Effects of nutrient enrichment on Georgetown Lake plant communities
by Peter Laurens Boveng

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biological Sciences
Montana State University
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Abstract:
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in

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MONTANA STATE UNIVERSITY
Bozeman, Montana

March 1985

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4/2/85
Date

Daniel Goodman
Chairperson, Graduate Committee

Approved for the Major Department

3 April 1985
Date

Robert C. Moore
Head, Major Department

Approved for the College of Graduate Studies

4-4-85
Date

M P Malone
Graduate Dean

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Date 27 MARCH 1985

ACKNOWLEDGMENTS

I offer my most sincere gratitude to my advisor, Dr. Daniel Goodman, for inspiration, for prompt and helpful critiques, and most of all, for his patience. I thank the other members of my committee, Dr. C. M. Kaya, Dr. T. W. Weaver, and Dr. M. A. Hamilton for their many helpful comments and especially for accomodating my frantic schedule in the few weeks prior to finishing. Dr J. C. Priscu kindly analyzed macrophyte tissue samples, and provided helpful comments on a draft.

Dr. Paul Garrett, in addition to providing guidance as Project Scientist of the Georgetown Lake Project, shared in the long hours of field and lab work and was a fine companion. The Biology Department staff, Dee Griffith and Gisela Knupp, steered me through innumerable administrative curves. I thank fellow graduate students for inspiration and encouragement and I am particularly grateful to Chris Randolph for the brute force which he was able to apply when the time came to remove experimental apparatus from the field.

My parents have given me freedom, encouragement, and support of many kinds. They have born the burden of my whims and fancies throughout my education. My debt to them is immeasurable.

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ABSTRACT

The Georgetown Lake Clean Lakes Project was designed to evaluate macrophyte control measures including herbicides, harvesting, and winter drawdown of the water level. Each of these measures has the potential for release of nutrients to the water. In the summer of 1982, enrichment experiments were conducted on isolated communities of macrophytes and phytoplankton to determine the short term fate of added phosphorus. Measurements of common limnological parameters including pH, alkalinity, conductivity, dissolved and total phosphorus, ammonia nitrogen, and chlorophyll were made at the enclosed sites. Similar measurements were made at open water sites to provide continuity with previous studies. Phytoplankton species composition and succession are described.

Limnological conditions in 1982 were similar to those described in studies made in 1973-1975 and 1981. The enrichment studies showed that some of the added phosphate appeared in the particulate fraction within several hours. However, most of the phosphorus was still unaccounted for at the end of the experiment and it appears that much of it may have simply precipitated owing to conditions of high pH and available calcium. No increase in nitrogen or phosphorus content was observed in the macrophyte tissue from the enriched site. Enrichment resulted in elevated densities of phytoplankton but did not cause appreciable shifts in the species composition. Rather, the major differences in species composition were between enclosed and open water sites.

INTRODUCTION

The fate of a nutrient such as phosphorus or nitrogen, released into a freshwater lake, is an important aspect of the ecology of aquatic plant communities. Consider an atom of phosphorus, dissolved as phosphate ion in the water column. Whether its source was natural or cultural, its existence in the dissolved phase would likely be short lived. Planktonic and benthic plants and bacterioplankton are capable of taking dissolved phosphorus directly from the water column. In addition to biological processes which can remove nutrients from the dissolved phase, there are physical processes such as adsorption to suspended solids or to the sediments. This thesis describes a study of some of these processes as they occurred in Georgetown Lake, Montana in 1982.

Georgetown Lake is a reservoir located approximately 27 km northwest of Anaconda, Montana. The reservoir's importance as a multiple use resource has prompted several limnological studies (eg. Knight et al. 1975, Foris 1976, Garrison 1976, Geer 1977, Knight 1980, and Garrett 1983a,1983b). The data presented in this paper were collected as part of the most recent study, the Georgetown Lake Project, which was sponsored by the Environmental Protection Agency's Clean Lakes Program.

The Georgetown Lake Project sought, among other objectives, to evaluate the options available for controlling macrophyte growth while

maintaining the multiple use characteristics (Garrett 1983a). Among the alternatives considered for macrophyte control were treatment with herbicides, mechanical harvesting, and winter drawdown of the water level.

Each of these control measures has the potential for release of substantial quantities of nutrients to the water column. Herbicide treatment and mechanical harvesting, if not accompanied by removal of dead plant material, would release nutrients when the macrophyte tissue decayed. Nutrient release after a winter drawdown would probably be increased by the physical effects of ice disturbing the exposed littoral sediments (Dunst et al. 1974) as well as decomposition of plant material.

Economic considerations would probably limit harvesting or herbicide treatment to specific problem areas of the reservoir where dense macrophytes interfere most with recreational uses (Garrett 1983a). Consequently, under these treatments, there would be large portions of the lake in which undisturbed macrophyte communities would remain along with the corresponding plankton communities.

Winter drawdown would, likewise, only kill macrophytes in a limited area. The associated pulse of released nutrients would occur in the spring, at an early stage in the macrophyte's seasonal development, as contrasted with the summer release of nutrients from a harvest or herbicide application. These considerations lead to questions about the effect of increased nutrient load on both the attached and planktonic plants of Georgetown Lake.

With respect to the macrophytes, there is an obvious need to know whether spatially or temporally localized treatment of plants would simply aggravate problems with macrophyte density elsewhere, or at a later time. To a large extent, this would be determined by the effectiveness of phytoplankton competition with the macrophytes for the released nutrients.

Enrichment of a lake with nutrients may cause both quantitative and qualitative responses in the phytoplankton (Schindler and Fee 1974; Edmondson 1972). Quantitative responses are expressed as increased growth rates and/or increased standing crops. Such increases can be detrimental due to loss of aesthetic and recreational qualities. Qualitative responses are expressed as changes in the species composition of the phytoplankton community. More specifically, the frequencies of taxa which are capable of causing nuisance conditions (such as tastes, odors and toxins) often increase in lakes with increased nutrient loads (eg. Edmondson 1972). As Lynch and Shapiro (1981) have shown, the relative intensities of the quantitative and qualitative responses are dependent on a number of factors including the abundance of herbivores and their predators.

Experiments to determine the effects of nutrient enrichment on plant communities have been done on a 'whole lake' basis (Schindler 1974), but this was not a practical option for Georgetown Lake for several reasons. First, the heavy use of the reservoir for recreational purposes and of the shoreline for residential purposes, made a whole lake fertilization experiment unacceptable due to

potentially dramatic impacts on the users. Second, the size of the lake would make it economically difficult. Accordingly, it was decided in this study to enclose small portions of the lake for experimentation.

Enclosures of various types have apparently been used successfully in studies of nutrient dynamics (Lean and Charlton 1977) and aquatic plant community ecology (Lie 1979). Marine researchers have used enclosures to study the effects of metals and organic pollutants on several trophic levels from bacteria to fish (Menzel and Case 1977; Menzel 1977). Although enclosures provide advantages such as reducing the size of costly experiments, reducing complexity, and containing of harmful agents, the isolating structures themselves can have their own effects on the experimental system.

For example, during the 1981 field season of the Georgetown Lake Project, several enclosed littoral communities, which were scheduled to receive different treatments in a study of nutrient cycling, failed to track conditions in the natural communities by such a wide margin that they were deemed useless for the intended purpose. Because the use of enclosures --or mesocosms, as they are sometimes called-- is an attractive strategy (Odum 1984), this study will serve as an evaluation of the several types of enclosures used during the course of Georgetown Lake Project experiments.

Summarizing the ideas above, the objectives of this study were to:

1. Measure and describe relevant limnological parameters

in the reservoir during the course of Georgetown Lake Project experiments.

2. Describe the effects of nutrient enrichment on the density of phytoplankton.
3. Test the hypothesis that enrichment with nitrogen and phosphorus will lead to increased proportions of blue-green algae in the species composition.
4. Estimate the rate of removal of phosphorus from artificially enriched water by plant communities consisting of a) isolated phytoplankton, and b) macrophytes with phytoplankton.
5. Trace the fate of phosphorus in the plant communities on the time scale of a few hours, and attempt to construct a phosphorus budget for the entire growing season.
6. Evaluate the effectiveness of using enclosures for aquatic plant ecology research.

DESCRIPTION OF THE STUDY AREA

The historical, geographical, and geological features of Georgetown Lake and its drainage basin have been described several times, perhaps most completely by Knight (1980) and Garrett (1983b). Only a brief summary is given here.

Georgetown Lake is a reservoir located at latitude 46°10'16" N and longitude 113°10'42" W. The first impoundment was built in 1885 and was raised to its present level in 1919. At full pool, the mean depth is 4.89 m and maximum depth is 10.7 m. The surface area is 1219.2 ha and the surface elevation is 1959.7 m.

The area of the drainage basin is about 14,000 ha. Uses of the reservoir include summer and winter recreation, and permanent and seasonal residence. Logging, mining, and ranching are practiced in the surrounding basin.

METHODS AND MATERIALS

Sampling Sites and Schedule

Sampling sites were of two types, enclosed and open. The sites which were not enclosed will be refered to as open water sites, regardless of distance to shore or macrophyte coverage. Names and locations of sampling sites are shown in Figure 1. Site I was in open water near the dam at the deepest point (10 m) in the reservoir. The bottom at site I was smooth and silty, with no macrophyte growth. This site was sampled to provide continuity with the other Georgetown Lake studies, as it is the only one which has been consistently sampled (Knight, et al 1976; Garrett 1983b).

Several vinyl "limnocorrals" of various sizes were purchased from Kepner Plastics, Inc., Torrance, California. These enclosures were fabric-reinforced vinyl curtains with a flotation collar at the top and a heavy steel chain sewn into the bottom. The flotation collar extended above the water surface and the weighted bottom was embedded in the sediments to isolate the water column. The integrity of the seal was not tested directly, but the persistence of chemical, physical, and biological conditions which were dramatically different from the conditions outside the enclosures used in 1981 (Garrett 1983b; this study) implies that there was no substantial mixing.

Rigid frames were installed around all of the enclosures. These

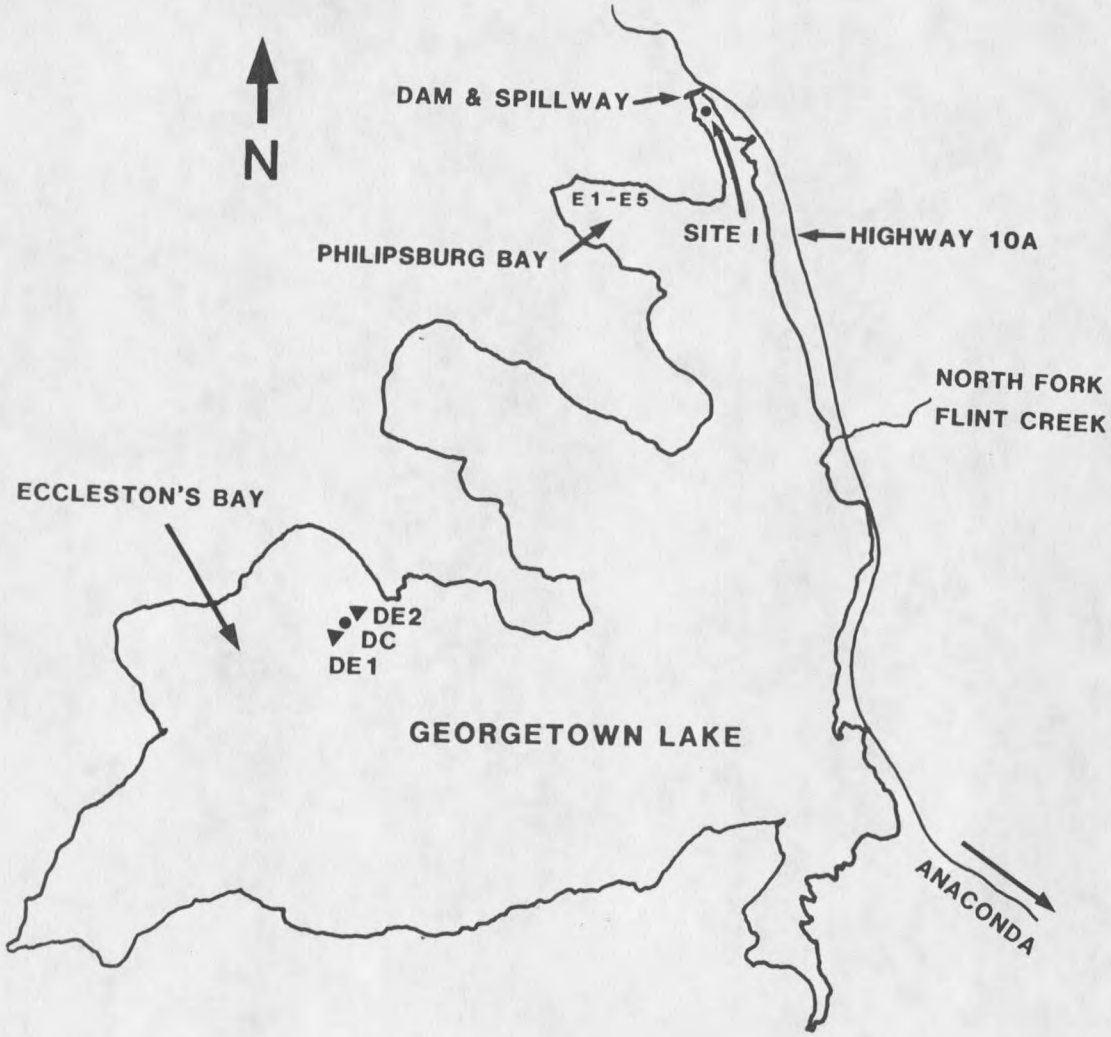

Figure 1. Map of Georgetown Lake showing sites sampled, 1981-82.

frames were wooden, in the form of triangles, 3.67 m on a side.

Five of the triangular enclosures were installed in Philipsburg Bay (designated E1-E5), surrounding shallow (about 2 m) macrophyte beds dominated by of Elodea. These five enclosures were maintained and sampled from July 1981 to June 1982. Garrett (1983a;1983b) reported some of the findings from analyses of water chemistry and other limnological parameters at these sites; Boveng (1983) reported on the phytoplankton communities in these enclosures. This study will summarize data relevant to evaluation of the performance of the enclosures.

For the summer 1982 field season, two new enclosures were made for use in deep water macrophyte communities. These enclosures were 5 m deep but otherwise the dimensions were the same as E1-E5. Clear vinyl windows were installed over about 85% of the wall surface area. These enclosures, designated DE1 and DE2, were installed over communities consisting entirely of Potamogeton praelongus in 4.7 m of water near the mouth of Eccleston's Bay (Figure 1). Site DE2 was chosen for fertilization treatment with phophorus and nitrogen. Site DE1 was used as an unfertilized control site to determine the effects of the enclosure itself on the community within. A third site at this location, designated DC, was an open water control site next to the enclosures, with the same type of plant community as DE1 and DE2.

Table 1 shows the dates during the summer of 1982 on which particular sites were sampled for water chemistry, chlorophyll, and phytoplankton. Site DC was sampled on 9 July 1982 to establish the

initial conditions at the experimental enclosure area. Enclosures DE1 and DE2 were installed immediately after sampling DC. At site DE2, all sampling for water chemistry and other limnological parameters was done immediately before each fertilization event. In addition to the routine sampling schedule reported in Table 1, three experiments were done to determine the short term fate of phosphorus added on 14 August, 26 August, and 9 September.

Table 1. Sampling schedule, summer 1982.

Date	Site			
	DC	DE1	DE2	I
9 July	X			X
21 July	X	X	X	X
28 July	X	X	X	X
3 August	X	X	X	X
13 August	X	X	X	X
25 August	X	X	X	X
7 September	X	X	X	X

Site DE2 was fertilized with phosphorus and nitrogen. Phosphorus was added as KH_2PO_4 and nitrogen was added as KNO_3, according to the schedule shown in Table 2. The fertilization rates were intended to fall in the range of concentrations that might be expected from nutrient release caused by the macrophyte control methods discussed in the introduction. These rates were based on an estimated 65 % areal coverage of macrophytes, a mean depth of 4.89 m, an average of 250 g/m^2 dry weight macrophyte biomass, 0.25 % phosphorus content, a P:N mass ratio of 1:7 (molar ratio of 1:15.5), and an 8 week decomposition period (Garrett 1983b).

