

## Spring phytoplankton photosynthesis, growth, and primary production and relationships to a recurrent coastal sediment plume and river inputs in southeastern Lake Michigan

Steven E. Lohrenz,<sup>1</sup> Gary L. Fahnenstiel,<sup>2</sup> David F. Millie,<sup>3</sup> Oscar M. E. Schofield,<sup>4</sup> Tom Johengen,<sup>5</sup> and Trisha Bergmann<sup>4</sup>

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[1] A recurrent coastal sediment plume (RCP) is an episodic event in the southern basin of Lake Michigan that typically coincides with the spring diatom bloom. Strong winter storm activity during El Niño conditions in 1998 resulted in a large and intense RCP event. Consistently higher values of the light-saturated rate of photosynthesis,  $P_{\max}^B$ , were observed in spring 1998 compared to 1999 and 2000. Higher values of  $P_{\max}^B$  in 1998 appeared to be related to increased availability of phosphorus, as evidenced by significant correlations of  $P_{\max}^B$  with soluble reactive phosphorus (SRP). Light-saturated growth rates were also significantly correlated with SRP concentrations. These findings were consistent the view that the RCP was a source of enrichment. However, incubation experiments involving lake water enriched with sediments showed relatively small increases in growth and photosynthetic parameters, while enrichments with river water exhibited elevated rates. This result, along with increased levels of river discharge in 1998 and high levels of dissolved phosphorus in river water, supported the view that riverine inputs rather than the RCP were responsible for the higher photosynthetic parameters and growth seen for coastal margin assemblages. Despite the higher levels of  $P_{\max}^B$  in 1998, model analyses revealed that reduced light availability resulting from the intense RCP event constrained phytoplankton growth rates and primary production during this season and apparently suppressed the development of a typical spring bloom. These findings indicate a potential for reduced ecosystem productivity in response to extreme storm events, the frequency of which may increase with projected long-term climate changes. *INDEX TERMS:* 4855

Oceanography: Biological and Chemical: Plankton; 4845 Oceanography: Biological and Chemical: Nutrients and nutrient cycling; 4552 Oceanography: Physical: Ocean optics; 9345 Information Related to Geographic Region: Large bodies of water (e.g., lakes and inland seas); *KEYWORDS:* Lake Michigan, phytoplankton, primary production, Lake Michigan phytoplankton processes

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### 1. Introduction

[2] A recurrent coastal plume (RCP) that occurs within the southern basin of Lake Michigan is an episodic event that coincides with the spring diatom bloom [Mortimer, 1988; Eadie *et al.*, 1996, 2002]. The plume consists largely of suspended sediments that are believed to originate from

the silt and clay materials eroded from bluffs along the shores of Lake Michigan and from glacial clay deposits in shallow waters [Mortimer, 1988]. Strong northerly winds and associated waves accompanying the advent of late winter storms are believed to initiate the plume in the southern basin [Beletsky *et al.*, 1999].

[3] The correspondence in time between the RCP and the phytoplankton spring bloom has led to speculation that the RCP may be important for the development of the spring bloom. Suggested mechanisms include increased availability of limiting nutrients, principally phosphorus [Eadie *et al.*, 1984; Cotner *et al.*, 2000; Eadie *et al.*, 2002; Millie *et al.*, 2002a, 2002b, 2003], and introduction of meroplanktonic taxa associated with sediment resuspension [Eadie *et al.*, 1996; Millie *et al.*, 2002a, 2002b, 2003]. However, recent studies examining relationships between phytoplankton photosynthesis, growth, and community structure within and outside of plume-impacted waters did not find enrich-

<sup>1</sup>Department of Marine Science, University of Southern Mississippi, Stennis Space Center, Mississippi, USA.

<sup>2</sup>National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, Muskegon, Michigan, USA.

<sup>3</sup>Fish and Wildlife Research Institute, Saint Petersburg, Florida, USA.

<sup>4</sup>Coastal Ocean Observation Lab, Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick, New Jersey, USA.

<sup>5</sup>Cooperative Institute of Limnology and Ecosystems Research, University of Michigan, Ann Arbor, Michigan, USA.

ment of typical bloom species in association with the plume [Millie *et al.*, 2002b, 2003]. Indeed, during El Niño conditions in 1998, a large and intense RCP event was observed [Winkelman *et al.*, 1998], and a typical spring bloom phytoplankton assemblage never fully developed [Millie *et al.*, 2002b, 2003]. Furthermore, while apparent stimulation of phytoplankton growth and photosynthetic parameters has been observed at stations impacted by high sediment concentrations, it remains unclear whether this was attributable to sediment resuspension or infusion of phytoplankton and nutrients associated with tributary inflows [Millie *et al.*, 2003].

[4] Here, we examine effects of sediments and river water on phytoplankton growth and photosynthetic parameters in an effort to isolate potential mechanisms for enhancement of spring phytoplankton populations in southeastern Lake Michigan. We consider these findings in the context of observed relationships to phosphorus and other key environmental variables during spring 1998, 1999, and 2000 within and outside of plume-impacted waters. In addition, we explore implications of observed variability for regional primary production through sensitivity analyses of models.

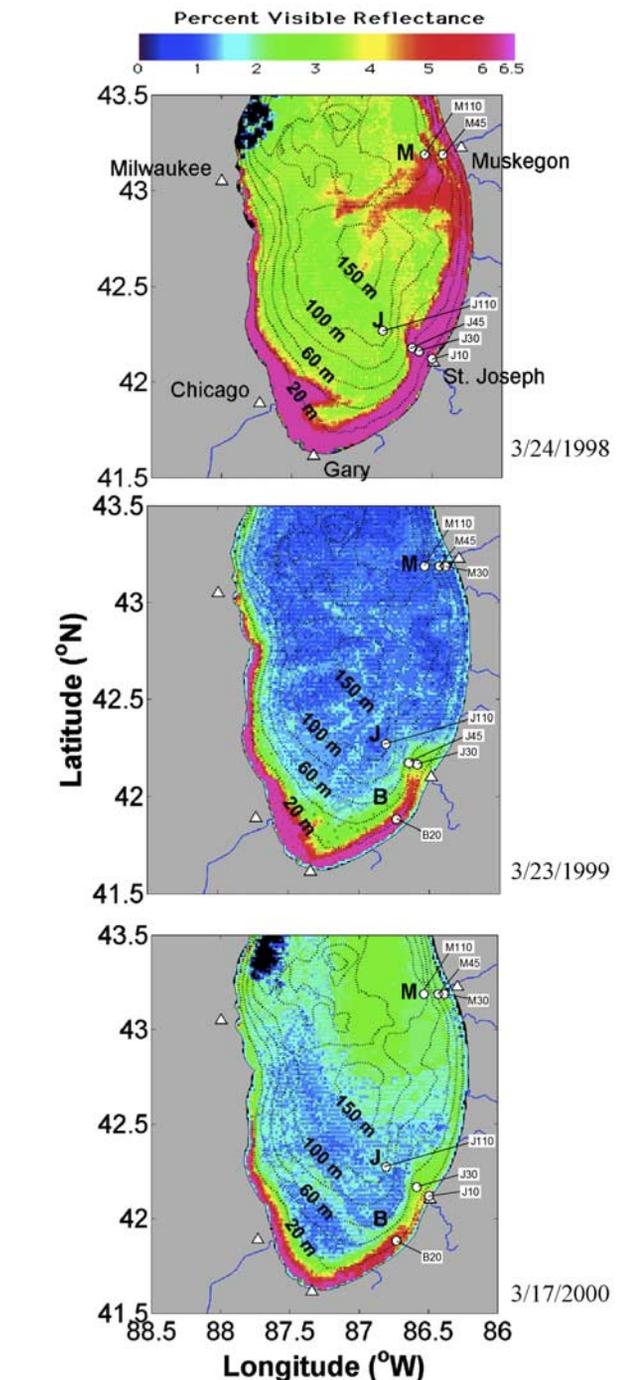
## 2. Methods

### 2.1. Cruise Operations

[5] Studies were performed in conjunction with the Episodic Events in the Great Lakes Experiment (EEGLE). Cruises were conducted aboard the R/V *Laurentian* during the spring isothermal period in 1998, 1999, and 2000 in southeastern Lake Michigan. Data for this study included that acquired during the spring in 1998 (16–19 March, 22–28 March, and 4–11 April), 1999 (24–26 March, and 14–15 and 22–24 April), and 2000 (17–19 March). Samples were collected in the sediment plume and adjacent waters at locations off Muskegon (“M” transect), St. Joseph (“J” transect), and New Buffalo (“B” transect) (Figure 1). At each station, profiles of conductivity, temperature and depth (CTD) were conducted using an instrument package consisting of a Seabird SBE 911plus CTD equipped with a SeaTech transmissometer and Biospherical Instruments scalar photosynthetically available radiation (PAR, 400 to 700 nm) sensor. Estimates of diffuse attenuation coefficient for downwelling scalar irradiance ( $K_{PAR}$ ,  $m^{-1}$ ) were estimated as the linear slope of natural logarithm-transformed vertical profiles of PAR [Fahnenstiel *et al.*, 2000; Wetzel, 2001]. Modified Niskin bottles (all rubber parts were replaced with Teflon-coated or silicone [Fahnenstiel *et al.*, 2002]) were used to collect water samples.

