Phytoplankton photosynthesis and biomass in Lake Superior: Effects of nutrient enrichment[1]

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Introduction

Several investigators have measured the rate of photosynthesis in Lake Superior during the past two decades (Putnam & Olson 1966, Parkos et al. 1969, Verduin 1975, Nalewajko et al. 1981, Fahnenstiel & Glime 1983, Nalewajko & Voltolina 1986). Neither experimental approaches nor methods for data reporting have been consistent among investigators (Fahnenstiel et al. 1989) and thus, not all rates are comparable. Furthermore, the factor(s) controlling the rate of photosynthesis in Lake Superior may still be open to question.

The role of nutrients and in particular, phosphorus, in controlling photosynthesis and phytoplankton yield in Lake Superior has been documented. Schelske et al. (1972) performed a series of large enclosure experiments that were designed to determine the limiting element in the Great Lakes. In these experiments, large volumes of water (> 1000 l) were spiked with various combinations of plant nutrients and the response of the phytoplankton community in terms of chlorophyll, phytoplankton abundance, and photosynthesis was monitored. Results from these experiments suggested that phosphorus was the limiting element in the Great Lakes. These and other nutrient enrichment studies on the Great Lakes (Schelske 1979) provided the scientific cornerstone for eutrophication control.

More recent information, however, has questioned the role of phosphorus in controlling primary production and algal growth in Lake Superior. Nalewajko et al. (1981) suggested that phytoplankton growth in Lake Superior was not limited by phosphorus but by light, and even suggested that the entire concept of phosphorus control to maintain phytoplankton biomass at present levels may need to be reevaluated. Light control of primary production was suggested to occur even in the epilimnion during thermal stratification. In a subsequent paper, Nalewajko & Voltolina (1986) suggested that physical factors were more important than phosphorus in controlling primary production during isothermal mixing periods.

The purposes of this study were: 1) to examine the photosynthesis-irradiance (P-I) parameters for Lake Superior phytoplankton, and 2) to determine the role of nutrients in controlling the P-I parameters and phytoplankton biomass during thermal stratification. Photosynthesis-irradiance curves are commonly used to characterize the pattern (Jassby & Platt 1976, Platt et al. 1980) and to understand the controls (Côté & Platt 1984) of photosynthesis.

Methods

Samples were collected at an offshore station (47° 27′ 48″ N, 88° 34′ 42″ W) located 25 km from the north entry of the Portage Ship Canal on 18 May and 24 August, 1981. The water depth at this station was 230 m.

In May, samples were collected in the early evening from 10 m and 150 m and were stored in 20-l carboys. The carboys were transported to the lab without any interruption in the day-night cycle. The carboys were maintained at 2.8 °C and illuminated with 0.36 Einst. $m^{-2} \cdot h^{-1}$. Starting at dawn the next day, three P-I experiments were performed on samples from each carboy.

In August, samples were collected in the evening from the epilimnion (5 m) and hypolimnion (25 m) and were stored in four 20-l carboys. One carboy from each depth served as the control; the other two received daily nutrient additions of 0.75 µg $\cdot$ l^{-1} of phosphorus, 7.0 µg $\cdot$ l^{-1} of EDTA, 1 µg $\cdot$ l^{-1} of Fe, and 0.1 µg $\cdot$ l^{-1} of Mn on days 0–3 which resulted in total additions to the nutrient carboys of 3.0 µg $\cdot$ l^{-1} of P, 28 µg $\cdot$ l^{-1} of EDTA, 4 µg $\cdot$ l^{-1} of Fe, and 0.4 µg $\cdot$ l^{-1} of Mn. These daily nutrients enrichment levels were chosen in order to provide relatively little perturbation while, if nutrients were limiting, still prompting significant nutrient response (see Schelske 1984). The carboys from 5 m were maintained at 18.5 °C, 0.4 Einst. m$^{-2} \cdot$ h^{-1}, and 14:10 light-dark cycle, while the carboys from 25 m were maintained at 5.8 °C, 0.09 Einst. m$^{-2} \cdot$ h^{-1}, and 14:10 light-dark cycle.