Table 2. Fertilization schedule for site DE2, summer 1982. Enclosure DE2-S is described in the phosphorus fate section. Additions to enclosure DE2-S were counted in cumulative additions to DE2 because DE2-S was emptied into DE2 after each phosphorus fate experiment.

Date	Site	Phosphorus Added (g)	Cumulative P Added to Site DE2	Nitrogen Added (g)	Cumulative N Added to Site DE2	Target [P] (mg/l)
21 Jul	DE2	0.347	0.347	2.427	2.427	0.01
28 Jul	DE2	0.347	0.694	2.427	4.854	0.01
3 Aug	DE2	1.735	2.429	12.145	16.999	0.05
14 Aug	DE2-S	0.055		0.384		0.10
"	DE2	3.412	5.986	23.884	41.267	0.10
26 Aug	DE2-S	0.027		0.189		0.05
"	DE2	1.706	7.629	11.942	53.398	0.05
9 Sep	DE2-S	0.025		0.173		0.05
"	DE2	1.504	9.158	10.528	64.099	0.05

Sampling methods

All water samples were collected through Tygon tubing with a battery powered peristaltic pump. Depth stratified samples were made by lowering the end of the tube to the desired depth and then pumping, allowing time for the overlying water to flush through the pump. Depth integrated samples were collected by pulling the tube end through the desired range of depths while pumping. Samples for community metabolism studies were depth-stratified. All other samples were depth integrated from the surface to about 10 cm above the bottom.

A portion of each sample was filtered in the field using Whatman GF/C filters. The filters were placed in 90% aqueous acetone for extraction of chlorophyll. The filtrate was saved for determination of dissolved nutrients in the laboratory.

Water Chemistry

Analyses for phosphorus were done by the ascorbic acid method (APHA 1980). Soluble inorganic phosphorus (SIP) was defined as that quantity detectable in a filtered sample. Total soluble phosphorus (TSP) was that quantity detectable in a filtered sample after digestion with potassium persulfate. Total phosphorus (TP) was the quantity detectable in an unfiltered sample after persulfate digestion. Concentrations of all phosphorus species were computed and expressed as mg P/l.

Ammonia nitrogen was measured in filtered samples by the

phenolhypochlorite method (Solorzano, 1969). Concentrations of ammonia nitrogen were computed and expressed as mg N/l.

Alkalinity was measured using the pH potentiometric method (APHA 1980) with an endpoint of 4.5. Alkalinity values were computed and expressed as milliequivalents per liter (meq/l).

Conductivity was measured in the laboratory with a Yellow Springs Instruments model 31 conductivity bridge.

Chlorophyll

Measured volumes of water from each site were filtered with glassfiber (Whatman GF/C) filters in the field. The filters were immediately immersed in 20 ml of 90% acetone, placed on ice for transport to the laboratory, and stored in a freezer until analysis.

The optical densities of the acetone extracts were measured at 750 and 665 nm before and after acidification with 6 N HCl (Strickland and Parsons 1968). A recent study (Wilkinson 1983) has shown that the older acidification procedure is too vigorous and results in an absorbance shift for chlorophyll a greater than that which corresponds to the commonly used maximum acid ratio of 1.70 (The maximum acid ratio is the ratio of the absorbance of pure chlorophyll a before acidification to the absorbance after acidification.) From the results of Wilkinson (1983) a maximum acid ratio of 1.84 was computed for the chlorophyll a calculations of this study.

The equation used to compute chlorophyll a corrected for phaeopigments was

$$\text{Chl } a = (E_a - E_b) * (t/t-1) * k * (v/V * l)$$

where E_a is the extract absorbance at 665 nm minus the absorbance at 750 nm before acidification and E_b is the corresponding quantity measured after acidification, t is the maximum acid ratio (1.84), k is 1000 divided by the specific absorption coefficient (89 l*g/cm), v is the extract volume, V is the volume of water filtered, and l is the optical path length in cm (Wilkinson 1983).

Phytoplankton

A 125 ml subsample of the water collected for chemical analyses at each site was preserved with 3.0 ml of a mixture (FAA) of formalin, acetic acid, ethanol, and distilled water as in Prescott (1978). Fresh material, for use in taxonomic identification, was taken directly from the water chemistry samples in the laboratory.

Appropriate volumes of the preserved samples, dependent on the density of cells, were stained with iodine-potassium iodide solution (Prescott 1978) and concentrated onto Millipore HA membrane filters (25 mm diameter, 0.45 um pore size). Vacuum was limited to 167 mbar in order to minimize cell damage. Permanent microscope slide mounts were prepared from the filters after clearing with immersion oil (McNabb 1960).

A computer program was used to choose random coordinates on the slides for enumeration of the plankton. These coordinates were in

terms of the units on the Vernier scales of a movable microscope stage. The coordinates were checked for overlapping fields which were not counted. Records were kept of the locations of fields counted for each sample so that counts or taxonomy could be checked or repeated if necessary.

Counts were made under at least two magnifications between 150X and 1350X, depending on the size distribution of the predominant taxa. At each magnification, a number of fields sufficient to ensure observation of at least 100 individuals of the most abundant taxon were counted. Concentrations of phytoplankton in the lake were calculated by scaling the area counted to the total area on the filter and accounting for the volume of sample filtered.

Estimates of the standing crop of phytoplankton were made on a cell volume basis by multiplying cell numbers by an estimate of the representative cell volume for each taxon. Representative cell volumes were calculated in two ways. If the geometry of a cell was a simple one with a known volume formula, the appropriate cell dimensions were measured and the volume computed accordingly (Wetzel 1975). More complex shapes were modeled in sculptor's clay, and the displacement volumes of the models were scaled according to the actual cell dimensions.

Because preserving, staining and filtering distorts the cells of some taxa, fresh material from each sample was examined after concentration by gentle centrifugation. Lists of the taxa present and rough estimates of their relative abundance in the fresh material

were used to check the taxonomy of the preserved slides. Prescott (1962,1978), Patrick and Reimer (1966), Hustedt (1930), and Smith (1950) were used for taxonomic identification.

Phosphorus fate experiments

For the short term (approximately 36 hr) phosphorus experiments (14 August, 26 August and 9 September 1982), planktonic communities were isolated from macrophytes and sediments by using small-volume enclosures made from clear vinyl. These enclosures were tubes, 0.42 m in diameter and 4.0 m deep. The tubes were suspended vertically from float rings, and flat bottoms were sealed into the tubes with large pipe clamps. A bucket was used to fill each small enclosure with water from the appropriate site.

One of the small enclosures (DE2-S) was placed inside enclosure DE2, thereby isolating a fertilized plankton community from a fertilized whole community. Another small enclosure (DC-S) was placed at site DC, isolating a previously unfertilized plankton community from the intact community at the control site. The small enclosures were in place only during the three phosphorus experiments (i.e. were removed between experiments).

In the first phosphorus experiment, on 14 August, DE2-S was spiked with 54.8 mg of P and 383.6 mg of N (Table 2). In this, and the other two phosphorus experiments, DC-S was fertilized at the same rate as DE2-S. The community inside DE2 but excluded by DE2-S was spiked with an additional 3.412 g of P and 23.884 g of N (Table 2).

Monitoring the concentration of SIP at those sites during the subsequent 24 hours served to establish that in all sites there were detectable losses of P from the soluble inorganic pools.

In the other two phosphorus experiments (26 August, 9 September), the same enclosures were spiked according to the schedule in Table 2. In order to determine the fate of P disappearing from the dissolved inorganic pool, the levels of soluble inorganic phosphorus, total soluble phosphorus, and total phosphorus were all monitored. The P levels were measured immediately after spiking and at six times spread over the ensuing 36-38 hours in both experiments.

A laboratory experiment was conducted to determine whether orthophosphate is adsorbed by the vinyl material of the enclosure walls. Vinyl was incubated in known concentrations of phosphate ion at the same surface to volume ratio as existed in the enclosures. After 48 hours, no difference could be detected between the phosphate concentrations in solutions exposed to the vinyl and those not exposed to the vinyl.

Community metabolism

Measurements of community metabolism were made concurrently with the second and third phosphorus fate experiments by the diel pH-CO_2 method (Odum and Hoskin 1958; Park et al 1958; Beyers et al 1963). This method uses changes in pH to infer quantities of CO_2 fixed or released by the community. Community metabolism was measured in the enclosures (DE1, DE2) and the control (DC), as well as in plankton

isolates at each site (DE1-S, DE2-S and DC-S). Solar insolation during the community metabolism measurements was recorded with a Kipp and Zonen Model CM-3 pyranometer (Garrett 1983b) at the Montana Department of Fish, Wildlife and Parks cabin where U. S. Highway 10A crosses the North Fork of Flint Creek (Figure 1).

Macrophyte biomass and tissue analysis

On 28 July 1982 the heights of all *Potamogeton praelongus* stems in sites DE1 and DE2 were measured to the nearest 0.1 m. The measurements were made by SCUBA diving outside the enclosures and sighting against markers fixed in the enclosures.

The entire stands of *Potamogeton praelongus* at sites DE1, DE2, and DC were harvested at the termination of the field study on 20 September 1982 by SCUBA diving and gathering the plant stems into bags by hand. All the above-sediment biomass was collected from each site. The roots of this species are generally small and easy to pull from the sediments but a few stems broke in the harvesting process, leaving a small but unquantified portion of the root biomass in place.

The samples were frozen until just prior to analysis when they were dried at 70° C. Dry weights were recorded for each sample. Samples of leaf tissue and representative samples (approximately 20 g) of whole plant tissue were ground with a mortar and pestle and stored in a dessicator.

The samples were analyzed for carbon and nitrogen content using a Carlo-Erba model 1106 elemental analyzer standardized with

acetanilide by Dr. John C. Priscu, Biology Department, Montana State University. Total phosphorus was measured by the ascorbic acid method (APHA 1980) after ashing with magnesium nitrate and digestion in sulfuric acid.

RESULTS AND DISCUSSION

Conductivity

The specific conductance of the water decreased at all sites during the 1982 summer season (Figures 2 and 3). The conductance at site I (Figure 2), was lower initially but did not decrease by the end of the summer to levels as low as those at the sites in the experimental area (Figure 3). The trend was interrupted by an increase in conductance on 3 August at all sites. This increase occurred at the same time as the observed peak in phytoplankton standing crop at most sites.

There was an initial drop in conductance in the enclosures (DE1 and DE2) relative to the control (DC), but by 25 August the three sites were nearly the same. The conductance continued to decrease in fertilized DE2 but increased slightly at DC and DE1 by 7 September.

Alkalinity and pH

At most sites, the general trend was a decrease in alkalinity as the summer season progressed (Figures 4 and 5). The alkalinity increased slightly at site I at the beginning of the season and increased at site DC on the last sampling date. The alkalinity at DC was slightly higher than in the enclosures except on 25 August when the levels were 1.60 meq/l at DC and 1.64 meq/l in DE2.

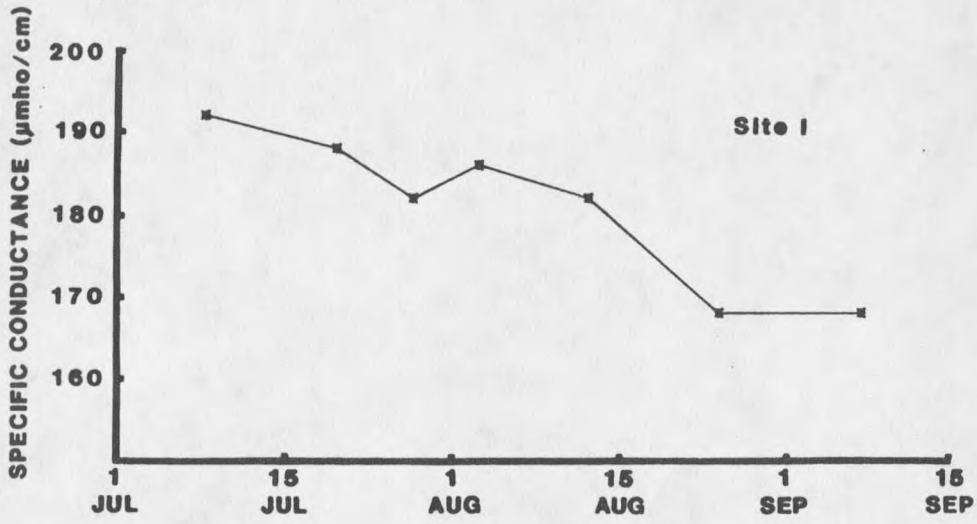

Figure 2. Specific conductance at site I.

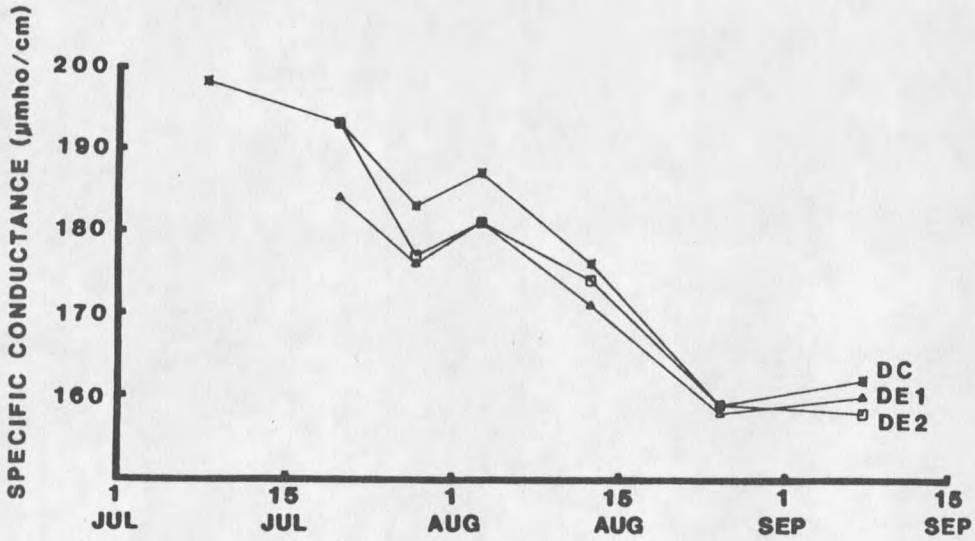

Figure 3. Specific conductance at sites DC, DE1, and DE2.

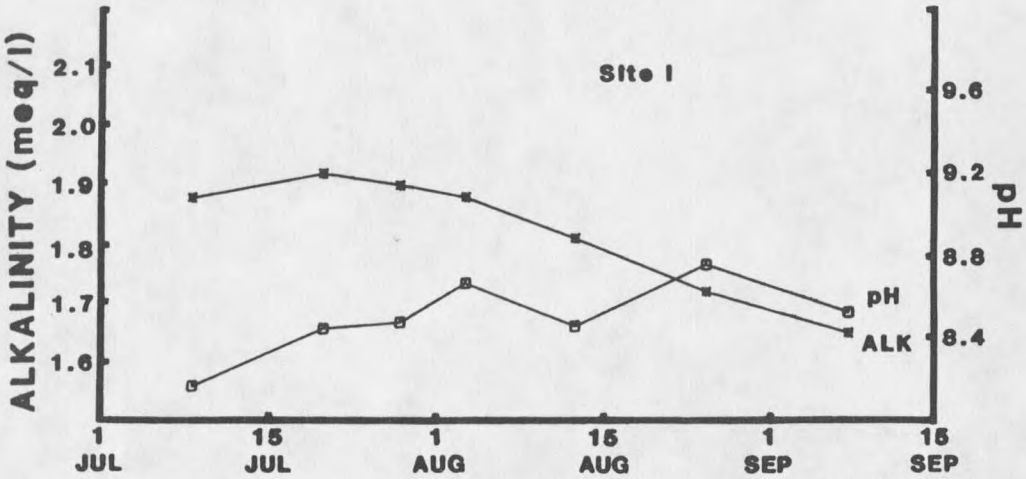

Figure 4. Alkalinity and pH at site I.

The pH values increased with time but the trends were somewhat less regular than those of the alkalinities. There was a peak in pH value common to all sites on 25 August. The highest pH observed was 9.16, at DE2 on that date (Figure 5). The pH values in Figures 4 and 5 were measured in the lab as initial points for the alkalinity titrations. Higher pH's were measured in situ during diel community metabolism measurements but they are not directly comparable to the lab values. As Knight (1981) and Garrett (1983b) showed, the high pH values of Georgetown Lake during periods of high production represent a condition of undersaturation of CO_2. The pH's measured in the lab may have have been lowered by absorption of atmospheric CO_2 after collection, but this should not have affected the alkalinity measurements (Stumm and Morgan 1981).