### 2.2. Chemical Analyses

[6] Total dissolved phosphorus (TDP) and soluble reactive phosphorus (SRP) were measured using an Auto Analyzer II [Davis and Simmons, 1979]. Aliquots for TDP were stored in acid-cleaned Pyrex test tubes at 5°C, digested in an autoclave, and measured as SRP [Menzel and Corwin, 1965]. Total CO<sub>2</sub> was determined from alkalinity and pH measurements [Vollenweider, 1974]. Chlorophyll *a* concentrations were determined fluorometrically on 90% acetone extracts [Strickland and Parsons, 1972] using a Turner Model 10 fluorometer [Holm-Hansen *et al.*, 1965]. Calibrations were made using a pure chlorophyll *a* standard



**Figure 1.** Sediment reflectance (channel 2 – channel 1) as measured by the advanced very high resolution radiometer onboard the NOAA 14 Orbiter satellite. Images were provided courtesy of NOAA Coastwatch.

(Sigma). All chlorophyll analyses were done in duplicate. Mean coefficients of variation for replicate chlorophyll analyses were 6.9%, 4.7%, and 5.4% in 1998, 1999, and 2000, respectively.

### 2.3. Phytoplankton Absorption

[7] Particulate absorption coefficients were determined using the transmission-reflectance (T-R) filter pad method

[Tassan and Ferrari, 1995] using the approach given by Lohrenz et al. [2003]. The T-R method accounts for losses due to backscatter and eliminates the need for baseline subtraction. This method was reported to be less subject to artifacts related to variable sediment content [Tassan and Ferrari, 1995]. Briefly, samples were filtered onto a 25 mm Whatman glass fiber filter and stored in liquid nitrogen until analysis. Measurements were made with a Perkin Elmer Lambda 18 spectrophotometer equipped with a Labsphere 150 mm integrating sphere (RSA-PE-18 Reflectance Spectroscopy Accessory). For transmittance measurements, filters moistened with filtrate were placed on a quartz slide at the entrance of the sphere and scanned from 350–800 nm at a scan speed of 120 nm/min. Slit width was 2 nm. A blank filter was used as a reference. Measurements of reflectance were made with the filters positioned at the back of the integrating sphere. Correction for path length amplification was made as described by Lohrenz et al. [2003]. Following measurement of transmittance and reflectance of the filters, pigments were extracted from the filter pad using a 15 min extraction in hot methanol. The extracted filters were rinsed with Milli-Q® water to remove residual methanol and phycobiliproteins, and then moistened with filtrate. Measurements of transmittance and reflectance were repeated to obtain the absorption spectrum of the particulate detrital material. Spectral absorption due to phytoplankton pigments in their particulate form,  $a_{ph}(\lambda)$  ( $m^{-1}$ ), was determined by subtraction of absorption due to detrital particulate material (material remaining after methanol extraction) from total particulate spectral absorption. The shape vector for phytoplankton absorption,  $\hat{a}_{ph}(\lambda)$ , was calculated by normalizing  $a_{ph}(\lambda)$  to  $a_{ph}(440)$ .

#### 2.4. Photosynthesis Parameters

[8]  $^{14}C$ -based photosynthetic measurements were derived from aliquots of water incubated within a photosynthesizer, after the technique described by Fahnenstiel et al. [1995, 2000] for Great Lakes assemblages. Water samples were inoculated with  $^{14}C$ , and subsamples of 3 mL were incubated in acid-cleaned scintillation vials for 40 min over a range of light levels (ca. 1 to 1,800  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ ). The spectrum and intensity of the tungsten halogen light source was adjusted using theatrical gel and neutral density vinyl screening. After incubation, samples were acidified and sparged with air for 15 min and radioactivity determined by liquid scintillation counting (counting efficiency = 92–95%). Time zero and blanks were determined and subtracted from all light values. Photosynthesis-irradiance (P-E) parameters were derived from relationships of photosynthetic rates normalized to chlorophyll (Chl) to incubation irradiances.  $P_{\text{max}}^B$  (the maximum light-saturated photosynthetic rate in units of  $\text{gC gChl a}^{-1} \text{h}^{-1}$ ) and  $\alpha^B$  (the photosynthetic efficiency, defined as the initial, light-limited slope of the P-E curve in units of  $\text{gC gChl a}^{-1} \text{h}^{-1}$  ( $\mu\text{mol quanta m}^{-2} \text{h}^{-1}$ ) $^{-1}$ ) were calculated after Fahnenstiel et al. [1989].

#### 2.5. Quantum Yield Calculations

[9] Maximum photosynthetic quantum yield for carbon fixation,  $\phi_{\text{max}}^C$  ( $\text{mol C fixed mol quanta}^{-1}$ ), was determined by dividing  $\alpha^B$  by the chlorophyll-specific absorption cross-section weighted by the tungsten halogen spectrum of the

photosynthesizer,  $\bar{a}_{ph}^*$  ( $\text{m}^2 \text{ mg Chl a}^{-1}$ ). The value of  $\bar{a}_{ph}^*$  was determined in a manner similar to that of Sosik [1996] using the following equation:

$$\bar{a}_{ph}^* = \frac{\int_{PAR} a_{ph}(\lambda) E_{ps}(\lambda) d\lambda}{\text{Chl} \int_{PAR} E_{ps}(\lambda) d\lambda}, \quad (1)$$

where  $E_{ps}(\lambda)$  is the spectral irradiance of the photosynthesizer. The photosynthesizer spectrum was determined using a Li-Cor LI1800UW scanning spectroradiometer.

#### 2.6. Scalar Spectral Irradiance

[10] Spectral diffuse attenuation coefficients for downwelling irradiance,  $K_d(\lambda)$  ( $\text{m}^{-1}$ ), were determined using two methods. During 1999 and 2000, measurements of  $K_d(\lambda)$  were made as described by Bergmann et al. [2004] using a Satlantic OCP200 profiling spectral radiometer. In March 1998, a Li-Cor LI1800UW underwater scanning spectroradiometer was deployed at selected stations. This instrument provided a measure of downwelling spectral irradiance,  $E_d(z, \lambda)$ , at 2 nm wavelength intervals. Scans were acquired during midday at two or more depths (usually 5 and 10 m) and diffuse attenuation of downwelling spectral irradiance was estimated as

$$K_d(\lambda) = \frac{\log\left(\frac{E_d(z_2, \lambda)}{E_d(z_1, \lambda)}\right)}{(z_2 - z_1)}, \quad (2)$$

where  $z_1$  and  $z_2$  were the depths at which the scans were acquired. Because attenuation was high, there was not always sufficient light at all wavelengths to yield a valid estimate of  $K_d$  for the depth increment between 5 and 10 m. In such cases, a scan in air made on 24 March 1998 was used as an estimate of surface incident irradiance ( $E_d(0^+, \lambda)$ ) and attenuation was computed for the 0 to 5 m depth increment. To account for changes in the magnitude of surface incident irradiance between stations and losses associated with air-sea transmission, the magnitude of the  $K_d$  spectrum for the 0 to 5 m depth interval was adjusted to agree with measurements made between 5 and 10 m for those wavelengths where there was sufficient light penetration. Implicit in this approach were the assumptions that spectral variations in surface irradiance associated with sky conditions and air-sea transmission were relatively small compared to water column attenuation effects, and that the water column was vertically homogeneous, which was generally supported by physical and optical data [cf. Bergmann et al., 2004].

#### 2.7. Phytoplankton Carbon-Specific Growth Rates

[11] Carbon-specific growth rates ( $\mu^C$ ,  $\text{d}^{-1}$ ) were determined from  $^{14}C$ -labeling into chlorophyll *a* [Redalje and Laws, 1981; Goericke and Welschmeyer, 1993] following the technique of Fahnenstiel et al. [2000] for Great Lakes assemblages. Water samples were collected 1–4 hours before dawn from the 5 or 10 m depth at all stations, and over a range of depths at selected stations. Samples were dispensed into clean 2-L polycarbonate bottles after which 300  $\mu\text{Ci}$  of  $^{14}C$  was added. Bottles were incubated under simulated in situ conditions of light and temperature. Light levels and quality

were adjusted using a combination of theatrical gel and neutral density screening and ranged 3–65% of surface incident irradiance. A growth irradiance plot was constructed using growth rates and incubation irradiances from all experiments [cf. *Fahnenstiel et al.*, 1989, 2000].

## 2.8. Phosphorus Uptake Kinetics

[12] During the 1999 and 2000 field studies, uptake kinetics of inorganic phosphorus were determined by incubation of samples with  $^{33}\text{P}$ -orthophosphate. Phosphorus turnover and the maximum uptake velocity ( $V_{\max}$ ) were determined following the methods of *Millard et al.* [1996a, 1996b] and *Cotner et al.* [1997]. Phosphorus turnover was determined by adding carrier-free  $^{33}\text{P}$ - $\text{KH}_2\text{PO}_4$  (final concentration  $0.8 \text{ kBq mL}^{-1}$ ) to cleaned vials (20 mL) containing raw lake water and incubating these samples for 1–30 min. At least 6 different time intervals were used for each sample. The samples were then filtered onto presoaked (10 mM  $\text{KH}_2\text{PO}_4$ ),  $0.2 \mu\text{m}$  polycarbonate membrane filters. Radioactivity on each filter was counted with a scintillation counter. Killed samples, 1 mL of 50% TCA added to each vial, were used as controls for all incubations. The natural logarithm of the percentage of isotope left in the filtrate was regressed against time and the initial slope was used as the rate constant for phosphorus uptake. Turnover time was computed as the reciprocal of the rate constant.

