected with 1 ml of acid Lugol's solution to halt cellular activity. Upon their return to the laboratory the bottles were treated in one of two ways. Either the entire contents of the bottle were filtered with a single filter of 0.45 μ nominal porosity (Millipore HA) or the contents were poured through a series of three filters (Fig. 3) to separate the phyto-

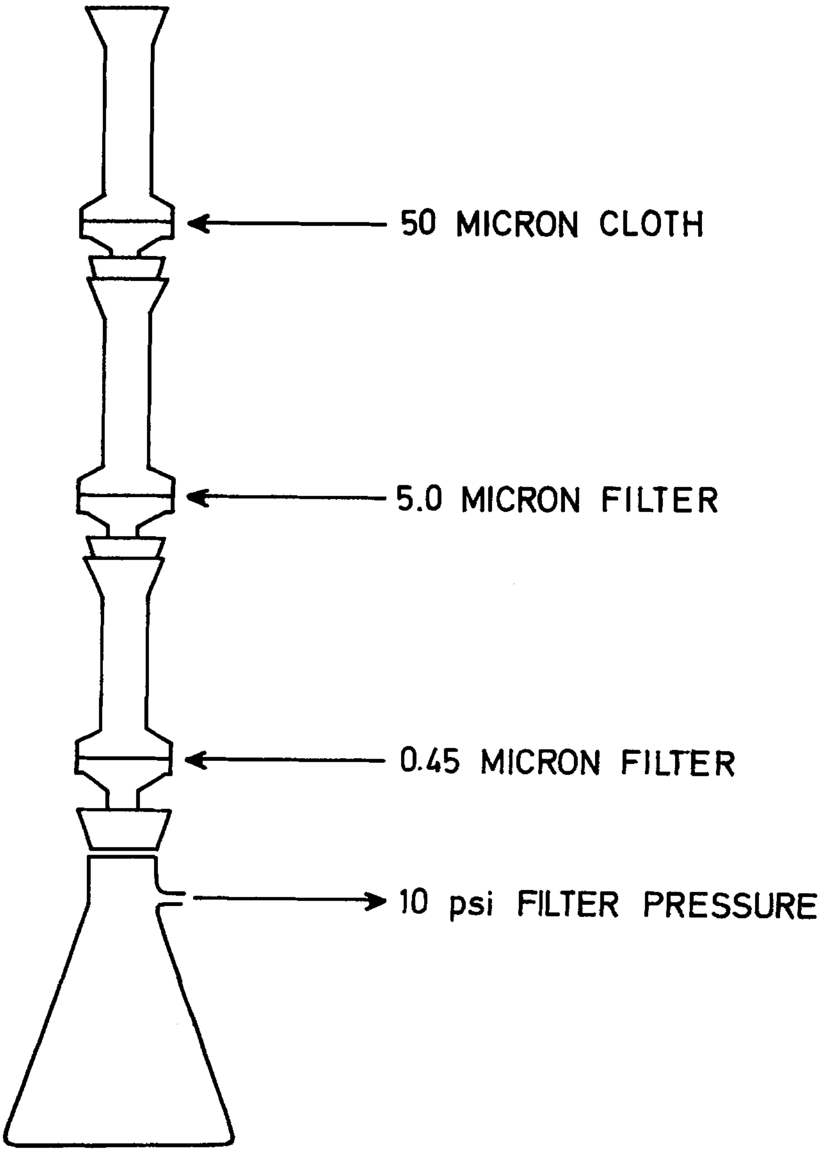

Fig. 3. Arrangement of 25-mm-diameter filters and filter holders for the fractional filtration of phytoplankton samples.

plankton into three size classes. The top filter was made by punching a 2.5 cm circle from 50 μ Nitex netting. The second was a 5.0 μ nominal porosity Millipore filter, and the third was a 0.45 μ nominal porosity Millipore filter. The filters were washed with 10 ml of distilled water, glued to planchettes, and stored in a desiccator for up to 25 days. Radioactivity was determined with a thin-window, gas-flow beta counter.

Total available stable inorganic carbon, the pool from which the tracer ^{14}C measures carbon uptake by plants, was determined from pH and alkalinity measured within half an hour of sampling. Correction for temperature was included by recalculation of the carbonate system dissociation constants using a nonlinear best fit regression equation obtained for data published in STUMM & MORGAN (1970).

Chlorophyll *a* was measured by the fluorometric technique of STRICKLAND & PARSONS (1968). A 100- or 200 ml volume of lake water was filtered through a 0.45 μ Millipore filter or through the stack of 3 filters as previously described. The sample was then desiccated for three days after which the chlorophyll *a* was extracted in 90% acetone. A Turner Model 110 fluorometer was used to measure the fluorescence of the extract.