Water temperatures at depth were determined with a bathythermograph and thermistor. Surface water temperatures were taken from two National Oceanic and Atmospheric Administration Data Buoys located at 48.0 °N, 87.6 °W and at 47.3 °N, 90.0 °W.

Chlorophyll concentrations were determined fluorometrically on 90 % acetone extracted samples (STRICKLAND & PARSONS 1972). Triplicate chlorophyll samples were taken from each carboy.

Phytoplankton samples were preserved with Lugol's solution and prepared for enumeration (DOZIER & RICHERSON 1975). Abundances were first converted to volume by geometric approximation of algal shape, and then to biomass by assuming a specific weight of one.

Phosphate turnover times were measured immediately after sample collection by adding carrier-free ^{33}P-PO_4 to fresh lake water and then filtering small subsamples at appropriate intervals (LEAN et al. 1983). The uptake rate constant is the natural logarithm of the percent ^{33}P in the filtrate regressed against time; the reciprocal is the turnover time.

Phytoplankton photosynthesis was estimated with the ^{14}C technique (VOLLENWEIDER 1974). Samples were dispensed from the carboys into 300-ml BOD bottles and inoculated with $10-20 \mu Ci$ of $H^{14}CO_3^-$. Bottles were incubated in a laboratory incubator with seven light levels, ranging from $0.02-1.35$ Einst. $m^{-2} \cdot h^{-1}$. Incubation temperature was maintained within 1 °C of lakewater temperature. In the lowest light compartment, a dark BOD bottle was spiked with ^{14}C and used as the control. The uptake of ^{14}C in this dark bottle did not exceed 5 % of the light-saturated rate. Two experiments were conducted daily for each treatment and depth. The first experiment, replicate # 1, was conducted in morning and the second experiment, replicate # 2, was conducted in early afternoon. Total CO_2 was determined from alkalinity and pH measurements (VOLLENWEIDER 1974).

After a $1-2$ h incubation, three subsamples from each bottle were filtered onto $0.45-\mu m$ Millipore filters, decontaminated with 0.5 ml of 0.5 N HCL for $4-6$ h, placed in separate scintillation vials with scintillation cocktail, and counted with a scintillation counter. External standards were used to correct for quench.

Photosynthetic rates, normalized to chlorophyll-a from triplicate samples of each bottle, were pooled to construct a single photosynthesis-irradiance (P-I) curve. The following equation was used to parameterize the P-I relationship (PLATT et al. 1980):

$$P^B = P_S^B \cdot (1-e^{-\alpha i/P_S^B} \cdot e^{-\beta i/P_S^B})$$

where P^B = specific photosynthetic rate at irradiance i (mg C $\cdot$ mg Chl$^{-1} \cdot h^{-1}$); P_S^B = the maximum potential photosynthetic rate (same units as P^B); α = the initial linear slope at low irradiances (mg C $\cdot$ mg Chl$^{-1} \cdot$ Einst^{-1} $\cdot m^2$); and β = the negative slope at high irradiances (same units as α). P_S^B is a scaling parameter with little ecological significance. The more commonly used parameter, P_M^B, the maximum photosynthetic rate at light saturation, was determined from P_S^B with the following equation:

$$P_M^B = P_S^B \cdot [\alpha/(\alpha + \beta)] \cdot [\beta/(\alpha + \beta)]^{\beta/\alpha}$$

In the absence of photoinhibition, $P_M^B = P_S^B$. If $\beta > 0$, then $P_S^B > P_M^B$, and P_S^B represents the maximum obtainable photosynthetic rate in the absence of photoinhibition.

One derived parameter was also of interest; I_K. I_K is the light saturation parameter (TALLING 1957), defined as P_M^B/α with units of Einst$^{-1} \cdot m^2 \cdot h^{-1}$. This parameter has been used to characterize the phytoplankton in terms of light adaptation (YENTSCH & LEE 1966). Phytoplankton with lower I_K values were generally assumed to be more low-light adapted than phytoplankton with higher I_K values.