There was an initial drop in pH of the enclosed sites relative

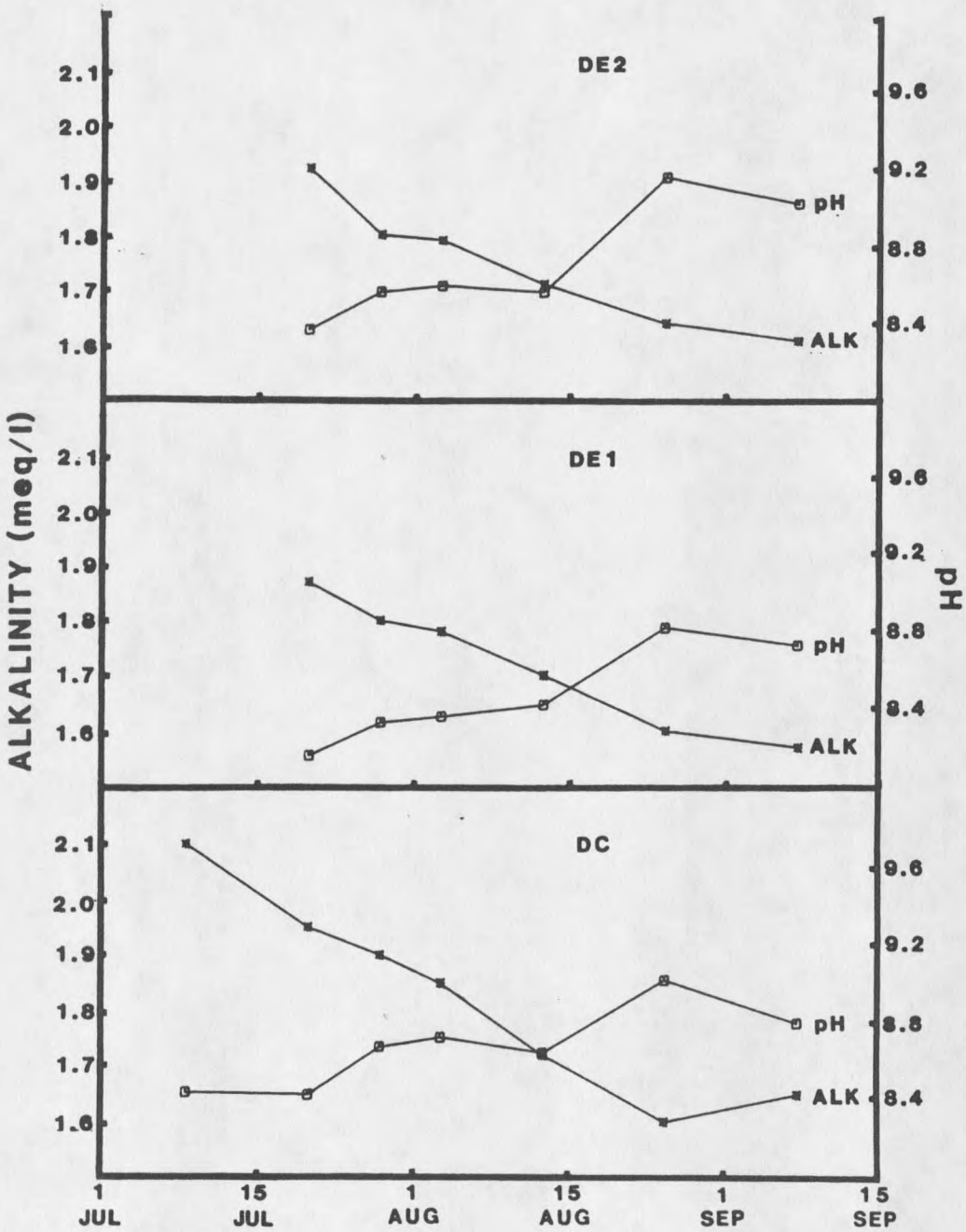

Figure 5. Alkalinity and pH at sites DC, DE1, and DE2.

to the control. The pH in DE1 remained below that of DC, but in DE2, the fertilized enclosure, the pH increased to levels above those of DC by the end of the experiment.

The observed trends in conductivity, alkalinity, and pH are commonly observed and can all be related to plant production and the inorganic carbon system of a calcium carbonate dominated lake such as Georgetown (Knight 1981). Photosynthetic removal of carbon dioxide from the water causes an increase in pH and, if accompanied by uptake of bicarbonate, ammonium, and phosphate, a decrease in alkalinity (Stumm and Morgan 1981). In addition, the increased pH can cause precipitation of calcium carbonate onto macrophyte leaf surfaces or in water from which it settles to the bottom (Wetzel 1975). The dissolution of $CaCO_3$ is much slower than the precipitation reaction which, along with the slow rate of invasion of atmospheric CO_2, produces a condition of undersaturation of CO_2 for much of the summer season. The observed decreases in conductivity presumably were the result of these biologically mediated removals of ionic species from the water column.

Ammonia nitrogen

Nitrogen detectable as ammonium ion (Table 3) dropped rapidly to levels below the detection limit at all sites by 28 July. The ammonium levels remained below detectable levels until 25 August, at which time there were low but detectable quantities at all sites. By 7 September, there were moderate levels of nitrogen detectable as ammonium at all sites.

Table 3. Concentrations of nitrogen present as ammonium ion, 1982. Dashed entry indicates concentration below level of detection.

Date	Ammonia Nitrogen (mg N/l) DC	DE1	DE2	I
9 July	.017			.005
21 July	---	.013	---	---
28 July	---	---	---	---
3 August	---	---	---	---
13 August	---	---	---	---
25 August	.001	.005	.003	.003
7 September	.007	.011	.007	.007

Phosphorus

The most notable features in the trajectory of soluble inorganic phosphorus (SIP) at site I were the two peaks occurring on 28 July and 25 August (Figure 6). On those dates, SIP constituted a relatively large portion of the total phosphorus (TP). SIP was low at sites DC and DE1 (Figure 7), except for a level of .009 mg P/l on 3 August. SIP increased in the fertilized enclosure to .012 mg P/l on 25 August and dropped to .007 mg P/l on 7 September.

The total soluble phosphorus (TSP) levels, which include both organic and inorganic fractions, seemed to track the SIP levels at all sites. This indicates that the soluble organic phosporus (TSP-SIP) maintained a fairly constant level and the fluctuations in total soluble phosphorus levels were primarily due to variation in the inorganic portion.

Variation in total phosphorus (TP) was generally slight when compared to the corresponding variation in the soluble components

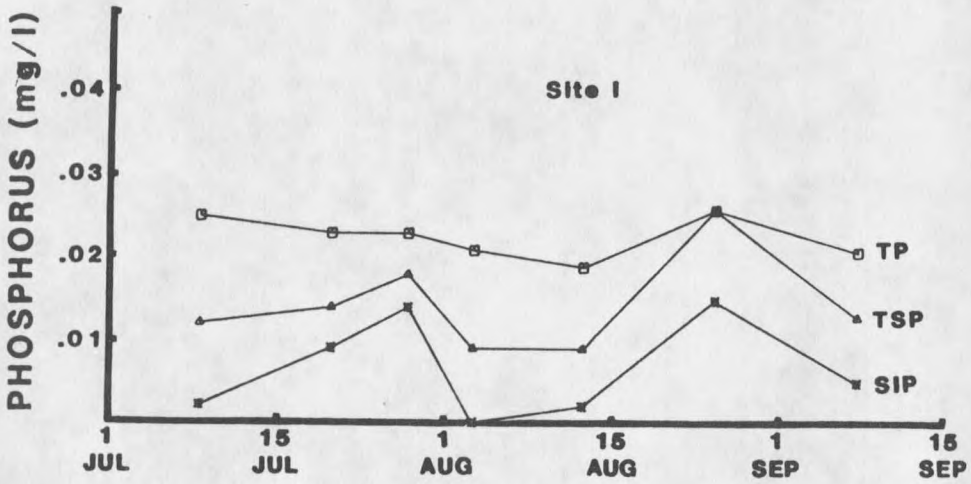

Figure 6. Levels of soluble inorganic P (SIP), total soluble P (TSP), and total P (TP) at site I.

(Figures 6 and 7). However, at site DE2, the fertilized enclosure, total phosphorus showed the greater variation, increasing to about 0.045 mg P/l on 25 August 1982. Discussion of these results is presented in the phosphorus budget section.

Phytoplankton standing crop

Chlorophyll

Chlorophyll a (Chl a) levels, corrected for phaeopigments, are presented in Figures 8 and 9. At site I, Chl a ranged between 3 and about 9 mg/m^3, with peaks on 3 August and 25 August. At site DC, the open water control for the enclosures, the concentration of Chl a ranged between about 3 and 6 mg/m^3, but there was a steady, gradual increase rather than two peaks. Chl a at both of the enclosed sites dropped to low levels (relative to DC) at the onset of the experiment.

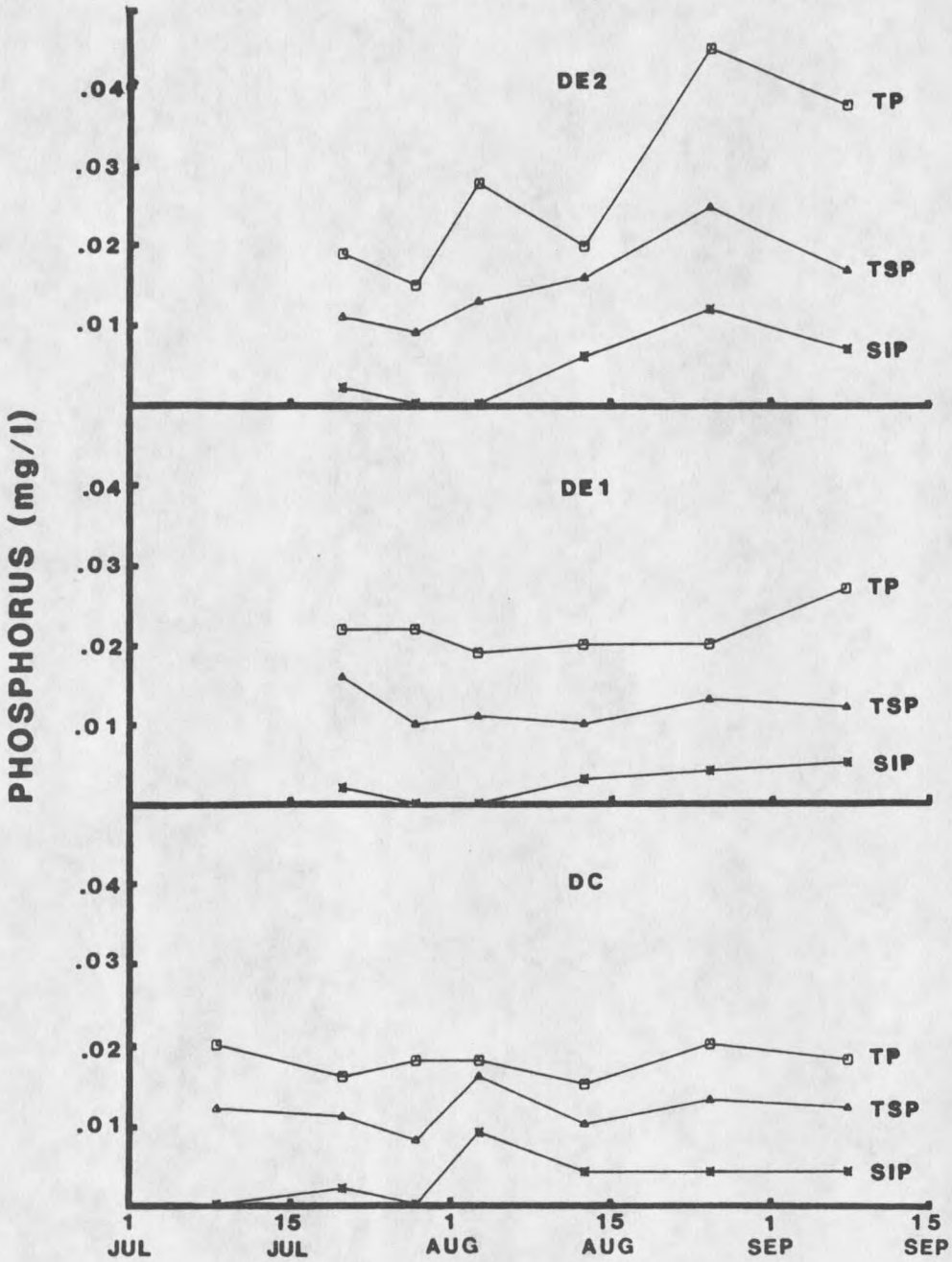

Figure 7. Levels of soluble inorganic P (SIP), total soluble P (TSP), and total P (TP) at sites DC, DE1, and DE2.

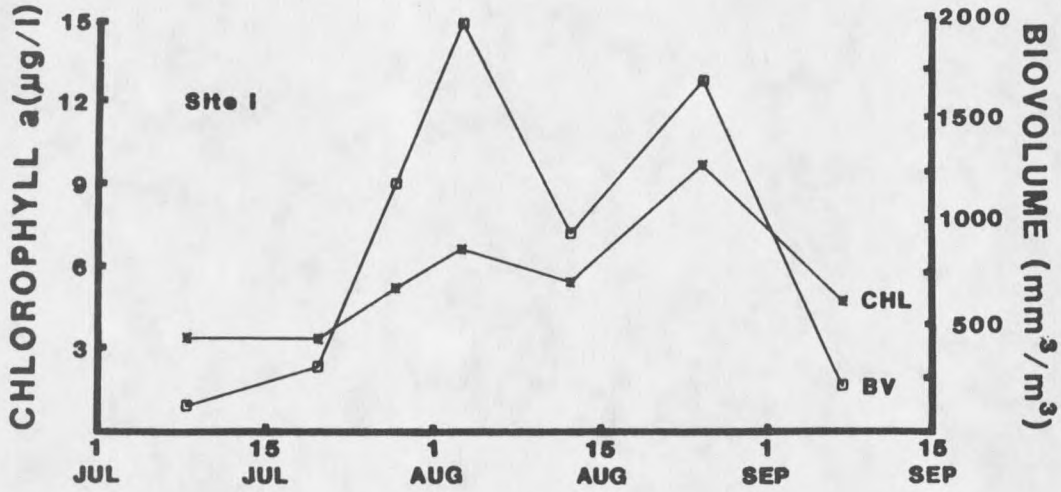

Figure 8. Chlorophyll a and total cell volume (biovolume) of the 10 most commonly occurring phytoplankton genera at site I.

However, following the initial decline, the chlorophyll concentrations in both of these enclosures increased steadily. At site DE1, the unfertilized enclosure, the Chl a levels on 7 September were nearly the same as those of the surrounding open water (site DC). Chl a in DE2, the fertilized enclosure, increased to about twice the levels of the two nearby sites.