[13]  $V_{\max}$  for phosphorus uptake was measured at saturating concentrations of dissolved inorganic phosphorus. Previous work in Lakes Ontario [*Lean and White*, 1983] and Lake Michigan (*Fahnenstiel*, unpublished) has demonstrated that  $V_{\max}$  usually occurs at inorganic phosphorus concentrations of 200–300 nM. Based these findings,  $V_{\max}$  was determined in this study by adding 500 nM of  $\text{KH}_2\text{PO}_4$ , along with carrier-free  $^{33}\text{P}$ -orthophosphate, to cleaned vials and incubating samples for 30 min to 4 hours. After the incubation (at least four time intervals for each sample) the samples were processed in the same manner as the phosphorus turnover experiments. The rate constant for phosphorus uptake was multiplied by the phosphorus concentration (500 nM) to yield  $V_{\max}$ .

## 2.9. Primary Production Modeling

[14] Primary production was estimated using both a wavelength-resolved model (WRM) and wavelength-independent model, in the terminology of *Behrenfeld and Falkowski* [1997a, 1997b]. The WRM [cf. *Lohrenz et al.*, 1993, 2002] consisted of a semianalytical wavelength-resolved primary production algorithm:

$$P(z, t) = \text{Chl}(z) P_{\max}^B [1 - \exp(-PUR(z, t) a_{ph}^*(440) \cdot 12000 \phi_{\max}^C / P_{\max}^B)] / 1000. \quad (3)$$

The factor of 12000 was required to convert moles of carbon in the quantum yield term to milligrams carbon. The divisor of 1000 converts productivity in milligrams carbon to grams carbon. Photosynthetically utilizable radiation for a given depth and time,  $PUR(z, t)$ , was determined by integrating the product of the absorption shape vector,  $\hat{a}_{ph}(\lambda)$ , and spectral irradiance over 400 to 700 nm as

$$PUR(z, t) = \int_{PAR} \hat{a}_{ph}(\lambda) E_0(z, t, \lambda) d\lambda, \quad (4)$$

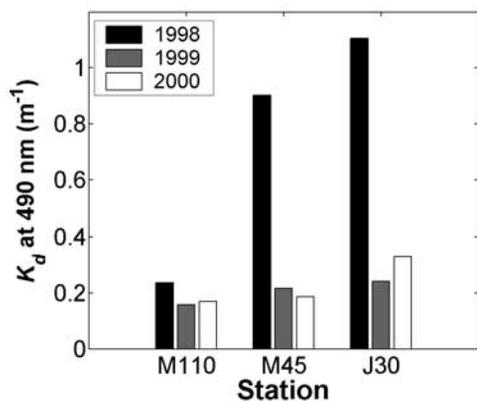
where  $E_0(z, t, \lambda)$  is the subsurface scalar spectral irradiance. An average  $\hat{a}_{ph}(\lambda)$  was used for each year for estimation of primary production by the WRM. Diffuse and direct components of surface incident spectral irradiance were approximated using the clear-sky model of *Gregg and Carder* [1990] and scaled such that the modeled downwelling surface irradiance integrated from 400 to 700nm was equivalent to the mean of the measured downwelling irradiance as recorded using a Li-Cor LI-1000 data logger and a LI-190SA quantum sensor. The resulting downwelling spectral irradiance was converted to scalar spectral irradiance by multiplying by an approximate geometric conversion factor (1.4) determined from simulations using the radiative transfer model, Hydrolight version 4.1 (Sequoia Scientific, Inc.). Spectral attenuation coefficients for determining the subsurface irradiance field were estimated by dividing  $K_d(\lambda)$  by either the cosine of the solar zenith angle for the direct component of irradiance or by the average cosine for the diffuse component of irradiance as described by *Sathyendranath and Platt* [1988].

[15] The wavelength-independent model was the Great Lakes Production Model (GLPM) [*Fahnenstiel et al.*, 1995; *Lang and Fahnenstiel*, 1996]. This model utilized the measured surface incident downwelling irradiance and measured  $K_{PAR}$  ( $\text{m}^{-1}$ ) for attenuation of the subsurface irradiance field.

[16] For both models, daily primary production was determined by integration in hourly time steps over the photoperiod. Water column primary production was determined by trapezoidal integration to the 0.1% light level, or to the bottom depth if shallower.

## 2.10. Enrichment Incubation Experiment

[17] An enrichment incubation experiment was conducted to isolate effects of river water and resuspended sediments as factors influencing phytoplankton photosynthetic parameters and growth rates. Water was collected during the night from Station B45 on 20 March 2000. This station was chosen so as to minimize river influence in the ambient water. Water was also collected from the mouth of the St. Joseph River. Water was transported back to the shore laboratory in Muskegon. Each treatment was initially mixed in a 500 L plastic container and 120 L of sample was prepared for each treatment. After preparation, the sample material was transferred in triplicate to 20 L polycarbonate carboys. Samples were subjected to four different treatments including the following: 1) an unenriched lake water control; 2) a river-enriched treatment consisting of 96-L lake water and 24-L river water; 3) a sediment-enriched treatment prepared by adding a 1 L slurry of sediment to 119 L of lake water to yield transmittance values similar to that of the RCP; and 4) a combined treatment enriched with both sediment and river water in the same manner as the individual treatments. Sediment used in the experiment was collected from Station B45 using an Ekman grab sampler. The carboys were held in a rotating incubator under simulated in situ conditions of temperature and light, with light levels adjusted to 12% of incident irradiance and spectrally matched using a combination of theatrical gels and neutral density vinyl screening. Following an initial 24 h acclimation period, determinations were made of chlorophyll, P-E parameters including  $P_{\max}^B$  and  $\phi_{\max}^C$ , and carbon-



**Figure 2.** Spectral diffuse attenuation ( $K_d$ ) at 490 nm compared between stations and years in southeastern Lake Michigan. The sites differed in location relative to the region of highest suspended sediment, with J30 being the most impacted, M45 being intermediate, and M110 being the least impacted.

specific growth rate ( $\mu^C$ ). After incubation of the treatment carboys for 13 days, final determinations were made of chlorophyll,  $P_{max}^B$  and  $\mu^C$  ( $\phi_{max}^C$  was not determined on day 13). For initial growth rate determinations, duplicate 2-L bottles from each treatment were incubated. For final growth rate determinations, triplicate 2-L incubations were done, one from each of the triplicate treatment replicates. Average coefficient of variation for replicate growth rate determinations was 10% (range 0–17%). Only a single P-E determination was made for each treatment on day 1, while P-E determinations were made in duplicate on day 13. The average coefficient of variation for replicate P-E measurements was 24% (range 1–42%) for both  $P_{max}^B$  and  $\alpha^B$ .

### 3. Results

#### 3.1. Physical Environment

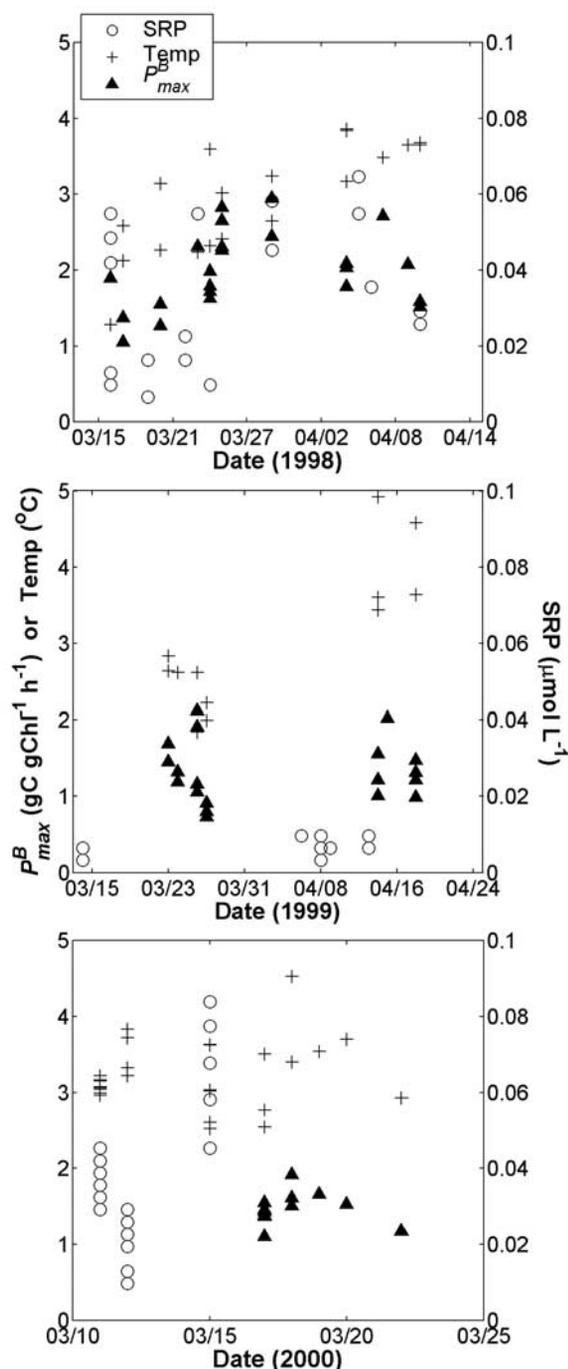
[18] Sediment plume events, originating from resuspension associated with late winter storms, were observed in all the three field years during March. Temperature profiles were isothermal or near isothermal at all stations and years, indicating holomictic conditions (data not shown). The most intense plume event occurred during March 1998 (Figure 1). Higher values of diffuse attenuation,  $K_d(\lambda)$  ( $m^{-1}$ ), were observed at Stations J30 and M45 as compared to the offshore Station M110 (Figure 2). The high attenuation in coastal waters could be attributed to both high suspended sediment as well as high turbidity associated with river outflow. Nearshore-offshore differences in attenuation in coastal waters during 1999 and 2000 were less pronounced (Figure 2). From examination of Figure 1, it can be seen that the sediment plume most heavily impacted Station J30, while M45 and M110 were less impacted. Diffuse attenuation at Station J30 was slightly higher than at M45 and M110 during 1999 and 2000 (Figure 2).

