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With 21 figures and 3 tables in the text

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I. Productivity

Primary productivity studies in Lake Tahoe, California

CHARLES R. GOLDMAN and RICHARD ARMSTRONG

With 21 figures and 3 tables in the text

Lake Tahoe, California-Nevada, is among the clearest alpine lakes in the world and has long been esteemed for its scenic beauty. During the last few decades there has been a sizable increase of the human population in its watershed and the first signs of accelerating eutrophication of this extremely oligotrophic lake are now discernible. The most visible evidence of the increase in the lake's fertility has been the great increase in littoral zone periphyton largely composed of the diatom *Gomphonema constrictum* v. *capitatum* and the fungus *Apostemidium guernisacl.* The periphyton growth is the subject of a separate study. The primary productivity of the lake has been studied intermittently since 1958 (GOLDMAN & CARTER 1965), and areal variation in productivity was first documented by two synoptic cruises in 1962. The following study has been designed to investigate the major sources of enrichment and to work out with greater precision the areal variability in the productivity of the lake as influenced by tributary streams. Evidence is presented for a general increase in fertility over the past nine years. By directing the investigation toward determining what factors are most important in causing higher rates of production in certain areas of the lake, we should be able to evaluate the role of eutrophicating nutrients in the lake as a whole and determine how the process might most effectively be slowed.

Considerable evidence has accumulated for the importance of nitrogen as a limiting factor for phytoplankton growth in the lake. Nitrogen limitation has been investigated through a series of bioassay experiments utilizing the lake's natural phytoplankton population, with stream water as well as preparations of inorganic nitrogen used as a nutrient additive.

To further investigate the dispersion of stream borne nutrients in the lake and their influence on primary productivity, a series of productivity measurements were made at the mouths of streams. In each of these experiments twenty-odd stations were arranged along a transect extending from the mouth of the stream to a depth of 85 meters.

Methods

Primary productivity was measured with the ^{14}C method (STEEMANN-NIELSEN, 1951) as modified by GOLDMAN (1963). All calibrations were done in terms of absolute activity as determined by gas-phase analyses to eliminate serious errors associated with counting (GOLDMAN 1968). Cultures of the lake water's natural phytoplankton population were incubated in an incubator with rotating shelves under 5000 lux. In addition to incubation, in situ productivity samples from the transect runs were incubated for four hours in the same constant temperature and light incubator. Incubation temperature was that of the surface lake water temperature. Calcium, magnesium, sodium and potassium were determined by atomic absorption spectrophotometry. Ultraviolet absorbance was measured with a Beckman DBG spectrophotometer. Nitrate determinations were made with the cadmium reduction method of STRICKLAND & PARSONS (1965). Ammonia determinations were made by STRICKLAND & PARSONS' hypochlorite method (1965).

Results

Primary productivity in Lake Tahoe was measured in situ on a weekly basis during 1967—68 at an index station near Homewood, California. Fig. 1 shows the location of the index station as well as other locations where productivity measurements were made. Examination of the productivity data from various stations indicates that the index station provides a good average productivity value for the

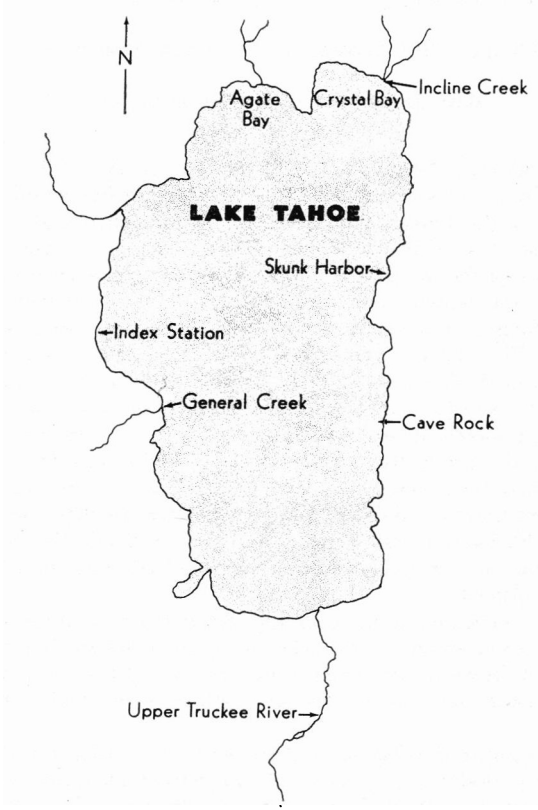

Fig. 1. Lake Tahoe, California-Nevada. All locations mentioned in the text are indicated on this map.

lake. Ten measurements at other stations were at least 10 % lower than the index station, eight measurements were more than 10 % higher, while nine measurements were within 10 % of the index station values.

The degree of areal variability at Tahoe from August through November 1967 is indicated in Fig. 2. During this period the primary productivity at the index station varied from 110 to 238 mg $C \cdot m^{-2} \cdot day^{-1}$ calculated on the basis of integration of in situ measurements to 90 m depth. Since the productivity measurements at the other five stations were made under somewhat different light conditions than at the index station, the best comparison can be made by calculating their relative photosynthetic efficiencies and by comparing them with the photosynthetic efficiency measured at the index station which is taken as the standard

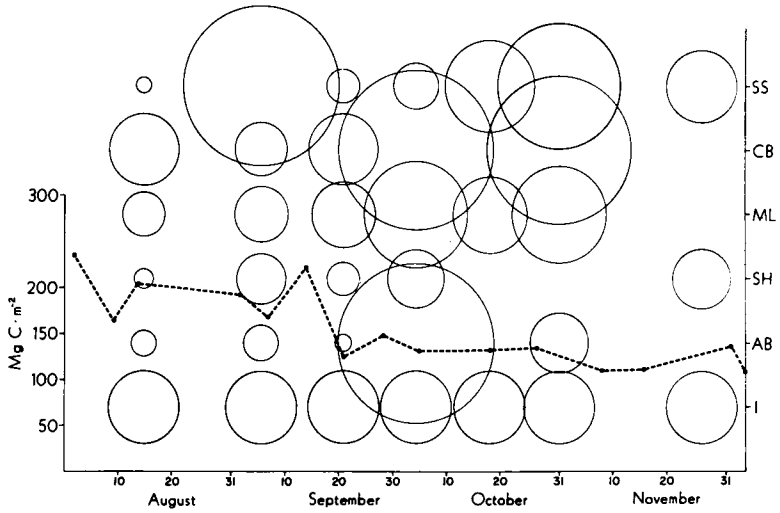

Fig. 2. 1967 productivity measurements made at the Index Station (dashed line). Productivity was calculated by integrating the results of four-hour in situ measurements throughout the photic zone (0—90 m). Circles superimposed on the productivity curve indicate the photosynthetic efficiency at other stations relative to the index station.

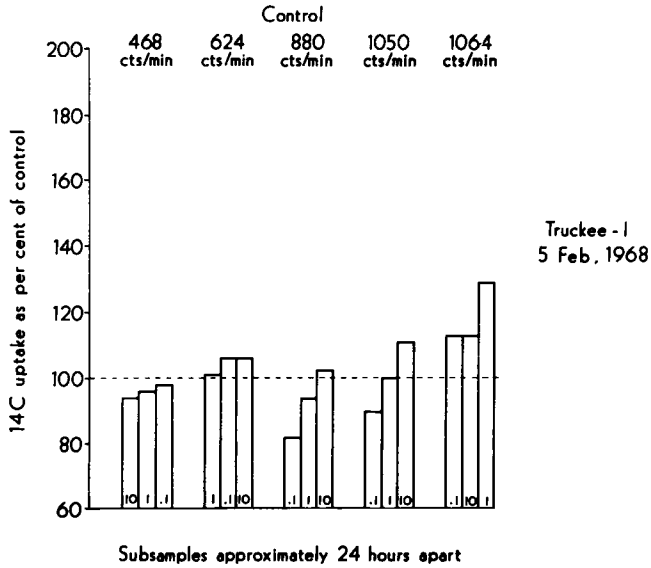

Fig. 3. Bioassay of Upper Truckee River water. The river water was collected on 5 February 1968 and added to pelagic lake water in different proportions (0.0 %, 0.1 %, 1.0 % and 10.0 %). Phytoplankton growth as estimated by ^{14}C uptake is shown for the different treatments over a five-day period. Experimental results are given as a percentage of the control in each case. Absolute growth of the cultures is indicated by the increasing radioactivity of the control. The small differences between experimentals and controls do not appear to be significant.

