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H. J. CARRICK AND R. L. LOWE

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Response of Lake Michigan Benthic Algae to in situ Enrichment with Si, N, and P¹

Hunter J. Carrick^{2,3} and Rex L. Lowe²

Department of Biological Sciences, Bowling Green State University, Bowling Green, OH 43403-0212, USA

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The possibility that benthic algae in the nearshore area of Lake Michigan might be growth limited by Si was tested using nutrient-releasing substrata. Nutrient treatments were Si, N+P, Si+N+P, and controls (CONT) and were sampled after 7, 14, and 31 d of exposure. Addition of Si alone had little stimulatory effect on algal biomass, while enrichment with Si+N+P led to the greatest increase in chlorophyll *a*, particulate Si, total biovolume, and diatom biovolume after 14 d of incubation ($P < 0.0001$). By day 31, communities on CONT and Si substrata exhibited little change in biomass and remained dominated by diatoms (98% of total biovolume), while algal biomass on both N+P and Si+N+P substrata increased more than eightfold ($P < 0.0001$) and consisted mainly of *Stigeoclonium tenue* (Chlorophyta) and *Schizothrix calcicola* (Cyanophyta). These results indicate that benthic diatoms in Lake Michigan are not currently limited by Si, but may become Si limited following enrichment with N+P.

On a vérifié la possibilité que la croissance des algues benthiques de la zone littorale du lac Michigan soit limitée par le Si, à l'aide de substrats libérateurs de bioéléments. Ces substrats, contenant du Si, du N+P et du Si+N+P ainsi que les sédiments témoins ont été échantillonnés après 7, 14 et 31 j d'exposition. L'apport de Si a eu peu d'incidence stimulante sur la biomasse algale tandis que l'enrichissement avec du Si+N+P a entraîné la plus grande augmentation de la concentration de chlorophylle-*a*, de Si particulaire, du biovolume total et du biovolume des diatomées après 14 j d'incubation ($P < 0,0001$). Après 31 j, les communautés poussant sur des substrats témoins et enrichis de Si ont montré peu de variations de la biomasse et étaient surtout constituées de diatomées (98 % du biovolume total) tandis que la biomasse algale sur les substrats enrichis de N+P et de Si+N+P a augmenté plus de 8 fois ($P < 0,0001$) et se composait surtout de *Stigeoclonium tenue* (Chlorophytes) et *Schizothrix calcicola* (Cyanophytes). Ces résultats révèlent que les diatomées benthiques du lac Michigan ne sont pas actuellement limitées par la concentration de Si mais peuvent le devenir par suite d'un enrichissement au N+P.

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The role nutrients play in shaping phytoplankton communities has received much attention (Kilham and Kilham 1978; Tilman 1982). Investigators have demonstrated that the availability of one to a few nutrients limits phytoplankton growth and leads to shifts in community composition (Dillon and Rigler 1974; Schindler 1977). Although less thoroughly understood, nutrients have been shown to limit benthic algal productivity (Krewer and Holm 1982). However, nutrients commonly limiting to phytoplankton (i.e. P) are often times less well correlated with benthic algal biomass (Cattaneo 1987), perhaps suggesting that nutrient supplies available to benthic algae may differ from the open water (Alexander et al. 1982; Pringle 1985). Recent work by Pringle (1987) suggests that

nutrients supplied from substrata interact with nutrient supplies in the water column to mediate the response of benthic algae to enrichment.

Results from several bioassay techniques have demonstrated benthic algal growth stimulation with additions of P (Krewer and Holm 1982; Fairchild and Lowe 1984), N (Grimm and Fisher 1986), and both P and N (Stockner and Shortreed 1978; Pringle and Bowers 1984). Silicon may be another important nutrient to benthic algae, particularly because diatoms dominate most benthic algal assemblages (Stockner and Armstrong 1971; Round 1981) and dissolved Si concentrations are very low in many aquatic systems (Alexander et al. 1982; Schelske et al. 1986). While very little information exists on the role Si plays in regulating benthic algal growth and community dynamics (e.g. Hooper-Reid and Robinson 1978), Si demand by phytoplankton can serve as an index of eutrophication (Kilham 1971).

In Lake Michigan, the growth of planktonic diatoms and subsequently their rate of Si utilization has been shown to increase following P enrichment (Schelske and Stoermer 1972; Schelske et al. 1986). This phenomenon has been suggested as a

¹Contribution No. 541, Great Lakes Environmental Research Laboratory.