#### 3.2. Intra-annual and Interannual Variation in Photosynthesis-Irradiance Parameters

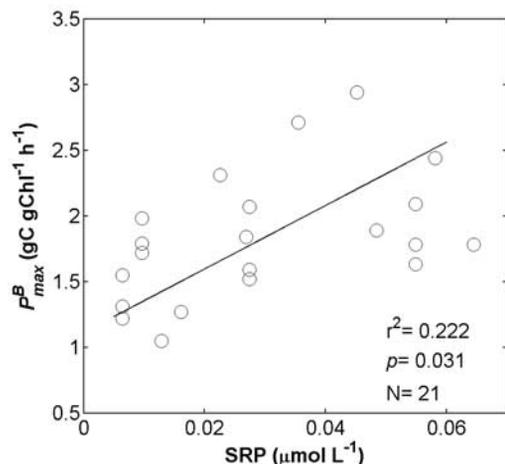
[19] Light-saturated rates of photosynthesis,  $P_{max}^B$ , in the upper water column exhibited interannual differences, particularly between 1998 and the other years (Figure 3), with a

higher range of values of  $P_{max}^B$  observed in 1998 (range 1.0–2.9, mean = 2.0  $gC\ g\ Chl^{-1}\ h^{-1}$ ) than in 1999 (range 0.72–2.1, mean = 1.3  $gC\ g\ Chl^{-1}\ h^{-1}$ ) and 2000 (range 1.0–1.9, mean = 1.5  $gC\ g\ Chl^{-1}\ h^{-1}$ ). There was no statistically significant temperature dependence in  $P_{max}^B$  for the range of temperatures encountered during the spring cruises (results not shown).

[20] Temporal variations in both SRP and temperature during 1998 initially coincided with increases in  $P_{max}^B$  (Figure 3). Subsequent decreases in phosphorus were



**Figure 3.** Temporal variability in  $P_{max}^B$ , soluble reactive phosphorus (SRP) and temperature for the period of sampling in each of the field years.



**Figure 4.** Relationship of  $P_{\max}^B$  to soluble reactive phosphorus (SRP) for the 1998 field year.

accompanied by decreases in  $P_{\max}^B$ , even as temperature remained relatively constant. That higher values of  $P_{\max}^B$  in 1998 were related to phosphorus availability was supported by a weak, but significant, relationship between  $P_{\max}^B$  and SRP (Figure 4). SRP concentrations were generally lower during 1999, and  $P_{\max}^B$  values remained relatively low despite increases in temperature (Figure 3). In 2000, SRP measurements were available only for the week prior to when the P-E measurements were made. Despite some relatively high SRP concentrations comparable to those seen in 1998, observed values of  $P_{\max}^B$  in 2000 were consistently low (Figure 3).

[21] Possible sources of variation in phosphorus included discharge from rivers and desorption from suspended sediments. A comparison of seasonal discharge from Muskegon and St. Joseph Rivers (Figure 5) showed relatively high discharge during 1998, as compared to 1999 and 2000. Consistent with the view that river inputs were a source of phosphorus was the observation that total dissolved phosphorus concentration at the St. Joseph River mouth on 11 March 2000 was high,  $0.14 \mu\text{mol L}^{-1}$ , relative to lake concentrations of  $<0.1 \mu\text{mol L}^{-1}$ .

[22] There were no systematic differences between years in the mean spectral shape of phytoplankton absorption,  $\hat{a}_{ph}(\lambda)$  (data not shown). The coefficients of variation among the yearly means of  $\hat{a}_{ph}(\lambda)$  were less than 14% for all wavelengths over the spectral range from 350–700 nm. Coefficients of variations of  $\hat{a}_{ph}(\lambda)$  within individual years were less than 35% in 1998 and less than 30% in 1999 and 2000, with largest variation observed at wavelengths less than 400 nm. The overall mean spectral values for  $\hat{a}_{ph}(\lambda)$  for all three years are given in Table 1. Phytoplankton absorption at 440 nm ( $a_{ph}(440)$ ,  $\text{m}^{-1}$ ) varied in relationship to chlorophyll concentrations (Figure 6) in a manner consistent with that reported by Bricaud *et al.* [1995] for oceanic waters.

[23] Maximum photosynthetic quantum yield,  $\phi_{\max}^C$ , generally ranged between 0.02 and  $0.06 \text{ mol C mol quanta}^{-1}$ . Variation observed within a given year was comparable to interannual variation (Figure 7). Examination of relationships of  $\phi_{\max}^C$  with SRP and optical depth (here defined as the product of  $K_{PAR}$  and depth) yielded no significant correlations (results not shown). The lack of significant

correlation may be due to the fact that data from various days and times were pooled for statistical analyses, and day-to-day and within day variation was sufficiently large (see Figure 7) so as to obscure depth dependencies or nutrient relationships.

### 3.3. Relationships of Carbon-Specific Growth Rates to Irradiance and SRP

[24] Carbon-specific growth exhibited a light saturation response when plotted against photosynthetically available radiation (Figure 8a). Data were fit to the equation:

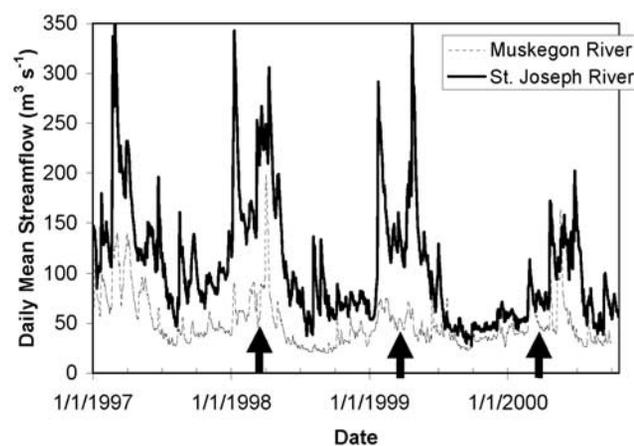
$$\mu^C = \mu_{\max}^C \left[ 1 - e^{(-PAR/E_{k-\mu})} \right], \quad (5)$$

where  $\mu_{\max}^C$  is the maximum (light-saturated) growth rate and  $E_{k-\mu}$  is the light saturation constant for growth. The value of  $E_{k-\mu}$  was  $0.9 \text{ mol quanta m}^{-2} \text{ d}^{-1}$  and  $\mu_{\max}^C$  was  $0.12 \text{ d}^{-1}$ . There were no systematic differences in light-saturated carbon-specific growth rates between years (Figure 8a) and, as for  $\phi_{\max}^C$ , variation observed within a given year was comparable to interannual variation. From the scatter in the data about the fitted curve, it was evident that variations in incubation irradiance accounted for only a portion of the variability in observed values of  $\mu^C$ .

[25] Phosphorus availability appeared to be a factor influencing the observed variation in light-saturated carbon-specific growth rates. To examine this, values of  $\mu^C$  were selected for incubation irradiances  $>2$  (to avoid effects of light limitation) and  $<20 \text{ mol quanta m}^{-2} \text{ d}^{-1}$  (to avoid effects of photoinhibition). The relationship of these growth data to SRP concentrations was found to be significant (Figure 8b).

### 3.4. Phosphorus Uptake Kinetics

[26] Turnover times of  $^{33}\text{P}$ -orthophosphate were generally less than 24 h at all stations (Table 2). Shorter turnover



**Figure 5.** Streamflow at St. Joseph and Muskegon Rivers from 1997 through 2000. Data were obtained from the U.S. Geological Survey (USGS) through the National Water Information System. Data for St. Joseph were from USGS station 04101500 at Niles, Michigan. Data for the Muskegon River were from the USGS station 04121970 near Croton, Michigan. Arrows show the approximate timing of the field operations.

