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PHOSPHORUS, SILICA, AND EUTROPHICATION OF LAKE MICHIGAN[1]

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ABSTRACT

Natural phytoplankton assemblages enclosed in large plastic bags responded, as measured by carbon-14 uptake and cell counts, to experimental treatments of nitrogen, phosphorus, and silica; nitrogen and phosphorus; and phosphorus alone. Effects were measured with treatments as small as 20 mg PO_4-P m^{-3}, 200 mg NO_3-N m^{-3}, and 700 mg SiO_2 m^{-3}. Increases in cell numbers and rates of carbon fixation were accompanied by decreases in soluble NO_3-N and SiO_2 and increases in particulate PO_4-P, indicating biological utilization of these elements. Silica was reduced to limiting levels but nitrogen was not. A highly significant correlation occurred between rate of carbon fixation and particulate phosphorus. Ratios of phosphorus to silica present in tributary inputs indicate that phosphorus is supplied in quantities 10 to 20 times larger than ratios of phosphorus to silica required by diatoms in phytoplankton assemblages. These data indicate that phosphorus has been the limiting nutrient that has controlled eutrophication, resulting in lower concentrations of silica in the lake. With continued depletion of silica, diatoms will be replaced in the phytoplankton by nonsiliceous forms, probably blue-green and green algae.

INTRODUCTION

Environmental changes in the Great Lakes, particularly Lake Erie, are well known. Changes associated with accelerated eutrophication have been reviewed and summarized recently (Beeton 1969). Changes in Lake Michigan have not been as severe as those in Lake Erie and Lake Ontario, but are greater than those that have occurred in Lake Superior and Lake Huron.

Changes in planktonic diatom assemblages since 1880 are indications of eutrophication that have been documented recently (Stoermer and Yang 1969). These floristic changes may reflect not only increased nutrient supplies and availability, but also the entire spectrum of ecological changes including thermal effects and increases in conservative elements. In this paper, we consider only nutrient effects and use the term *eutrophication* in this context, although we recognize that the practical consequences of nutrient pollution cannot be separated entirely from other environmental insults.

Eutrophication, particularly accelerated eutrophication of a body of water, is controlled at any given time by a limiting nutrient. The concept of a limiting nutrient is easily understood—the difficulty in applying the concept for practical problems lies in the questions of how to study or measure limiting nutrients and, in instances of advanced eutrophication, how to determine what nutrients were limiting during the past history of the lake. Our paper is concerned with the determination of limiting nutrients in Lake Michigan at the present time, which can be approached in three ways.

First is chemical assay, in which the chemical characteristics of the environment are measured and used to deduce why phytoplankton grow and reproduce. There are many elements that might be measured and there are many problems in interpretation. Do we know all the variables that must be measured? Do the analyses of water measure biological availability? Often overlooked is the fact that nutrient concentration in the water represents only the balance between supply and utilization of nutrients by phytoplankton. Concentrations of criti-

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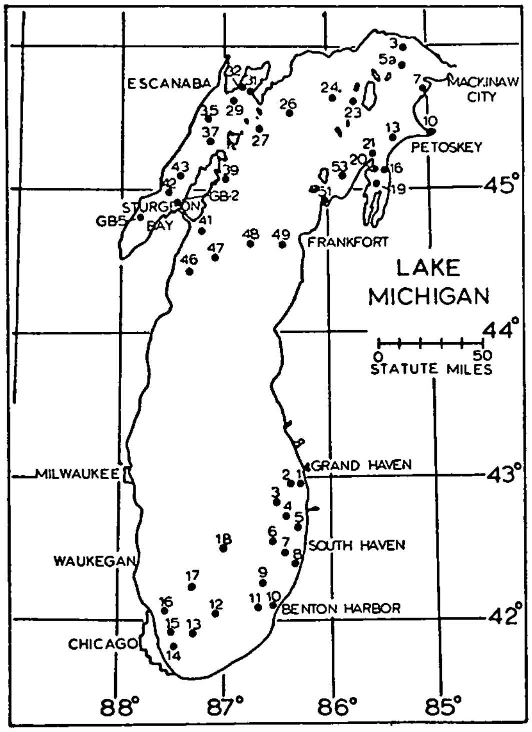

FIG. 1. Map showing location of stations in southern Lake Michigan. Figure from Schelske and Callender (1970).

cal nutrients in phytoplankton, on the other hand, are a valid measure of carrying capacity and degree of eutrophication.

Second is the biological assay, in which pure cultures with known growth requirements are used in formulating questions about the trophic state (nutrient concentrations) of an environment. One advantage of this approach is that the biologically available fraction of the nutrient supply is measured for the conditions of the experiment. Problems include extrapolation to a wide variety of environments with many species, each of which may have different nutrient requirements; competition among species in the natural environment; and different responses of species depending on their previous light, nutrient, temperature, and other environmental history. Recently attempts have been made to use biological assay to determine potential algal productivity of different waters, the so-called PAAP test (Joint Industry/Government Task Force on Eutrophication 1969).

Third is the ecological perturbation experiment, which is conducted by treating or perturbing natural phytoplankton assemblages in natural lake water with different nutrients and then observing, measuring, and describing the results of these perturbations. It combines the favorable features of the first two approaches. The Great Lakes are too large to use the ecological perturbation approach directly, so we conducted experiments by perturbing phytoplankton assemblages contained in large plastic bags. Our approach is unique in that we have measured balances of materials, demonstrated several effects related to eutrophication, and utilized natural phytoplankton populations under conditions that closely simulate those of Lake Michigan.

METHODS AND MATERIALS

Nutrient enrichment experiments were performed in 1969 and 1970 by studying the effect of nutrient treatments on natural phytoplankton populations. Stations used in the study are shown in Fig. 1. Nutrient enrichment experiments in 1969 were conducted at stations 1 and 2 located near Grand Haven, Michigan. The inshore station was 1.2 km from the shoreline at a depth of 16 m and the offshore station was 6.7 km from the shoreline at a depth of 60 m. Both stations were located on an east-west line, 6.3 km south of Grand Haven. Experiments in 1970 were conducted in northern Lake Michigan at a station located near Petoskey in the mouth of Little Traverse Bay. The depth at this station was 55 m.

Nutrients were added to large plastic bags constructed of 4-mil polyethylene. Bags used in 1969 had a volume of approximately 4000 liters and a diameter of 2 m. The volume of bags used in the 1970 experiments were smaller, approximately 1000 liters.