A nonlinear least squares estimation package was used to determine both the maximum likelihood estimates of the parameters and the variance-covariance matrix. In many cases, the three-parameter model described above, including a photoinhibition parameter, may not be necessary to adequately fit P-I data (PLATT et al. 1980). Many phytoplankton communities do not exhibit significant photoinhibition at incubation irradiances, and the simple two-parameter model with P_M^B and α is adequate. Whether the photoinhibition parameter, β, should be included in our model was determined by fit of the model, based on R^2 values, and the significance of β.

Results

May experiments

Despite a completely isothermal water column at 2.8 °C, there were notable differences between phytoplankton communities at 10 m and 150 m. Chlorophyll and phaeophytin values were 0.67 ± 0.08 mg $\cdot$ m^{-3} and 0.10 ± 0.02 mg $\cdot$ m^{-3}, respectively, at 10 m; but were 0.13 ± 0.03 mg $\cdot$ m^{-3} and 0.43 ± 0.06 mg $\cdot$ m^{-3}, respectively, at 150 m. Similarly, phytoplankton abundance and biomass were approximately $4-5$ times higher at 10 m than at 150 m. The phytoplankton community at 10 m was dominated by *Cyclotella* spp., small flagellates $(3-10 \mu m)$, and *Oscillatoria* spp.; at 150 m *Rhodomonas minuta* constituted over half the biomass.

The samples from 150 m were more susceptible to photoinhibition and had lower alpha and P_M^B values than samples from 10 m (Fig. 1; Table 1). The three-parameter model including photoinhibition was needed to adequately fit all P-I curves from 150 m but in only one case was the three-parameter model needed to fit P-I curves from 10 m. Alpha and P_M^B values for 10 m were approximately $2-3$ times higher than values for 150 m (Table 1).
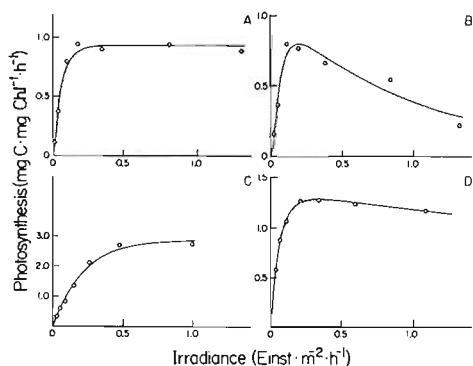
Fig. 1. Examples of P-I curves from each sampling period and depth. A) May, 10 m, nutrient treatment, day 1, replicate 1, B) May, 150 m, control, day 1, replicate 1, C) August, 5 m, control, day 1, replicate 1, D) August, 25 m, control, day 1, replicate 1.

August experiments

The August samples were collected at the time of maximum surface temperature (Fig. 2) to examine P-I parameters and the role of nutrients in controlling photosynthesis during thermal stratification. The 5 m sample was taken from the middle of a 10 m thick epilimnion.

Epilimnetic phytoplankton communities exhibited approximately half the chlorophyll and phytoplankton biomass of hypolimnetic phytoplankton communities (Figs. 3 and 4). The phytoplankton communities were somewhat similar with epilimnetic communities dominated by *Cyclotella* spp., small flagellates (3 – 10 μm) and lesser amounts of Cryptophytes; while the hypolimnetic community was dominated by phytoflagellates (small flagellates and Cryptophytes)

Table 1. Photosynthesis-irradiance parameters for experiments performed in May and August, 1981. The day and type of treatment (C = control, N = nutrient), replicate number, P_M^B (mg C · mg Chl^{-1} · h^{-1}) α (mg C · mg Chl^{-1} · $Einst.^{-1}$ · m^{-2}), I_k (Einst. m^{-2} · h^{-1}), β (same units as α), and the R^2 of regression are given for each P-I curve. Error estimates are standard deviations.