²Also, University of Michigan Biological Station, Pellston, MI 49769, USA.

³Also, Great Lakes Environmental Research Laboratory, NOAA, 2205 Commonwealth Blvd., Ann Arbor, MI 48105, USA (present address).

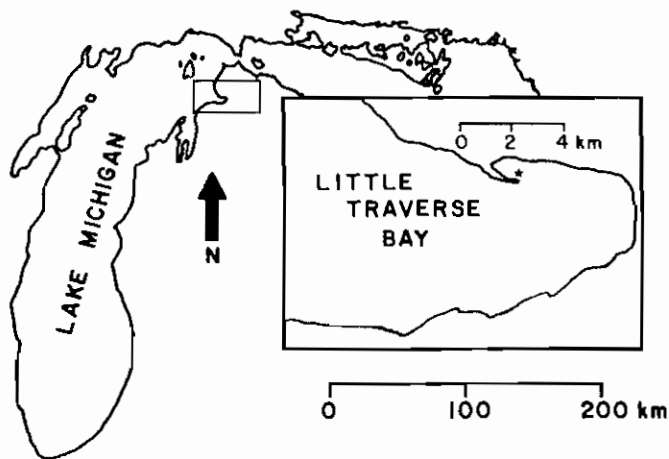


FIG. 1. Lake Michigan with Little Traverse Bay enlarged displaying the study site, indicated with a star (after Schelske and Callender 1970; Rea and Pigula 1979).

mechanism partially responsible for seasonal shifts from a diatom-dominated assemblage during spring mixing to dominance by phytoplankton without growth requirements for Si following thermal stratification (Schelske and Stoermer 1971; Fahnenstiel and Scavia 1987a). Because diatoms also dominate Lake Michigan benthic algal assemblages (Stevenson and Stoermer 1981; Kingston et al. 1983), elevated P inputs might induce similar shifts in benthic algal community composition. Thus, the present study utilized substrata which release combinations of Si, N, and P in the littoral zone of Lake Michigan in order to determine (1) whether benthic diatoms are Si limited and (2) if a shift from a diatom-dominated community to one composed of algae without Si requirements (i.e. green and blue-green algae) is observed following N + P enrichment.

Materials and Methods

Nutrient-releasing substrata were constructed as described by Fairchild and Lowe (1984) from clay flower pots (internal volume = 245 mL) that were autoclaved and soaked in deionized water for 48 h. Each substratum was filled with a hot 2% agar-deionized water solution containing one or a combination of 0.05 M NaNO₃ (N), 0.05 M NaH₂PO₄ (P), and 0.1 M Na₂SiO₃ (Si).

Nutrient Release Experiments

Release rates of each ion were determined under laboratory conditions in order to characterize the pattern and magnitude of nutrient release over a time period comparable with that of the in situ experiment. Release of NO₃-N (average release = 254 μmol·d⁻¹) was higher than PO₄-P (82 μmol·d⁻¹); however, both decreased through time (Fairchild et al. 1985). Release of SiO₂ was determined by filling three replicate substrata with agar and 0.1 M Na₂SiO₃ (Si) and three more with just agar (CONT). The Si and CONT substrata were placed in 4-L plastic containers filled with 1.5 L of deionized water. The water in each jar was changed daily for 23 d. On days 1, 2, 3, 6, 9, 12, 15, 18, 21, and 23 of the experiment, water samples were filtered through washed 0.45-μm Millipore® filters, stored in acid-washed polyethylene bottles, and refrigerated. These samples were analyzed for SiO₂ colorimetrically using a Technicon II autoanalyzer (Davis and Simmons 1979).

In situ Nutrient Manipulation

Forty-eight nutrient-releasing substrata were constructed for field experiments: 12 contained Si as a nutrient addition (Si substrata), 12 had both N and P added (N + P substrata), 12 had all three nutrients added (Si + N + P substrata), and the remaining 12 served as controls, with no nutrients added (CONT substrata). On 15 July 1984, all substrata were placed approximately 0.5 m apart in a grid at a depth of 10 m off Harbor Point in Little Traverse Bay, Lake Michigan, using SCUBA (Fig. 1). Each substratum was secured into the sediments by a wooden dowel at its base. Four substrata of each treatment were gently collected after 7, 14, and 31 d in 1-gal zip-lock plastic bags by divers, taking care to include as little lake water (and suspended algae therein) as possible with each substratum.