Bags were filled and sampled underwater by SCUBA divers. Bags were anchored at a depth of 7 m and filled at a rate of 200 liters min^{-1} with nonmetallic pumps positioned on the deck of a ship. To ensure complete mixing, nutrient treatments were added to the water as it was being pumped into the bags. While anchored at depth, bags were sampled with a nonmetallic submersible pump powered by a 12-v battery. SCUBA divers inserted the sampling hose into the bags through a filler tube. After the hose and pump were flushed other workers in a small boat positioned over the bags collected samples. Samples were collected on the day of filling and as frequently as possible thereafter. The same procedure was used to sample lake water outside the bags so environmental changes in the lake could be measured to assess variability in the lake environment.

Experiments conducted in 1970 differed from the 1969 experiments in that duplicate treatments were used in the experimental design in 1970. Bags with the duplicate treatments were positioned on the same line, one bag at a depth of 7 m and the other at about 4 m.

Experiments with plastic bags were thus conducted under existing light and temperature regimes in the lake. Phytoplankton were brought to the surface only very briefly during the filling process and when the bags were sampled to determine the effects of the different treatments.

The technique of using bags for these experiments proved to be worth while. Difficulties encountered were due mainly to the failure of some bags to withstand for two weeks the rigorous physical conditions of Lake Michigan, and to delays caused by sea conditions that made it impractical for divers to work safely. An anticipated problem, fouling of the polyethylene by attached organisms, did not materialize. Several bags were left in the lake for more than five weeks with no growth being evident on the polyethylene. Algae, however, were present on the manila lines that went from the bags to the floats at the surface of the water.

Divers observed the condition of the bags during sampling and, if the volume of water was reduced through leakage to approximately one-fourth or less, the results were no longer considered valid. Data from samples collected on 8 September 1969 were not used in interpretation of results for the offshore station but are presented later (see Fig. 3) to illustrate the problem of leakage. Whether the large silica values are due to regeneration, to movement of lake water into the bag, or to some other factor is not known. In the interpretation of results it is logical that in general the validity of the results becomes more questionable with time after the start of the experiment. We are confident of results obtained during the first few days of an experiment, but generally would question their validity after 10 days.

TABLE 1. *Nutrient enrichments used in 1969 experiments with Lake Michigan phytoplankton*

Treatment	Chemical form	Concentration in bags
N	$NaNO_3$	0.200 mg N liter^{-1}
P	Na_3PO_4	0.020 mg P liter^{-1}
Si	$Na_2SiO_3 \cdot 9H_2O$	0.70 mg SiO_2 liter^{-1}

Only sodium salts were used in the nutrient treatments. Sodium was chosen because it should affect water chemistry and responses of phytoplankton less than any other cation. The chemical form and concentration of the nutrients used in the 1969 experiments are given in Table 1. Different concentrations of the same nutrients were used in the experiments in 1970.

Concentrations of silica and nitrate nitrogen and rates of carbon fixation were measured on samples removed from the bags with methods described previously (Schelske and Callender 1970). Bags were sampled in the morning between 7:00 and 10:00 AM and experiments were usually concluded by 3:00 PM. Silica and nitrate were determined on samples which had been filtered through an HA Millipore® filter and then frozen. Nitrate nitrogen was reduced to nitrite and measured on the day samples were thawed, and silica was measured at a later date. Silica, nitrate plus nitrite, and phosphate were measured colorimetrically with an Autoanalyzer. Nitrite and ammonia were not measured separately because measurements that were performed indicated the concentrations were small relative to the amounts of added nitrate. Measurements of reactive orthophosphate are not reported because they were generally less than 2 μg P liter^{-1} or undetectable even in treated bags, indicating that added soluble phosphate was removed rapidly by phytoplankton or by chemical processes.

Material remaining on the filter was used to determine the concentration of particulate phosphorus. Filters were charred or digested with 1.0 ml of concentrated nitric acid in a porcelain crucible, and then ashed for 3 hr at 450C. Residues were dissolved in 50% HCl with warming and diluted to volume so the final concentration of HCl was 5%. Samples were treated with hydrogen peroxide and heated if color was present. This procedure was followed to concentrate trace metals for chemical analysis and allowed 10- to 20-fold concentration of particulate matter.

Phytoplankton were concentrated on AA Millipore® filters and cleared for identification and enumeration as described by Stoermer et al. (in press).

NUTRIENT ENRICHMENT EXPERIMENTS

Four treatments were used at each station in 1969: Si; N,P; N,P,Si; and control. In 1970, experiments were conducted with different concentrations of phosphate.

Nitrogen, phosphorus, and silica enrichments, 1969

Inshore and offshore waters at the two stations near Grand Haven were different biologically and chemically (Schelske et al. in press). At the inshore station, the influx of nutrients from upwelling was evident from greater concentrations of nutrients and rates of primary productivity than were observed at the offshore station. Larger standing crops of phytoplankton were also present at the inshore station than at the offshore station; this was evident from cell counts, rates of carbon fixation, and Secchi disk transparency. These differences must be considered in the interpretation of data from experiments at each station.

Offshore station. A significant increase in carbon fixation and cell counts resulted from the N,P,Si treatment (Fig. 2). Cell counts, plotted on a log scale, increased about 10 to 15 times. Carbon fixation also increased about 15 times, indicating that, for the N,P,Si treatment, changes in rates of carbon fixation were a good representation of increases in cell counts and possibly biomass.

Effects of perturbation measured in terms of carbon fixation were greater in the N,P treatment than in the Si treatment, but the Si treatment apparently caused a larger increase in cell counts than the N,P treatment (Fig. 2). Carbon fixation in the Si treatment was only slightly larger than the controls. These results, as discussed later, indicate that the species composition and at least the volume of each species must be considered in the interpretation of experimental results.

During the course of the experiment, growth of phytoplankton affected the chemical characteristics of the water. Silica decreased from the enriched level of 0.86 ppm SiO_2 to 0.05 ppm SiO_2 in the N,P,Si treatment, which had the largest increase in cell counts and carbon fixation of the treatments (Fig. 2). In the Si treatment, silica decreased from 0.86 to 0.56 ppm SiO_2, reflecting an increase in diatoms. A decrease in silica in the N,P treatment from 0.10 to 0.05 ppm SiO_2 also occurred.

Silica decreased in the N,P,Si treatment in relation to increases in cell numbers. The largest increase in absolute counts of cells occurred between July 21 and 25. The greatest decrease in concentrations of silica was in this period.