**Table 1.** Mean Shape Vector for Phytoplankton Absorption for All Years Normalized Such That the Value at 440 nm Was Unity ( $\hat{a}_{ph}(\lambda)$ ,  $m^{-1}$ )

| $\lambda$ | $\hat{a}_{ph}(\lambda)$ |
|-----------|-------------------------|
| 350       | 0.601                   |
| 355       | 0.596                   |
| 360       | 0.605                   |
| 365       | 0.621                   |
| 370       | 0.643                   |
| 375       | 0.671                   |
| 380       | 0.702                   |
| 385       | 0.722                   |
| 390       | 0.735                   |
| 395       | 0.750                   |
| 400       | 0.773                   |
| 405       | 0.816                   |
| 410       | 0.866                   |
| 415       | 0.909                   |
| 420       | 0.933                   |
| 425       | 0.951                   |
| 430       | 0.984                   |
| 435       | 1.011                   |
| 440       | 1.000                   |
| 445       | 0.938                   |
| 450       | 0.868                   |
| 455       | 0.824                   |
| 460       | 0.797                   |
| 465       | 0.763                   |
| 470       | 0.716                   |
| 475       | 0.663                   |
| 480       | 0.622                   |
| 485       | 0.597                   |
| 490       | 0.575                   |
| 495       | 0.542                   |
| 500       | 0.494                   |
| 505       | 0.434                   |
| 510       | 0.376                   |
| 515       | 0.329                   |
| 520       | 0.291                   |
| 525       | 0.264                   |
| 530       | 0.245                   |
| 535       | 0.229                   |
| 540       | 0.213                   |
| 545       | 0.199                   |
| 550       | 0.183                   |
| 555       | 0.165                   |
| 560       | 0.149                   |
| 565       | 0.138                   |
| 570       | 0.130                   |
| 575       | 0.123                   |
| 580       | 0.117                   |
| 585       | 0.115                   |
| 590       | 0.112                   |
| 595       | 0.108                   |
| 600       | 0.105                   |
| 605       | 0.109                   |
| 610       | 0.119                   |
| 615       | 0.131                   |
| 620       | 0.141                   |
| 625       | 0.145                   |
| 630       | 0.149                   |
| 635       | 0.149                   |
| 640       | 0.148                   |
| 645       | 0.146                   |
| 650       | 0.155                   |
| 655       | 0.186                   |
| 660       | 0.252                   |
| 665       | 0.347                   |
| 670       | 0.429                   |
| 675       | 0.450                   |
| 680       | 0.407                   |
| 685       | 0.309                   |
| 690       | 0.191                   |
| 695       | 0.109                   |

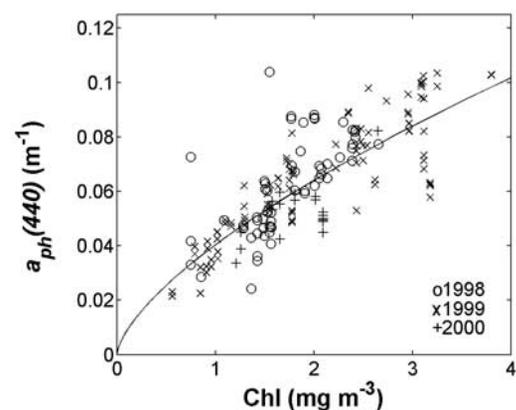
**Table 1.** (continued)

| $\lambda$ | $\hat{a}_{ph}(\lambda)$ |
|-----------|-------------------------|
| 700       | 0.066                   |
| 705       | 0.044                   |
| 710       | 0.030                   |
| 715       | 0.023                   |
| 720       | 0.018                   |
| 725       | 0.014                   |
| 730       | 0.010                   |
| 735       | 0.009                   |
| 740       | 0.007                   |
| 745       | 0.005                   |
| 750       | 0.004                   |

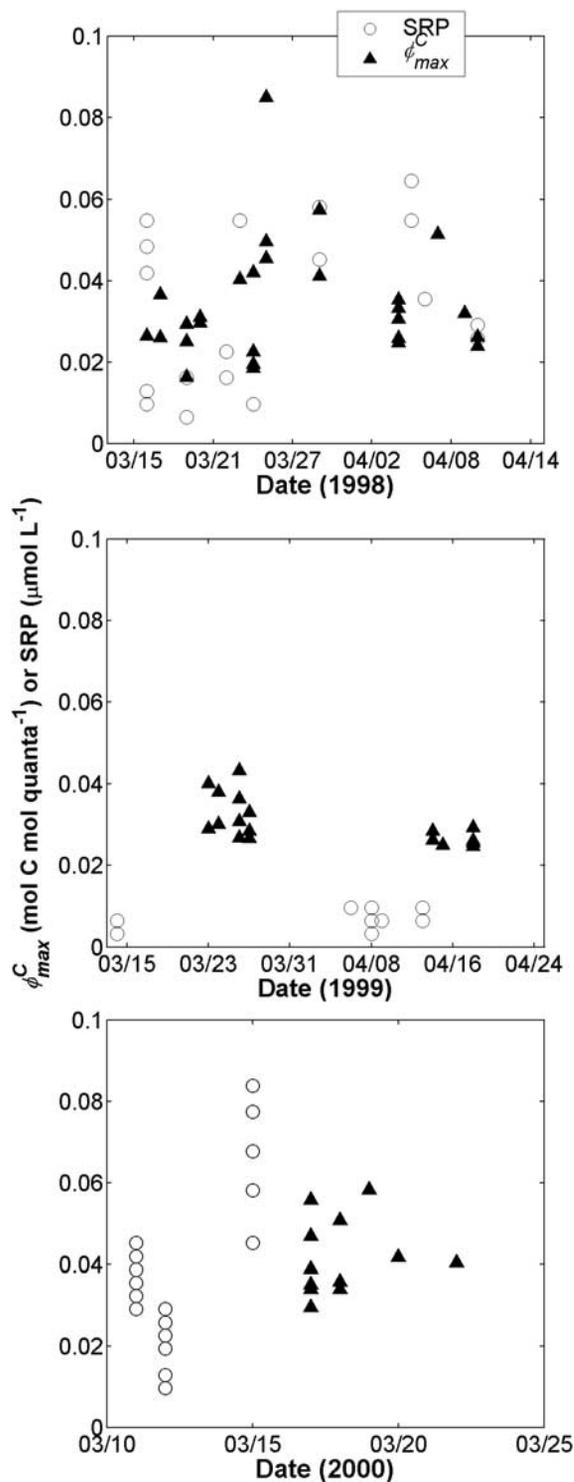
times were observed at nearshore stations, particularly for plume-impacted stations J10, J30, and B20 (Table 2), where turnover times were less than 5 h. Maximum uptake rates tended to be higher for these stations as well. Longest turnover times were observed at offshore stations J110 and M110, with values ranging from 7.5–28 hours.

### 3.5. Effects of Enrichment With Sediments and River Water

[27] Initial chlorophyll concentrations were higher in the river-supplemented and sediment-supplemented treatments relative to controls (Table 3), an indication that both river water and sediments harbored sizable concentrations of chlorophyll. An ANOVA examining variability in chlorophyll and carbon-specific growth rate,  $\mu^C$ , for day 1 showed significant effects of treatment for chlorophyll ( $F = 510$ ,  $p < 0.0001$ ) and for  $\mu^C$  ( $F = 18.4$ ,  $p = 0.020$ ). Both chlorophyll and  $\mu^C$  were higher in the treatments containing river water (i.e., river water and combined treatments) compared to either the lake water control or sample augmented with sediment alone (Table 3). Similarly, determinations on day 1 of photosynthetic parameters,  $P_{max}^B$  and  $\phi_{max}^C$ , revealed higher values in the treatments with river water compared to other treatments (Table 3). Reexamination on day 13 revealed largest increases in chlorophyll concentrations in



**Figure 6.** The relationship of phytoplankton pigment absorption at 440 nm to chlorophyll *a*. The solid curve represents the plotted relationship  $a_{ph}(440) = 0.0403(\text{chlorophyll})^{0.668}$  as given by Bricaud *et al.* [1995] for various oceanic waters. The  $r^2$  of the correlation between observed values of  $a_{ph}(440)$  and those estimated with the Bricaud expression was 0.824 ( $p < 0.0001$ ,  $N = 180$ ).



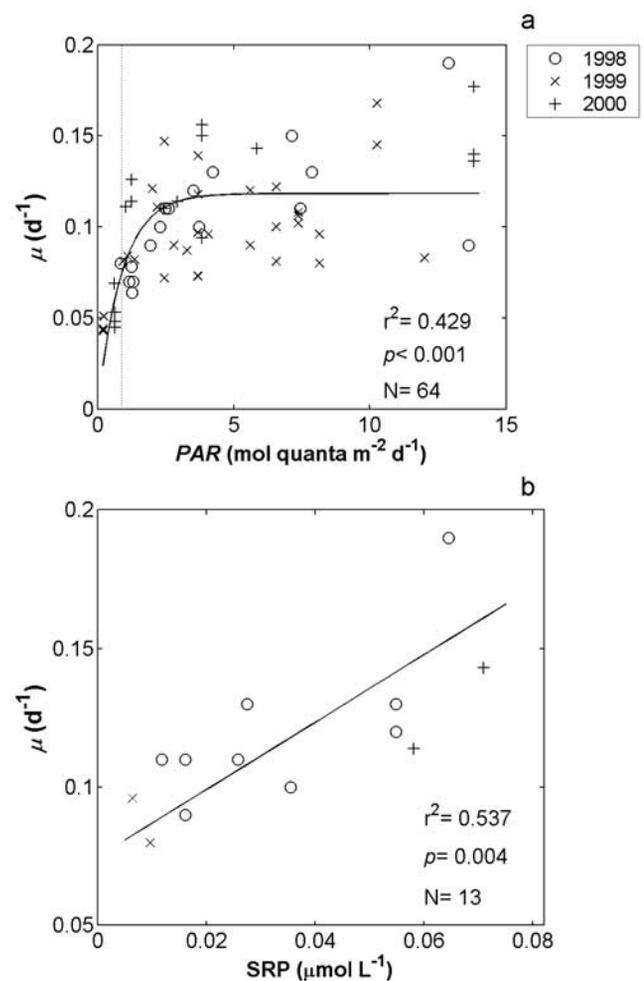
**Figure 7.** Temporal variability in maximum photosynthetic quantum yield of carbon fixation,  $\phi_{\max}^C$ , and soluble reactive phosphorus (SRP) for the period of sampling in each of the field years.

river supplemented and river + sediment supplemented treatments (Table 3). A small increase in chlorophyll was also seen in the sediment-augmented treatment. An ANOVA examining variability in chlorophyll and carbon-specific growth rate,  $\mu^C$ , for day 13 showed significant effects of

treatment ( $F = 86.5$ ,  $p < 0.0001$ ) for chlorophyll, but not for  $\mu^C$  ( $F = 1.22$ ,  $p = 0.36$ ). Values of  $P_{\max}^B$  and  $\mu^C$  were similar for all treatments on day 13. Turnover times of inorganic phosphorus were dramatically shorter on day 13 compared to initial values (Table 3) as well as in comparison to values observed in the field (Table 2).