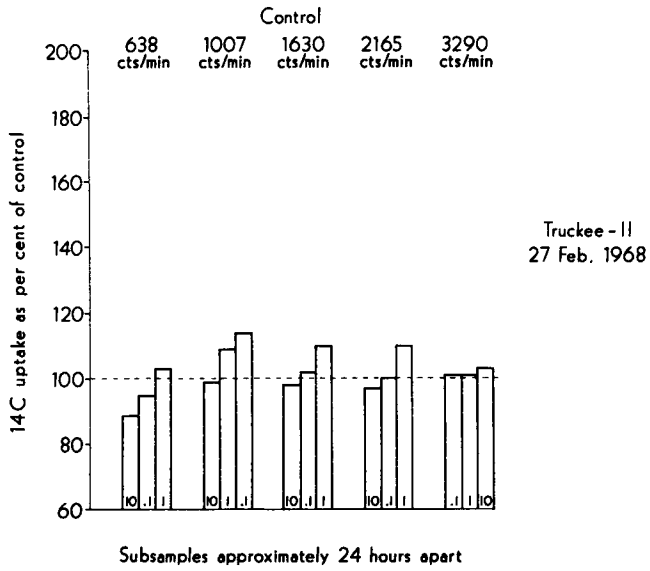

Fig. 4. Bioassay of Upper Truckee River water collected on 27 February 1968. There appeared to be no stimulation of the lake's phytoplankton by the addition of river water.

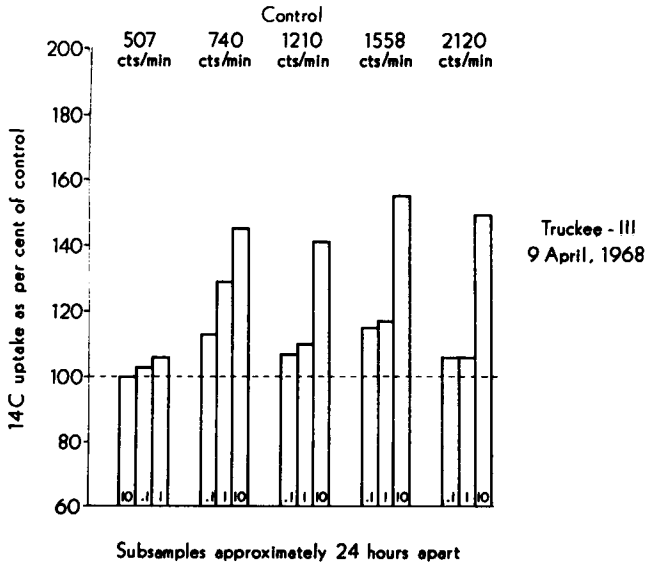

Fig. 5. Bioassay of Upper Truckee River water collected on 9 April 1968. The stimulatory effect of a 10 % addition of river water is particulary well marked.

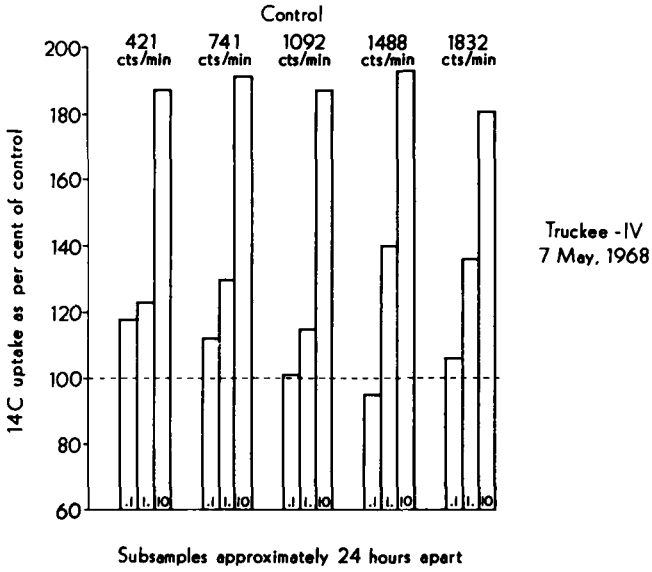

Fig. 6. Bioassay of Upper Truckee River water collected on 7 May 1968. Both the 1 % and 10 % addition were stimulatory in these experiments and there is a suggestion that the 0.1 % addition was also but that its stimulatory potential was exhausted during the first two days.

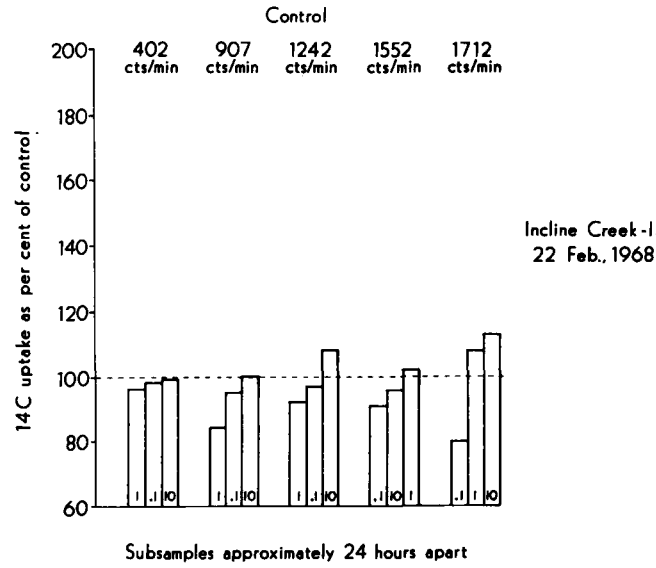

Fig. 7. Bioassay of Incline Creek water collected on 22 February 1968. There was no stimulation of the lake's phytoplankton by the addition of the stream water.

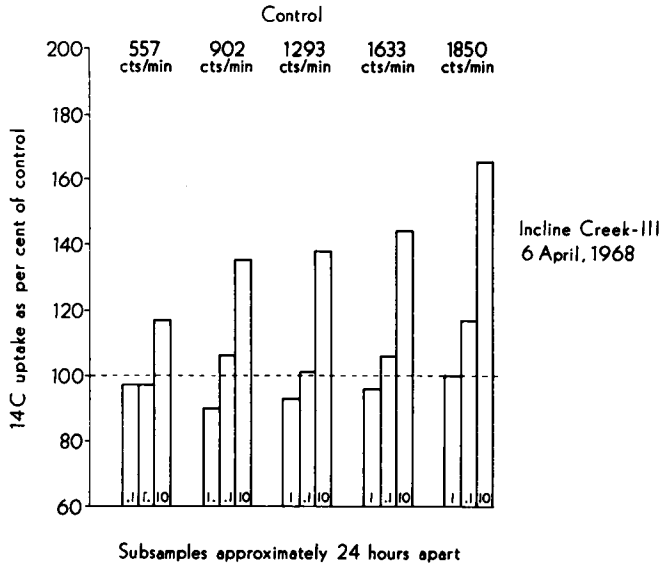

Fig. 8. Bioassay of Incline Creek water collected on 6 April 1968. The culture containing 10 % (v/v) of stream water supported appreciably more photosynthesis than the control.

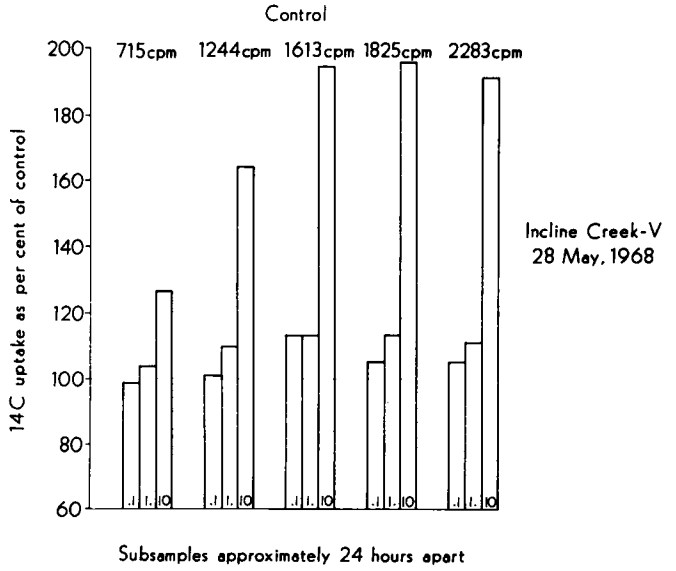

Fig. 9. Bioassay of Incline Creek water collected on 28 May 1968. Increased photosynthesis in the 10 % culture was even more evident than in the previous month's experiment.