Reductions in the concentrations of NO_3-N do not show consistent trends for two reasons. First, chemical analyses were quite variable, possibly because of our inability to perform some analyses as soon as frozen samples were thawed. Analyses could not be rerun to check questionable results. Second, relatively small increases in absolute cell numbers as compared with the inshore experiment, which will be discussed next, resulted in small changes in soluble NO_3-N. In spite of these difficulties, it seems apparent that nitrate nitrogen

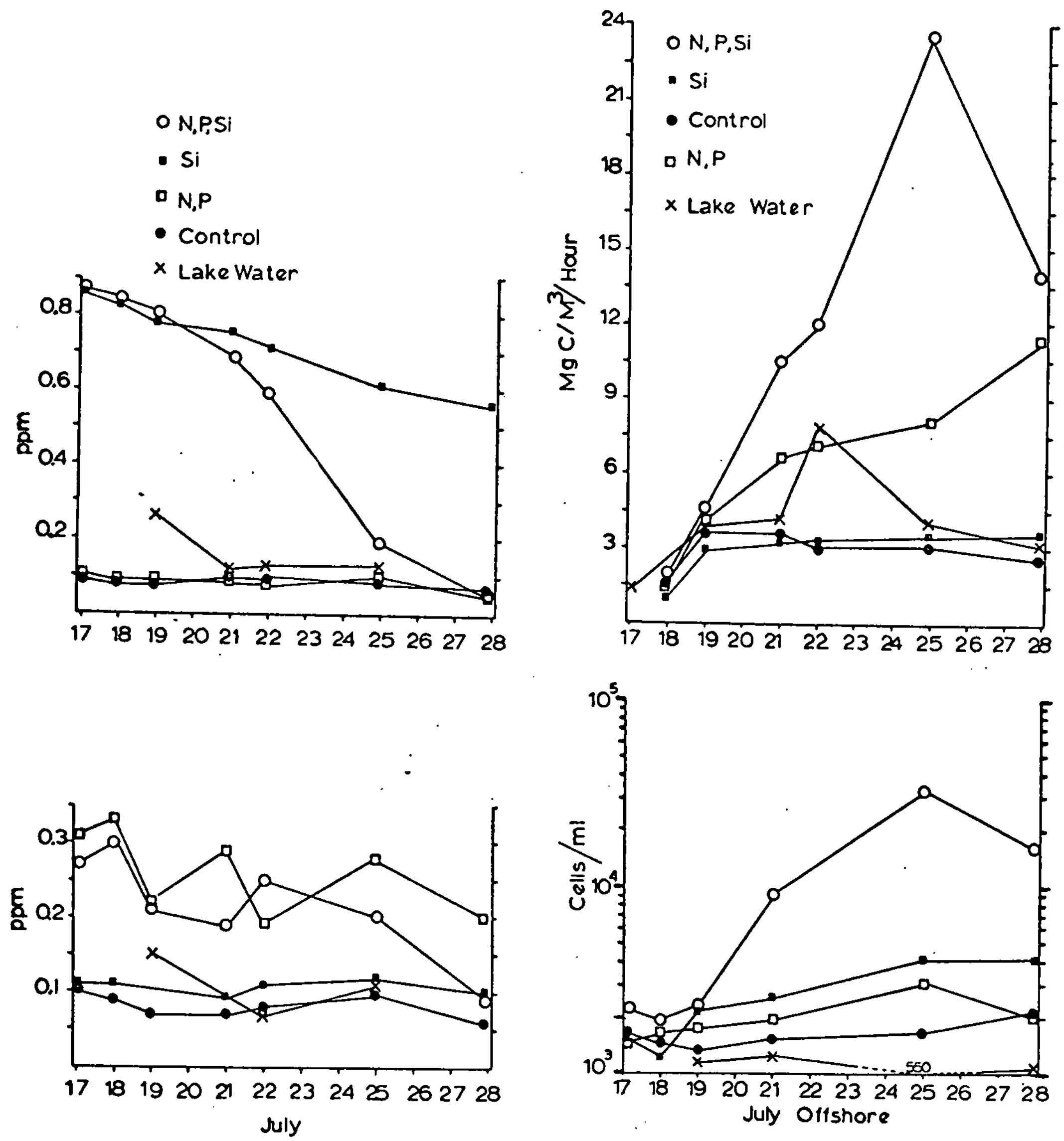

FIG. 2. Results of nutrient enrichment experiments at offshore station, July 1969. Experiment started July 17. Upper left corner, soluble SiO_2 in ppm. Lower left corner, soluble NO_3-N in ppm. Upper right corner, rates of carbon fixation in mg C m^{-3} hr^{-1}. Lower right corner, total cell counts in cells per ml.

decreased in the N,P,Si treatment and may have decreased in the N,P treatment.

Inshore station. Environmental conditions at the initiation of the experiment at the inshore station in August were different from those at the offshore station in late July. The standing crop of diatoms was greater than at the offshore station and the differences in standing crops were reflected in the rates of carbon fixation (Figs. 2, 3). Cell counts initially were about 1700 cells ml^{-1} at the offshore station and averaged more than 3000 cells ml^{-1} at the inshore station (Stoermer et al. in press). Carbon fixation in the control treatments averaged about 3 mg C m^{-3} hr^{-1} at the offshore station