Insolation was determined at the University of Washington campus with an integrating Epply pyrheliometer. It is recognized that the distance between the campus and the research site (93 km) resulted in inaccuracies when applied to the lake. On several occasions, however, insolation measurements were made at the lake with a portable pyrheliometer. The values observed ranged from +9% to —11% of those obtained over the same time interval at the campus. The weather during the periods of measurement ranged from clear and sunny, through broken clouds, to rainy. Thus the use of values obtained at the campus seems accurate to about 10%.

Samples were collected in acid-washed polyethylene plastic bottles. Samples for ortho-phosphorus, nitrate plus nitrite-nitrogen, and reactive silicate analyses were filtered through an 0.45 μ membrane filter and then frozen prior to analysis. Samples for ammonia-nitrogen analysis were fixed with a 2% solution of mercu-

TABLE I

Methods used for nutrient analysis

Ortho-P	phosphomolybdate
Total-P	persulfate digestion, phosphomolybdate
NO_3-NO_2-N	cadmium-copper reduction column, diazotization
NH_3-N	phenol-hypochlorite
SiO_3-Si	silicomolybdate- oxalic acid

ric chloride at the time of sampling. Table I summarizes the methods used for nutrient analysis. Samples collected after September 1972 and all those for ammonia were analysed with a Technicon Auto-analyzer. Nutrient content reported in this paper are weighted means for the 25 m water column.

Results and discussion

Findley Lake is dimictic with pronounced thermal stratification in summer and in winter (Fig. 4). On 24 July, 1971, approximately 2 m of slushy snow was still floating on the surface of the lake. By 10 August the lake was completely snow free and had a surface temperature of 20°C. The lake remained open until mid-November when snow began to accumulate on top of a thin layer of ice. The maximum snow accumulation observed was 3.5 m on 20 March 1972. When a hole was drilled through the snow, it was found that there was no ice supporting the snow. The upper meter of snow was dry and rather well compacted, while just below this was a 2 cm layer of hard-frozen snow marking the top of the zone of water penetration. Below this frozen layer the snow was saturated with water although the large ice crystals were still densely packed. Apparently the surface ice never attained a thickness of more than a

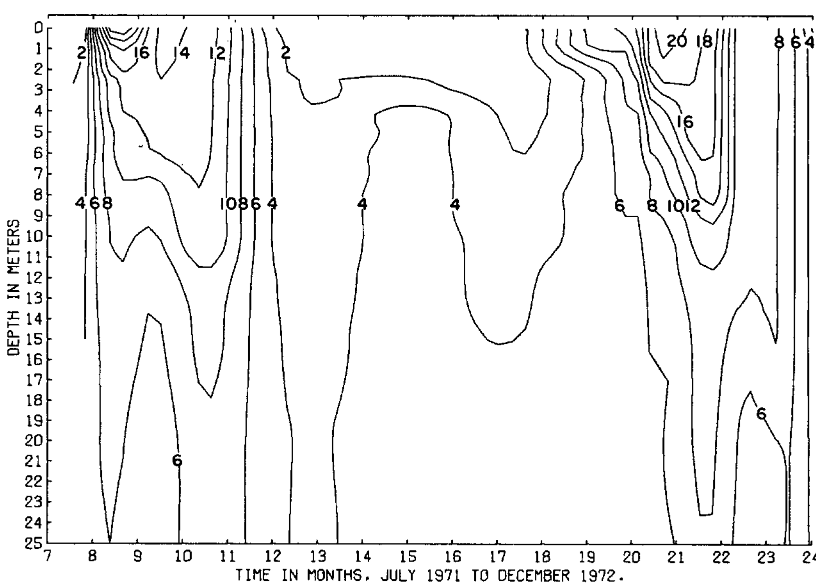

Fig. 4. Temperature contour in Findley Lake, 1971/1972, in intervals of 2°C.

few centimeters, and when this was insulated from the cold air by a blanket of snow, the residual heat in the lake melted away the ice.

On 7 June, 2 m of snow remained on the lake, and by 7 July the lake was completely open again with a surface temperature of 11.0°C. A complete turnover and restratification occurred in the space of a few weeks. The lake was well stratified in the summers; the maximum depth of the epilimnion occurred at approximately 10 m in 1971 and 8 m in 1972. Refreezing occurred on 17 November 1972, which marked the termination of this portion of the Findley Lake study.

Complete occlusion of light from the lake because of the snow cover prevented phytoplankton production. A submarine photometer was used to measure the light penetration through the snow and into the lake in mid-winter. Only a slight deflection of the indicator needle was apparent immediately below the floating snow.