Upon returning to the laboratory, the contents from each zip-lock bag were transferred to a 1-L wide-mouth jar. Organisms were removed from the surface of each substratum with a razor blade and toothbrush and washed into the jar with deionized water. Each sample was diluted to a known volume, from which subsamples were removed to determine concentrations of chlorophyll *a*, particulate Si (PSi), and algal biovolume (Stoermer and Kreis 1980). The remaining slurry was concentrated by settling and diatom reference slides were prepared (Patrick and Reimer 1966).

Chlorophyll subsamples were filtered (0.45-μm Millipore), sonicated, centrifuged, extracted in 90% acetone buffered with MgCO₃, and analyzed using a Turner 111 fluorometer. Samples were subsequently acidified and assayed a second time for phaeopigments (Strickland and Parsons 1968). Subsamples for PSi were filtered (0.40-μm Nuclepore®), transferred to plastic vials, and frozen. Samples were later subjected to NaOH extraction and acid neutralization and analyzed with an autoanalyzer for dissolved SiO₂ (Krause et al. 1983).

Algal densities were estimated from each prepared slide by enumerating between 350 and 3000 algal cells using a Leitz Dialux® research microscope at 1250× magnification. Biovolume estimates were obtained for taxa by determining the mean cell dimensions of at least 10 randomly chosen cells. Average biovolume was calculated from the mean cell dimensions and was multiplied by cell densities to obtain the total biovolume for each taxon.

Estimates of algal biomass were analyzed using one-way analysis of variance (ANOVA), with nutrient treatments considered a fixed factor and sampling intervals treated as a blocked factor. Data were log transformed to meet the assumptions of homoscedasticity, and Student–Newman–Keuls multiple range tests ($P < 0.05$) were used to evaluate sources of significant variation (Zar 1983).

Physicochemical Analyses

Duplicate 1-L lake water samples were collected on days 1, 7, 14, and 31 of the experiment from depths of 1, 5, and 10 m using a 2-L Van Dorn bottle. Lake water samples (100 mL) were analyzed for chlorophyll, following which the filtrate was analyzed for NO₃-N, soluble reactive P (SRP), Cl⁻, and SiO₂ using a Technicon II autoanalyzer (Davis and Simmons 1979). An additional 100 mL of lake water was filtered onto membrane filters to determine PSi concentrations.

Also, on days 7, 14, and 31, pH, dissolved oxygen, temperature, and conductivity were determined at 1-m intervals from the surface to depths of between 6 and 12 m using a

TABLE 1. Pooled estimates for chemical and biological parameters measured on four dates from duplicate water samples taken at three depths (1, 5, and 10 m) in Little Traverse Bay, Lake Michigan (und = undetectable).

Date (1984)	SiO ₂ (mg·L ⁻¹)	Cl ⁻ (mg·L ⁻¹)	NO ₃ -N (μg·L ⁻¹)	SRP (μg·L ⁻¹)	PSi (mg·L ⁻¹)	Chl <i>a</i> (μg·L ⁻¹)
15 July	0.36	8.77	182.8	und	2.14	1.11
22 July	0.41	8.77	193.1	1.00	2.81	1.65
29 July	0.35	8.62	199.4	1.20	1.55	1.15
15 August	0.37	8.23	198.0	und	1.24	0.79
Mean	0.38	8.59	193.3	1.10	1.94	1.18
SE	0.01	0.13	3.7	0.10	0.35	0.19

Hydrolab®. Water transparency was measured with a white and black Secchi disk (diameter = 20 cm).

Results

Silica (SiO₂) liberation from Si and CONT substrata was characterized by high initial release, followed by relatively constant release. The magnitude of SiO₂ release from Si substrata (254 μmol·d⁻¹) was more than 25-fold higher than that released from CONT substrata (10 μmol·d⁻¹).

Physicochemical Conditions of Lake Michigan Water

Concentrations of SiO₂, Cl⁻, NO₃-N, and SRP showed little temporal or spatial variability (Table 1). Levels measured were similar to those reported from other nearshore areas in northern Lake Michigan (Schelske and Callender 1970) and are indicative of extreme P limitation (Tilman 1982). Concentrations of PSi and chlorophyll were highest on 22 July and declined thereafter, indicating a decrease in phytoplankton standing crop (i.e. diatoms) typical of summer epilimnetic populations in Lake Michigan (Fahnenstiel and Scavia 1987a).