### 3.6. Spatial and Interannual Variation in Primary Production and Sensitivity Analysis

[28] Estimates of primary production from the Great Lakes Production Model (GLPM) and wavelength-resolved model (WRM) agreed well (Table 4 and Figure 9), although the GLPM tended to produce slightly higher estimates particularly in 1999 and 2000. Productivity was lowest during 1998, when the sediment plume was most intense. During other years, there was a general pattern of lower productivity at inshore stations more heavily impacted by the sediment plume (J30, J45, B20). This reflected a



**Figure 8.** (a) Variations in carbon-specific growth rate in relationship to photosynthetically available radiation. The solid curve is a fit of the data to equation (5). The dashed vertical line corresponds to  $E_{k_{\mu}}$ . The value of  $E_{k_{\mu}}$  was  $0.9 \text{ mol quanta m}^{-2} \text{ d}^{-1}$ , and  $\mu_{\max}^C$  was  $0.12 \text{ d}^{-1}$ . (b) Relation of light-saturated carbon-specific growth rate to soluble reactive phosphorus (SRP). Only data for light levels  $>2$  and  $<20 \text{ mol quanta m}^{-2} \text{ d}^{-1}$  were used.

**Table 2.** Maximum Uptake Rates ( $V_{\max}$ ) and Turnover Times Determined From Incubations With  $^{33}\text{P}$ -Orthophosphate

| Date          | Station | $V_{\max}$ , nmol P h <sup>-1</sup> | Turnover, hours |
|---------------|---------|-------------------------------------|-----------------|
| 24 March 1999 | M30     | 3.2                                 | 15.4            |
| 24 March 1999 | M110    | 1.9                                 | 28.0            |
| 27 March 1999 | J30     | -                                   | 2.2             |
| 27 March 1999 | J110    | -                                   | 7.5             |
| 27 March 1999 | B20     | 4.4                                 | 4.4             |
| 18 March 2000 | M30     | 3.4                                 | 4.1             |
| 18 March 2000 | M110    | 1.3                                 | 21.2            |
| 19 March 2000 | J10     | 18.2                                | 0.25            |
| 19 March 2000 | J30     | 6.2                                 | 1.6             |
| 19 March 2000 | J110    | 1.6                                 | 18.8            |
| 20 March 2000 | B20     | 9.1                                 | 0.83            |

combination of higher attenuation and lower chlorophyll concentrations at these stations. An exception to this in 2000 was Station J10, near the mouth of the St. Joseph River, which had a higher chlorophyll concentration and slightly higher values of  $P_{\max}^B$  (1.9 gC gChl a<sup>-1</sup> h<sup>-1</sup>) and  $\phi_{\max}^C$  (0.051 mol C fixed mol quanta<sup>-1</sup>) relative to other stations.

[29] A sensitivity analysis was conducted using the WRM to examine the relative importance of variables and parameters that would affect primary production estimates. Estimates of productivity from the WRM were most sensitive to variations in  $K_d$  and chlorophyll concentrations (Table 4). Variations of plus or minus 50% in these terms resulted in variations of 40–50% in estimates of productivity. Sensitivity to variation in  $P_{\max}^B$  and quantum yield of plus or minus 50%, ranges comparable to that encountered in our measurements, was relatively small, contributing only about 15–20% variation in productivity estimates.

#### 4. Discussion

[30] While availability of phosphorus evidently influences photosynthetic parameters and growth rates of spring phytoplankton populations in southern Lake Michigan, resuspension of sediments within the RCP does not appear to be an important stimulus for phytoplankton growth and photosynthesis. Rather, our findings provide evidence that river discharge had a more significant impact on phytoplankton physiology. A variety of types of evidence support

this view. Highest values of  $P_{\max}^B$  were observed in 1998 (Figure 3), when river discharge was substantially higher than other years (Figure 5). Enrichment experiments during the 2000 field season (Table 3) indicated that growth rates and photosynthetic parameters were elevated in river water-augmented samples, while sediment alone provided minimal, if any, stimulation of phytoplankton activity.

[31] The potential importance of river inputs in influencing phytoplankton processes has been noted in various prior investigations. *Mortimer* [1988] observed that rivers, including the Muskegon and St. Joseph Rivers, deliver substantial quantities of nutrients, dissolved organic matter, sediments and chlorophyll along the eastern shore of southern Lake Michigan. *Schelske et al.* [1980] noted that the St. Joseph River, among others, was a significant source of soluble PO<sub>4</sub> to coastal waters of southeastern Lake Michigan, and found higher abundances of phytoplankton as well as differences in species composition in nearshore waters influenced by river outflow. *Millie et al.* [2003], while acknowledging positive associations of photosynthetic parameters ( $P_{\max}^B$  and  $\alpha^B$ ) and light-saturated carbon-specific growth rates with sediment-impacted stations, pointed out that these results were heavily influenced by data from nearshore stations along the St. Joseph transect. Such stations would have been subject to the influence of the St. Joseph River outflow. *Biddanda and Cotner* [2002] also noted the importance of rivers as source of phosphorus and dissolved organic carbon, and concluded that terrestrial inputs may support 10–20% of in-lake heterotrophic and autotrophic requirements.

[32] Our findings that river water enhanced the growth of phytoplankton populations were consistent with prior work by *Schelske et al.* [1984], who examined phytoplankton community responses to treatments of lake water with river water from the Grand River, the mouth of which is located south of Muskegon. They found that lake water enriched with 10% river water showed a doubling of chlorophyll above initial levels over a 7 d period, but no further increase between 7 and 13 d, presumably because nutrient supplies were depleted. These findings were analogous to our observed level of increase in chlorophyll in lake water samples augmented with river water between day 1 and day 13 (Table 3). Furthermore, our findings of low growth rates and extremely rapid phosphorus turnover times on

**Table 3.** Influence of Sediment and River Water Additions on Photosynthetic Parameters, Carbon-Specific Growth Rates, and Phosphorus Uptake Parameters for Lake Water Collected From Station B45 in March 2000 and Incubated Under Simulated Ambient Irradiance and Temperature

| Treatment              | Parameter                                 |  |  |         |                                     |                |  |
|------------------------|---|--|--|---------|-------------------------------------|----------------|--|
|                        | Chlorophyll <i>a</i> , mg m <sup>-3</sup> | $P_{\max}^B$ mg C mg chlorophyll <sup>-1</sup> h <sup>-1</sup> | $\phi_{\max}^C$ , mol C mol quanta <sup>-1</sup> | $\mu^C$ | $V_{\max}$ , nmol P h <sup>-1</sup> | $\tau$ , hours |  |
| <i>Initial (Day 1)</i> |   |  |  |         |                                     |                |  |
| Control                | 1.2                                       | 1.2  | 0.04   | 0.11    | 3.9                                 | 6.3            |  |
| +River water           | 7.4                                       | 2.6  | 0.077  | 0.16    | 14                                  | 7.3            |  |
| +Sediment              | 2.6                                       | 1.5  | 0.016  | 0.11    | 5.5                                 | 7.2            |  |
| +Both                  | 6.1                                       | 3.3  | 0.056  | 0.16    | 12                                  | 6.7            |  |
| <i>Final (Day 13)</i>  |   |  |  |         |                                     |                |  |
| Control                | 1.4                                       | 1.0  | na   | 0.084   | 14                                  | 0.82           |  |
| +River water           | 15  | 1.1  | na   | 0.064   | 54                                  | 0.10           |  |
| +Sediment              | 4.6                                       | 1.2  | na   | 0.082   | 16                                  | 0.55           |  |
| +Both                  | 21  | 0.95   | na   | 0.074   | 62                                  | 0.08           |  |