Growing Season

The most striking feature of the phytoplankton productivity was the peak observed immediately following the clearing of snow from the lake surface. Figure 5 indicates the patterns of the phytoplankton productivity, chlorophyll concentration, and the ratio of carbon assimilated to chl. *a* (x 20 for scale) throughout the study

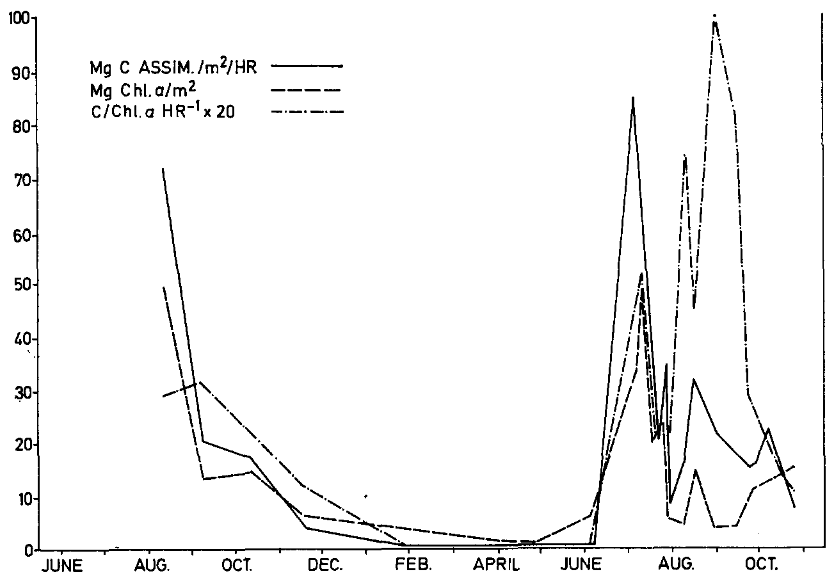

Fig. 5. Hourly phytoplankton productivity, chlorophyll *a*, and productivity/chl. *a* ratio observed in Findley Lake, 1971/1972.

period. The maximum values of productivity on 10 August 1971 and 7 July 1972, both taken just after the clearing of snow from the surface, were 72, and 86 mg m^{-2} hr^{-1}, respectively. Both of these peaks were followed by rapid declines in the rates of productivity. Chlorophyll *a*, attained peak levels of 51 mg/m^2 on 10 August 1971 and 48 mg/m^2 on 11 July 1972. The simultaneous occurrence of both the observed maximum biomass and productivity levels in 1971 implies that the actual maximum productivity was not observed; maximum productivity probably occurred earlier, closer to the date of clearing. Biomass accumulation usually follows increased productivity as was observed in 1972. Productivity and biomass obtained some lesser peaks during the remainder of the growing season. As snow began to accumulate on the surface of the lake in November and insolation decreased, productivity became insignificant. Thus the growing season is restricted to the period of open water, which was 3.5 months in 1971 and 4.5 months in 1972.

Autotrophic Capacity

The autotrophic capacity is often used to classify a lake as to its trophic type and to make comparisons between lakes. VOLLENWEIDER (1970) suggests that the annual autotrophic production per unit area be used to standardize data for comparisons. A value for carbon assimilation obtained in an incubation period of a few hours is converted to daily production for this purpose. The following equation may be used for this transformation:

$$C_d = (I_d/I_p)C_p \qquad (1)$$

where C_d = productivity per unit area per day, I_d = insolation in langleys for the entire day, I_p = insolation in langleys for the incubation period, and C_p = productivity during the incubation period.

Plotting the daily productivity values, as in Fig. 6, allows the calculation of annual production by integration of the area under the curve with a polar planimeter. This was done for the period 10 October 1971 to 21 October 1972, in Findley Lake, and an annual production of 36 g carbon per m^2 was obtained for the 25 m water column. A productivity rate of 50 g m^{-2} yr^{-1} has been considered the upper limit for oligotrophic lakes (VOLLENWEIDER, 1970). This productivity value cannot be applied to the lake as a whole since only at the deepest part of the lake is the light level diminished to 1% of the surface intensity.

The relationship between productivity and nutrient concentration in Findley Lake, compare Fig. 5 to Fig. 7, is not entirely clear. First of all the orthophosphorus concentration is quite low and at times approaches the lower detection limit of the analytical method.

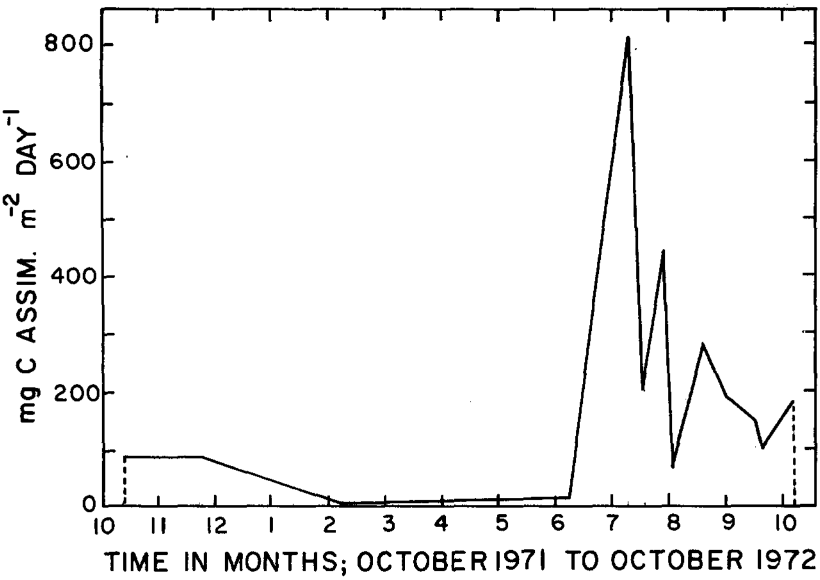

Fig. 6. Daily phytoplankton productivity rates in Findley Lake 1971/1972 integrated over the 25-m water columns and plotted over the year. The units are mg C m-[2] day-[1] versus months.