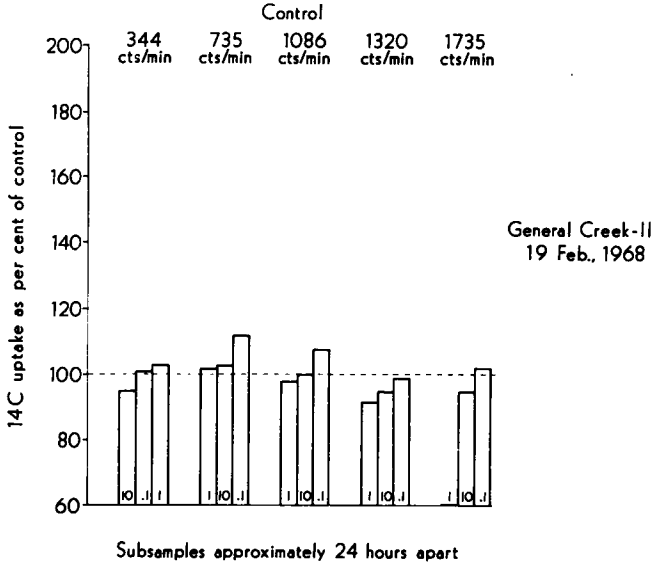

Fig. 10. Bioassay of General Creek water collected on 19 February 1968. General Creek was selected as the best example of an unpolluted stream available. The stream water did not affect the lake's phytoplankton in this experiment.

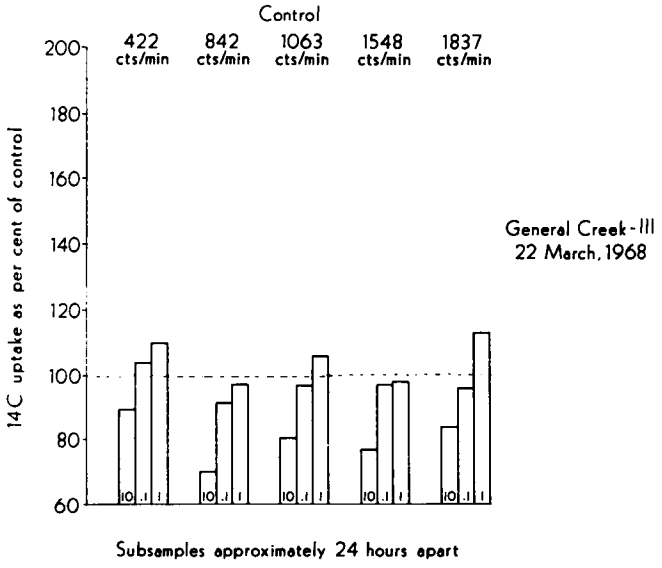

Fig. 11. Bioassay of General Creek water collected on 22 March 1968. It appears from these results that addition of stream water had a negative effect on phytoplankton growth.

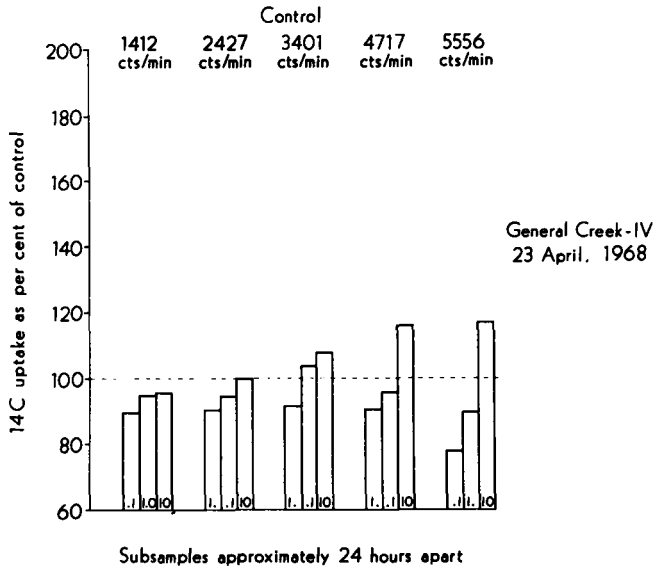

Fig. 12. Bioassay of General Creek water collected on 23 April 1968. There is still some suggestion of inhibition of ^{14}C uptake caused by the stream water, especially in the early part of the experiment.

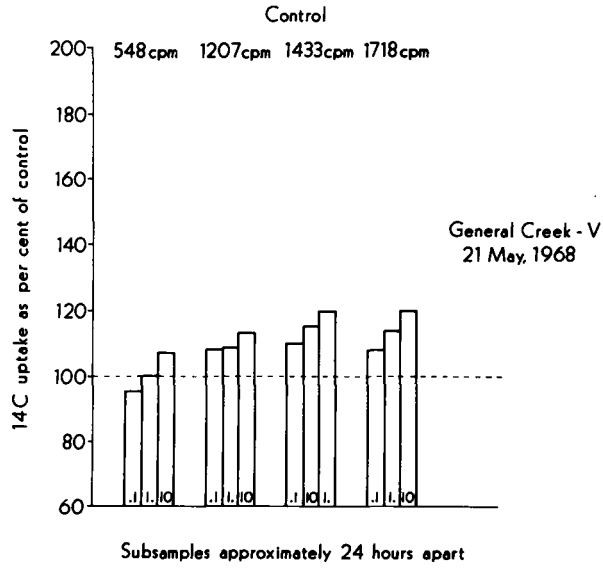

Fig. 13. Bioassay of General Creek water collected on 21 May 1968. The stream water had a stimulatory effect in all proportions but this was slight compared to the effects seen in the May experiments with water from Incline Creek and Upper Truckee River.