**Table 4.** Comparison of Chlorophyll and Productivity Estimated Using the Great Lakes Primary Production Model (GLPM) and the Wavelength-Resolved Model (WRM)<sup>a</sup>

| Date          | Station | Chl, mg m <sup>-3</sup> | PP, gC m <sup>-2</sup> d <sup>-1</sup> |       | Sensitivity Analysis |       |              |       |       |       |       |       |
|---------------|---------|-------------------------|--|-------|----------------------|-------|--------------|-------|-------|-------|-------|-------|
|               |         |                         | GLPM                                   | WRM   | Quantum Yield        |       | $P_{\max}^B$ |       | $K_d$ |       | Chl   |       |
|               |         |                         |  |       | +50%                 | -50%  | +50%         | -50%  | +50%  | -50%  | +50%  | -50%  |
| 24 March 1998 | J30     | 1.8                     | 0.086                                  | 0.080 | 0.090                | 0.071 | 0.106        | 0.060 | 0.053 | 0.120 | 0.121 | 0.054 |
| 20 March 1998 | M45     | 2.7                     | 0.136                                  | 0.136 | 0.155                | 0.118 | 0.177        | 0.103 | 0.091 | 0.204 | 0.204 | 0.091 |
| 20 March 1998 | M110    | 1.4                     | 0.201                                  | 0.186 | 0.213                | 0.160 | 0.241        | 0.142 | 0.124 | 0.279 | 0.279 | 0.124 |
| 26 March 1999 | J30     | 1.5                     | 0.227                                  | 0.176 | 0.200                | 0.152 | 0.229        | 0.133 | 0.117 | 0.257 | 0.263 | 0.117 |
| 27 March 1999 | J45     | 1.8                     | 0.175                                  | 0.168 | 0.190                | 0.147 | 0.221        | 0.127 | 0.112 | 0.252 | 0.253 | 0.112 |
| 27 March 1999 | J110    | 3.1                     | 0.595                                  | 0.481 | 0.561                | 0.407 | 0.611        | 0.374 | 0.320 | 0.721 | 0.721 | 0.321 |
| 24 March 1999 | M45     | 2.5                     | 0.569                                  | 0.355 | 0.411                | 0.302 | 0.454        | 0.274 | 0.237 | 0.532 | 0.533 | 0.237 |
| 24 March 1999 | M110    | 2.8                     | 0.710                                  | 0.539 | 0.627                | 0.457 | 0.685        | 0.418 | 0.360 | 0.809 | 0.808 | 0.359 |
| 18 March 2000 | J10     | 5.0                     | 0.513                                  | 0.373 | 0.423                | 0.324 | 0.486        | 0.282 | 0.249 | 0.542 | 0.560 | 0.249 |
| 18 March 2000 | J30     | 1.6                     | 0.241                                  | 0.190 | 0.217                | 0.165 | 0.247        | 0.144 | 0.127 | 0.285 | 0.285 | 0.127 |
| 18 March 2000 | M45     | 2.1                     | 0.452                                  | 0.409 | 0.468                | 0.352 | 0.528        | 0.312 | 0.272 | 0.605 | 0.613 | 0.272 |
| 18 March 2000 | M110    | 2.1                     | 0.628                                  | 0.316 | 0.366                | 0.270 | 0.405        | 0.244 | 0.211 | 0.474 | 0.474 | 0.211 |
| 20 March 2000 | B20     | 1.7                     | 0.272                                  | 0.237 | 0.268                | 0.207 | 0.311        | 0.179 | 0.161 | 0.331 | 0.356 | 0.158 |

<sup>a</sup>A sensitivity analysis illustrated the effect of various parameters on production estimated with the WRM. Values represent production estimated with the WRM for a 50% increase or decrease in each parameter shown.

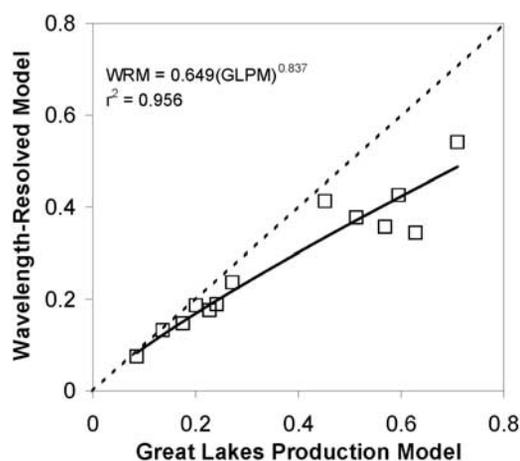
day 13 (Table 3) were consistent with intense cycling and possible depletion of available phosphorus in the incubated samples, consistent with the inferences of *Schelske et al.* [1984].

[33] Other evidence that phosphorus availability was a controlling variable under light-saturated conditions during the spring period in Lake Michigan included observations in 1998 that temporal variations in soluble reactive phosphorus (SRP) coincided with variations in  $P_{\max}^B$  (Figure 3), and that  $P_{\max}^B$  was weakly, but significantly, correlated with SRP (Figure 4). The view that phosphorus was a controlling variable was also supported by observation of positive correlations between light-saturated carbon-specific growth rates,  $\mu^C$ , and SRP concentrations (Figure 8). A lack of coincident nutrient data during 1999 and 2000 limited our ability to examine relationships to photosynthetic param-

eters and growth during those seasons. Furthermore, despite some relatively high initial SRP concentrations in 2000, values of  $P_{\max}^B$  were consistently low during this season (Figure 3). Such results may be attributable to spatial heterogeneity of episodic nutrient inputs. Both the Muskegon and St. Joseph Rivers exhibited an episodic peak in discharge prior to our period of sampling in 2000 (Figure 5). Some of the highest SRP concentrations in March of 2000 were observed on 15 March (Figures 3 and 7), which immediately followed the small peak in river discharge. It is possible that these high SRP concentrations were localized and, as well, may have declined during the period of our measurements.

[34] A further difficulty in relating SRP concentrations to phytoplankton rates is that SRP measurements may overestimate the true available phosphate concentrations [Hudson *et al.*, 2000]. However, that the true available phosphorus levels may have been even lower than measured SRP concentrations only strengthens arguments in favor of phosphorus as a controlling variable. The role of phosphorus in limiting microbial production in lakes is well recognized [e.g., *Schelske et al.*, 1974], and founded on the knowledge that, unlike carbon and nitrogen, no biological mechanisms exist for compensating deficiencies in phosphorus from atmospheric sources [Schindler, 1977]. Moreover, recent reductions in phosphorus loading in Lake Michigan and other Laurentian Great Lakes have increased the potential for phosphorus limitation [Johengen *et al.*, 1994; Fahnenstiel *et al.*, 2000; Barbiero *et al.*, 2002].

[35] Our experimental results showing minor responses of light-saturated rates of photosynthesis and growth to sediment addition (Table 3) seem at odds with prior findings of high particulate phosphorus levels in waters impacted by the RCP [Eadie *et al.*, 1996, 2002] and modeling studies suggesting the importance of plume-released nutrients in maintaining nutrient levels [Ji *et al.*, 2002]. Studies in other lake systems provide conflicting evidence regarding the role of suspended particles as a source of P for phytoplankton. Phytoplankton populations in Lake Apopka, FL were found to be more P limited with reduction of particles by dilution with filtered lake water [Carrick *et al.*, 1993]. Schallenberg



**Figure 9.** A comparison between primary production estimated using the wavelength-integrated Great Lakes Production Model (GLPM) and the Wavelength-Resolved Model (WRM) demonstrated that the two models produced comparable results. However, the Great Lakes Production Model yielded higher estimates at high-productivity stations. Units were gC m<sup>-2</sup> d<sup>-1</sup>.

and Burns [2004] found for a shallow New Zealand lake that sediment additions had a relatively small impact on available nutrients, releasing phytoplankton from limitation in only two out of four experiments. We did observe a small increase in chlorophyll concentration in the sediment-augmented samples between day 1 and day 13 (Table 3), suggesting that sediments may provide a limited capacity to enhance phytoplankton yields. Our observations of rapid turnover of soluble inorganic phosphorus, determined using  $^{33}\text{P}$ -orthophosphate, at plume-impacted stations (Table 2) were consistent with the view that the microbial communities in these waters were efficiently cycling available phosphorus. Sediment resuspension appears to support enhanced elevated heterotrophic bacterial activity in our region of study [Cotner *et al.*, 2000; Biddanda and Cotner, 2002]. It is possible that increased bacterial competition for uptake in the RCP largely nullified beneficial effects of sediment-entrained nutrients for phytoplankton communities in our study.

[36] While resuspension of sediments did not appear to substantially enhance light-saturated rates of photosynthesis and growth, evidence from prior studies does indicate a substantial impact of resuspension on phytoplankton community composition. Phytoplankton communities in waters impacted by the RCP exhibited greater prevalence of small, centric diatoms (*Cyclostephanos* spp., *Cyclotella* spp.), whose meroplanktonic life histories suggest a possible sedimentary origin [Millie *et al.*, 2003]. In contrast, the typical spring bloom species, including the larger diatoms, *Aulocoseira islandica* and *A. italica*, were typically more abundant at nonimpacted stations and during the 1999 season when resuspension was less intense [Kelly, 2001; Millie *et al.*, 2003]. That sediments represented a significant reservoir of chlorophyll was evident from our laboratory studies showing elevated chlorophyll in lake water augmented with sediments (Table 3). Similar findings of increased chlorophyll in sediment-augmented samples were reported by Schallenberg and Burns [2004].