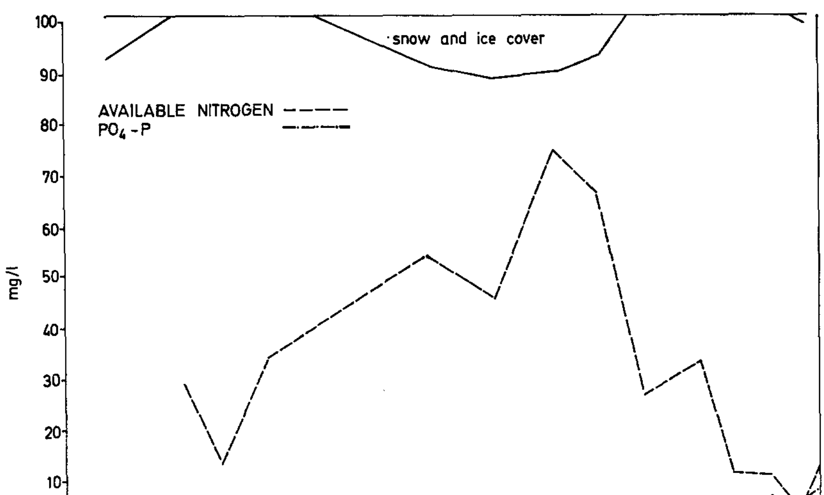

Fig. 7. Weighted mean concentrations of Ortho-P and available N ($NO_3 + NO_2 + NH_3$) in Findley Lake, 1971/1972, in milligrams per cubic meter.

Variations in the concentration are not great over the year, however, the weighted means ranging from 0.5 mg/m^3 to 8.3 mg/m^3, as P. Nitrogen concentration, on the other hand, fluctuates considerably over the year (Fig. 7). Following the decline in productivity and toward the end of the growing season in 1971, the weighted mean concentration of available nitrogen, obtained by summing the concentrations of NO_3, NO_2, and NH_3 forms of nitrogen, began to increase. From the minimum level of 12 mg N/m^3 in September, the concentration climbed more or less steadily to a peak at 76 mg/m^3 in late March of 1972. The breaking up of the summer stratification in the fall and consequent mixing is probably responsible for the increased N concentration at that time. Diminishing daily insolation plus the increasing snow cover in November contribute to the reduction of the nitrogen loss rate by removal through plant growth, while heterotrophic organisms remineralize organic forms of the nutrients through the winter. The nitrogen concentration declined rapidly as the major outburst of growth occurred following snow clearing of the lake surface and continued to decline as the growing season progressed in 1972.

In vitro batch culture tests to determine the limiting nutrient were carried out on the natural phytoplankton in water obtained from the lake on 30 August 1972. The results of these experiments indicated that nitrogen and phosphorus were most limiting to phytoplankton growth. The addition of P alone, however, *did* bring about a stimulation of growth, although much less than N and P together, while the addition of N alone had no effect. Since P was at all times rather low in concentration (maximum of 5 mg/m^3) and its addition caused a measurable increase in growth, and since N alone did not produce a measurable growth response, it appears that the supply rate of P (and perhaps of N at times) is controlling the growth of the phytoplankton during the latter part of the growth season. The occurrence of a low and rather constant level of P at the same time that the concentration of N is sharply declining suggests that the turnover rate for P is much greater than of N.

Light Inhibition

The variation in productivity with depth is illustrated in Fig. 8 and Table II. Data for this plot were obtained by averaging the productivities at each 5 m interval over the growing season. Generally, a peak occurs near the 15 m depth. Theoretically, the depth of maximum productivity should coincide with the depth at which light saturation occurs. RODHE (1965) found this to lie between 30 and 70% of the incident radiation, as a general rule. But the light intensity at 15 m, as can be seen from Fig. 9, is only about 10% of