| Exp.	Depth	Day	Treat.	R	P_M^B		α	I_k	β	R_2
Aug.	5	1	C	1	2.9±	0.1	13.3±1.0	0.22	–	0.99
			C	2	3.2±	0.2	16.5±1.4	0.19	–	0.98
			N	1	2.7±	0.1	13.1±1.2	0.21	–	0.98
			N	2	3.1±	0.2	15.0±1.4	0.21	–	0.98
		4	C	1	3.7±	0.2	18.0±1.8	0.20	–	0.98
			C	2	3.8±	0.3	19.9±3.2	0.19	–	0.95
			N	1	4.9±	0.3	18.6±2.1	0.26	–	0.97
			N	2	5.6±	0.5	22.2±4.5	0.25	–	0.94
		10	C	1	3.7±	0.3	22.0±1.9	0.17	–	0.99
			C	2	4.0±	0.4	22.8±2.9	0.18	–	0.99
			N	1	3.5±	0.2	18.8±2.1	0.19	–	0.97
			N	2	3.7±	0.2	23.2±1.3	0.16	–	0.97
Aug.	25	1	C	1	1.2±	0.1	14.0±1.2	0.09	0.35±0.16	0.98
			C	2	1.3±	<0.1	20.2±0.6	0.06	0.17±0.03	0.99
			N	1	1.0±	<0.1	12.8±0.9	0.08	0.08±0.05	0.98
			N	2	1.2±	<0.1	15.4±0.6	0.08	0.27±0.05	0.99
		4	C	1	1.4±	<0.1	15.7±0.5	0.09	0.12±0.04	0.99
			C	2	1.6±	0.2	14.3±1.2	0.11	–	0.90
			N	1	1.6±	0.1	13.5±0.5	0.12	0.52±0.13	0.99
			N	2	2.0±	0.2	14.7±1.8	0.14	–	0.93
		10	C	1	1.7±	0.3	18.0±3.1	0.09	0.38±0.51	0.92
			C	2	1.5±	0.2	16.1±4.0	0.09	0.23±0.50	0.89
			N	1	2.4±	0.2	17.7±3.2	0.14	–	0.93
			N	2	2.6±	0.2	20.6±3.4	0.13	0.44±0.80	0.95
May	10	1	C	1	1.9±	0.1	30.4±3.8	0.06	–	0.97
			C	2	2.5±	0.2	35.9±4.8	0.07	0.32±0.26	0.97
			C	3	2.6±	0.1	38.0±7.7	0.07	–	0.94
	150	1	C	1	1.3±	0.3	14.3±4.1	0.09	0.76±0.51	0.89
			C	2	0.9±	0.1	15.8±4.1	0.06	0.92±0.31	0.94
			C	3	1.0±	0.2	12.2±2.0	0.08	0.72±0.39	0.96
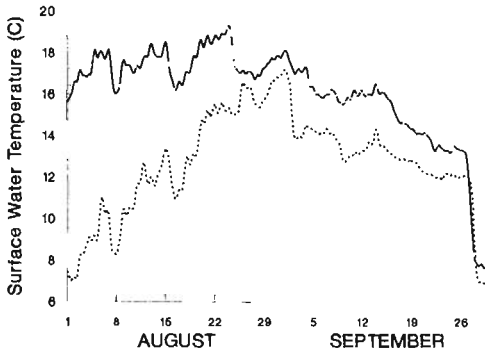
Fig. 2. Surface temperatures in Lake Superior for August and September taken from NOAA Weather Buoys # 1 and # 6. Data from Buoy # 1 (48.0 °N, 87.6 °W) are indicated by dotted lines and data from Buoy # 6 (47.3 °N, 90.0 °W) are indicated by solid line.
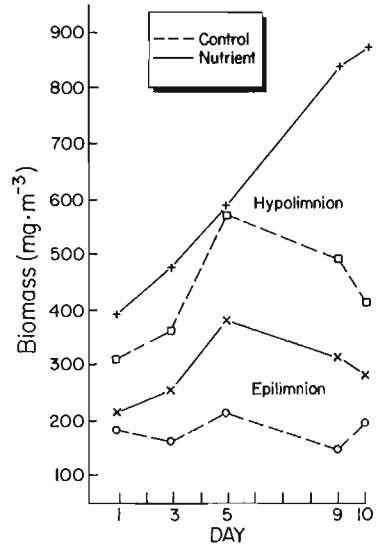

Fig. 4. Phytoplankton biomass (mg · m^{-3}) in nutrient-treated and control carboys from experiments conducted with epilimnetic and hypolimnetic phytoplankton communities. Experiments conducted in August 1981.