Estimates ($\bar{X} \pm SE$) of conductivity (286.7 ± 2.1 μmho·cm⁻¹ at 25°C), pH (7.97 ± 0.13), and dissolved oxygen (8.4 ± 1.3 mg·L⁻¹) changed very little by depth and through time. Water transparency (Secchi depth = 5–6 m) also showed little temporal variability. Temperature profiles (20.2 ± 0.7°C) indicated that surface waters in the bay warmed very little during the study and that the thermocline was below 10 m (Carrick 1985).

Algal Biomass Estimates

Changes in algal biomass among nutrient treatments over all sampling periods as determined by chlorophyll, PSi, and total biovolume yielded consistent results (Table 2; Fig. 2). Samples on day 7 were not different in terms of total biovolume and PSi; however, chlorophyll concentrations were highest on Si + N + P substrata. By day 14, algal biomass was greatest on either Si + N + P (chlorophyll and PSi) or Si and Si + N + P treatments (biovolume). On day 31, all three biomass estimates were greater on N + P and Si + N + P substrata over CONT and Si treatments.

Division-Level Responses

Biovolume of three divisions of algae (blue-green algae, green algae, and diatoms) did not vary significantly among nutrient treatments following 7 d of incubation (Table 3). After 14 d of exposure, diatom biovolume was highest on Si + N + P

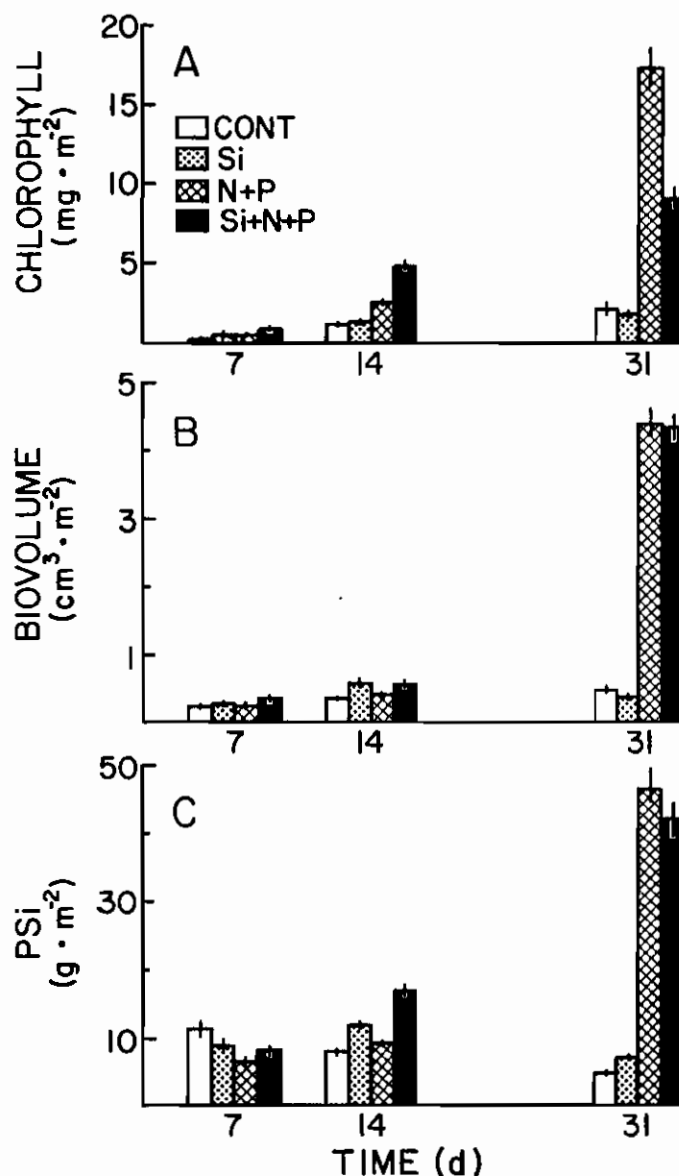


FIG. 2. Average (A) chlorophyll *a* concentrations, (B) total biovolume estimates, and (C) PSi concentrations among four nutrient treatments collected over three successive sampling periods. Vertical bars denote 1 SE from the mean.

and Si substrata over the other two treatments. By day 31, blue-green and green algae both demonstrated a significant increase in biovolume on N + P and Si + N + P over Si and CONT substrata (Fig. 3).

TABLE 2. Results from one-way analysis of variance (ANOVA) comparing estimates of algal biomass among nutrient treatments for each sampling date. Treatments joined by underlining were not significantly different from one another when assessed with the Student-Newman-Keuls (SNK) multiple means range test (at $P < 0.05$). *** $P < 0.0001$.