[37] In addition to its impact on phytoplankton community structure, the recurrent coastal sediment plume had a profound impact on the irradiance field in southeastern Lake Michigan (Figure 2) with consequences for growth and primary production. This was evident in the comparison between the 1998 results, when the RCP was most intense and attenuation values were highest, with the 1999 and 2000 field years (Table 4). River discharge, which was higher during 1998, may also have contributed to increased turbidity in nearshore stations. Outflow from the St. Joseph River has been implicated in higher turbidity of nearshore waters in that region of the lake [Schelske *et al.*, 1980; Bergmann *et al.*, 2004].

[38] It is evident from the results of the sensitivity analysis (Table 4) that the higher values of attenuation in 1998 were primarily responsible for the lower productivity observed during the 1998 season. Despite similar concentrations of chlorophyll at Stations J30 and M45, primary production in 1998 was less than half that of other years. The lower integral primary production in 1998 could not be attributed to differences in photosynthetic parameters. Values of  $P_{\text{max}}^B$  during 1998 were similar to or higher than values observed during 1999 and 2000 (Figure 3). Parameters related to light-limited photosynthesis, including

$\phi_{\text{max}}^C$  and  $\hat{a}_{ph}(\lambda)$ , did not appear to exhibit systematic differences among years or in relation to environmental variables. The range of values of  $\phi_{\text{max}}^C$  seen in 1998 was comparable to that observed in other years (Figure 7) and similar to ranges reported for lakes [Bannister and Weidemann, 1984; Fahnenstiel *et al.*, 1984] and oceanic systems [Schofield *et al.*, 1993; Sosik, 1996]. Similarly, relationships of values of phytoplankton absorption at 440 nm ( $a_{ph}(440)$ ,  $\text{m}^{-1}$ ) were consistent among different years and agreed well with observations from various other oceanic waters (Figure 6). Thus it appears the variation in availability of light was the likely factor contributing to interannual differences in primary production in our study. Millie *et al.* [2003] similarly noted a strong association between  $K_{PAR}$  and suspended particulate matter (SPM) concentrations, and negative relationships between integral primary production and  $K_{PAR}$  and SPM.

[39] We addressed the question of light limitation as a constraint on phytoplankton growth by considering observed growth-irradiance relationships (Figure 8). Our derived light saturation constant for growth,  $E_{k_{\mu}}$ , of 0.9 mol quanta  $\text{m}^{-2} \text{d}^{-1}$  is close to that reported by Fahnenstiel *et al.* [2000] for Lake Michigan of 1.0 mol quanta  $\text{m}^{-2} \text{d}^{-1}$ . Thus we feel confident that the value of 0.9 mol quanta  $\text{m}^{-2} \text{d}^{-1}$  represents a reasonable threshold for irradiance limitation of growth in southern Lake Michigan waters. On the basis of comparisons to modeled ambient irradiances (not shown), phytoplankton growth during 1998 would have been constrained by light at Station J30 for depths below 5.4 m, while saturating light levels would have extended to depths of 20 m during 1999 and 15.5 m during 2000. From this, we concluded that a major portion of the water column was light limited during the 1998 season.

[40] Our evaluation of productivity algorithms demonstrated the importance of accurate descriptions of water column attenuation and subsurface irradiance fields in Great Lakes environments. The comparison between the Great Lakes Production Model (GLPM) and the Wavelength-Resolved Model (WRM) revealed that the two algorithms produced comparable results (Table 4 and Figure 9). However, the GLPM yielded higher estimates at high-productivity stations. The GLPM uses a constant value for attenuation at depth, and consequently may overestimate irradiance in surface waters. This may explain the differences between the two algorithms. Accounting for differences in in situ spectral quality does not appear to be a key factor in differences between the models [Bergmann *et al.*, 2004]. Rather, the major strength of the spectral model is improved characterization of the irradiance field. Spectral attenuation models provide greater accuracy and the ability to describe irradiance variations on the basis of measurements from in situ optical instruments or quantities derived from remote sensing.

[41] In addition to being sensitive to accurate representation of irradiance fields, productivity estimates also exhibited a relatively high sensitivity to estimates of chlorophyll (Table 4). Initial results support the view that realistic estimates of chlorophyll concentrations can be derived from water leaving radiances [Bergmann *et al.*, 2004], although presence of some phytoplankton taxa may require modified algorithms. Given accurate estimates of chlorophyll  $a$ , a reasonable estimate of phytoplankton

absorption can be derived on the basis of average relationships (Figure 6).

[42] Our findings of altered productivity, growth and phytoplankton community structure during the 1998 season have profound implications for effects of long-term climate change on the structure and function of the Lake Michigan ecosystem. The intense RCP event in 1998 was associated with weather conditions influenced by an unusually strong El Niño event [Kerr, 1998; McPhaden, 1999]. Global climate model analyses suggest that greenhouse warming may lead to increased frequency of El Niño events [Timmermann *et al.*, 1999] and associated alterations in weather, including increased frequency and severity of storm events [Hanley *et al.*, 2003]. Although there is great uncertainty in such extrapolations, the 1998 observations highlight the possibility that climate-related increases in extreme weather events could in turn diminish overall autotrophic productivity and shift phytoplankton community structure away from the typical large diatom bloom structure toward the smaller, centric diatom assemblages. An additional variable is regional precipitation, which is projected to increase in response to global warming [Allen and Ingram, 2002]. Increased precipitation would result in elevated levels of terrestrial inputs of dissolved inorganic and organic nutrients, stimulating both autotrophic and heterotrophic production. In any case, it is likely that long-term changes in weather events have the potential to profoundly alter the trophic dynamics of the lake ecosystem.

[43] A key to monitoring regional change in Lake Michigan and the other Great Lakes will be accurate, regionally specific approaches for estimation of primary production from satellite ocean color in Lake Michigan. Our results should provide a solid basis from which to develop regional satellite primary production algorithms for southeastern Lake Michigan. While satellite algorithms for estimating primary production have been used extensively in oceanic waters [Morel, 1991; Longhurst *et al.*, 1995; Antoine and Morel, 1996; Behrenfeld and Falkowski, 1997a, 1997b], they have been used infrequently in the Great Lakes [Lesht *et al.*, 2002]. Remote sensing approaches will undoubtedly be valuable for characterization of both long-term trends and episodic changes in ecosystem properties in future studies.

## Notation

|                         |   |
|-------------------------|---|
| $a_{ph}(\lambda)$       | Spectral absorption due to phytoplankton pigments in their particulate form, $m^{-1}$ .   |
| $\hat{a}_{ph}(\lambda)$ | Shape vector for phytoplankton pigment absorption, dimensionless.   |
| $\bar{a}_{ph}^*$        | Chlorophyll-specific absorption cross-section weighted by the spectrum of the photosynthetron ( $m^2 \text{ mg Chl } a^{-1}$ ).   |
| $\alpha^B$              | Photosynthetic efficiency, defined as the initial, light-limited slope of the P-E curve $gC \text{ gChl } a^{-1} h^{-1}$ ( $\mu\text{mol quanta } m^{-2} h^{-1}$ ) $^{-1}$ ). |
| $E_{k_{\mu}}$           | Light saturation constant for phytoplankton growth, $\text{mol quanta } m^{-2} d^{-1}$ .  |
| $P_{\max}^B$            | Maximum light-saturated photosynthetic rate, ( $gC \text{ gChl } a^{-1} h^{-1}$ ).  |
| $\phi_{\max}^C$         | Maximum photosynthetic quantum yield for carbon fixation, $\text{mol C fixed mol quanta}^{-1}$ .  |

|                |   |
|----------------|---|
| $K_d(\lambda)$ | Spectral diffuse attenuation coefficients for downwelling irradiance, $m^{-1}$ .                          |
| $K_{PAR}$      | Diffuse attenuation coefficient for downwelling scalar photosynthetically available radiation, $m^{-1}$ . |
| $\mu^C$        | Phytoplankton carbon-specific growth rate, $d^{-1}$ .   |
| $\mu_{\max}^C$ | Maximum (light-saturated) growth rate, $d^{-1}$ .   |

[44] **Acknowledgments.** We are grateful to M. Tuel, K. Kelley, A. Brown, R. Stone, L. Boihem, A. Kotlewski, and G. Lang for technical assistance in data collection, management, and processing of samples. C. L. Schelske, H. Carrick, and two anonymous reviewers provided valuable suggestions and insight. We also thank the crew of the R/V *Laurentian*. Funding was provided by NSF (OCE-9727341 and OCE-9727342), NOAA through the Coastal Ocean Program Great Lakes Initiative, and by the U.S. Department of Agriculture.

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- T. Bergmann and O. M. E. Schofield, Coastal Ocean Observation Lab, Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick, NJ 08901, USA. (oscar@ahab.rutgers.edu)
- G. L. Fahnenstiel, NOAA Great Lakes Environmental Research Laboratory, 1431 Beach Street, Muskegon, MI 49441, USA. (gary.fahnenstiel@noaa.gov)
- T. Johengen, Cooperative Institute of Limnology and Ecosystems Research, University of Michigan, Ann Arbor, MI 48109, USA. (johengen@glrl.noaa.gov)
- S. E. Lohrenz, Department of Marine Science, University of Southern Mississippi, Stennis Space Center, MS 39529, USA. (steven.lohrenz@usm.edu)
- D. F. Millie, Fish and Wildlife Research Institute, 100 Eighth Avenue S.E., Saint Petersburg, FL 33701, USA. (david.millie@fwc.state.fl.us)