Fig. 3. Chlorophyll concentrations (mg · m^{-3}) in nutrient-treated and control carboys from experiments conducted with epilimnetic and hypolimnetic phytoplankton communities. Experiments conducted in August 1981.
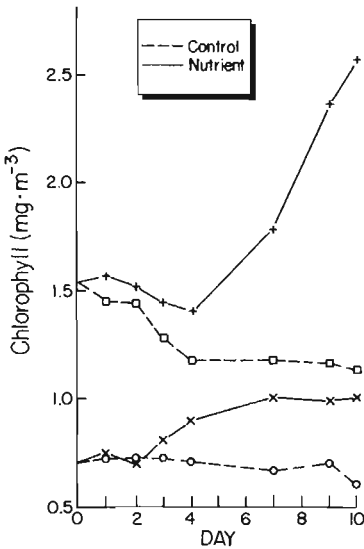
with lesser amounts of *Cyclotella* spp. and *Oscillatoria* spp. Epilimnetic phytoplankton were more P-deficient than hypolimnetic communities, as indicated by faster ^{33}P turnover times, 14 minutes vs. 30 minutes.

All epilimnetic P-I curves were adequately fit with the two-parameter model (no photoinhibi-

tion), whereas the majority of hypolimnetic P-I curves required the three-parameter model (Fig. 1; Table 1). Hypolimnetic P_M^B values were lower than epilimnetic values, but were similar to May values. Alpha values were similar for both epilimnetic and hypolimnetic communities, and were similar to the May 150-m sample but less than the May 10-m sample.

Nutrient enrichment increased chlorophyll and phytoplankton biomass for both epilimnetic and hypolimnetic communities (Figs. 3 and 4). For the hypolimnetic community, chlorophyll and biomass concentrations were approximately 2 times initial or control values after ten days; for the epilimnetic community, chlorophyll and biomass values were approximately 1.5 times initial or control values. Epilimnetic communities responded earlier to the nutrient additions than hypolimnetic communities. Maximum chlorophyll and biomass values were found on days 5–7 for the epilimnetic community and on day 10 for the hypolimnetic community. The chlorophyll and biomass concentrations in the epilimnetic control remained relatively constant throughout the experiment. On the other hand, the hypolimnetic control exhibited a marked decrease in chlorophyll but an increase in phytoplankton bio-
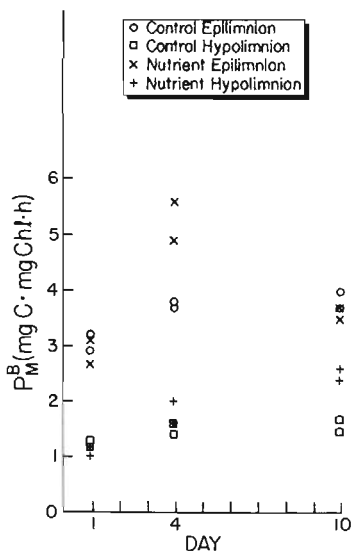
Fig. 5. P_M^B values $(mg C \cdot mg Chl^{-1} \cdot h^{-1})$ in nutrient-treated and control samples from experiments conducted with epilimnetic and hypolimnetic phytoplankton communities. Experiments conducted in August 1981.