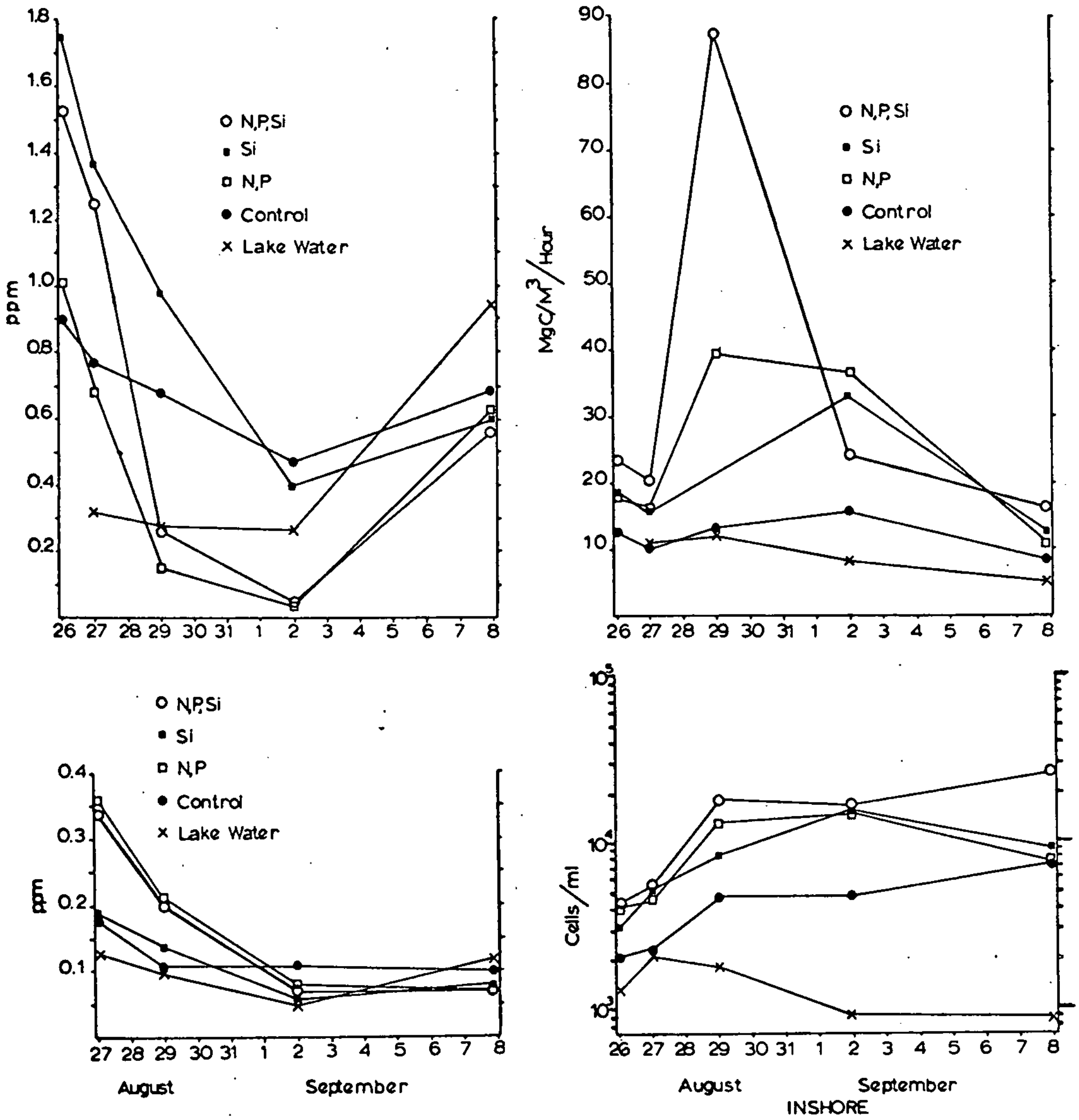

FIG. 3. Results of nutrient enrichment experiments at inshore station, August and September 1969. Experiment started August 26. Upper left corner, soluble SiO_2 in ppm. Lower left corner, soluble NO_3-N in ppm. Upper right corner, rates of carbon fixation in mg C m^{-3} hr^{-1}. Lower right corner, total cell counts in cells per ml.

and more than 10 mg C m^{-3} hr^{-1} at the inshore station. Silica concentrations at the inshore station were greater initially than the enriched treatments at the offshore station. Concentrations of nitrate nitrogen were also greater at the inshore station than at the offshore station.

Even though the initial conditions for the two stations were different, the effects of the treatments were essentially the same. At the inshore station, the greatest increase in rates of carbon fixation and cell counts occurred in the N,P,Si treatment (Fig. 3). The N,P treatment had the next greatest effect. Cell numbers and carbon fixation also seemed to increase in the Si treatment

TABLE 2. *Summary of relative increases in cell counts at offshore station in Lake Michigan in response to nutrient enrichment, July 18 to July 28, 1969**

Species	Abundance	Control	Si	N, P	N, P, Si
Cyclotella stelligera	(1)		3X		XX
C. michiganiana	(6)				3X
Fragilaria crotonensis	(4)	<2X	6X	<2X	XX
Tabellaria flocculosa					4X
T. fenestrata	(2)		2X		3X
Dinobryon divergens	(3)	6X	XX	3X	
Flagellates	(5)			4X	2X
Unidentified green colony		6X	5X	XX	8X

* Experiment started July 17. Abundance indicates rank of cell counts from highest to lowest in control treatment. Key to symbols: 6X = 6-fold increase from July 18 to July 28; XX = > 10-fold increase from July 18 to July 28.

although concentrations of silica were apparently adequate at the beginning of the experiment.

Interpretation of the silica effect is related to the dynamic state of the phytoplankton assemblage when the experiment was started. Increases in cell counts and rates of carbon fixation in the control treatment indicate that the experiment at the inshore station was started during a phytoplankton bloom (Fig. 3). Sufficient nutrients were present initially, therefore, for phytoplankton growth and utilization of silica. In the control treatment cell counts increased from 2000 to 4800 cells ml^{-1} and silica decreased from 0.95 to 0.48 ppm SiO_2. In the presence of added nitrogen and phosphorus (N,P,Si and N,P treatments), the concentration of silica was reduced to about 0.05 ppm SiO_2 by September 2, or about the same level found in these treatments in the experiments at the offshore station (Fig. 2).

As a result of large increases in absolute numbers of phytoplankton early in the experiments, concentrations of nitrate nitrogen were reduced in all treatments at the inshore station (Fig. 3). In the two treatments that contained nitrogen, NO_3-N decreased from 0.35 to 0.08 ppm. If nitrate lost from the water was utilized in phytoplankton production, the quantities utilized were 270 mg m^{-3} in the two treatments containing nitrogen, 120 mg m^{-3} in the silica treatment, and 80 mg m^{-3} in the control treatment.

Species composition of phytoplankton assemblages

More than 50 taxonomic entities were identified and counted in some treatments, but in most experiments six or seven species comprised 80% or more of the counts. Individual species responded differently to the various treatments.

Cell numbers of two diatoms, *Cyclotella stelligera* and *Fragilaria crotonensis*, increased more in the two treatments containing silica than in the two that contained no silica (Table 2). On the other hand, *Dinobryon divergens* increased more in treatments that contained no phosphorus than in those treated with phosphorus. Diatoms require silica for frustule formation and *D. divergens* is a species that reportedly thrives on low levels of phosphorus (Hutchinson 1967). Unidentified flagellates and an unidentified green colony increased in the N,P and control treatments or those treatments lacking silica. The stimulatory effect of the Si treatment on *D. divergens* may be due to the incorporation of silica in the lorica and to utilization of silica in cyst formation, or to both.

In these two sets of experiments in Lake Michigan (Figs. 2 and 3) growth of phytoplankton was enhanced by the presence of silica in combination with nitrogen and phosphorus. Whether phosphorus or nitrogen limited growth was not determined directly. Because the concentration of soluble nitrate nitrogen in all experiments could be reduced below pretreatment levels,

TABLE 3. *Concentrations of particulate phosphate phosphorus in mg PO_4-P m^{-3} in nutrient enrichment experiments at offshore station, July 1969**

Treatments	Dates 17	18	19	21	22	25	28
N, P, Si	4.0	6.3	7.7	9.6	11.0	14.8	20.4
N, P	3.9	6.6	8.6	7.8	9.2	7.7	—
Si	4.4	3.5	3.3	2.9	3.0	3.8	—
Control	4.6	3.6	3.9	3.6	4.2	4.2	—

* Experiment started on July 17.