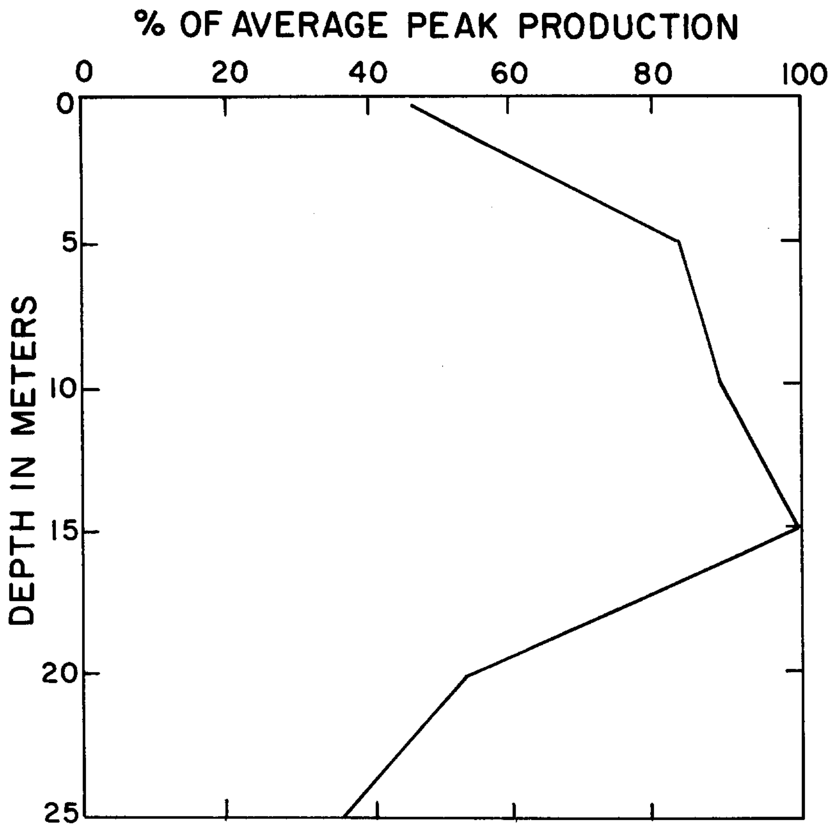

Fig. 8. Phytoplankton production values (in milligrams per cubic meter per hour) at each incubation depth in Findley Lake are averaged over the period 7 July to 21 October 1972. Each average is then plotted as a percentage of the peak value, which occurred at 15 m.

TABLE II

Phytoplankton production rates for the 1972 growing season. Maximum observed production rates and the averages of the production rates observed at each depth are listed in columns 2 and 3 (in milligrams per cubic meter per hour). The percentage of production relative to the 15-m maximum is given for the seasonal averages in column 4.

Depth (m)	Max. C assim.	Av. C assim.	C assim. at 15 m (%)
0	2.24	0.65	46
5	4.51	1.19	84
10	5.12	1.27	90
15	5.93	1.42	100
20	2.36	0.82	58
25	0.96	0.51	36

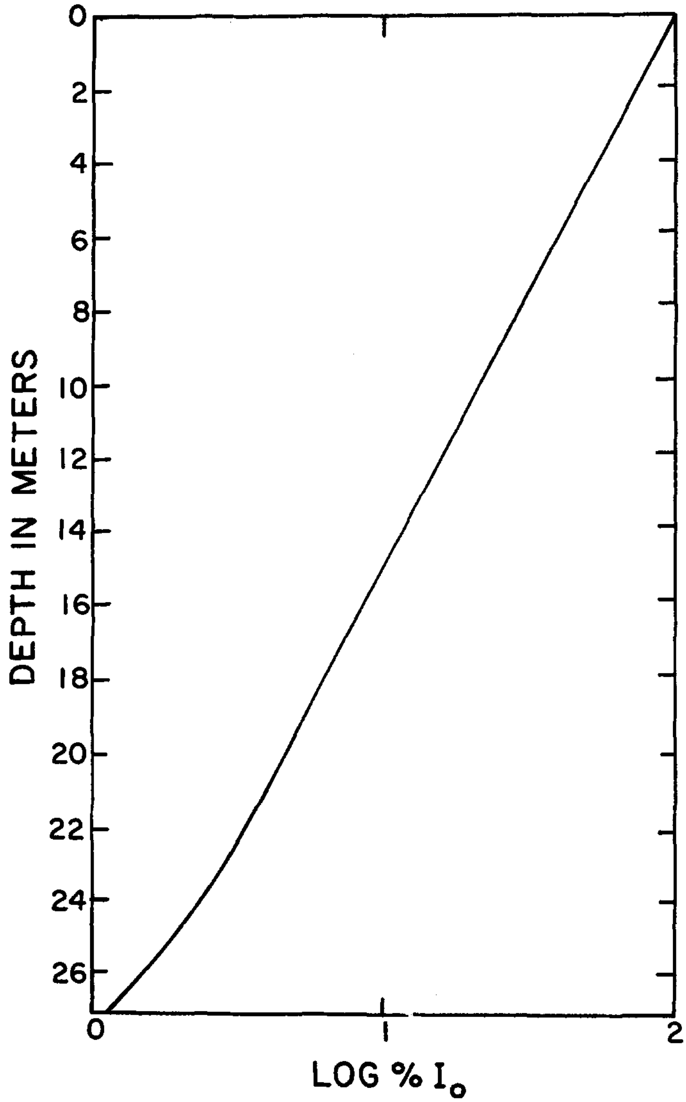

Fig. 9. Light penetration in Findley Lake, 21 October 1972. Log_{10} of the percentages of surface insolation observed through the water column are plotted against depth.