Biovolume

Total biovolume of the 10 most commonly occurring genera is shown for site I in Figure 8 and for DC, DE1, and DE2 in Figure 9 (Note the difference in scales). At site I there were two prominent peaks corresponding to the chlorophyll peaks at that site. The magnitudes of the biovolume peaks were not very different from each other and did not reflect the relative magnitudes of the chlorophyll peaks of which the second was the larger. Biovolume at sites DC, DE1, and DE2

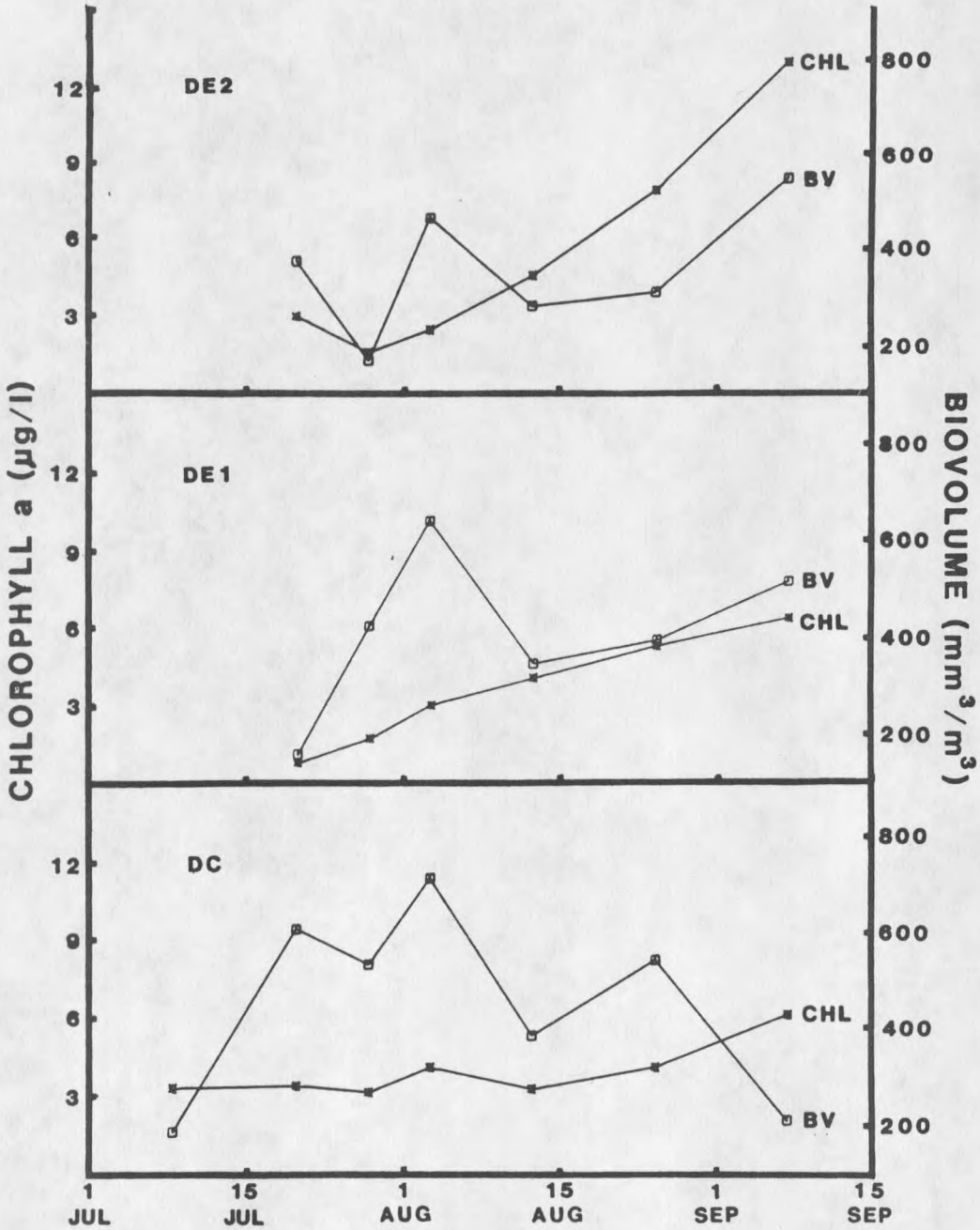

Figure 9. Chlorophyll a and total cell volume (biovolume) of the 10 most commonly occurring phytoplankton genera at sites DC, DE1, and DE2.

exhibited the 3 August peak but only site DC had a peak on 25 August.

Comparison of standing crop estimates

Correlation between biovolume and Chl a was weak at sites DC, DE1, and DE2. Correlation coefficients were -.26, .29, and .56, respectively. At site I the correlation coefficient was .81.

Low correlations between biomass and chlorophyll might be attributed to 3 factors. These include: 1) changing chlorophyll content of cells as an adaptatation to changing light intensity (Brown and Richardson 1968; Steeman-Nielson and Jorgensen 1968), 2) nutrient limitation (Wright 1960; Harris 1978), and 3) species differences in chlorophyll content or differences in the efficiency of extraction of chlorophyll from different species (APHA 1980). Knight (1981) attributed variation in the chlorophyll to carbon ratio of the Georgetown Lake phytoplankton in 1973-1975 to light adaptation or nutrient limitation processes.

The correlations between Chl a and biovolume in this study were based on samples collected in July, August, and September, a period of relatively high light intensities. It seems unlikely that the differences in light intensity experienced by the plankton during this study were sufficient to cause correlations as low as those observed.

Likewise, at least in fertilized site DE2, the plankton were almost certainly not limited by P or N yet the correlation between chlorophyll and biovolume was still low.

Species composition changed markedly during the period, from diatoms early in the summer to blue-greens later (see next section). The taxonomic differences in pigment composition and concentrations between the major algal divisions and the differential extraction efficiencies (the filters were not ground) were probably responsible for the lack of correlation in this study.

The apparent ambiguity in the estimates of phytoplankton biomass at site DE2 (high chlorophyll, moderate cell volume) complicated the interpretation of the effects of fertilization. The cell volumes near the end of the experiment were not markedly different between sites DE1 and DE2. On the other hand, comparing levels of Chl a in DE2 with those in DE1, it would seem that there was a clear quantitative response to fertilization.

Variation in cell chlorophyll content with environmental conditions and between species notwithstanding, Chl a is probably a more precise measure of biomass than cell volume. Total cell volume as reported here was only the total for the 10 most commonly occurring genera. Although the important biomass and successional variation was probably well represented by these taxa, there may have been times when neglecting the other genera caused appreciable errors in estimates of the total biomass. The phytoplankton counts on which the biovolume estimates are based probably represent an even greater source of error. Even with randomly distributed organisms, several hundred would usually need to be counted to achieve levels of statistical confidence normally associated with other measures (Lund

et al. 1958). The non-randomness of the distributions of colonial organisms aggravates the precision problem when the colonies are of indeterminate size.

The trajectories of total phosphorus (Figure 7) provide additional evidence which can be brought to bear on the question of whether chlorophyll or cell volume was the better estimate of phytoplankton standing crop. The disparity between total phosphorus levels in DE1 and DE2 is more consistent with chlorophyll than with biovolume. This, coupled with the fact that the reported levels of Chl a were corrected for degradation products, indicates that the elevated levels of these parameters was not simply due to increased senescing algae. It seems that the chlorophyll estimate was the more reliable indicator of algal biomass and that there was a quantitative response to fertilization of DE2.

Phytoplankton species composition and succession

The 70 taxa which were identified to genus level or below are listed in Table 4. The divisions Chlorophyta and Chrysophyta were the most commonly encountered, with members generally present in every sample. The Euglenophyta were represented by several species of the genus Trachelomonas. No other euglenoid genera were observed. Two species of Pyrrophyta were observed, and although they were present only periodically, they occasionally made a substantial contribution to the total cell volume. The remaining two groups, the division Cyanophtya and the class Cryptophyceae were each observed in approximately half of the samples.

Table 4. Phytoplankton taxa observed from Georgetown Lake, Montana during 1981 and 1982. Representative cell volumes are given for all taxa which were present more than rarely.

Taxon	Representative cell volume (μm^3/cell)
Division Chlorophyta	
Class Chlorophyceae	
Order Volvocales	
Family Chlamydomonadaceae	
Carteria sp.	
Chlamydomonas sp. Ehrenberg	52
Family Volvocaceae	
Eudorina sp.	
Pandorina morum (Muell.) Bory	
Volvox aureus Ehrenberg	40
Order Tetrasporales	
Family Palmellaceae	
Gloeocystis sp.	38
Order Chlorococcales	
Family Hydrodictyaceae	
Pediastrum boryanum (Turp.) Meneghini	
Pediastrum sp.	
Family Oocystaceae	
Ankistrodesmus falcatus (Corda) Ralfs	15
Chodatella sp.	500
Closteriopsis longissima Lemmerman	1059
Oocystis sp.	400
Quadrigula lacustris (Chod.) G.M. Smith	70
Tetraedron minimum (A.Brown) Hansgirg	50
Tetraedron sp.	
Family Scenedesmaceae	
Scenedesmus sp.	50
Order Zygnematales	
Family Zygnemataceae	
Spirogyra sp.	
Family Desmidaceae	
Cosmarium sp.	
Pleurotanium sp.	
Staurastrum sp.	
Xanthidium sp.	

Table 4. (continued)

Taxon	Representative cell volume (μm^3/cell)
Division Euglenophyta	
Class Euglenophyceae	
Order Euglenales	
Family Euglenaceae	
Trachelomonas lacustris Drezepolski	
Trachelomonas sp. 1	
Trachelomonas sp. 2	
Trachelomonas sp. 3	
Division Chrysophyta	
Class Chrysophyceae	
Order Ochromonadales	
Family Ochromonadaceae	
Chlorochromonas sp.	
Family Synuraceae	
Mallomonas pseudocoronata Prescott	1400
Mallomonas alpina Pascher, Ruttner	1963
Class Bacillariophyceae	
Order Centrales	
Family Coscinodiscaceae	
Cyclotella antiqua W.Sm.	565
C. bodanica Eulenst.	
C. catentata Brun.	123
C. sp.	1200
Stephanodiscus astrea (Ehr.) Grun.	2000
Order Pennales	
Suborder Fragilarineae	
Family Fragilariaceae	
Asterionella formosa Hass	300
Diatoma sp.	
Fragilaria capucina Desm.	447
F. construens (Ehr.) Grun.	269
F. crotonensis Kitton	400
Synedra acus Kutz.	60
S. acus var. *angustissima* Grun.	1525
S. capitata Ehr.	16620
S. ulna (Nitz.) Ehr.	1937

Table 4. (continued)

Taxon	Representative cell volume (μm^3/cell)
Family Achnanthaceae	
Achnanthes sp.	
Cocconeis placentula Ehr.	353
Suborder Naviculineae	
Family Naviculaceae	
Navicula sp.	
N. radiosa Kutz.	
Pinnularia sp.	
Stauroneis anceps Ehr.	
Family Gomphonemataceae	
Gomphonema constrictum Ehr.	1000
G. sphaerophorum Ehr.	1000
Family Cymbellaceae	
Cymbella sp.	
Epithemia sorex Kutz.	3421
E. turgida (Ehr.) Kutz.	20106
E. zebra (Ehr.) Kutz.	393
Rhopalodia gibba (Ehr.) O. Mull.	110835
Division Pyrrophyta	
Class Dinophyceae	
Order Peridiniales	
Family Peridiniaceae	
Peridinium cinctum (Muell.) Ehr.	40000
Family Ceratiaceae	
Ceratium hirundinella (Muell.)Dujardin	37396
Division Cyanophyta	
Class Mixophyceae	
Order Chroococcales	
Family Chroococcaceae	
Aphanocapsa sp.	
Chroococcus sp.	
Microcystis sp.	
Gomphosphaeria sp.	28
Order Oscillatoriales	
Family Oscillatoriaceae	
Arthrospira sp.	

Table 4. (continued)

Taxon	Representative cell volume (μm^3/cell)
Order Nostocales	
Family Nostocaceae	
Anabaena circinalis Rabenhorst	14
A. flos-aquae (Lyngbye) DeBrebisson	38
A. macrospora var. robusta Lemmermann	
A. spiroides Klebahn	165
A. sp.	
Division Uncertain	
Class Cryptophyceae	
Order Cryptomonadales	
Family Cryptochrysidaceae	
Rhodomonas lacustris Pascher, Ruttner	35
Family Cryptomonadaceae	
Cryptomonas erosa Ehr.	493
C. ovata Ehr.	2500

The phytoplankton succession will first be described as it occurred in the summer of 1982 at site I. Similarities between sites I and DC, the open water sites, will be noted. Then the differences between site I and the experimentally enclosed sites will be discussed.

At site I on 9 July, the phytoplankton community was composed primarily of *Mallomonas* (Chrysophyceae) and *Cryptomonas* (Cryptophyceae), remnants of the populations which were observed under the ice in March and early May (Boveng 1983). These taxa were joined and eventually replaced by the diatoms *Asterionella* and *Fragilaria*. *Asterionella* declined quickly but *Fragilaria* maintained

high densities (>500 mm^3/m^3) through 25 August. The dinoflagellates Peridinium and Ceratium reached moderately high densities (>100 mm^3/m^3) on 13 August but declined quickly and were barely detectable by 7 September. The blue-green alga Anabaena reached its maximum density on 25 August but was still present in large numbers on 7 September, accompanied by Microcystis.

Mallomonas and Cryptomonas are motile forms which have been found to adapt well to low temperatures and light intensities (Morgan and Kalff 1975; Rodhe 1955; Wright 1964). Mallomonas, in particular, was present in relatively large numbers during the winter of 1982 and was probably responsible for the high levels of oxygen and chlorophyll found under the ice (Garrett 1983a). Initiation of the spring maximum by these forms and persistence into the summer occurs commonly in small, shallow lakes (Wetzel 1975, p. 325).

An early season pulse of the diatom Asterionella is a frequently observed phenomenon. The cause for declining diatom numbers which signal the end of the spring bloom has been attributed to limitation by silica in some lakes (Lund 1964). However, in Georgetown, this seems unlikely because the Asterionella peak was followed immediately by an even larger peak of Fragilaria. Parisitism may have contributed to the decline of Asterionella; colonies observed in Georgetown in 1981 and 1982 often seemed to be parasitized. No positive identifications of the parasites were made but they resembled chytrid fungi which have been reported to attack Asterionella and to be partially responsible for its replacement by Tabellaria and

Fragilaria (Lund 1949; 1950).

The bloom of Fragilaria in 1982 was a major feature of the phytoplankton succession. The maximum standing crop (as cell volume) was recorded at the open water site I on 3 August during this bloom. There was a substantial decline in numbers of Fragilaria on the next sampling date, 13 August. As is often the case, this decline of the early season diatom peak was accompanied by increases in the abundance of chlorophytes (Wetzel 1975). These green algae (Oocystis and Gloeocystis) reached their maximum abundance along with the dinoflagellates, Peridinium and Ceratium on 13 August but they were immediately replaced by the blue-green alga Anabaena and surprisingly, a second peak of Fragilaria on 25 August.

Brown and Austin (1973) found that succession of Fragilaria crotonensis was related to nitrate levels. Although nitrate nitrogen was not measured in this study, several observations indicate that nitrate concentrations may have played a causal role in the second Fragilaria bloom at sites I and DC. First, at both sites the pH decreased between 3 August and 13 August (Figures 4 and 5); this was the only decrease measured between 9 July and 25 August. At the same time, alkalinity was still increasing. These conditions are consistent with those which would result from nitrification, a process by which nitrate and hydrogen ions are released (Stumm and Morgan 1980). Furthermore, the level of phaeophytin (which was estimated in the analysis for chlorophyll a) was at a maximum --about 2 μg/l -- on 13 August at site I, indicating that some degradation of

plant material had taken place. Finally, the abundance of Anabaena at the open water sites was lower than at the enclosed sites which did not have a second Fragilaria peak. The nitrogen fixing Anabaena may not have been able to compete as well with the diatoms in the presence of available nitrogen.

The final event in the phytoplankton succession was the appearance of substantial numbers of Microcystis colonies at all sites on 7 September. This blue-green, which does not fix nitrogen, probably depended on the ammonia nitrogen which began to reach detectable levels on 25 August.

The basic pattern in the phytoplankton succession, outlined above for site I, consisted of an early summer diatom bloom, a diverse community at mid-season, including chlorophytes, diatoms, dinoflagellates, and blue-greens, followed by increased densities of diatoms and blue-greens in late summer. The fundamental qualitative difference between this pattern and the one observed in the enclosed sites DE1 and DE2, was that there was not a second Fragilaria peak in the enclosures and the densities of Anabaena were higher in DE1 and DE2. A quantitative consideration of variation in phytoplankton species composition is presented in the following section.

Principal components analysis of phytoplankton species composition

The 10 most commonly occurring phytoplankton taxa, expressed as cell volume per unit of water volume, were submitted to principal

components analysis (PCA). The same data were log transformed (after adding 1 to all observations) and again submitted to PCA. All observations at sites DC, DE1 and DE2 were pooled for the PCA and computation of component scores.

The first principal component (PC I) of the original (not transformed) variables explained about 65% of the variance and was overwhelmingly a Fragilaria axis with a portion of the Anabaena abundance subtracted (Table 5). The second PC accounted for an additional 23% of the variance and was dominated by Anabaena. The higher order PC's accounted for smaller proportions of the variance and were considered unimportant.