TABLE 4. *Concentrations of particulate phosphate-phosphorus in mg PO_4-P m^{-3} at inshore station, August and September 1969**

Treatments	Dates 26	27	29	2
N, P, Si	10.8	27.6	21.3	25.6
N, P	9.6	21.5	20.7	14.7
Si	7.2	8.2	6.8	5.3
Control	5.6	6.6	11.3	—

*Experiment started on August 26.

it seems unlikely that nitrate nitrogen was limiting phytoplankton growth in the lake at the beginning of the experiment. On the other hand, when N,P was used as a treatment, phytoplankton growth was stimulated, indicating that phosphorus was the critical element. The same conclusion was reached from results of four other sets of experiments conducted during the period from early June to late September 1969.

EXPERIMENTS WITH PHOSPHORUS

If nitrate nitrogen was not limiting, it seems logical to conclude that the effect of N,P treatments was due primarily to phosphate phosphorus. Measurements of soluble orthophosphate in the water could not be used to substantiate this conclusion because uptake of phosphate by phytoplankton may be due to luxury consumption or to other factors not related to growth. Measurements of total particulate phosphorus, however, were related to growth of phytoplankton as measured by cell counts and to rates of carbon fixation by phytoplankton.

Changes in particulate phosphorus

In the offshore experiment, the concentration of particulate phosphorus in the four treatments averaged 4.2 mg PO_4-P m^{-3} at the beginning of the experiment (Table 3). Results of measurements made during the course of the experiment indicate that greater increases in concentration occurred in the two treatments which contained phosphorus than in those which contained no phosphate. The greatest increase was in the N,P,Si treatment, which also had the largest increase in cell numbers (Fig. 2). In the N,P,Si treatment, particulate PO_4-P increased 16 mg m^{-3}, which represents about 80% of the 20 mg m^{-3} added in the treatment. It should be noted that the average difference between the Si and control treatments is not considered significant.

Particulate phosphorus was present initially in much greater concentrations at the inshore than at the offshore station (Table 4). Initial concentrations in the four treatments probably averaged about 6.4 mg PO_4-P m^{-3}, the average of the two treatments with no added phosphorus; larger concentrations in the N,P and N,P,Si treatments probably reflect rapid uptake of added phosphorus by the large, rapidly dividing phytoplankton assemblage (Fig. 3). Further evidence of rapid accumulation of added phosphorus by the phytoplankton is indicated by the levels of particulate phosphorus, more than 20 mg m^{-3}, in the N,P and N,P,Si treatments on the first day after enrichment (Table 4). The maximum amount of phosphorus in the particulate fraction was 27.6 mg PO_4-P m^{-3} in the N,P,Si treatment and was reached only one day after the start of the experiment. It is apparent that most of the 20 mg PO_4-P m^{-3} added was accumulated in the particulate fraction. For the N,P and N,P,Si treatments, increases in particulate phosphorus were related generally to the increase in cell numbers. As in the previous experiment, however, the increase in cell numbers in the Si treatment is not reflected by an increase in particulate phosphorus. In both experiments, concentrations of particulate phosphorus seem to be the same in the control and Si treatments, indicating that when the experiments were started the

TABLE 5. *Effect of phosphorus on C-14 carbon fixation in nutrient enrichment experiments in Little Traverse Bay near Petoskey, June 1970**

Treatments (in mg m⁻³)	Dates								
	8	9	10	11	12	13	14	15	17
20 P	3.0	1.9	7.5	9.1	10.4	10.8	11.9	19.2	25.4
20 P	2.6	2.2	7.2	8.4	9.9	12.7	9.9	17.5	20.7
40 P	2.5	4.9	6.2	9.8	9.9	9.9	6.6	14.4	24.2
40 P	2.4	5.7	6.6	10.0	9.3	10.0	9.1	20.4	25.1
80 P	1.9	1.3	4.8	8.3	8.0	10.8	10.5	14.9	20.7
80 P	1.5	1.6	5.1	6.1	6.9	9.5	8.1	14.6	19.8
400 N, 80 P	2.1	1.9	5.7	7.9	9.3	12.4	11.4	17.8	34.9
400 N, 80 P	2.0	2.4	5.3	7.6	8.9	11.8	9.6	18.9	25.5
Control	3.0	3.9	4.3	5.3	4.0	3.9	3.6	3.8	4.1
Control	3.1	4.7	4.5	3.9	4.3	3.8	3.0	4.5	4.4

* Experiment started on June 8.

phytoplankton assemblage had accumulated the supply of phosphorus available in the water.

Phosphorus enrichments, 1970

Experiments conducted in 1969 indicated that phosphorus limited growth of phytoplankton. In June 1970, the effect of treatments with phosphorus alone was tested in experiments conducted in Little Traverse Bay.

The effect of duplicate treatments of three concentrations of phosphorus on the rates of carbon fixation was tested (Table 5). Two or three days after the start of the experiment on June 8, the rate of carbon fixation was greater in all treatments than in the controls. After one week there was no apparent difference among the three levels of treatment with phosphorus nor did there appear to be a difference between the treatments with phosphorus alone and the duplicate treatments enriched with nitrogen and phosphorus. These results indicate that phytoplankton growth was limited by phosphorus and that nitrogen was not a limiting nutrient. Why differences in phytoplankton production were not reflected by different levels of phosphorus is not apparent, but nutrients other than phosphorus and nitrogen or other factors may have limited the response to the somewhat consistent level observed among the treatments. Additional data and data analysis for this set of experiments may provide an answer. Hughes and Lund (1962), in laboratory experiments with *Asterionella formosa*, also found that the size of the population was not proportional to the amount of phosphorus added.

Particulate phosphorus and carbon fixation

Phosphorus can be related to eutrophication of Lake Michigan by correlating rates of carbon fixation by phytoplankton with concentrations of particulate phosphorus. Data used were obtained on a cruise on southern Lake Michigan in July 1969 (Schelske and Callender 1970) and from samples of lake water collected in 1969 at the time nutrient enrichment experiments were being conducted. July 1969 data were obtained from stations 2–18 (Fig. 1); stations 7 and 14 were not included because of lack of data, and stations 5, 8, and 10 (Fig. 1) were plotted in Fig. 4 as inshore stations. The correlation coefficients for rates of carbon fixation with concentrations of particulate phosphorus (Fig. 4) were 0.80 for data from 14 stations in southern Lake Michigan and 0.68 for 20 stations including the 14 stations plus six stations collected in July, August, and September from inshore and offshore stations near Grand Haven. Both correlation coefficients are highly significant.