the surface intensity. The occurrence of productivity peaks deep in the water column and at such relatively low light levels is characteristic of many clear mountain lakes (Rodhe et al., 1966; Larson, 1972). Numerous authors have noted the phenomenon of surface inhibition of primary productivity (Talling, 1955) which is attributed to supraoptimal light intensities at all wave lengths. But it is believed that this inhibition deep in the water column is caused by the transmission of ultraviolet wavelengths to greater depths than in less transparent lakes and by the greater intensity of the ultraviolet component of the insolation as altitude increases. Penetration of the near ultraviolet light, 300 to 400 mμ, deep into oligotrophic lakes has been confirmed by measurement (ELSTER, 1965; RODHE et al., 1966), and its inhibitory effect on phytoplankton productivity has been demonstrated (STEEMANN NIELSEN, 1964).

That the deep productivity maximum is not caused by some factor such as temperature or nutrient depletion is seen from the occurrence of a productivity maximum at the surface on 15 August 1972. The relatively high value of 2.24 mg C assimilated m^{-3} hr^{-1} was considerably greater than any other observed surface value. This was a very dark, overcast day with intermittent rain. It appears that the diminution of inhibitory light by diffusion and absorption in the cloud cover allowed the phytoplankton to grow at a rapid rate in the surface waters.

This circumstantial evidence indicates that the occurrence of a production peak deep in the water column may be correlated not so much to the saturation of the photosynthetic processes with light of optimal wavelengths as it is to removal of inhibitory UV wavelengths by absorption in the overlying water.

With this inhibition in mind, phytoplankton production for the whole lake was determined. First, annual production at each depth was obtained planimetrically from plots of the daily productivity values; next, the volumes of the lake at the depth intervals indicated in Table III were obtained, using the planimetric areas from Fig. 2;

TABLE III

Findley Lake, Total production for the growing season, 7 July 1972 to 21 Aug. 1972.

a Incubation depth (m)	b Incubation zone limit (m)	c Zone thickness (m)	d Contour area* at c, x $10^3 m^2$	e Volume c x d (m^3 x 10^3)	f mg C/m^3**	Kg C e x f
0	0 — 3.5	3.5	72.00	252.0	629	158.5
5	3.5— 7.5	4.0	54.56	218.2	906	197.7
10	7.5—12.5	5.0	24.06	120.5	908	109.2
15	12.5—17.5	5.0	9.96	49.8	1031	51.3
20	17.5—22.5	5.0	3.32	16.6	727	12.1
25	22.5—27.5	5.0	0.43	2.1	550	1.2
		Total production for the 1972 growing season =				530.0 Kg

* Contour area is obtained for each zone center from Figure 2.
** The production at each incubation depth is integrated over the growing season.

then these two quanitities were multiplied for total production at each depth interval and the products were summed to obtain the total annual production of 530 kg per year for the entire lake.

From Fig. 9 it can be seen that the entire lake is shallower than the depth of 1% light intensity, and therefore is in the euphotic zone. Planimetric measurements of Fig. 2 indicate that approximately 90% of the lake volume lies above the 12.5 m depth contour and therefore may be subject to some degree of inhibitory radiation on sunny days. If the areal productivity of the 27 m water column had been applied to the total lake surface, annual production would have been over estimated by a factor of 6.

Phytoplankton Genera

Samples for phytoplankton analysis were collected from the depth of maximum productivity on several dates of interest. Counting of these organisms was made difficult by population densities of a few hundred cells per milliliter, with some samples as low as 10 cells per milliliter. Samples were centrifuged and the contents were concentrated by a factor of 100, and the relative abundance of the principle genera was determined using a 1 cm Palmer-Maloney counting chamber at 400X.

All of the samples contained small, irregularly shaped cells that appeared to belong to the Chlorophyceae. It was difficult to distinguish between these cells and detritus in preserved samples.

TABLE IV

Dominant genera of phytoplankton in Findley Lake observed at the depth of maximum production, exclusive of small green alga of 1—3 μm diameter.

Date	Genera	Relative Abundance (%)
10 October 1971	*Cyclotella*	100
18 November 1971	*Cyclotella*	100
7 June 1972	*Cyclotella*	33
	Melosira	33
	Gymnodinium	33
7 July 1972	*Trachelomonas*	67
	Gymnodinium	33
29 August 1972	*Cyclotella*	70
	Oocystis	15
	Gloeocystis	15
21 October 1972	*Gloeocystis*	25
	Cyclotella	25
	Oocystis	25
	Melosira	25

Their numbers increased severalfold during the growing seasons of both 1971 and 1972, however. Table 4 lists the relative abundance of genera, exclusive of the small cells described above, and Table V lists the genera identified so far in Findley Lake.