The PCA of the log-transformed data (Table 6) was less sensitive to the very abundant and variable taxa such as Fragilaria and Anabaena which dominated the analysis of the original variables. PC I in this analysis accounted for 39% of the variance and consisted of an association of early season taxa (Mallomonas and Asterionella) which were negatively correlated with late season taxa such as Anabaena and Oocystis. PC II accounted for an additional 20% and was composed mostly of a positive association between Fragilaria and the dinoflagellate Peridinium. PC III explained an additional 17% of the variance and was primarily determined by the observations in which Peridinium and Anabaena occurred in concert.

The component scores on the first two principal components were plotted by site and date to determine whether seasonal variation or experimental treatment was more important in determining

Table 5. Principal components analysis of biovolumes (not transformed) of the 10 most commonly occurring genera of phytoplankton. All observations at sites DC, DE1, and DE2 were pooled.

Genus	PC I	PC II	PC III
Fragilaria	.940	.274	.186
Oocystis	.011	.043	-.005
Gleocystis	-.000	-.008	.025
Asterionella	-.000	-.146	.221
Synedra	-.001	-.053	-.075
Ceratium	-.003	.002	-.018
Peridinium	-.029	.023	.118
Cryptomonas	-.032	-.053	-.214
Mallomonas	-.052	-.438	.831
Anabaena	-.336	.839	.400
Cumulative Variance (%)	65.1	88.1	95.8

Table 6. Principal components analysis of log-transformed biovolumes of the 10 most commonly occurring genera of phytoplankton. All observations at sites DC, DE1, and DE2 were pooled.

Genus	PC I	PC II	PC III
Anabaena	.429	.144	.551
Oocystis	.301	.220	.029
Cryptomonas	.150	-.135	-.164
Ceratium	.091	.173	.016
Peridinium	.058	.419	.507
Gloeocystis	-.070	.167	.248
Fragilaria	-.296	.806	-.375
Synedra	-.304	-.010	.248
Asterionella	-.485	-.018	.209
Mallomonas	-.521	-.173	.322
Cumulative Variance (%)	39.4	58.9	76.3

phytoplankton species composition. With the original variables, there were no distinct groupings by site or date (Figure 10). The component scores from the log-transformed PCA displayed a tendency to group by date but not by site (Figure 11).

The results from the log-transformed cell volumes are somewhat more satisfying than those from the non-transformed (original) cell volumes, because they suggest that phytoplankton community composition was determined more by the time of year than by the experimental treatments (control, enclosed, enclosed and fertilized). However, the principal components from the log-transformed data set are more difficult to interpret in biological terms. The principal components of the log-transformed data must be thought of as weighted products of the cell volumes, rather than weighted sums.

As another way of addressing the question of whether sample date or sample treatment was more important in determining the phytoplankton community structure, the cell volumes were plotted separately for the genus Fragilaria and the genus Anabaena in Figure 12. A comparison of Figure 12 with the curves for total biovolume of the 10 most commonly occurring genera in Figure 9 demonstrates that Fragilaria and Anabaena comprised the majority of the standing crop. The shapes and magnitudes of the curves for these two taxa alone are very similar to the shapes and magnitudes of the total biovolume curves. The point to be taken from Figure 12, which is not made by Figure 9, is that the fertilization of DE2 did not make a substantial difference in the composition of the primary constituents of the

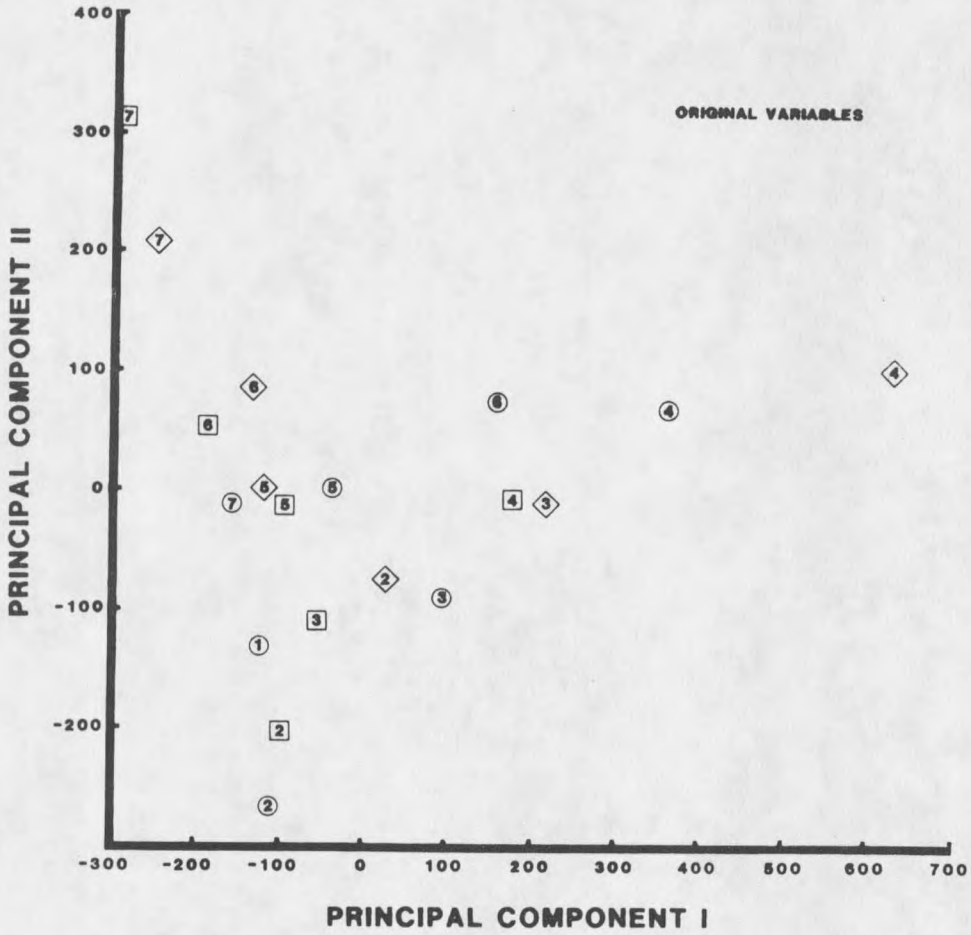

Figure 10. Component scores on the first two principal components from total cell volumes of phytoplankton, plotted by site and date. Symbols are sites: ○= DC, ◇= DE1, □= DE2. Numerals are dates: 1 = 9 July.....7 = 7 September.

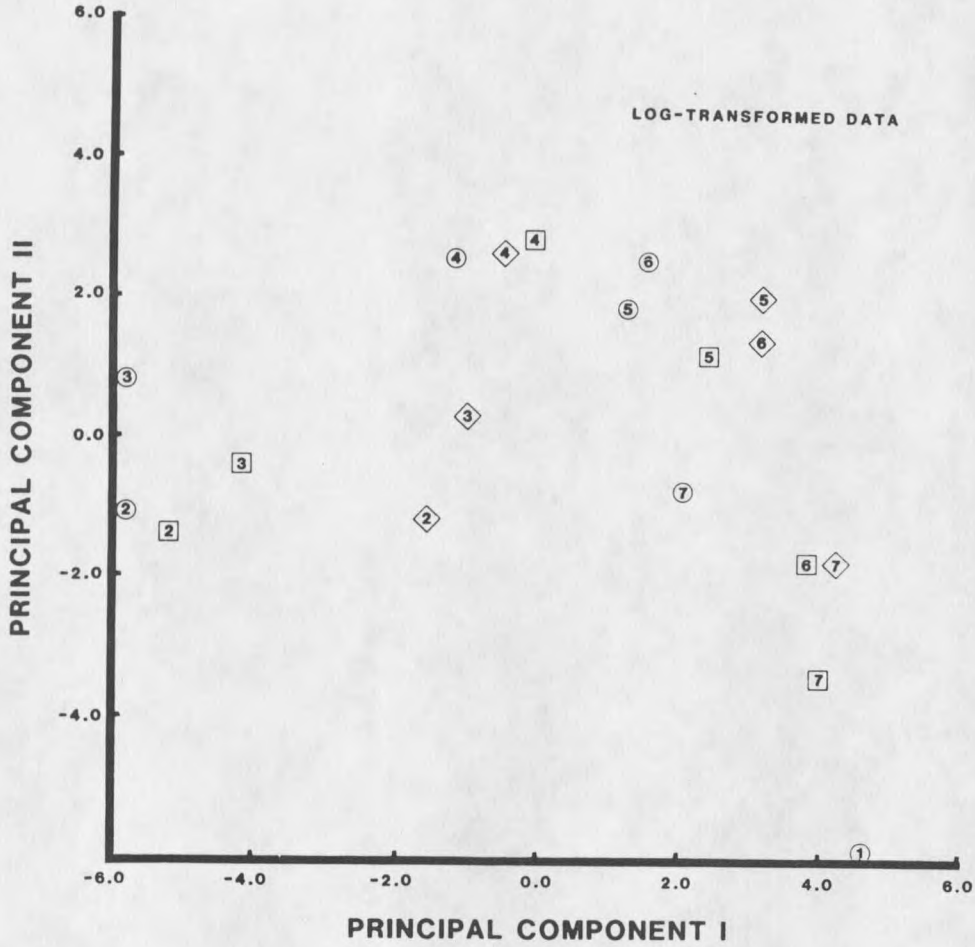

Figure 11. Component scores on the first two principal components from log-transformed total cell volumes of phytoplankton plotted by site and date. Symbols are sites: ○= DC, ◇= DE1, □= DE2. Numerals are dates: 1 = 9 July.....7 = 7 September.

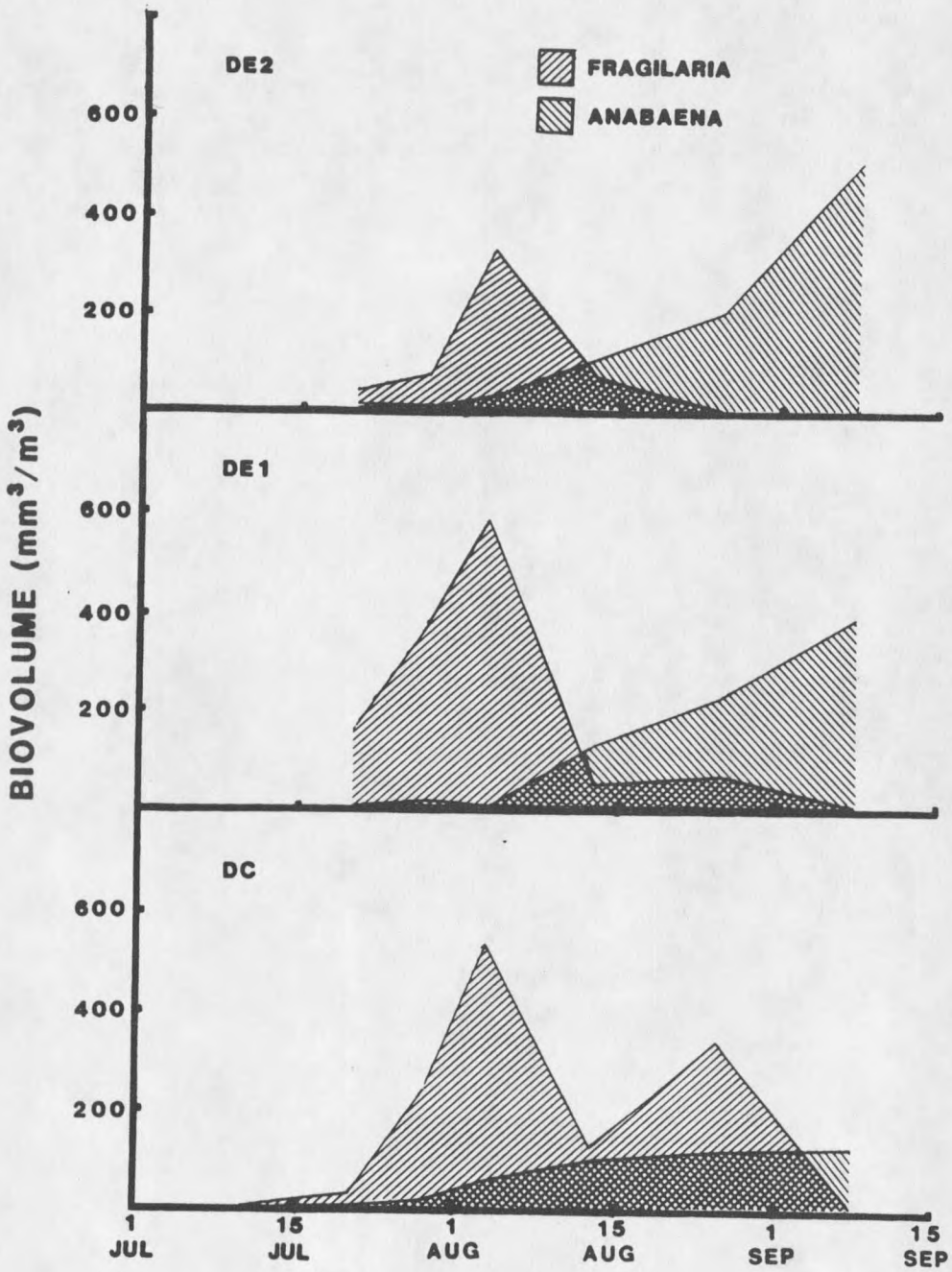

Figure 12. Biovolumes of Fragilaria and Anabaena plotted separately, sites DC, DE1, DE2.

phytoplankton community. In fact, the greater difference in community composition was between enclosed and non-enclosed sites. This observation is supported by the occurrence of a second Fragilaria peak at site I in late August which closely resembled the second Fragilaria peak at DC (Figure 13).

Neither the PCA, nor the cell volume plots indicated that fertilization had an appreciable affect on the phytoplankton species composition. These findings, and the reasons for the apparent lack of consistency with many cases of cultural eutrophication will be considered again after discussion of the phosphorus fate experiments and phosphorus budgets.

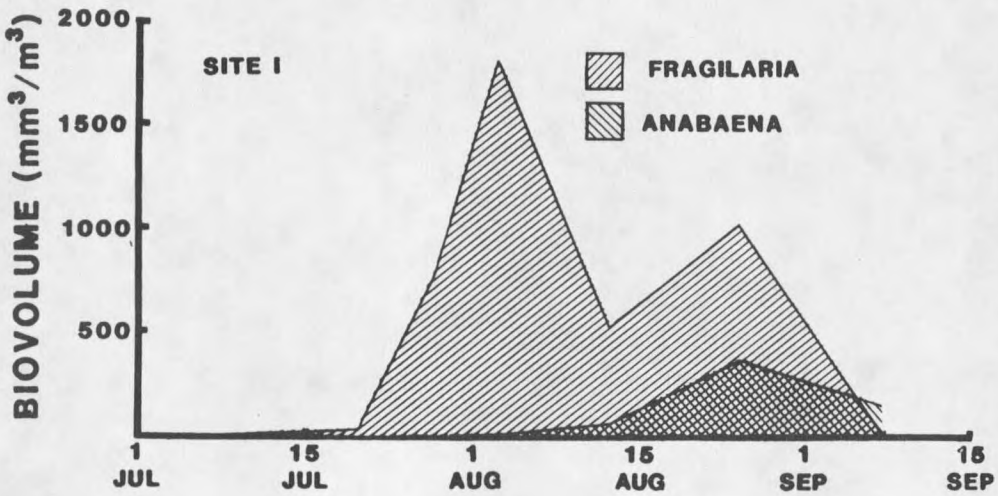

Figure 13. Biovolumes of Fragilaria and Anabaena plotted separately, site I.

Phosphorus fate experiments

The trajectories of soluble inorganic, soluble organic, and particulate phosphorus during the second and third phosphorus fate experiments (experiment II, 26 August; experiment III, 9 September) are plotted in Figures 14 and 15, respectively. Two differences between experiments II and III will be discussed prior to analysis of the main results.

First, the levels of particulate phosphorus (PP) in DE2 and DE2-S during experiment III were much higher than those in experiment II. This was consistent with the increase in the disparity between TP and TSP near the end of the summer in DE2 (Figure 7).