Five sets of data in Fig. 4 were not included in the analysis since four of the five had much higher rates of carbon fixation than the others and one had a very high

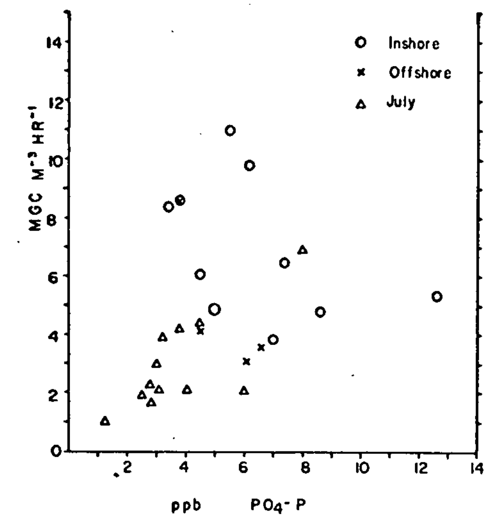

FIG. 4. Plot of rates of carbon fixation (mg C m^{-3} hr^{-1}) versus concentration of particulate PO_4-P (mg P m^{-3}) in samples collected in 1969. Triangles designate data from stations sampled during July in southern Lake Michigan. Crosses designate data from offshore station, and circles designate seasonal data from inshore station.

phosphorus value. The set with the highest rate of carbon fixation was collected August 27 during a phytoplankton bloom and the set with the highest amount of phosphorus was collected on September 8 after or during a period of upwelling (Schelske et al. in press). The fact that all the inshore data are not correlated significantly is probably a reflection of the variability of the inshore environment, which receives "slugs" of nutrients from tributary inflows and upwelled water. We have concluded that two variables cannot describe the dynamic and complex inshore environment (Schelske et al. in press).

No attempt was made to determine correlation coefficients for the data from the nutrient enrichment experiments because nutrients added as slugs would obviously bias particulate phosphorus data. Data in Table 4 indicate that phytoplankton may rapidly remove phosphate added to the water.

Data on rates of carbon fixation in the four upper Great Lakes published by Parkos et al. (1969) and our unpublished data can be used to indicate a relationship between rates of carbon fixation and particulate phosphorus. The rank of the lakes from lowest to highest with respect to carbon fixation rates is Lake Superior, Lake Huron, Lake Michigan, and Lake Erie. Green Bay and Saginaw Bay are more eutrophic and have higher rates of carbon fixation than Lake Michigan and Lake Huron, and are more characteristic of Lake Erie than the lakes of which they are parts. It is well known that concentrations of particulate phosphorus would appear in the same ranking. Our unpublished data on particulate phosphorus in Lake Superior for example, average 2.4 μg P liter^{-1} for 16 stations which had an average rate of carbon fixation of 0.39 ± 0.11 mg C m^{-3} hr^{-1} (Schelske and Callender 1970).

In addition, concentrations of nitrate nitrogen in the four upper Great Lakes can be used to show that nitrogen is not a pri-

TABLE 6. *Average concentrations of soluble silica and nitrate-nitrogen in the Great Lakes.*

Location	No. of stations	SiO_2 (ppm)		NO_3-N (ppb)	
		Surface	Bottom	Surface	Bottom
S. Lake Michigan, July 1969*	16	0.15	1.63	100	220
N. Lake Michigan, Aug. 1969*	16	0.26	1.26	120	220
Lake Superior, July 1969*	20	1.87	2.01	270	280
Lake Superior, July 1970†	34	2.25	2.27	260	260
Lake Huron, July 1970†	19	0.91	1.38	110	150
Lake Erie, W.B., July 1970†	12	0.78	1.00	90	110
Lake Erie, C.B., July 1970†	8	0.22	1.35	36	100
Saginaw Bay, July 1970†	6	1.08	1.06	21	72
Green Bay, Aug. 1969*	10	0.50	—	74	180

* Data from Schelske and Callender 1970. † Unpublished data collected by class in Great Lakes limnology from the University of Mich. Biol. Station, summer 1970.

mary factor in the eutrophication of the three upper Great Lakes. The largest concentrations of nitrate nitrogen in the Laurentian Great Lakes are found in Lake Superior (Table 6), because very little nitrate is utilized by the phytoplankton in the lake. In the other Great Lakes, however, nitrate is utilized by phytoplankton because of higher rates of carbon fixation and larger phytoplankton populations. As a result, lower levels of nitrate nitrogen are present. Our studies with phosphorus demonstrate that added phosphorus is required for the phytoplankton to be able to utilize the available supplies of nitrogen; consequently an inverse relationship would be expected between soluble nitrate nitrogen and total phosphorus or particulate phosphorus within the limits of nitrate supplies. Silica, in addition to nitrate nitrogen, is also present in abundant quantities in Lake Superior, where concentrations of phosphorus are probably too low for enhancement of silica utilization by diatoms.

DEPLETION OF SILICA AND ACCELERATED EUTROPHICATION

Lund (1969) found that Blelham Tarn became more eutrophic after farmers began to apply larger amounts of fertilizer to the surrounding farmland. The mean maximum concentration of phosphate increased threefold and the mean minimum concentration of silica decreased threefold. *Asterionella formosa* at the time of the vernal maximum is usually the dominant diatom, and in six out of 14 years since the trophic change its numbers were more than 10,000 cells ml^{-1}. Prior to the change in trophic state, the maximum population did not exceed 5000 cells ml^{-1}. Lund states, "It seems that this increase in phosphorus, so well known as a major factor in eutrophication, is responsible for the enhanced utilization of silica by the diatoms," but cautions that there is question as to whether the effect of phosphorus is direct or indirect. Larger standing crops of phytoplankton have resulted and concentrations of silica in the water are smaller in the summer than was the case before fertilization.

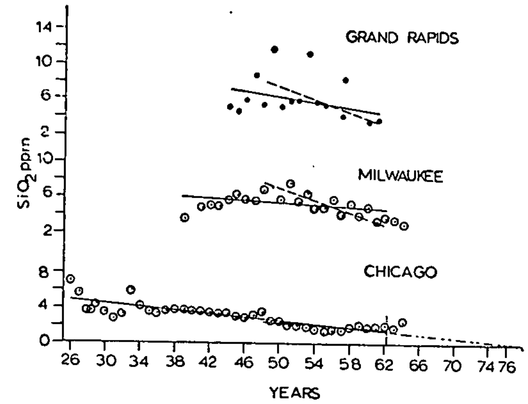

FIG. 5. Concentrations of SiO_2 (ppm) in water samples collected at municipal water intakes, Chicago (from Powers and Ayers 1967).