TABLE V

Genera of the various algal divisions found in Findley Lake. (Excluded from this list is a small cell of 1 to 3 µm diameter and tentatively assigned to the Clorophyta, and an observation of Oscillatoriacea).

Chlorophyceae	Bacillareophyceae	Dinophyceae
Kirchneriella	*Cyclotella*	*Gymnodinium*
Schroederia	*Navicula*	*Desmomastix*
Gloeocystis	*Cymbella*	*Massartia*
Tetraedron	*Melosira*	
Oocystis	*Gomphonema*	
Cosmarium	*Diatoma*	Euglenophyceae
Sphaerocystis	*Nitzschia*	
Treubaria	*Coconeis*	*Trachelomonas*
Mxyophyceae	Chrysophyceae	Chryptophyceae
Microcystis	*Chrysosphaerella*	*Chroomonas*
Aphanocapsa	*Synura*	
	Dinobryon	

Net-, Nanno-, and Ultraplankton

The ecological significance of cell size has been of considerable interest both in the marine environment and in freshwaters. A correspondence between the degree of eutrophy of an aquatic environment and the portion of total productivity contributed by cells of a particular size class has often been observed (RILEY, 1957; GOLDMAN & WETZEL, 1963; RODHE, et al., 1966; GLIWICZ, 1967; MALONE, 1971). The relationship is such that as eutrophy increases so does cell size.

Various terms have been used to describe particular size fractions of the phytoplankton community. These include net-, nanno-, micro-, and ultraplankton. For the purposes of this research, three size classes were defined. The term netplankton is taken to mean those cells that were retained on a net of 50 µ nominal porosity. Nannoplankton refers to cells that passed through the 50 µ net but were retained on a membrane filter of 5.0 µ nominal porosity. The ultraplankton were those cells that passed through the previous two filters but were retained by a membrane filter of 0.45 µ nominal porosity.

These size class definitions may differ from those given by other authors. For example, microplankton was defined by LUND (1961) as plankton less than 15 µ in size. GOLDMAN & WETZEL (1963) set

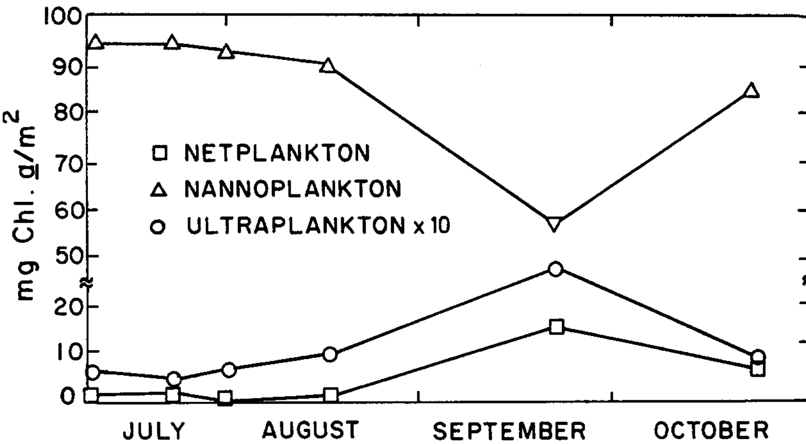

Fig. 10. Chlorophyll *a* content of three size classes of the phytoplankton community in Findley Lake (1972), expressed as percentages of the whole community chlorophyll *a* concentration.

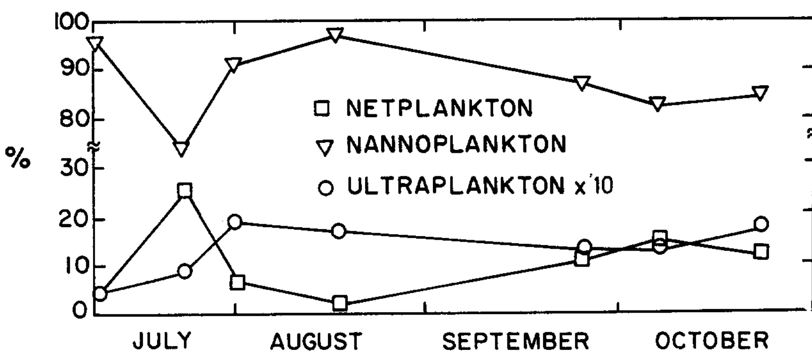

Fig. 11. Carbon assimilation of three size classes of the phytoplankton community in Findley Lake (1972), expressed as percentages of the whole community carbon assimilation.

ultraplankton at less than 5—15 μ. These size classes are no more than functional size groupings based on the laboratory procedures used to separate the plankton community. Functional definitions of this sort do not mean that the sizes of the phytoplankton are limited to exactly the 50-, 5-, and 0.45 μ dimensions. Some long, slender diatoms of more than 50 μ in length sneak into the nannoplankton category while others of the same species are retained by the 50 μ net. A second problem is that the membrane filters do not necessarily pass particles of the nominal pore size. The Millipore 5.0 μ membrane filter can be expected to retain some particles of less than 1 μ diameter (Sheldon, 1972).