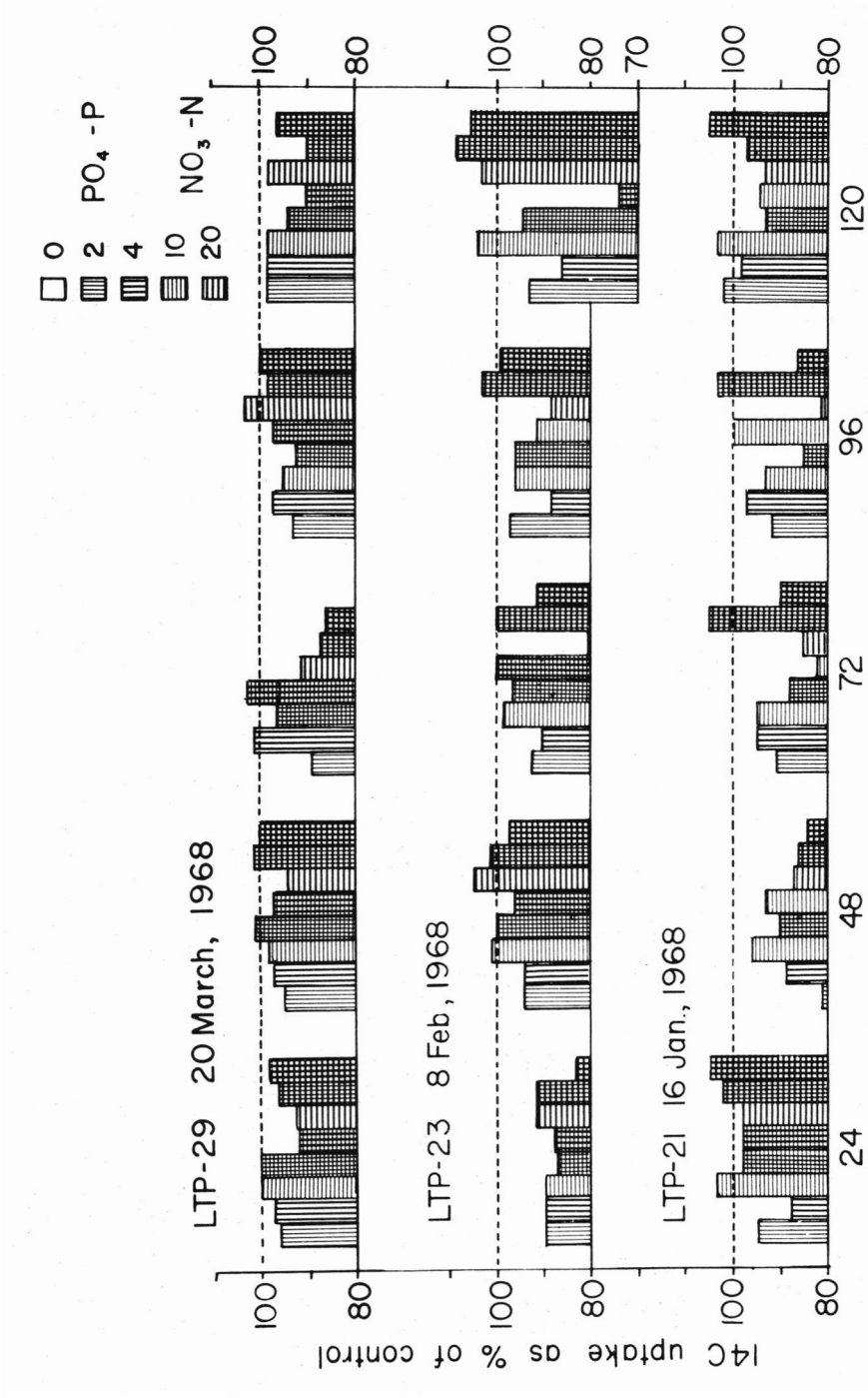

Fig. 14. Nitrate and phosphate bioassay experiments using pelagic Lake Tahoe water. In these experiments the ambient concentrations of nitrate and phosphate were approximately doubled (by adding 10 ppb NO_3-N or 2 ppb PO_4-P) or tripled (by adding 20 ppb NO_3-N or 4 ppb PO_4-P). All experimental results are shown relative to results obtained from a control culture.

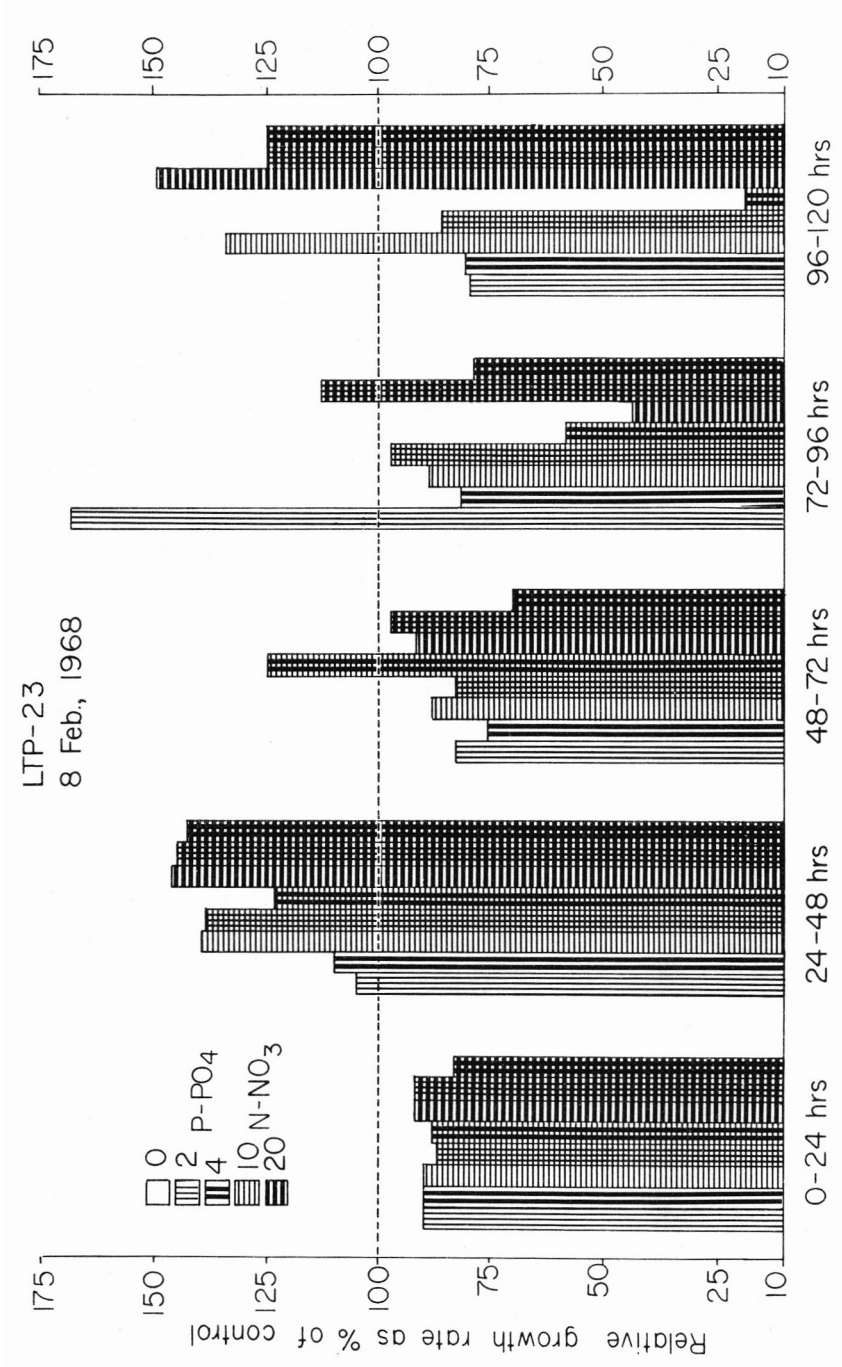

Fig. 15. Nitrate and phosphate bioassay experiment performed on pelagic Lake Tahoe water collected on 8 February 1968. Each set of histograms indicates the relative rate of photosynthesis during a 24-hour interval.

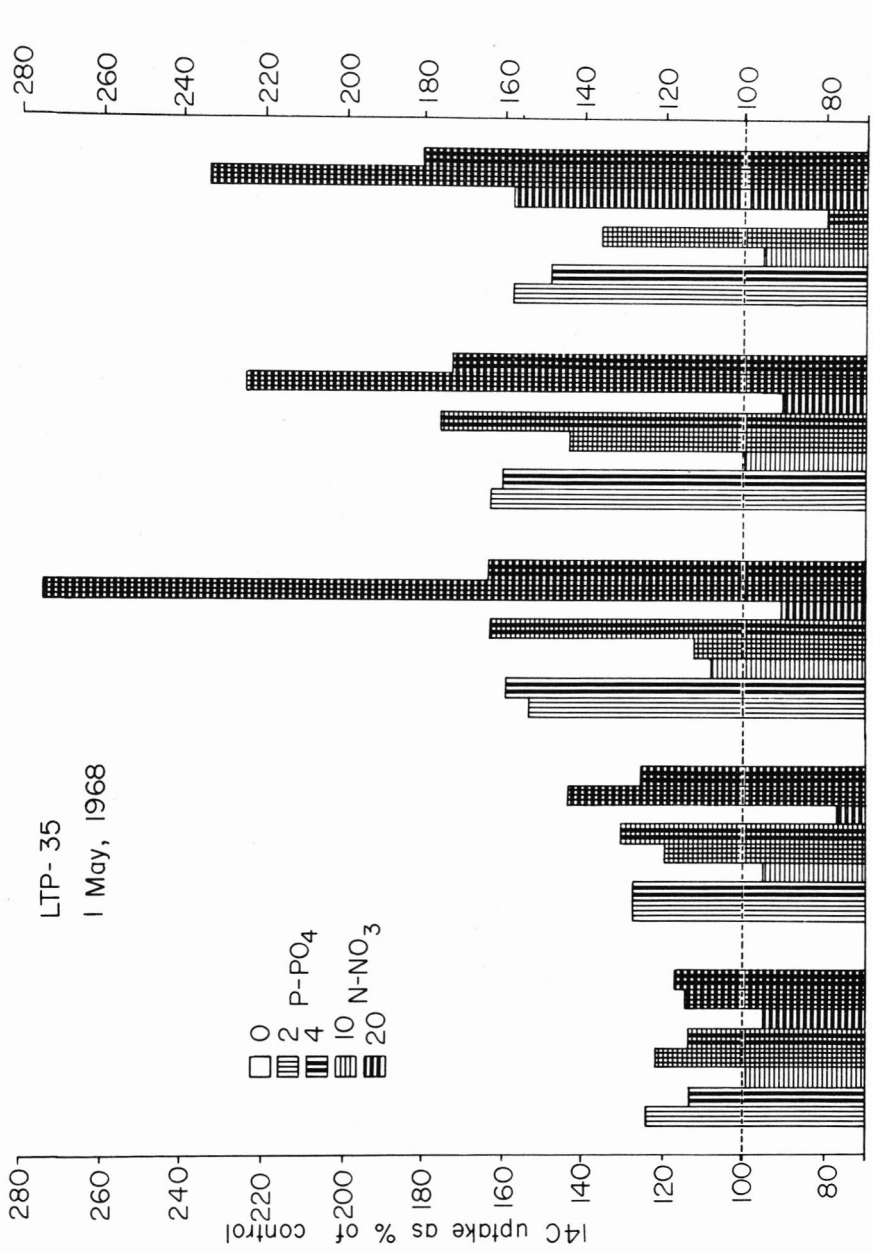

Fig. 16. Nitrate and phosphate bioassy experiment performed on pelagic Lake Tahoe water collected on 1 May 1968. The histograms show the cumulative ^{14}C uptake of the experimental cultures relative to the cumulative ^{14}C uptake by the controls.