It has been shown recently that ambient silica concentrations may influence the seasonal succession and dominant species of diatoms (Kilham 1971). Kilham has suggested also that "some measure of silica demand could be used as an index of increasing eutrophication." His data for ambient silica concentrations and species composition may not be applicable for the Great Lakes because silica concentrations as large as the mean of 13.4 mg SiO_2 $liter^{-1}$ cited for *Melosira granulata* do not occur in the Great Lakes (Table 6). *Melosira granulata* (Ehr.) Ralfs and *M. granulata* var. *angustissima* O. Müll., however, do occur as dominants in the plankton; furthermore, these two taxa are indicative in Lake Michigan of highly eutrophic situations (Stoermer and Yang 1970) and not of the early stages of eutrophication, as suggested by Kilham's hypothesis. *Melosira islandica* O. Müll. and *M. italica* subsp. *subarctica* O. Müll., on the other hand, reflect more oligotrophic conditions in Lake Michigan than either of the two taxa of *M. granulata* (Stoermer and Yang 1970). Kilham's hypothesis about demand for silica being a measure of trophic state appears to fit the current situation in Lake Michigan. In Lake Michigan the demand for silica by diatoms is largely controlled by phosphorus.

Concentrations of silica in Lake Michigan have decreased from average levels of tributary inputs (Fig. 5) and we have concluded that the decline resulted from increases in inputs of phosphorus to the lake (Schelske and Stoermer 1971). Data on phosphorus and silica inputs were collected in 1963–1964 by the U.S. Public Health Service and summarized by Ayers (1970). Daily inputs were 5.9×10^3 kg PO_4-P and 5.5×10^5 kg SiO_2; the ratio of SiO_2 to PO_4-P equals 93. Lund (1969) reported that *Asterionella formosa* utilizes silica and phosphorus in a ratio of more than 2000:1. These ratios indicate that 10 to 20 times more phosphorus is being supplied to Lake Michigan than can be utilized by diatoms with the given inputs of silica. The net result is continued depletion of the available silica pool. Obviously in the cycle of each nutrient some fraction of each is returned to the water; but unless the rate of regeneration is much greater for silica, its supply will decrease. It is not likely that silica is regenerated at a greater rate than phosphorus.

Diatoms contain large amounts of silica and the amount varies with species (Lund 1965). On a dry-weight basis, means for different species ranged from 26 to 63%. Amounts per cell varied more among different species—means ranged from 41 to 8500 μg SiO_2 per 10^6 cells. Means for most species, however, were less than 400 μg SiO_2 per 10^6 cells. *Asterionella formosa* contained 140 μg SiO_2 per 10^6 cells, which indicates that other species of diatoms might utilize larger amounts of silica relative to phosphorus than does *A. formosa*.

In both nutrient enrichment experiments, the N,P,Si treatments resulted in the reduction of silica to about 0.05 ppm (Figs. 2,3). Ratios of utilized SiO_2 to particulate PO_4-P were 51:1 in the offshore experiment and 84:1 in the inshore experiment. Greater ratios undoubtedly would have been obtained if larger supplies of silica had been present, since in both cases silica was probably reduced to limiting levels. Depletion of silica with treatments of 20 mg P m^{-3} is also a strong indication that inputs of phosphorus to the lake have caused the observed decline in silica (Fig. 5). Concentrations of particulate phosphorus were generally less than 10 mg PO_4-P m^{-3} and averaged less than 6 mg m^{-3} in 1965 at inshore and offshore stations in Lake Michigan between Ludington and Sturgeon Bay (Holland 1968).

We have also concluded that the changing chemical environment will result in a series of undesirable changes in the biology of Lake Michigan (Schelske and Stoermer 1971). Data for this conclusion were obtained from four sources.

First, phytoplankton assemblages in the past have consisted chiefly of diatoms. All available data and collections of phytoplankton from Lake Michigan dating back to the turn of the century point to this fact (Stoermer 1967). Stoermer and Kopczynska (1967) found that on the basis of cell counts 70% or more of the phytoplankton in the lake in 1962–1963 were diatoms. A supply of silica is essential for the growth and reproduction of diatoms. Recent collections indicate a decrease in dominance of diatoms. Out of 22 samples collected in the fall of 1969, only one contained more than 50% diatoms (Table 7). Half the samples contained less than 15% diatoms. In 1969 the species composition at our offshore station, station 2 near Grand Haven (Fig. 1), also shifted to a smaller percentage of diatoms in August and September (Schelske et al. in press). Blue-green and green algae comprised from 56 to 85% of the total cell counts in late August and early September, and from 30 to 45% of the total cell counts in late September. It is significant to note that the collections with a predominance of blue-green and green algae are also collections that have relatively low cell counts.

Second, the supply of silica in the surface waters has declined over the past 40 years. Powers and Ayers (1967) compiled data collected at municipal water intakes and these data for the South Filtration Plant at Chicago show the downward trend (Fig. 5). The slope of the regression line in Fig. 5 represents a yearly decrease of 0.10 ppm SiO_2. Extrapolation of this line to zero has little meaning since supplies of silica in the surface waters are replenished annually

TABLE 7. *Percentage of diatoms in cell counts of Lake Michigan phytoplankton, 1969**

Station	Position	Date of collection	
		Aug. 23–Oct. 15	Oct. 25–Nov. 9
F-5	45°44.0′N, 86°03.2′W	1.8 (174)	34.0 (244)
EF-2	45°05.5′N, 86°09.0′W	3.6 (167)	26.4 (193)
E-2†	44°37.0′N, 86°20.0′W	11.5 (52)	21.1 (241)
D-1†	43°55.9′N, 86°38.5′W	52.0 (148)	16.6 (647)
D-4	43°48.0′N, 87°01.3′W	10.7 (215)	4.3 (93)
CD-3	43°29.8′N, 86°47.7′W	3.6 (142)	13.3 (135)
CD-6†	43°22.2′N, 87°46.8′W	38.9 (139)	24.3 (300)
C-3	42°48.6′N, 86°29.0′W	7.3 (248)	19.4 (560)
B-4	42°23.5′N, 87°01.5′W	2.1 (144)	6.3 (316)
A-4	42°03.5′N, 87°06.5′W	2.7 (296)	—
AB-1‡	42°08.3′N, 87°33.0′W	29.1 (431)	—
D-6‡	43°43.9′N, 87°39.2′W	24.6 (332)	—
EF-4	45°10.4′N, 86°51.8′W	9.1 (177)	—

* Numbers in parentheses are total cell counts per milliliter; Data supplied by J. C. Ayers. † Inshore station, eastern side. ‡ Inshore station, western side.

during the winter overturn. It does seem logical, however, that the supply in the lake as a whole may be decreasing also, and the limited data available support this line of reasoning (Schelske and Stoermer 1971). Values of less than 0.10 ppm were obtained in southern Lake Michigan in July 1969 (Schelske and Callender 1970).