Second, there were increases in SIP on the last measurement in DE2 and DC-S during experiment III which did not occur in DE2-S or in any site during experiment II. Experiment III began at 2200 hrs on 9 September 1985 and was run until about 1300 hrs on 11 September. The bulk of the experiment was run on 10 September during which the sky was overcast (see Community metabolism section). There may have been some release of SIP following the overcast day but this does not explain why no increase in SIP was observed in DC-S. The time elapsed between the last measurement and the one previous to it was about 13 hours --longer than the time span between any other successive measurements. This made it impossible to determine whether the apparent increases in SIP were due to a genuine trend during that time or simply analytical artifacts of the final measurements.

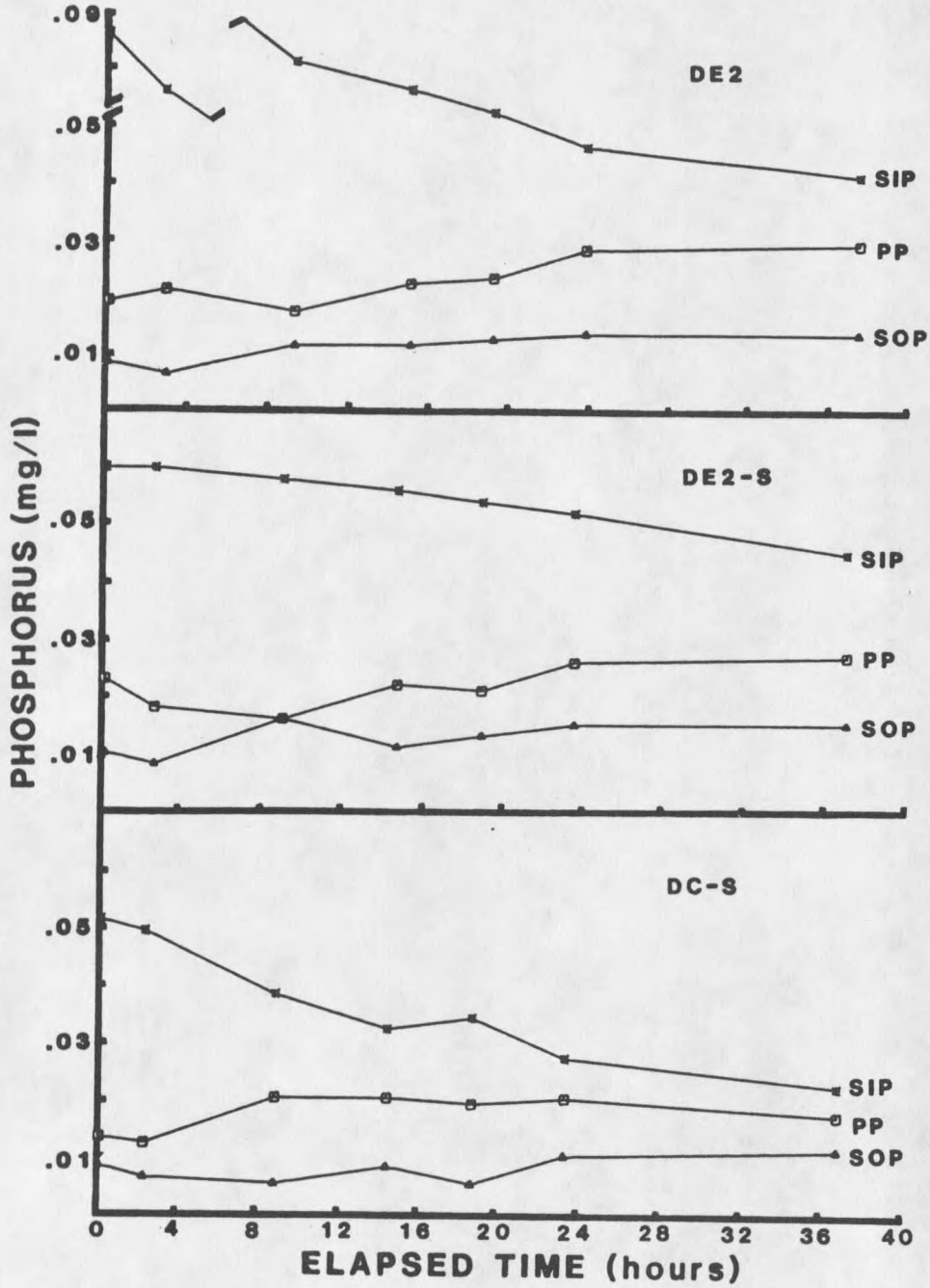

Figure 14. Trajectories of soluble inorganic P (SIP), soluble organic P (SOP), and particulate P (PP) in phosphorus fate experiment II.

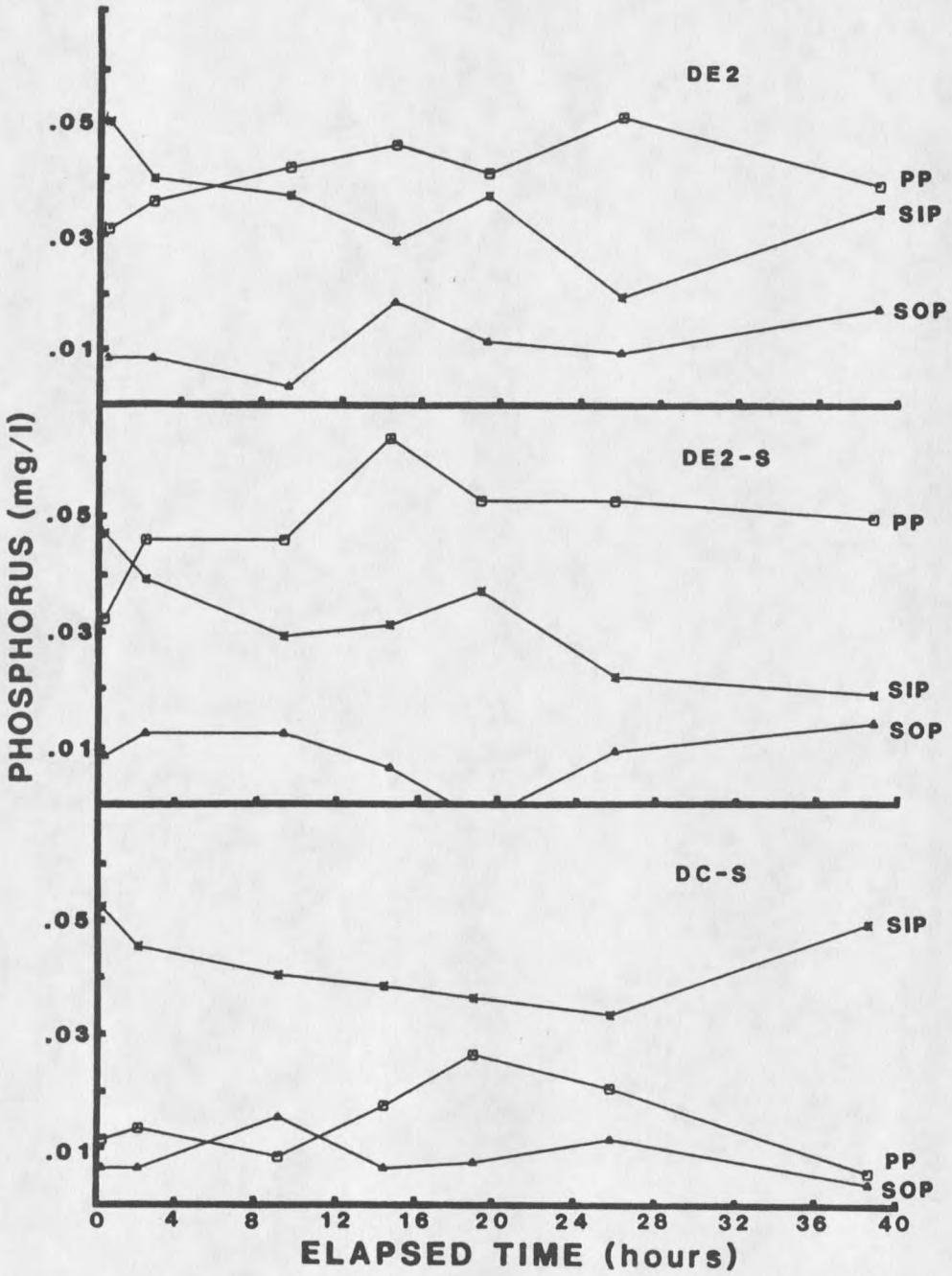

Figure 15. Trajectories of soluble inorganic P (SIP), soluble organic P (SOP), and particulate P (PP) in phosphorus fate experiment III.

Kuhl (1962) and Currie and Kalff (1984) have documented diel variation in uptake of phosphorus by phytoplankton. To avoid biasing the results of the phosphorus fate experiments toward a particular portion of the day, and because the increases in SIP observed in the last measurement of experiment III seemed out of character with the other observations, the discussion of the main results of the phosphorus fate experiments will focus primarily on the first 24 hours of the experiments (about 26 hours for experiment III).

The purpose of isolating a plankton community inside DE2 was to allow investigation of the relative ability of a planktonic community compared to an intact system of plankton and rooted macrophytes to remove inorganic P from the water. If uptake by the plankton (increase in particulate P) and loss of SIP were the same in both community types, the conclusion would be that the plankton determined the fate of added phosphate on the time scale of a few hours. On the other hand, if the increase in PP were the same in both communities but the loss of SIP were greater in the intact community, the conclusion would be that some component of the whole community (macrophytes, sediments, benthic algae), in addition to the plankton, was able to remove appreciable quantities of inorganic phosphorus. In other words, the slopes of the SIP curves in the two communities could be compared to determine whether the plankton or another component was most important in SIP removal.

Figures 14 and 15 show that in all cases, there were net increases in the levels of phosphorus measured as particulate (PP)

over the first 24 hours. However, in linear regressions of PP on elapsed time (Table 7), only two PP curves (DC-S, experiment II and DE2, experiment III) produced significantly positive slopes at the 5 percent level. The apparent slopes were so shallow that more than one sample per observation would probably be necessary to achieve significance. Thus, it seems clear from the consistency with which increases in PP occurred, that the increases were genuine; but due to the general lack of statistical significance, the actual rate estimates are difficult to compare.

Table 7. Linear regressions of particulate phosphorus (PP) on time elapsed since spiking in the phosphorus fate experiments. Slope coefficients in μg/l/hr are given with P-values for the test, Ho: slope = 0 versus Ha: slope > 0.

Site	26 August		9 September	
	Slope	P-value	Slope	P-value
DE2	0.31	.071	0.64	.015
DE2-S	0.19	.331	0.74	.134
DC-S	0.34	.044	0.49	.096

It would be useful to know if the observed increases in the PP component were realistic for phytoplankton communities. The slopes shown in Table 7 range between about 0.1 and 0.7 μg/l/hr with 0.4 being approximately representative of the group. Maximum rates of phosphorus uptake by planktonic algae have been measured in a few instances (Kuenzler and Ketchum 1962; Mackereth 1953; Rhee 1973; Lehman et al. 1975). Lehman et al. (1975) suggested a value of about 3×10^{-8} μg/cell/hr for blue-green algae. The phytoplankton in DE2

during experiments II and III were composed primarily of Anabaena, with densities ranging between about 5 X 10^6 and 13 X 10^6 cells/l. Taking 9 X 10^6 cells/l as representative, the community uptake rate would be 0.27 μg/l/hr. The observed value of about 0.4 seems close enough to conclude that the observed increases in PP could have been due to uptake by the phytoplankton.

The PP curves at sites DE2 and DE2-S from experiment II were very similar in appearance, with the exception of the initial sample (Figure 14). This similarity is not surprising because DE2-S was filled with water from DE2 at the beginning of the experiment. However, the corresponding SIP curves were different; SIP declined at a much higher rate in DE2 than in DE2-S (Figure 14; Table 8). This indicates that some component of the intact ecosystem, in addition to the plankton, removed a substantial portion of the SIP from the water in DE2.

Table 8. Linear regressions of soluble inorganic phosphorus on time elapsed since spiking in the phosphorus fate experiments. Slope coefficients in μg/l/hr are given with P-values for the test, Ho: slope = 0 versus Ha: slope < 0.

Site	26 August		9 September	
	Slope	P-value	Slope	P-value
DE2	-1.59	.001	-0.93	.022
DE2-S	-0.35	.000	-0.70	.063
DC-S	-1.01	.002	-0.66	.005

The trajectories of PP in DE2 and DE2-S for the first 26 hours of experiment III (Figure 15) did not exhibit as much similarity as those from experiment II (Figure 14). The initial and 26 hour PP levels were nearly the same in both curves, making the average rate of increase about the same. However, the PP levels at intermediate sampling times differed by as much as 0.018 mg P/l (at 15 hours) between DE2 and DE2-S (Figure 15).

The time courses of SIP levels in DE2 and DE2-S from experiment III (Figure 15) were nearly identical (with the exception of the final observations, discussed above). The 9 hour sample differed by 0.008 mg P/l between the sites, but no other sample in the first 26 hours differed by more than 0.003 mg P/l. The net losses of SIP during the first 26 hours of experiment III were 0.031 mg P/l in DE2 and 0.025 mg P/l in DE2-S. The PP levels increased by 0.020 mg P/l and 0.021 mg P/l, respectively, implying that the bulk of the SIP loss could be accounted for by incorporation into the PP fraction. The amount unaccounted for was greater in DE2 (0.011 mg P/l) than in DE2-S (0.004 mg P/l), suggesting that the macrophytes or sediments were responsible for part of the removal of SIP in DE2.

Several studies have shown that the nutrient content, or 'cell quota', of microorganisms in culture regulates the rate of nutrient uptake (Rhee 1973; Lehman et al. 1975; Brown and Harris 1978). These studies demonstrated an inverse relationship between the nutrient content of a cell and the uptake of that nutrient. Based on these findings, the expected rate of P uptake following enrichment of an

unfertilized plankton community would be greater than the uptake rate following a spike in a community with a history of heavy enrichment. The purpose of isolating a previously unfertilized plankton community (DC-S) and adding nutrients to it was to test this hypothesis.

The increase in PP in DC-S during the first 24 hours of experiment II, was slight but linear regression showed the slope to be significantly greater than zero (Figure 14, Table 7). By the argument given above, the increase in PP was of a realistic magnitude for a phytoplankton community. Statistical comparison of the PP trajectories in DC-S and DE2-S showed that there was no significant difference between the slopes (P=.484) from experiment II. Likewise, PP increased in DC-S during experiment III but the increase was not significantly different (P=.600) from the increase observed in DE2-S (Figure 15). Thus, the unfertilized open-water plankton community did not take up phosphorus at a significantly greater rate than the fertilized community in either experiment.

There are several possible explanations for the lack of agreement between this study and the literature reports of decreased rates of uptake with increased cell nutrient content. First, it is apparent from the discussion above that the techniques used in this study --monitoring the levels of P fractions using the ascorbic acid-molybdate method-- were of limited sensitivity. The predicted effects may have occurred in the experimental system but were obscured by variability in the measured parameters.

Second, as shown in the section on phytoplankton community

composition and succession, the plankton communities captured in DC-S and DE2-S were similar in composition and density but not entirely the same. The proportion of diatoms was higher in DC-S than in DE2-S. Lehman et al. (1975) estimated that the maximum uptake rates for a generalized diatom was 3 times that for a blue-green but differences between species within the major groups may vary by more than a factor of 3 (Rhee 1973; Lehman et al. 1975).

The cell nutrient contents were not measured directly in these experiments. It was assumed that algal cells in a heavily fertilized community would have higher nutrient contents than those in the open water. However, if phosphorus had been readily available in the open water, or, if phosphorus in the fertilized enclosure was not as available as expected from the quantity added, the cell P content might have been similar in the two communities. In that case, theory (Rhee 1973; Lehman et al. 1975; Brown and Harris 1978) would predict that the rates of uptake would probably be similar.

There is some evidence supporting the possibility that the availability of P in the fertilized enclosure was not proportional to the amount of P added. Figures 16 and 17 show the levels of total phosphorus (TP) during the second and third phosphorus fate experiments, respectively. In closed containers such as the small enclosures DC-S and DE2-S, TP was expected to remain constant. In fact, there were net losses of TP from the water in both small enclosures in both experiments. The losses were generally slight; an exception was the case of DC-S on 26 August which lost 0.02 mg P/l in 37 hours.