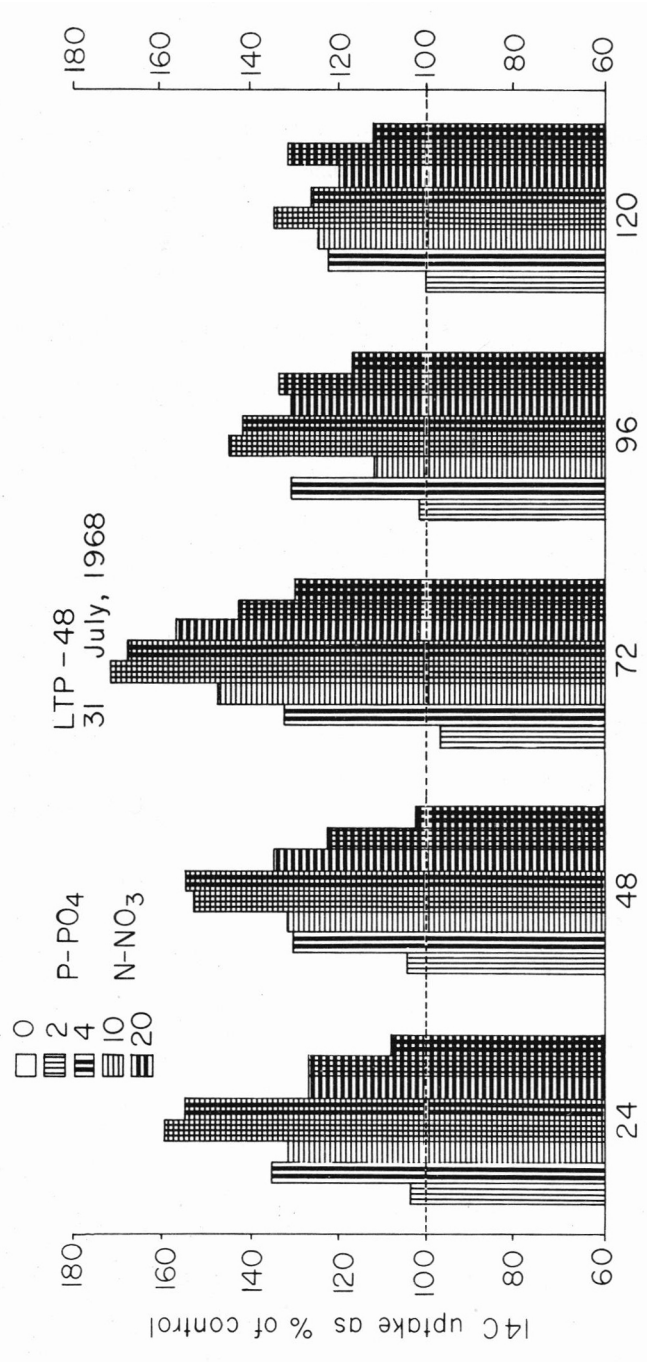

Fig. 17. Nitrate and phosphate bioassay experiment performed on pelagic Lake Tahoe water collected on 31 July 1968. The histograms show the cumulative ^{14}C uptake of the experimental cultures relative to the cumulative ^{14}C uptake by the controls.

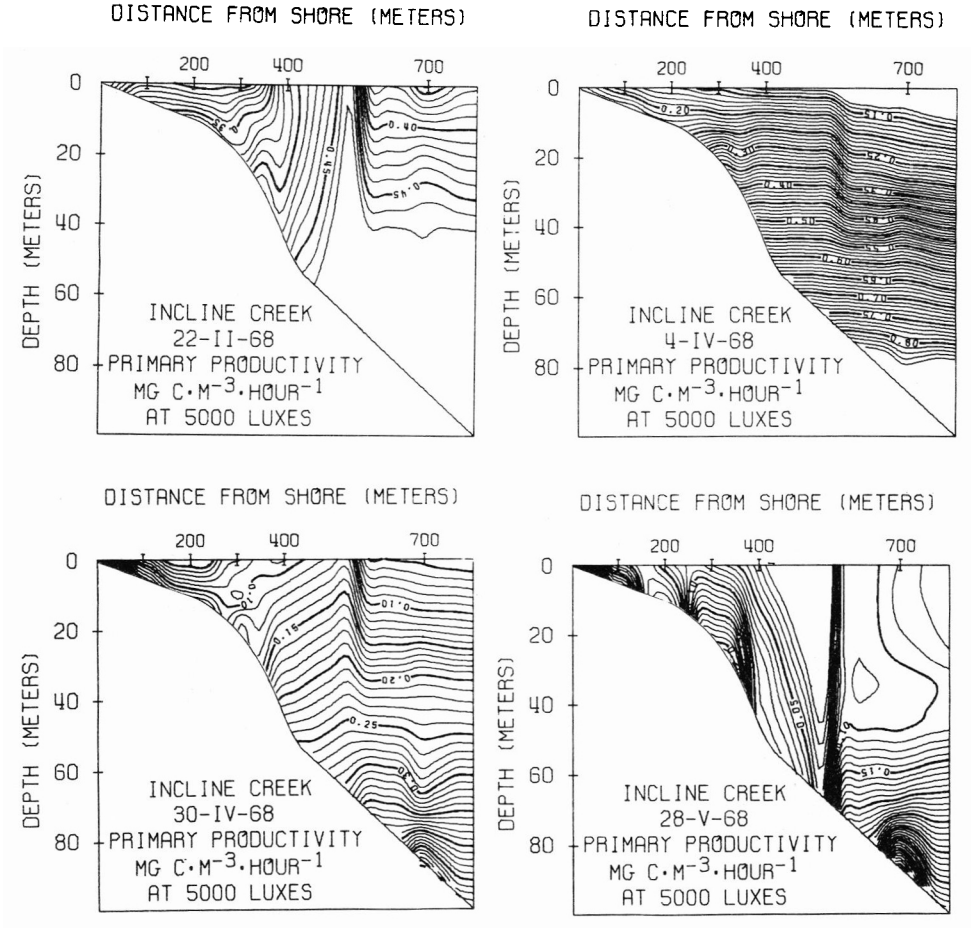

Fig. 18. Primary productivity off the mouth of Incline Creek. The isopleths connect points having equal productivity. The heavy diagonal line represents the lake's bottom.