Fig. 6. Alpha values $(mg C \cdot mg Chl^{-1} \cdot Einst.^{-1} \cdot m^2)$ in nutrient-treated and control samples from experiments conducted with epilimnetic and hypolimnetic phytoplankton communities. Experiments conducted in August 1981.
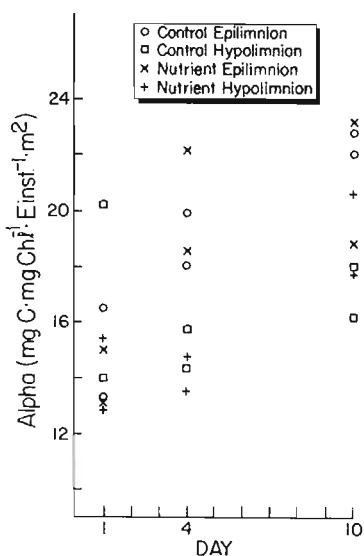
mass. Phytoplankton species composition did not change markedly with either nutrient treatment. Taxa that were especially responsive to nutrient additions included an *Ochromonas*-like flagellate, *Oscillatoria* spp., and *Synedra* spp.

P-I curves also demonstrated marked response to nutrient enrichment (Figs. 5 and 6). Epilimnetic and hypolimnetic P_M^B values were higher with nutrient treatments than control values during the period of biomass and chlorophyll increases. Epilimnetic P_M^B values from nutrient treatments were higher than control values on day 4; hypolimnetic community nutrient P_M^B values were higher on day 10. Alpha values did not demonstrate any nutrient response (Fig. 6); there was, however, a general increase with time in alpha values for all treatments and depths.

Discussion

The photosynthetic characteristics of Lake Superior phytoplankton observed in this study are similar to those reported in recent studies from Lake Superior. Our mean and range of surface P_M^B values (2.7 and 1.9 – 3.2 mg C · mg Chl^{-1} · h^{-1}, respectively) are similar to P_M^B values and assimilation numbers reported by FAHNENSTIEL & GLIME (1981) and NALEWAJKO & VOLTOLINA (1986). FAHNENSTIEL & GLIME (1981) reported a mean assimilation number of 2.4 mg C · mg Chl^{-1} · h^{-1} with a range of 0.5 – 3.5 mg C · mg Chl^{-1} · h^{-1} and NALEWAJKO & VOLTOLINA (1986) reported a P_M^B range of 0.1 – 5.0 mg C · mg Chl^{-1} · h^{-1} with mean values of 1.2 and 2.5 mg C · mg Chl^{-1} · h^{-1}, respectively, during isothermal and thermally stratified periods. Our I_K values for epilimnetic communities, 0.15 – 0.30 Einst. m^{-2} · h^{-1}, overlap the range of 0.27 – 0.36 Einst. m^{-2} · h^{-1} reported by NALEWAJKO et al. (1981).

One of the more surprising results of this study was the remarkable difference between phytoplankton from 10 m and 150 m in an isothermally "mixed" water column. The phytoplankton from 150 m were more low light adapted, as indicated by lower I_K values and more photoinhibition (HARRIS 1978), and also had reduced chlorophyll and phytoplankton biomass compared to phytoplankton from 10 m. Most of the chlorophyll found at 150 m was phaeophytin. This indicates that the phytoplankton had spent sufficient time out of the euphotic zone to actually start "dying", and therefore, that the mixing time was greater than the phytoplankton generation time. An isothermal water column does not imply that the

water column is necessarily well mixed but rather that viscous forces rather than buoyancy may be the greatest inhibition to deep mixing. The relationship between mixing times and phytoplankton generation times should be examined in more detail in deep lakes. Whatever the relationship, it is clear that light is an important factor limiting phytoplankton growth in deep lakes during isothermal mixing periods (NALEWAJKO & VOLTO-LINA 1986).