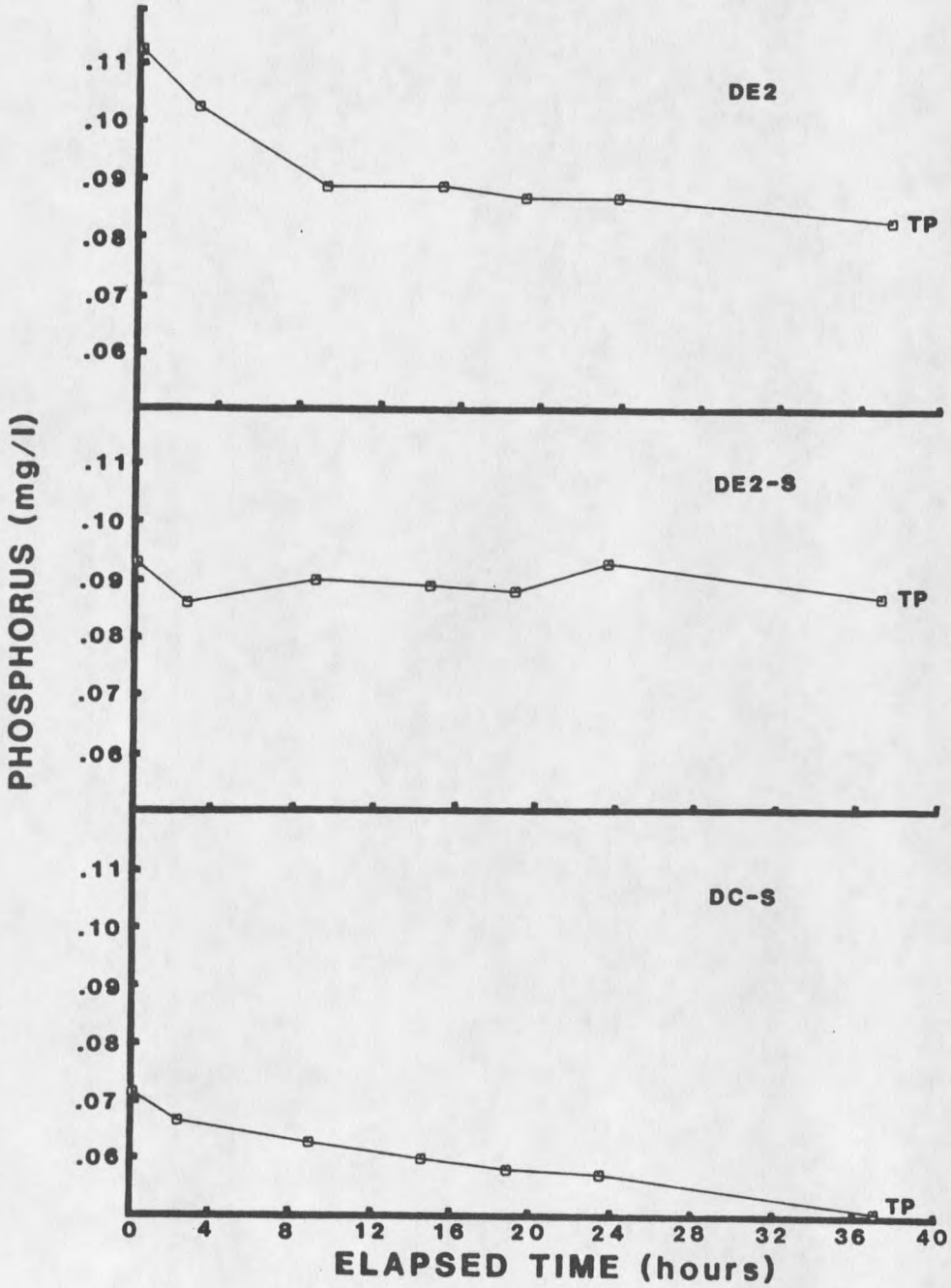

Figure 16. Trajectories of total P in phosphorus fate experiment II.

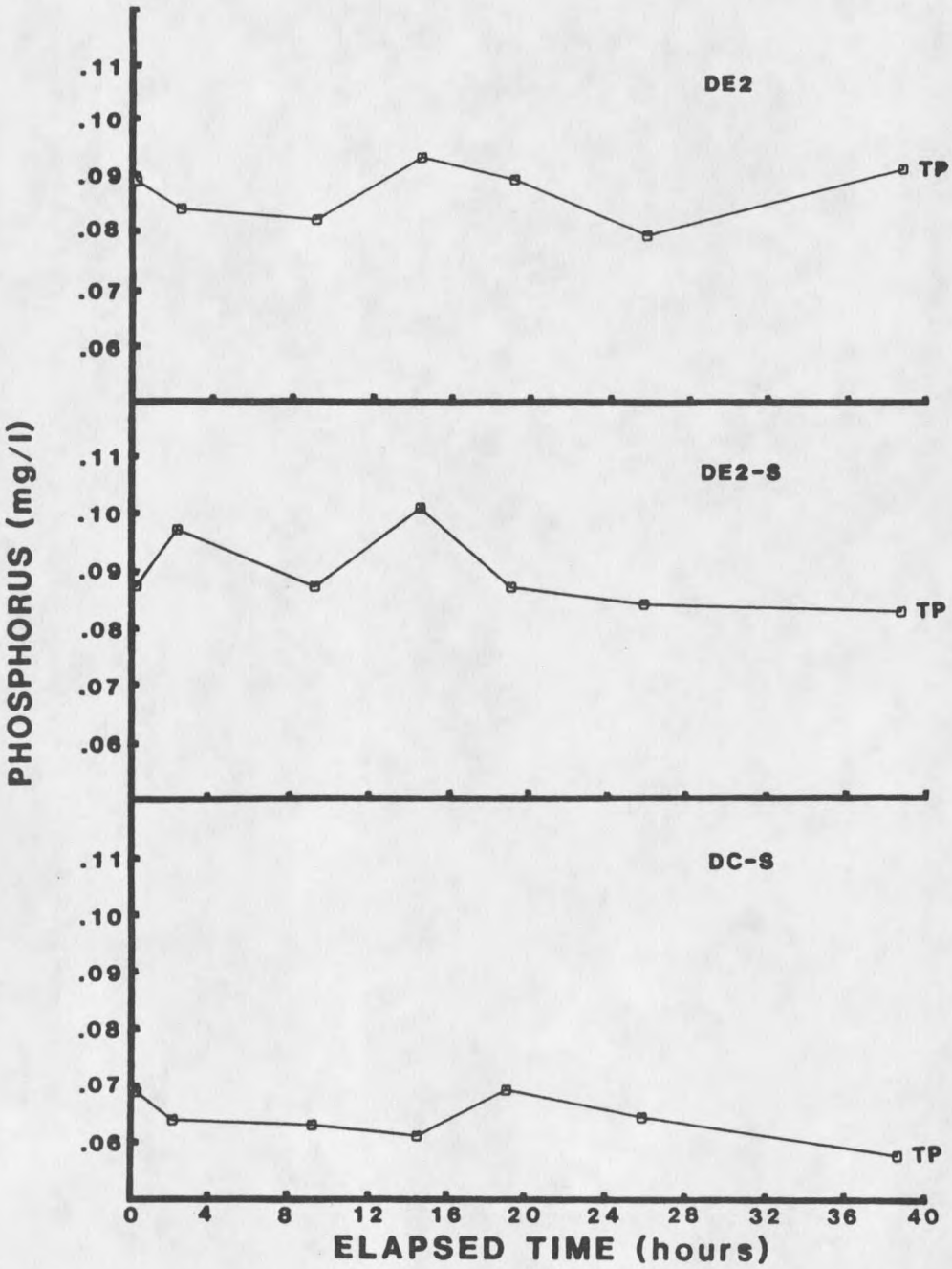

Figure 17. Trajectories of total P in phosphorus fate experiment III.

Because the vinyl from which the enclosures were made was shown not to adsorb inorganic P in the lab, these losses were attributed to settling of particulate P. A sediment film was observed on the bottom plates of the enclosures at the end of each experiment, but it was not analyzed.

Total P was not necessarily expected to remain constant in enclosure DE2 which contained macrophytes and was open to the sediments. There was, in fact, a substantial decrease in TP of the water column in DE2 on 26 August. The decline appears to have been driven almost entirely by the decline in SIP (Figure 16).

The phosphorus fate experiments can now be summarized. Removal of SIP from the water column occurred at all sites during the first 24 hours of both experiments. Some of the loss of SIP could be accounted for by increases in PP but variability in PP precluded rigorous quantification of the amount taken up or the uptake rate. Despite the uncertainty in those values, it seems clear that the SIP loss was much greater than the accumulation of PP, in at least two cases -- sites DC-S and DE2 in experiment II. In the case of DC-S, settling of particulate was probably the cause. In DE2, settling to the bottom or uptake by macrophytes could have been responsible for the difference between the loss of SIP and the accumulation of PP.

Macrophyte biomass and tissue analysis

The stem height measurements made on 28 July revealed 72 *Potamogeton* stems in enclosure DE1 with a mean height of 4.22 m

(standard deviation of 0.281 m). In DE2, the fertilized enclosure, there were 65 stems with a mean height of 3.72 m and a standard deviation of 0.54 m. Even assuming that the variances were not significantly different (patently a poor assumption) the mean stem heights were appreciably different in the two enclosed communities (despite efforts to choose sites as similar as possible).

The dry weights of the macrophyte biomass harvested on 20 September from sites DC, DE1, and DE2 were 412.7 g, 2030 g, and 1677 g, respectively. Accordingly, the ratio of macrophyte biomass in DE1 to that in DE2 was 1.21. Using the total of all stem heights in each enclosure on 28 July as an index of biomass, the ratio of biomass in DE1 to DE2 was 1.26, remarkably similar to the final value. These data suggest that biomass of the macrophytes in DE2 did not increase appreciably in response to fertilization.

The content of carbon, nitrogen, and phosphorus in Potamogeton praelongus from sites DC, DE1, and DE2 are given in Table 9. As would be expected, N and P were more concentrated in the leaves than in the 'whole-plant' samples, large portions of which were composed of stem tissue.

If the percent nitrogen in the leaf tissues from sites DE1 and DC are taken as replicates of unfertilized communities, an estimate of the variance is available. The resulting standard deviation should be corrected for the small sample size by the factor C_n given by Sokal and Rohlf (1981, p. 53, attributed to Gurland and Tripathi (1971)). This factor inflates the standard deviation by about 25

Table 9. Carbon, nitrogen and phosphorus content of *Potamogeton praelongus* at sites DC, DE1 and DE2, expressed as percent of dry weight.

Site	% C	% N	% P
DC (whole plant)	38.24	1.52	0.19
DE1 (whole plant)	42.56	1.43	0.18
DE2 (whole plant)	42.15	1.42	0.18
DC (leaves only)	42.14	3.08	0.25
DE1 (leaves only)	42.14	3.09	0.28
DE2 (leaves only)	45.48	3.15	0.28

percent for a sample size of 2. Using the corrected standard deviation and the t test for comparison of a single observation with the mean of a sample (Sokal and Rohlf 1981, p. 231), the value of 3.15 % nitrogen in the fertilized leaf tissue was not significantly greater than the mean nitrogen content (3.085 %) in the unfertilized leaves (P=0.053).

The same test on the phosphorus content of leaf tissue indicated that the P content of the fertilized leaves (0.28 %) was not significantly different from the mean P content (0.265 %) of the unfertilized leaves (P=0.363).

Phosphorus budget

Construction of a budget of the phosphorus added to DE2, the fertilized enclosure, was attempted using information from the seasonal trajectories of dissolved and suspended P (Figure 7), the findings from the short term phosphorus fate experiments, and the macrophyte biomass and tissue analysis.

The increase in TP at DE2 was far too small to account for all the phosphorus added. Table 10 shows the amount of phosphorus not accounted for by the levels of TP in the water column, computed by subtracting the TP levels at DE1 to allow for enclosure effects. The deficit ranged from 56 percent to 168 percent of the phosphorus added.

Table 10. Phosphorus deficits at DE2, calculated as the difference between total amount of P added and the amount by which concentration of total P in DE2 exceeded that in DE1 (to account for enclosure effects).

Date	Total P (g) (DE2-DE1)	Added P (g) (cumulative)	P Deficit (g)
21 July	-0.102		
28 July	-0.238	0.347	0.585
3 August	0.306	0.694	0.388
13 August	0.000	2.429	2.429
25 August	0.850	5.986	5.136
7 September	0.374	7.629	7.255

The phosphorus fate experiments showed that in at least two cases --sites DC-S and DE2 in experiment II-- loss of SIP was much greater than accumulation of PP. Trajectories of TP in the small enclosures, DE2-S and DC-S, suggest that some of the added P was lost due to settling. In DE2, the possible repositories for the missing P included both the sediments and the macrophytes.

Analysis of the macrophyte tissue harvested from DE2 at the end of the summer indicated that the fate of the majority of added P in DE2 was not resolved by increased biomass or P content of the macrophytes. The dry weight of macrophyte tissue which could account for the 7 g of missing P would amount to about 3500 g which is more

than the dry weight of the entire macrophyte stand in DE2.

Several possibilities for the fate of added phosphorus have been eliminated. A complete budget of the added P could not be constructed because the P content of the other major pool of phosphorus, the sediment, was not monitored. However, interpretation of the chemical conditions which occurred during this study and the findings from other studies (Golterman 1982; Stumm and Morgan 1980) indicated that the sediments were likely the repository of the majority of missing phosphorus.

According to Stumm and Morgan (1980) and Golterman (1982), the concentration of phosphate which will cause precipitation of apatite at pH 9 in a calcium carbonate system lies somewhere between 0.001 and 0.015 mg P/l as phosphate (the range is due to uncertainty in the estimates of the equilibrium constant for formation of apatite from calcite). The quantity of P measured as SIP in Georgetown Lake never exceeded this range but on several occasions was above the midpoint of the range (Figure 7) making pH controlled precipitation of P a likely mechanism for explaining the loss of P from enriched sites.

If, in fact, the majority of the added P simply precipitated, the results of this fertilization study should not be extrapolated to situations in which macrophyte control programs result in release of dissolved nutrients. Fertilization was accomplished in this study with inorganic phosphate and nitrate salts. Release of these nutrients from decaying macrophyte tissue would be accompanied by release of CO_2 and a concomitant decrease in pH. At substantially

lower pH levels than those observed in DE2, the mineralized phosphorus species would not be as likely to precipitate and therefore would be more available to plants.

Community metabolism

The diel pH measurements made concurrently with the phosphorus fate experiments allowed estimation of net photosynthetic rates, averaged over daylight hours (Table 11). For all stations except DE2 and its plankton isolate, DE2-S, the photosynthetic rates were higher on 27 August than on 10 September. In DE2 the 10 September rate was higher and in DE2-S the rates were essentially the same on both dates.

Table 11. Estimates of daytime net photosynthetic rates from diel pH measurements on 27 August, and 10 September, 1982.

Site & Date	P_n (g C/m^3/hr)
26 August:	
DC	0.114
DE1	0.099
DE2	0.045
DC-S	0.052
DE1-S	0.055
DE2-S	0.045
9 September:	
DC	-0.047
DE1	0.051
DE2	0.074
DC-S	0.009
DE1-S	0.038
DE2-S	0.046

The general decrease in photosynthetic rates from the first measurement to the second was probably due to differences in the

quantities of solar insolation received on the two dates. Total solar insolation on 27 August was 470 g-cal/cm^2, about three times as much as that received on 10 September (157 g-cal/cm^2).

For the most part, the rates in the plankton isolates were at least half as large as the rates in the intact communities, suggesting that the phytoplankton were responsible for at least as much of the primary production in the system as the macrophytes.

Enclosure performance

The first use of enclosures on the Georgetown Lake Project was in 1981 (see Methods section). Enclosures E1, E2, E3, E4 and E5 isolated communities consisting primarily of *Elodea* in about 2 m of water in Philipsburg Bay (Figure 1). The chemical results from those stations, described by Garrett (1983a; 1983b) are summarized below, along with observations on the phytoplankton communities (Boveng 1983).

Within a week of installation, enclosures E1-E5 began to show the effects of decomposition of the enclosed plant material (Garrett 1983a). Alkalinity and conductivity increased and pH decreased, exactly opposite of the trends which occurred in adjacent open-water controls. Levels of all measured species of phosphorus and nitrogen increased in the enclosures relative to the controls. Dissolved oxygen increased slightly, then declined sharply.