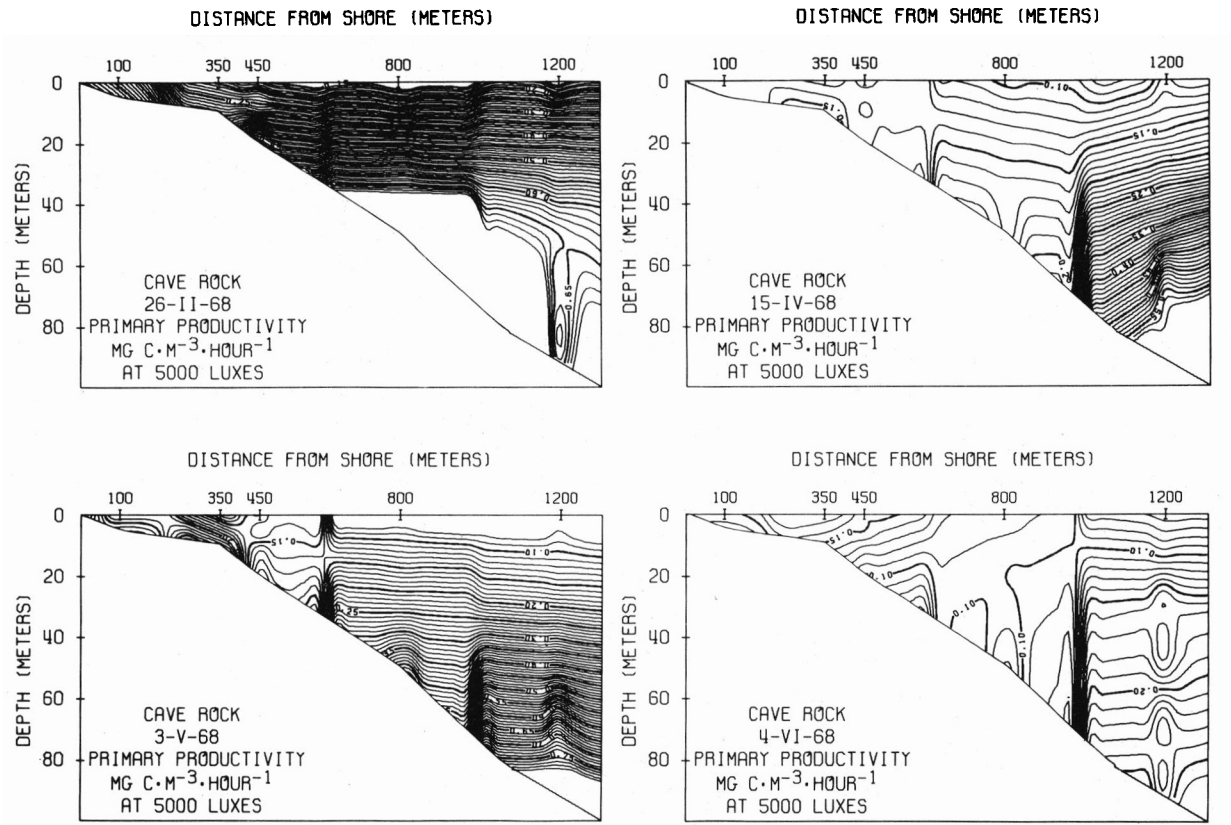

Fig. 19. Primary productivity off Cave Rock. The isopleths connect points having equal productivity. The heavy diagonal line represents the lake's bottom.

for each comparison. As in the two 1962 synoptic cruises there is no clear pattern in areal variation. Extremely high values (relative to the index station) occurred twice at the South Shore, twice at Crystal Bay, once at Agate Bay, and never at the mid-lake station or Skunk Harbor. This suggests that the South Shore and Crystal Bay may, on the average, be more productive than other parts of the lake.

The implications for the lake as a whole are serious when a comparison is made between this data and that collected during 1959 and 1960. The average daily value for the early study was 107.5 mg C · m^{-2} · day^{-1} while the average for 1967—68 is 162.3. There are insufficient data to say whether or not this simply reflects the high spring runoff of 1967 or whether it evidences an alarming increase in fertility over the last eight years. Continuing measurement in the lake will better define the annual variation in primary productivity and should indicate how significant this trend is.

A rough comparison of nitrogen and phosphorus values can be made from the data collected in 1962 with that of the present (Tab. 1). Although the sampling sites are different and the analytical techniques used are not the same, the results would certainly seem to suggest an increase in the lake's nitrogen during the last six years.

Tab. 1. A comparison of the nitrogen and phosphorus content of surface water in 1962 and 1968. The values given are in μg/l.

	1962			1968		
	Number of samples	Range	Mean	Number of samples	Range	Mean
NO_3-N	4	2—6.7	5.0	11	10.0—27.0	14.4
NH_3-N	< 4	—	< 2	10	11.0—43.0	21.8
P (total)	4	—	< 7.5	7	1.4— 1.9	1.7

To assess the relative influence of tributary waters three streams were selected for monthly bioassay. Mid-lake water was used as the culture medium with 0.1, 1, and 10 % by volume addition of the Upper Truckee River, Incline Creek, and General Creek. The Upper Truckee is the largest watershed, contributing one third of the annual runoff to the lake and one fifth of the total water input including precipitation on the lake surface. This stream drains a populated area which has previously been used for land disposal of sewage plant effluent. Although the effluent is now being diverted from the basin, the stream still carries a concentration of nitrate over three times that of the lake and an ammonia nitrogen content of over twice that of the lake (Tab. 2). Incline Creek also drains a highly disturbed

Tab. 2. Average nitrogen and phosphorus content of three streams draining the Tahoe watershed. Concentrations are given in ppb and have not been weighted for flow rate.

	Upper Truckee	Incline & 3rd Creeks	General Creek
NO_3-N	59.1	124	49.0
NH_3-N	45.4	41.0	40.3
P (total)	10.6	11.8	4.0
Annual Runoff $m^3 \times 10^6$	127 (103)*	9.5 (7.7)*	16.5 (13.4)*

* 1000's acre feet

area which has practiced land disposal of treatment plant effluent for golf course irrigation. It carries a nitrate concentration about twice that of the Upper Truckee River. General Creek was taken as a control stream since it drains a less disturbed area in land that is now a State Park. Fig. 3 through 13 show the results of these experiments.

Additions for Upper Truckee River water in February, April and May followed the same pattern of low stimulation in February (Figs. 3 and 4) with a large increase in April and May (Figs. 5 and 6). In these last two months the amount of increased growth was about proportional to the amount of stream water added and clearly shows that the Upper Truckee River is still a potent nutrient source.

Figs. 7, 8, and 9 give the results of the bioassay of Incline Creek for February. April and May. The trend of greater stimulation in April and May continues. Ten percent additions have a very marked effect on increasing productivity while 0.1 and 1 % provide less impressive stimulation to phytoplankton growth. Figs. 10 through 13 show the results of adding General Creek water to the lake. At no time did the water from this unpolluted control stream provoke the type of response observed in the experiments with Upper Truckee River and Incline Creek water. Only late in the spring was there a slight response following a 10 % addition. These bioassay experiments with the three streams clearly point out the necessity of doing culture experiments on a year round basis.

In the foregoing experiments the fertilizing effects of stream water additions to the lake have been demonstrated and the importance of their nitrogen or phosphorus content has been implied by their greater content of these elements. Special attention has been given in a second set of experiments to the relationship between nitrogen and phosphorus. Phosphorus has long received most attention as a limiting factor in aquatic environments, but nitrogen was found to be a more important limiting factor in Alaskan (GOLDMAN 1960) and Antarctic (GOLDMAN, MASON & HOBBIE 1967) lakes. Iron and nitrogen were both considered of importance in Tahoe by GOLDMAN & CARTER (1965).

In order to determine the effect of nitrate and phosphate on the lakes' phytoplankton, we began a series of experiments in which these nutrients were added to pelagic water both singly and in combination. The quantities added resulted approximately in a doubling or tripling of the ambient concentrations. Effect of the additions was determined, as before, by measuring the uptake of ^{14}C over a 5-day period. Fig. 14 shows the results of the first three experiments conducted during the winter months. At no time during these three months was there any stimulation of the lakes' phytoplankton by the addition of nitrate or phosphate (experimental results within 10 % of the control value can not be considered to differ significantly from the control). However, experimental cultures were frequently observed to fix less than 90 % as much ^{14}C as the control cultures. In the absence of a rigorous test of significance these low values can only be taken as suggestions of inhibition. They indicate that during the first two months tripling of either nitrogen or phosphorus alone was likely to cause inhibition. Of the 21 cases of inhibition, 5 occurred when the treatment was to triple the phosphate concentration without increasing nitrate and 5 occurred when the treatment was to triple nitrate without increasing phosphate. Doubling the nitrate concentration

without increasing phosphate did not lead to inhibition, but treatments in which nitrate was doubled and phosphate was doubled or tripled inhibited the cultures on six occasions.

Some clarity in interpretations is gained by decomposing these results to reveal the rate of growth of each culture averaged separately over each sampling interval. This manipulation introduces noise but it serves to resolve what may be important differences in the results for the various treatments. Fig. 15 shows the results of the 8 February experiment in this way. The heights of the histograms in Fig. 15 reveal the relative growth of each treatment during a single 24-hour light period instead of the relative cumulative growth since the start of the experiment as in Fig. 14. It can be seen from Fig. 15 that the experimentals all grew faster than the control on the second day although the increased growth with only phosphate added is unlikely to be significant. All of the treatments in which nitrate was added resulted in substantial increases in growth rate. Moreover, supplying the cultures with phosphate in addition to nitrate did not result in more stimulation than was gained by the addition of nitrate alone. There is even some indication that nitrate plus phosphate additions were less stimulating than nitrate additions alone. After the second day, growth of the treated cultures became erratic and was more often than not less than the control.