Third, most of the silica in the euphotic zone in Lake Michigan is apparently utilized early in the summer for diatom growth, as evidenced by low concentrations in surface waters in July (Table 5). Differences in the concentrations of silica between surface and bottom waters (Table 5) are attributable to diatom growth and utilization.

Fourth, enrichments of silica stimulate growth of diatom communities in the lake, as has been shown in the ecological perturbation experiments (Figs. 2, 3). In addition, the enrichment of lake water with small quantities of PO_4-P (20 mg m^{-3}) was sufficient to reduce silica levels to less than 0.10 ppm SiO_2.

These arguments lead to the conclusion that continuation of present inputs of phosphorus and the resultant decline in silica will cause dominant elements of the phytoplankton community of Lake Michigan to change from diatoms to less desirable blue-green or green algae. The exact nature of these changes cannot be predicted precisely on the basis of our studies. Not all the ecological factors that affect the qualitative aspects of the phytoplankton flora, as noted in the introduction, were treated, and our experiments were not designed to study the long-term aspects of species succession. The ability to assess fully the practical consequences of eutrophication induced by silica depletion will depend on additional research directed toward these questions.

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DISCUSSION

SHAPIRO: I wonder if you have calculations concerning what it would cost to raise the silica content in Lake Michigan to keep the population as diatoms instead of blue-greens?

SCHELSKE: This is the third time I have been asked that question in the past month. I now have the data to answer it. The daily input of silica to Lake Michigan is estimated to be 1.2 million pounds as SiO_2. If one wished to increase silica input (and I think we would want to increase it about 10 times), the cost would be the price of 10 million pounds of silica per day in addition to the expense of application.

GOLDMAN: What was your rationale for not using nitrogen and phosphorus separately in the first experiments?

SCHELSKE: The biggest factor was the human factor. We had divers who got very tired. We sampled eight bags a day; the divers filtered samples and did other lab work when they were out of the water. We were unable to run all the possible combinations.

MORTIMER: You were probably very wise in selecting Chicago intake as an early warning system, but what are the winter silica values in the northern part of the lake? What meager historical data are available seem to show that there hasn't been all that much change.

SCHELSKE: What concentrations do you think there are in the wintertime?

MORTIMER: Well, something on the order of 1.5–2.0 ppm as SiO_2. I think it probably shows up that high availability of analytical origin and I think the evidence for a catastrophic decrease in the main basin intake is not all that strong. The Chicago intake, of course, is right at the southern end of shallow water.

SCHELSKE: Figure 1 in the symposium paper indicates the areas we sampled in the summertime. I would agree with you that there aren't any reliable winter data. Table 6 provides data that I didn't point out during my presentation concerning averages in the southern and northern part of the lake. The values come from stations which, I would say, are representative of the whole lake. The values for northern Lake Michigan were exclusive of Green Bay and are a little higher than the stations in the southern part of the lake. In August we had more silica in the northern part than in the southern part in July but the reduction seems to be general over the lake. I would like to obtain some reliable data for the wintertime. We have some numbers from March 1970, but I can't tell you what they are right at this moment.

QUESTION: In the bag experiments, I take it that you didn't measure chlorophyll.

SCHELSKE: We have chlorophyll measurements for the 1970 experiments but not for 1969.

QUESTION: I wonder how your uptakes would look if you measured carbon uptake versus chlorophyll or even carbon uptake versus biomass or cell number? I think these would be more useful; I am sure they would confirm something that might look better. The second question I had concerns (I am not familiar enough with the annual cycle in Lake Michigan) whether you might have a situation where you have this kind of phosphorus-silica interaction at one part of the year, and perhaps a different situation another part of the year. I come from a lake where we can show rather nicely that the main spring phytoplankton that we get is determined by nitrogen, and at that time phosphorus does not appear to be limiting; whereas later on in the year phosphorus is much less in abundance and possibly limiting. So, as has been shown in other situations, you may have different factors being in force in different times of the year. I wonder if something like that might not be the case here?

SCHELSKE: We have done more experiments that we have reported at this meeting—a total of about seven different sets over a period of May through September. In September we did not follow any of the experimental designs shown here so it cannot be included. At all the other times of the year it appears that phosphorus is limiting. In addition, except for inshore areas, harbors, and areas like Green Bay, I have seen no nitrate values for Lake Michigan that are less than 0.1 ppm. I don't think that nitrate is limiting at that concentration.

VALLENTYNE: I just want to check to see if I have correctly understood what you said. You said that dissolved silica is decreasing in Lake Michigan. Am I correct in believing that your interpretation is that this is because other nutrients have been put in which then permit diatoms to take more silicon out?

SCHELSKE: It is primarily phosphorus, not other nutrients.

VALLENTYNE: Are you saying that it might be a good thing, where possible, to put some silicon in? That in this way growth could be shifted in favor of diatoms rather than blue-green algae?

SCHELSKE: No, I think this would increase the numbers of diatoms and Dr. Stoermer's work indicates that it would be the wrong kind of diatoms.

STOERMER: We already have nuisance blooms of diatoms but an increase in silica content would only increase the nuisance blooms.

EDMONDSON: Is that conclusion confirmed by observed changes in the rate of sedimentation of silica or of diatom counts in sediments?

SCHELSKE: Dr. Stoermer isn't close to the microphone; but, if I remember correctly, his work on the diatoms and sediments in Lake Michigan indicated that there aren't any diatoms in the sediments.

EDMONDSON: So where has the silica gone?

SCHELSKE: My theory on this, and it is only theoretical, is that because of water circulation patterns, deposition is not uniform throughout the lake.

SHAPIRO: Have you looked at the trace elements at all? I am leading up to something. We did experiments in Lake Superior; the only two things that stimulate the system in Lake Superior are phosphorus and manganese, alone or in combination. Silicate of course is very high and nitrate is very high. Iron has no effect. Is there any evidence of manganese being deficient?

SCHELSKE: I think that to answer that question I would like to go back to something that Dr. Vallentyne asked this morning—that is about taking things out of enrichments to study effects. My approach is that if you add one or more nutrients to a system and obtain a response, then those nutrients were limiting and were added at a level sufficient to cause the responses that were obtained. I don't think you have to add a number of things and then leave them out to determine if one is deficient. If the system responds, we have to assume that only the nutrients in the treatment were deficient at the time of the experiment. We did an experiment which shows the problem of adding a large number of nutrients. We added nitrogen, phosphorus, silicate, and several trace metals including manganese. We got nothing out of that experiment because we killed or inhibited the growth of the phytoplankton. I think the concentrations of trace metals were more suitable for algal cultures than they were for Lake Michigan phytoplankton. We have to realize that the phytoplankton populations, even though we say that Lake Michigan is becoming eutrophic, are adapted to low nutrient concentrations.