The dramatic changes in the water chemistry of enclosures E1-E5 were accompanied by shifts in the phytoplankton composition and

density (Boveng 1983). The proportions of diatoms in the community declined and the proportions of cryptophytes and chlorophytes increased. Maximum phytoplankton biomass in the open water surrounding the enclosures occurred as a diatom pulse in late July 1981. In contrast, the maximum phytoplankton biomass in E1 occurred as a bloom of Volvox in mid October 1981. In E2, on 9 September 1981, the phytoplankton was essentially a monoculture of Cryptomonas ovata.

Several other studies have reported that soon after installing enclosures, phytoplankton communities originally composed of diatoms were replaced by flagellated forms (Lund 1972; Takahashi et al. 1975; Thomas and Seibert 1977). These findings suggest that circulation patterns are affected by the enclosures, possibly in the manner proposed by Verduin (1969). Diatoms would tend to be lost from the water column in the less turbulent environs of the enclosure. Flagellates, on the other hand, would still be able to regulate their position in the water column. In addition to the advantage of motility, cryptomonads seem able to adapt effectively to conditions of low light (Rodhe 1955; Wright 1964; Morgan and Kalff 1975). This would help explain the dominance of Cryptomonas in some of the enclosures.

Blue-greens, which are not flagellated, but which can vary their densities over a broad range with gas vacuoles, did not appear in sites E1-E5. Perhaps the altered chemistry of the water offset any advantage which the blue-greens might have had from being able to

regulate bouyancy. For example, nitrogen fixing blue-greens, such as Anabaena often seem to appear in the seasonal succession of the plankton at times when they can exploit low ambient levels of dissolved nitrogen. The elevated levels of nitrate and ammonia in E1-E5 (Garrett 1983a) could have allowed the flagellated forms to compete more effectively in the enclosures than in the open water.

The decomposition of the macrophyte tissue, which seemed to drive the chemical and biological changes in E1-E5, appeared to have been caused by shading from the opaque enclosure walls. In late July 1981, E5 was removed from the lake and clear vinyl windows were installed over much of the wall area (Garrett 1983). After the enclosure was returned to the lake, the magnitudes of the effects noted previously were greatly reduced. Further evidence for the hypothesis that shading was the primary agent in the death of the macrophytes was gained from enclosures DE1 and DE2 which were used during the summer of 1982. These enclosures, which had clear windows over about 85% of the wall area, supported seemingly healthy macrophytes throughout the summer.

Despite the considerably improved performance of DE1 and DE2 over E1-E5, there were some phenomena observed in 1982 which appeared to be enclosure effects. There were initial declines in specific conductance in the enclosures relative to the open water, though the conductance seemed to parallel the control thereafter (Figure 3). The pH in DE1 was slightly depressed relative to DC (Figure 5), probably a reflection of decreased productivity of the macrophytes due

to the inability to completely eliminate shading. In DE2, pH levels were as high or higher than DC, suggesting that fertilization compensated for the enclosure effect.

The phenomena which appeared to be effects of DE1 and DE2 on the phytoplankton were described above in the section on species composition and succession. Briefly, they were an initial suppression of the diatom Asterionella and decreased proportions of Fragilaria accompanied by increased proportions of blue-greens later in the season. These results seem to be consistent with the hypotheses that decreased circulation hinders diatoms and that reduced shading mitigated the decay of macrophytes and subsequent release of nutrients.

The small enclosures used to isolate plankton communities (DC-S, DE1-S, and DE2-S) also seemed to have effects on the captured communities, even though they were left in place for less than two days at a time. The main effect observed was the apparent loss of phosphorus in the phosphorus fate experiments. If the loss of P was due to formation of insoluble P species, the small enclosures might have affected the rate at which the compounds were precipitated. Similarly, if the loss was due to settling of detrital or algal particles which were normally held in suspension by turbulence, the enclosures could have increased the rate of settling. These effects would probably become more pronounced in experiments of longer duration.

Use of the large enclosures such as E1-E5, DE1, and DE2, was

accompanied by several problems with deployment and maintenance. The most difficult to overcome were those problems caused by winds which are common on Georgetown Lake in the summer. Positioning the enclosures for installment, anchoring them, and sampling the enclosed communities were difficult or impossible during moderate winds. Additional problems with E1-E5 which were unexpected, but which could be overcome with suitable precautions, included damage to the float rings by muskrats and perching on the float rings by birds. The birds, primarily western grebes, defecated on the float rings and presumably, some of the excretions fell into the enclosed communities.

In summary, the enclosures used in this study allowed certain experiments to be conducted which would have been impossible without a container to isolate portions of the ecosystem. There were effects on the enclosed communities due simply to the method of isolation. As other workers have found, enclosures seem most useful for study of general ecosystem relationships and will be less useful for study of specific systems where the outcome of experiments depends heavily on precise agreement between control and enclosed communities.

CONCLUSIONS

Water chemical parameters measured in Georgetown Lake during the summer of 1982 were consistent with the findings of earlier studies which showed that the reservoir is a calcium carbonate dominated system. Conductivity, alkalinity, and pH all showed the effects of photosynthetic removal of dissolved inorganic carbon by the aquatic plants.

Enrichment with phosphorus and nitrogen of an enclosed community including macrophytes, phytoplankton and sediments resulted in an increase in the density of phytoplankton estimated by chlorophyll a levels. Cell volume estimates of the phytoplankton did not show the increase but this method of computing biomass seemed less accurate.

Unlike many documented cases of cultural eutrophication, enrichment of the enclosed sites did not result in dramatically increased levels of blue-green algae. The highest densities of blue-green algae observed seemed to be a response to isolation by enclosures rather than a response to fertilization.

Attempts to measure rates of phosphorus removal from the water and uptake by plants were largely confounded by a lack of sensitivity of the analytical technique. Furthermore, the chemical conditions present during most of the summer may have caused the majority of added phosphorus to precipitate. However, in experiments of about 24

hours duration, there was evidence that the phytoplankton were extracting phosphate from the water.

There was no detectable increase in total phosphorus of the macrophyte tissue harvested from the fertilized enclosure at the termination of the experiment. A rigorous budget of the added phosphorus could not be constructed because of the uncertainty associated with the insoluble abiotic pool which may have received much of the added P as a precipitate.

The isolated communities which were studied were subject to effects caused by the isolating mechanisms themselves. Enclosures used in 1981 provided information about the importance of natural light intensity to the plant communities and seemed to indicate that some of the effects are due to reduced circulation in the captured communities.

REFERENCES CITED

APHA. 1980. Standard methods for the examination of water and wastewater, 15th Ed. American Public Health Association, Washington, D. C. 1134 pp.

Beyers, R. J., J. L. Larimer, H. T. Odum, R. B. Parker, and N. E. Armstrong. 1963. Directions for the determination of changes in carbon dioxide concentration from changes in pH. Publ. Inst. Mar. Sci. Univ. Texas. 9:454-489.

Bold, H. C. and M. J. Wynne. 1978. Introduction to the algae. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 706 pp.

Boveng, P. 1983. Phytoplankton standing crop and taxonomy. In P. Garrett, Final Report: Georgetown Lake Clean Lakes Project, Phase 1. Deer Lodge County Planning Board, Anaconda, Montana. pp. 163-173.

Brown, E. J. and R. F. Harris. 1978. Kinetics of algal transient phosphate uptake and the cell quota concept. Limnol. Oceanogr. 23:35-40.

Brown, S. D. and A. P. Austin. 1973. Diatom succession and interaction in littoral periphyton and plankton. Hydrobiol., 43: 333-356.

Brown, T. E. and F. L. Richardson. 1968. The effect of growth environment on the physiology of algae: light intensity. J. Phycol. 4:38-54.

Currie, D. J. and J. Kalff. 1984. The relative importance of bacterioplankton and phytoplankton in phosphorus uptake in freshwater. Limnol. Oceanogr. 29:311-321.

Dunst, R., S. Born, P. Uttormark, S. Smith, S. Nichols, J. Peterson, D. Knauer, S. Serns, D. Winter, and T. Wirth. 1974. Survey of lake rehabilitation techniques and experiences. Technical Bulletin No. 75, Wisconsin Department of Natural Resources. Madison, Wisconsin.

Edmondson, W. T. 1972. Nutrients and phytoplankton in Lake Washington. Am. Soc. Limnol. Oceanogr. Spec. Symp. 1:172-193.

Foris, W. J. 1976. A comparison of diatoms on horizontal and vertical substrates in Georgetown Lake, Montana. M. S. Thesis. Montana State University, Bozeman, Montana. 106 pp.

Garrett, P. A. 1983a. Final report: Georgetown Lake Clean Lakes Project, Phase 1. Deer Lodge County Planning Board, Anaconda, Montana.

Garrett, P. A. 1983b. Relationships between benthic communities, land use, chemical dynamics, and trophic state in Georgetown Lake. Ph. D. Thesis. Montana State University. 149 pp.

Garrison, P. J. 1976. The role of the bottom sediments in the eutrophication of Georgetown Lake, Montana. M. S. Thesis. Montana State University, Bozeman, Montana. 123 pp.

Geer, W. H. 1977. The population dynamics and production of the net zooplankton in Georgetown Lake, Montana in 1974. M. S. Thesis. Montana State University, Bozeman, Montana. 141 pp.

Golterman, H. L. 1982. Loading concentration models for phosphate in shallow lakes. Hydrobiol., 91:169-174.

Gurland, J. and R. C. Tripathi. 1971. A simple approximation for unbiased estimation of the standard deviation. Amer. Stat., 25:30-32.

Harris, G. P. 1978. Photosynthesis, productivity and growth: The physiological ecology of phytoplankton. Ergebnisse der Limnologie, Heft 10, Verh. Int. Verein. Limnol. E. Schwiezerbart'sche Verlagsbuchhandlung (Nagele u. Obermiller). Stuttgart. 171 pp.

Hustedt, F. 1930. Bacillariophyta (diatomae). Heft 10. In A. Pa Pascher, Die Susswasser-flora mitteleuropas. Gustau Fisher, Jena, Germany; Reprint, 1976, Otto Koeltz Science Publishers, Koenigstein, West Germany.

Knight, J. C. 1980. An investigation of the general limnology of Georgetown Lake, Montana. Ph.D. Thesis. Montana State University, Bozeman, Montana. 139 pp.

Knight, J. C., P. J. Garrison and J. C. Wright. 1976. An investigation into the extent and cause of eutrophication in Georgetown Lake, Montana. Montana University Joint Water Resources Research Center, Bozeman, Montana. Report No. 77. 97 pp.

Kuenzler, E. J. and B. H. Ketchum. 1962. Rate of phosphate uptake by Phaeodactylum tricornutum. Biol. Bull. 123:134-135.

Kuhl, A. 1962. Inorganic phosphorus uptake and metabolism. In R. A. Lewin (ed.), Physiology and Biochemistry of Algae. Academic Press, New York. pp. 211-229.

Lean, D. R. S. and M. N. Charlton. 1976. A study of phosphorus kinetics in a lake ecosystem. In Nriagu, J., (ed.) Environmental

Biogeochemistry, Vol. 1. Ann Arbor Science Publishers, Inc., Ann Arbor, Michigan. p. 283-294.

Lehman, J. T., D. B. Botkin, and G. E. Likens. 1975. The assumptions and rationales of a computer model of phytoplankton population dynamics. Limnol. Oceanogr. 20:343-364.

Lie, G. B. 1979. The influence of aquatic macrophytes on the chemical cycles of the littoral. In Breck, J. et al. (eds.) Aquatic Plants, Lake Management, and Ecosystem Consequences of Lake Harvesting. Institute for Environmental Studies, University of Wisconsin. Madison, Wisconsin. p. 101-126.

Lund, J. W. G. 1949. Studies on Asterionella: I. The origin and nature of the cells producing the spring maximum. J. Ecol., 37: 389-419.

Lund, J. W. G. 1950. Studies on Asterionella: II. Nutrient depletion and the spring maximum. J. Ecol., 38:1-35.

Lund, J. W. G. 1972. Preliminary observation on the use of large experimental tubes in lakes. Verh. Int. Verein. Limnol. 18:71-77.

Lund, J. W. G., C. Kipling and E. D. LeCren. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrbiologia. 9:143-170.

Lynch, M. and J. Shapiro. 1981. Predation, enrichment, and phytoplankton community structure. Limnol. Oceanogr. 26(1):86-102.

Mackereth, F. J. 1953. Phosphorus utilization by Asterionella formosa. J. Exp. Bot. 4:296-313.

McNabb, C. D. 1960. Enumeration of freshwater phytoplankton concentrated on the membrane filter. Limnol. Oceanogr. 5:57-61.

Menzel, D. W. 1977. Summary of experimental results: Controlled ecosystem pollution experiment. Bull. Mar. Sci. 27(1):146-175.

Menzel, D. W. and J. Case. 1977. Concept and design: Controlled ecosystem pollution experiment. Bull. Mar. Sci. 27(1):1-7.

Morgan, K. and J. Kalff. 1975. The winter dark survival of an algal flagellate - Cryptomonas erosa (Skujo). Verh. Int. Verein. Limnol. 19:2734-2740.

Odum, E. P. 1984. The mesocosm. Bioscience. 34(9),558-562.

Odum, H. T. and C. M. Hoskin. 1958. Comparative studies of the metabolism in Texas bays. Publ. Inst. Mar. Sci. Univ. Texas. 5:16-46.

Park, K. H., D. W. Wood, and H. T. Odum. 1958. Diurnal pH variation in Texas bays and its application to primary production estimation. Publ. Inst. Mar. Sci. Univ. Texas. 5:47-64.

Patrick, R. and C. Reimer. 1966. The diatoms of the United States. Vol. I. Academy of Natural Sciences, Philadelphia. 688 pp.

Prescott, G. 1962. Algae of the Western Great Lakes area. W. C. Brown Co., Dubuque, Iowa. 977 pp.

Prescott, G. 1978. How to know the fresh-water algae. 3rd Edition. W. C. Brown Co., Dubuque, Iowa. 293 pp.

Rhee, G-Y. 1973. A continuous culture study of phosphate uptake, growth rate, and polyphosphate in Scenedesmus sp. J. Phycol. 9:495-506.

Rodhe, W. 1955. Can plankton production proceed during winter darkness in subarctic lakes? Verh. Int. Verein. Limnol. 12:117-122.

Schindler, D. W. and E. J. Fee. 1974. Experimental Lakes Area: Whole-lake experiments in eutrophication. J. Fish. Res. Bd. Can. 31:937-953.

Smith, G. 1950. The freshwater algae of the United States. 2nd Ed. McGraw-Hill, New York. 719 pp.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Company. San Francisco, California. 859 pp.

Solorzano, L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnol. Oceanogr. 14(5),799-801.

Steeman-Nielsen, E. and E. G. Jorgensen. 1968. The adaptation of plankton algae: I. General part. Physiol. Plant. 21:401-413.

Strickland, J. D. H. and T. R. Parsons. 1968. A practical handbook of seawater analysis. Fisheries Research Board of Canada, Bulletin, No. 167. 311 pp.

Stumm, W. and J. J. Morgan. 1981. Aquatic chemistry. John Wiley and Sons. New York. 780 pp.

Takahashi, M., W. H. Thomas, D. L. R. Seibert, J. Beers, P. Koeller, and T. R. Parsons. 1975. The replication of biological events in enclosed water columns. Arch. Hydrobiol. 76:5-23.

Thomas, W. H. and L. R. Seibert. 1977. Effects of copper on the dominance and the diversity of algae: Controlled ecosystem pollution experiment. Bull. Mar. Sci. 27:23-33.

Verduin, J. 1969. Critique of research methods involving plastic

bags in aquatic environments. Trans. Amer. Fish. Soc. 98:355-366.

Wetzel, R. 1975. Limnology. W. B. Saunders Company, Philadelphia. 743 pp.

Wilkinson, V. 1983. Chlorophyll manual. Taupo Research Laboratory, Division of Marine and Freshwater Science, Taupo, New Zealand.

Wright, J. C. 1960. The limnology of Canyon Ferry Reservoir. III. Some observations on the density dependence of photosynthesis and its cause. Limnol. Oceanog. 5:356-351.

Wright, R. T. 1964. Dynamics of a phytoplankton community in an ice-covered lake. Limnol. Oceanogr. 9:163-178.

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