The dominant phytoplankter throughout the experiment was *Fragilaria crotonensis*. This species had a population density of 71 cells/ml at the start of the experiment. At the end of the experiment it had increased to: 99 (control), 108 (0 NO_3—N : 2 ppb PO_4—P), 117 (0 : 4), 116 (10 : 0), 78 (10 : 2), 83 (10 : 4), 132 (20 : 0), 172 (20 : 2), and 127 (20 : 4). Increase in total cell number followed the same pattern; the initial total cell density was 123 cells/ml and increased to: 146 (control), 189 (0 : 2), 174 (0 : 4), 164 (10 : 0), 112 (10 : 2), 119 (10 : 4), 192 (20 : 0), 267 (20 : 2), 189 (20 : 4). The inferences that can be drawn from the count data are not the same as those that come from analyzing the cumulative ^{14}C results after the fifth day (Fig. 14). By either method treatments in which nitrates were tripled rank high with 20 ppb NO_3—N : 2 ppb PO_4—P being the most stimulatory of the treatments investigated. Likewise, by either method treatments (10 : 2) and (10 : 4) appear inhibitory. However, the cell count method of analysis indicates that additions of phosphate without any addition of nitrate can result in increases in cell number. The ^{14}C results indicate there was less photosynthesis in these cultures than in the control. Perhaps phosphate fertilization can stimulate cell division without leading to a correspondingly large stimulation of photosynthesis. A cautious summary of the midwinter state of the phytoplankton community would note that nitrate ion has some capacity to stimulate photosynthesis while phosphate alone probably does not. Phosphate, on the other hand, appears to have a marked capacity to provoke cell division, especially when it is added in moderate amounts. On the whole, nutrient enrichment in midwinter appears more likely to inhibit photosynthesis than to enhance it.

The response of the phytoplankton to similar manipulations carried out in mid-spring was quite different. Fig. 16 gives the results of a nitrate-phosphate bioassay experiment performed with pelagic water collected 1 May 1968. If nitrate was implicated as a stimulatory nutrient by the winter experiments, then phosphate

was unequivocally shown to stimulate CO_2 fixation during this springtime experiment. Cultures to which 2 or 4 ppb of PO_4—P alone were added had 50 to 60 % more ^{14}C uptake than the controls. Addition of NO_3—N alone either had no effect on the cultures or it had a slight inhibitory effect. When phosphate was doubled or tripled in conjunction with a doubling of nitrate (treatments 10 : 2 and 10 : 4), the stimulation was of a magnitude that could be accounted for by the phosphate addition alone. However, when the NO_3—N concentration was raised by 20 ppb the effect of phosphorus additions was much greater than when phosphorus was added alone. Greatest stimulation resulted from treatment 20 : 2 (20 ppb NO_3—N:2 ppb PO_4—P) while treatment 20 : 4 was only slightly more stimulating than treatment 0 : 4. Analysis of the phytoplankton population counts provide a similar, but by no means, identical, account. By the end of the incubation the total cell density in the control culture had increased from 103 cells/ml to 143 cells/ml while in the various experimental cultures the final cell densities were (in cells/ml): 164 (0 : 2), 108 (0 : 4), 107 (10 : 0), 168 (10 : 2), 146 (10 : 4), 222 (20 : 0), 244 (20 : 2), 140 (20 : 4). Both types of analysis picked treatment (20 : 2) as the most stimulating with 0 : 2 and 10 : 2 being about equally higher than the control. Cell counts for treatments involving addition of 4 ppb of phosphorus were surprisingly low relative to the controls considering the ^{14}C results. Apparently when the phosphorus concentration became quite high ^{14}C uptake continued at a high rate while population growth lagged behind. This tendency is well marked in 0 : 4 which took up 50 % more ^{14}C than the control but showed no population growth during the experiment. Treatments 10 : 4 and 20 : 4 both provided as much population growth as the control but no more. ^{14}C results with these cultures were 157 % and 179 % of the control.

These experiments were continued and by mid-summer a new type of response was evident in the results. Fig. 17 shows the results of a nitrate-phosphate bioassay performed with pelagic water collected on 31 July 1968. In this experiment the treatments were more distinctively separated from one another early in the incubation than they were at the end. This feature of the results probably is due to the failure of the cultures to grow appreciably after 72 hours. In fact, between 96 and 120 hours all but one of the cultures experienced a net loss in particulate ^{14}C. At the end of 72 hours the cultures which had fixed the most ^{14}C were those to which 10 ppb NO_3—N and either 2 or 4 ppb of PO_4—P had been added. All treatments except 0 : 2 appeared to increase ^{14}C uptake but the greatest enhancement of photosynthesis resulted from the addition of moderate amounts of both nitrogen and phosphorus. This was still true at the end of the experiment.

Analysis of the phytoplankton cell density data reveals a marked decline in total cell density in the control culture and in most of the experimental cultures. Initially the culture water contained 24 cells/ml and this figure dropped to 7 cells/ml in the control culture. The final cell densities in the experimental cultures were: 27 (0 : 2), 14 (0 : 4), 5 (10 : 0), 6 (10 : 2), 19 (10 : 4), 3 (20 : 0), 32 (20 : 2) and 23 (20 : 4). Thus, according to the cell count data the only cultures that supported net growth were 0 : 2 and 20 : 2 while the only cultures that ended the incubation with lower cell densities than the control were 10 : 0 and 20 : 0. The cell count data, therefore, suggest that phosphorus is the more in demand of the

two nutrient elements. The ^{14}C results show 2 ppb PO_4—P by itself to be ineffectual in stimulating photosynthesis but in combination with 10 or 20 ppb of NO_3—N to be the most effective treatment tested.

One purpose of the nitrate-phosphate bioassays was to find a rationale that could account for the results obtained in the stream water bioassay experiments. One of these results was that pelagic phytoplankton responded to stream water additions much more vigorously in the late spring and summer than they did in the winter. This result was duplicated in the nitrate-phosphate bioassay experiments. The winter phytoplankton showed no great response to any experimental manipulation while the spring and summer phytoplankton appeared to react to every change we made in their environment.

The amount of nitrogen and phosphorus added in the bioassay experiments was large compared to that added by even the most enriched streams entering the lake. In general the stream water was more stimulating than its nitrogen and phosphorus content alone would indicate. This may be due in part to organic growth factors or natural chelating agents which make such nutrients as iron more available.

Each time water from a stream was bioassayed a special productivity experiment was carried out in the lake near the mouth of the stream. Water samples were collected from the stream and at five stations along a transect extending from the mouth of the stream out to a point in the lake where the depth of the water was approximately 100 m. At each station samples were taken at regular intervals between the surface and the bottom so that a single transect encompassed 24—28 sampling points. Samples from each point included two light bottles and one dark bottle, all of which were taken back to the lab and incubated at constant light and temperature for four hours. An additional complete set of samples was collected from the deepest station and was incubated in situ under the prevailing light and temperature conditions. Results obtained with the constant light incubation were corrected for in situ light conditions on the assumption that the relationship between results obtained using artificial light and results obtained using in situ light was the same for all samples collected at a given depth regardless of distance from shore. The area off Cave Rock on the east of the lake was selected as a control area as there are no streams entering the lake near there and the shore is relatively undeveloped.

Fig. 18 shows the results obtained from four such transect experiments conducted at approximately monthly intervals off the mouth of Incline Creek. Productivity isopleths were drawn from the twenty-seven data points by a Calcomp® digital incremental plotter, Model 566, on an IBM 7044 computer using the General Purpose Contouring Program (GPCP)[1]. The measurements made late in February and early in April revealed no effect of the stream on the offshore waters. This is consistent with the results of the bioassay experiments which indicated that in the winter and early spring Incline Creek had little tendency to stimulate photosynthesis in the lake. However, by the end of April and especially at the end of May, the transect experiments suggested that stream water was

[1] Copyrighted 1968. California Computer Products, Inc., Anaheim, California.

having a stimulating effect on the lake water adjacent to the mouth. The results for May 25 indicate that the stream water entering the lake is denser than the lake water which by this date was thermally stratified. Fig. 19 shows the results of a comparable set of experiments conducted at Cave Rock where there is no stream entering the lake. There is no evidence from these experiments of a general "shore effect" which could confound the results from our other transect series.

The results obtained off General Creek and off the Upper Truckee River were comparable to those described for Incline Creek. Stimulation of photosynthesis by the stream water could be detected readily from measurements made in late spring or early summer but not at all from the winter and early spring data.