During thermal stratification, nutrients clearly limit the maximum photosynthetic rate and phytoplankton biomass in Lake Superior. Nutrient enrichment of both epilimnetic and hypolimnetic samples resulted in significant increases in P_M^B, phytoplankton biomass, and chlorophyll values several days after enrichment (Figs. 3–6). Although we examined the effect of a mixed nutrient enrichment (P, Fe, EDTA, and Mn), our ^{33}P results and those of SCHELSKE et al. (1972), LEAN et al. (1983), and NALEWAJKO & VOLTOLINA (1986) suggest that phosphorus is the specific nutrient that limits photosynthesis and phytoplankton biomass during thermal stratification. In a series of nutrient enrichment experiments, increases in photosynthesis and phytoplankton biomass were observed only when phosphorus was added, either alone or in combination with other nutrients (SCHELSKE et al. 1972). LEAN et al. (1983) reanalyzed NALEWAJKO et al. (1981) data and concluded on the basis of physiological evidence that the Lake Superior phytoplankton were severely phosphorus deficient. Furthermore, NALEWAJKO & VOLTOLINA (1986) reported Popt/Vmax ratios that also suggested the phytoplanton from thermal stratification were extremely phosphorus deficient. While we do not have estimates of Popt/Vmax, our relatively fast turnover times coupled with low phytoplankton biomass suggest that phosphorus is limiting (LEAN et al. 1983).

Because of similarities in the phytoplankton communities between our study and those of NA-LEWAJKO et al. (1981), our results have general application to the period of thermal stratification in Lake Superior, and therefore, to the question of nutrient-light control of photosynthesis and phytoplankton biomass. For both investigations, epilimnetic chlorophyll ranged between 0.7 and 1.0 mg · m^{-3} and phytoplankton biomass ranged between 0.12 and 0.2 g · m^{-3}. The physiological condition of the phytoplankton, in terms of nutrient and light regimes, was also similar. The phytoplankton communities studied by NALEWAJKO et al. (1981) exhibited phosphorus turnover times of

14–40 minutes, similar to our turnover times of 14–33 minutes. The P-I parameters, particularly I_K, reported in NALEWAJKO et al. (1981) and this study were also similar, as discussed earlier.

Because of these low I_K values and only moderate ^{33}P turnover times, NALEWAJKO et al. (1981) suggested that light is the primary factor limiting phytoplankton production in Lake Superior during thermal stratification. In our experiments, however, even the hypolimnetic phytoplankton which exhibited I_K values 3–5 times lower than those reported by NALEWAJKO et al. (1981) responded to nutrient enrichment. The fact that low-light adapted phytoplankton can respond to nutrient enrichment is not surprising, given the compensatory relationship between light and nutrient limitation. RHEE & GOTHAM (1981) demonstrated that within a range of growth rates, light and nutrients can compensate for each other to maintain a given growth rate. Excessive or added nutrients can help maintain a growth rate even under sub-optimal or low light conditions. A similar nutrient-light interaction was demonstrated for natural communities from the hypolimnion in Lake Michigan (FAHNENSTIEL et al. 1984) where a combination of light and nutrient levels were responsible for the final yield. Phytoplankton communities incubated at a light level as low as 0.03 Einst. m^{-2} · h^{-1} exhibited increased growth when given a nutrient addition. This light level is similar to average daily irradiance at 40 m in Lake Superior. Thus, just because a phytoplankton community is low-light adapted and exhibits only moderate ^{33}P turnover times does not preclude nutrient stimulation or phosphorus limitation.

The increase in P_M^B values with nutrient addition is consistent with the idea that Lake Superior phytoplankton are nutrient-limited. Using nutrient-limited cultures, SENFT (1978) demonstrated that Pmax, similar to P_M^B, was a function of the phosphorus status of the cell. On the other hand, our alpha values did not change relative to the controls in response to nutrient additions. Because alpha is a measure of the photochemical processes of photosynthesis we would not expect a change with nutrient enrichment. However, alpha values in both the controls and nutrients treatments did increase with time.

In conclusion, our results suggest that phosphorus management is the correct strategy for maintaining water quality in Lake Superior. Although a combination of physical, chemical, and biological factors control the rate of photosynthesis and phytoplankton biomass in the lakes, it is

our belief that the chemical factors, particularly phosphorus, are dominant in most cases and should remain the focus for controlling phytoplankton biomass in the Great Lakes. Even if one could demonstrate significant physical control of phytoplankton growth, such as those occurring during isothermal mixing periods, nutrients still play a role and offer more practical means of control than physical factors.

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