Figure 10 is a plot of the fraction of phytoplankton biomass in each of the three size classes during the 1972 growing season as determined by chlorophyll *a* concentrations. The nannoplankton portion varied from 58% to 94% of the whole community, with ultraplankton more important than netplankton in the remainder.

Figure 11 indicates the relative contributions of the three size classes to total phytoplankton productivity during the 1972 growing season. The nannoplankton accounted for from 74% to 95% of all production, with ultraplankton slightly more important than netplankton in accounting for the remainder.

It is interesting to note that the net- and ultraplankton increased in both percentage of contribution to the whole and in actual concentration of chlorophyll *a* as the season progressed. Conversely, the nannoplankton chlorophyll *a* undergoes a rapid decrease following the initial bloom. The increasing contribution from the netplankton appears to be due to an increase in the chain lengths of centric diatoms, primarily *Cyclotella* and *Melosira*, which may have been previously included in the nannoplankton when their chain lengths were shorter. There was an increase in relative abundance of very small chlorophyceae (1—3 μ), as noted above, which probably accounts for the increased importance of the nannoplankton over the growing season.

Interpretation

Just after surface clearing, when the nutrient supply is relatively high, the phytoplankton community grew rapidly until the excess nutrient supply was consumed. At this point the growth rate became regulated by the nutrient supply rate. Under these rate limited conditions a continual shift toward greater efficiency of resource utilization by the community occurred. This is indicated by the productivity per chlorophyll *a* ratio in Fig. 5. It is interesting to note that this specific productivity of the phytoplankton community became greater following the decline of the productivity peak.

There are two mechanisms by which the phytoplankton community could accomplish such an efficiency shift: physiological adjustment within the cells, and species succession when physiological change is no longer possible. A shift in the species composition toward smaller cell size was noted in plankton samples.

If natural conditions were static, as in a chemostat, the optimum efficiency could be maintained. But the nutrient supply, and probably its rate of renewal were diminishing at this time in Findley Lake. The rate of change in environmental conditions exceeded the capacity of the community to adapt to the new conditions and specific productivity declined.

References

Elster, H. J. - 1965 - Absolute and relative assimilation rates in relation to phytoplankton populations. *Mem. Ist. Ital. Idrobiol.*, 18 suppl.: 79—103.

Gliwitz, Z. M. - 1967 - The contribution of nannoplankton in pelagial primary production in some lakes with varying trophy. *Bull. Acad. Pol. Sci. Cl. II.*, 15(6).

Goldman, C. R. & Wetzel, R. G. - 1963 - A study of the primary productivity of Clear Lake, Lake County, California. *Ecology* 44(2): 281—294.

Larson, D. W. - 1972 - Temperature transparency and phytolankton productivity in Crater Lake, Oregon. *Limnol. Oceanogr.* 17(3): 410—417.

Lund, J. W. G. - 1961 - The periodicity of μ-algae in three English lakes. *Verh. Int. Verein. Limnol.* 14: 147—154.

Malone, T. C. - 1971 - The relative importance of nannoplankton and netplankton as primary producers in tropical oceanic and neritic phytoplankton communities. *Limnol. Oceanogr.* 16(4): 633—639.

Riley, G. A. - 1957 - Phytoplankton of the north central Sargasso Sea 1950—1952. *Limnol. Oceanogr.* 2: 252—270.

Rodhe, W. - 1965 - Standard correlations between pelagic photosynthesis and light. Mem. Ist. Ital. Idrobiol., 18 suppl.: 365—381.

Rodhe, W., Hobbie, J. E. & Wright, R. T. - 1966 - Phototrophy and heterotrophy in high mountain lakes. *Verh. Int. Verein. Limnol.* 16: 302—312.

Sheldon, R. W. - 1972 - Size separation of marine seston by membrane and glass fiber filters. *Limnol. Oceanogr.* 17(3): 494—498.

Steemann Nielsen, E. - 1964 - On a complication in marine productivity work due to the influence of ultraviolet light. *J. Cons. Perm. Int. Explor. Mer.* 29: 130—135.

Strickland, J. D. H. & Parsons, T. A. - 1968 - A Practical Handbook of Seawater Analysis. *Fish. Res. Board Can., Bull.* 167. 311 p.

Stumm, W. & Morgan, J. J. - 1970 - Aquatic Chemistry. New York, Wiley-Interscience. 583 p.

Talling, J. F. - 1955 - Photosynthetic characteristics of some freshwater plankton diatoms in relation to underwater radiation. *New Phytol.* 56: 29—50.

Vollenweider, R. A. - 1970 - Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. Organization for Economic Cooperation and Development, Paris.

Wolcott, E. E. - 1965 - Lakes of Washington Vol. 1, Western Washington. 2nd ed. Wash. State Dept. Conserv., Div. Water Resour., Olympia.