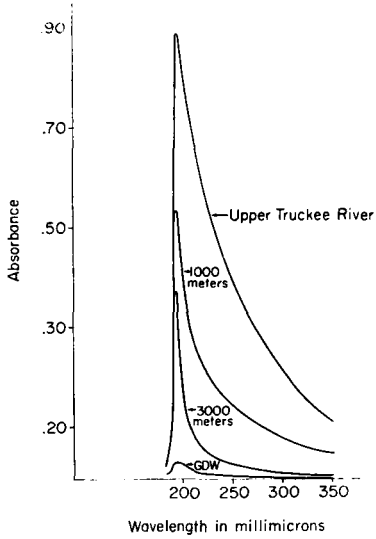

Fig. 20. Ultraviolett absorbance spectra of Upper Truckee River water and Lake Tahoe water 1000 meters and 3000 meters off the mouth of the river (pathlength = 40 mm; GDW = glass distilled water).

As part of the transect program the water from each sampling point was analyzed for Ca, Mg, Na, K and ultraviolet absorbance. The cation analyses did not provide any information that could contribute to the interpretation of the productivity measurements. In most cases the concentrations were practically uniform throughout the series. Ultraviolet absorbance, however, was much greater in the streams than in the lake and therefore offered greater promise of being a watermass indicator. Fig. 20 shows the UV absorbance spectra of Upper Truckee River water and Lake Tahoe water at 1000 and 3000 m from the mouth of the stream. Maximum absorbance of both stream and lake water was at 195 mμ. The absorbance of all water samples was measured at this wavelength, therefore, and the results were plotted by the Calcomp® plotter for easy comparisons with the productivity data. Fig. 21 shows the results of one such series of measurements together with the productivity values corrected for in situ conditions. The data were collected 7 June 1968 at the mouth of the Upper Truckee River. The similarity between the corrected productivity isopleths and the isopleths of absorbance at 195 mμ is striking. In order to see if this relationship was one that held throughout the entire series of experiments we calculated the linear correlation coefficient

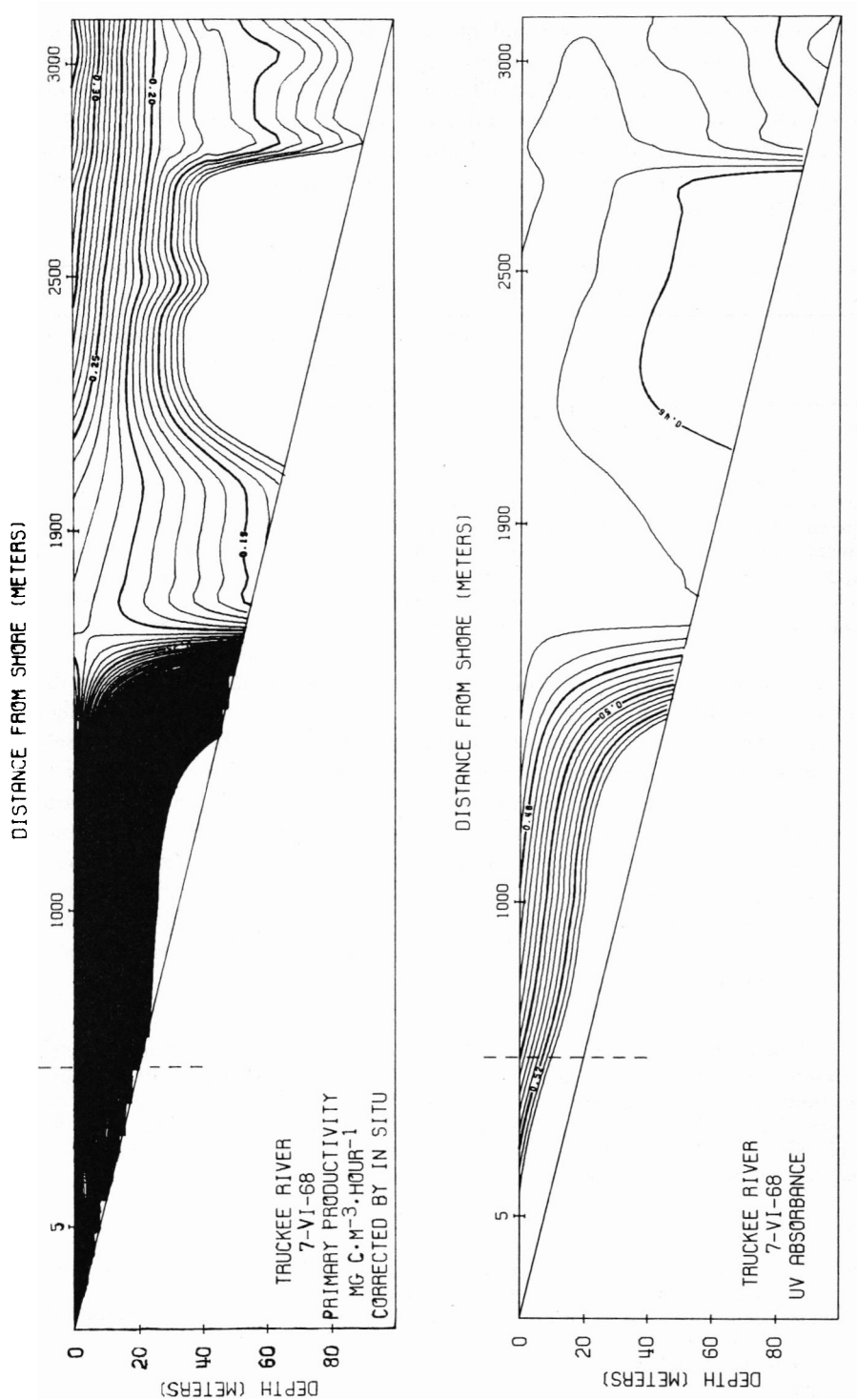

Fig. 21. (Upper) Primary productivity off the mouth of the Upper Truckee River. The values have been corrected to show the productivity under in situ light conditions. (Lower) Absorbance at 195 mμ by Lake Tahoe water off the mouth of the Upper Truckee River.

between absorbance at 195 mμ and primary productivity (both corrected and uncorrected). The results (Tab. 3) showed the relationship to be restricted to the waters around the mouth of the Upper Truckee River. Each time the measurements were made there was a significant correlation of absorbance with the corrected productivity values. It should be noted also that the strength of this correlation increased with time just as the stimulating effect of the stream water on photosynthesis increased.

Tab. 3. Linear correlation coefficients between absorbance at 195 mμ and productivity. (n. s. = not significant; percentage figures indicate level of significance.)

Location	Date	Correlation coefficient between absorbance and productivity			
		with uniform light		corrected for in situ light	
Incline Creek	4—IV—68	—.11210	n. s.	—.19386	n. s.
Incline Creek	30—IV—68	.08754	n. s.	.17997	n. s.
Incline Creek	28—V—68	—.11613	n. s.	.03766	n. s.
Cave Rock	3—V—68	—.17030	n. s.	—.11655	n. s.
General Creek	23—IV—68	—.20422	n. s.	—.37537	n. s.
General Creek	21—V—68	—.56567	1.0 %	—.26086	n. s.
Upper Truckee River	7—IV—68	—.06899	n. s.	.47880	5.0 %
Upper Truckee River	7—V—68	.17637	n. s.	.54218	2.0 %
Upper Truckee River	7—VI—68	.68705	0.1 %	.78299	0.1 %

At this time we have not identified the ultraviolet absorbing substances in the Upper Truckee River and have not completed experiments to determine whether they are in themselves responsible for stimulation of photosynthesis or are merely associated with other stimulating substances. Presumably the absorbance is due to the combined effect of several or many substances contained in the river water among which nitrate ions as well as organic compounds are likely to be important (OGURA & HANZA 1967). In view of the generally slight stimulating effect of nitrate solutions on pelagic water we are inclined to suspect the effect is brought about by some organic compound, possibly an iron containing compound, as Lake Tahoe phytoplankton have been observed to respond to additions of chelated iron (GOLDMAN 1964).

Acknowledgments

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Discussion

THOMAS: As Professor GOLDMAN showed, inorganic nitrogen increased from 1962 to 1968 from 7,0 to 36,2 μg/l (NO_3—N from 5,0 to 14,4; NH_3—N from 2 to 21,8) and phosphate decreased from 7,5 (?) to 1,7 µg/l. According to my opinion, in such a lake phosphate is the limiting factor for algal growth.

Authors: Within the restraints imposed by the concept of a single limiting factor, THOMAS' opinion is supported by the results of the nitrogen-phosphorous bioassays. However, the response to iron and much greater stimulation provided by minute amounts of stream water indicate the presence of stimulatory chemical species with far greater potency than phosphorous. Moreover, the changing pattern of response to all manipulations makes us question the adequacy of interpreting the lake's biology in terms of nutrient limiting factors alone.