Date	Biomass estimate	F (df = 3)	SNK range test
Day 7	Chlorophyll	13.29***	<u>CONT N+P Si</u> <u>Si+N+P</u>
	Biovolume	2.41	<u>CONT N+P Si</u> <u>Si+N+P</u>
	PSi	1.38	<u>N+P Si+N+P Si</u> <u>CONT</u>
Day 14	Chlorophyll	74.12***	<u>CONT Si</u> <u>N+P</u> <u>Si+N+P</u>
	Biovolume	13.35***	<u>CONT N+P Si</u> <u>Si+N+P Si</u>
	PSi	11.97***	<u>CONT N+P Si</u> <u>Si+N+P</u>
Day 31	Chlorophyll	29.22***	<u>Si</u> <u>CONT</u> <u>Si+N+P</u> <u>N+P</u>
	Biovolume	177.23***	<u>Si</u> <u>CONT</u> <u>Si+N+P</u> <u>N+P</u>
	PSi	140.18***	<u>CONT Si</u> <u>N+P</u> <u>Si+N+P</u>

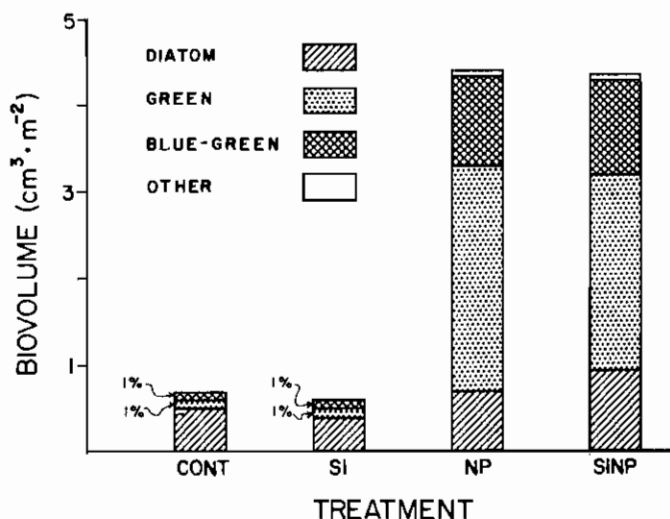


FIG. 3. Relative contribution of algal divisions to the total biovolume among four nutrient treatments after 31 d of exposure.

Population-Level Responses

The response of algal populations to nutrient enrichment following the 31-d incubation fell into four categories: species responding positively to either Si, N+P, or Si+N+P and species responding negatively to all three patterns of enrichment (Table 4).

Eleven species of diatoms displayed significant growth response to Si enrichment (Table 4A) and accounted for between 1 and 2% of the total biovolume on Si substrata. *Amphora ovalis* (Kütz.) Kütz., *Cocconeis diminuta* Pant., *Cymbella minuta* Hilse ex Rabh., and *Nitzschia bacata* Hust. underwent from 1.2- to 3.7-fold increases in biovolume following Si enrichment. The biovolume of *Navicula cryptocephala* var. *veneta* (Kütz.) Rabh. and *Synedra rumpens* Kütz. was comparable on CONT and Si substrata but was less variable on Si substrata. The remaining five species only occurred on Si substrata.

Two species responded strongly to enrichment with N+P and Si+N+P (Table 4B; Fig. 4). The growth of *Schizothrix calcicola* (Ag.) Gomont, a small filamentous blue-green alga, was enhanced over 2000-fold on N+P and Si+N+P substrata and comprised a substantial portion of the total biovolume (24

and 26%, respectively). *Stigeoclonium tenue* (Ag.) Kütz., a green filamentous alga, increased more than 600-fold on N+P and Si+N+P substrata and accounted for 59 and 50% of the total biovolume in each community.

The diatoms *Achnanthes minutissima* Kütz. and *Cocconeis placentula* Ehr. responded moderately to enrichment with N+P, but increased to the greatest extent when all three nutrients were supplied (Table 4C; Fig. 4). *Achnanthes minutissima* underwent a 1.5-fold increase in biovolume on N+P substrata and a 2.3-fold increase on Si+N+P substrata (6 and 9% of the total biovolume, respectively). *Cocconeis placentula* showed a similar response to enrichment, increasing in biovolume 8.4-fold on N+P and more than 14-fold on Si+N+P substrata (4 and 6%, respectively).

Eleven species of diatoms maintained stable populations on CONT substrata and either decreased or were sporadically represented or absent on Si, N+P, and Si+N+P treatments (Table 4D). *Achnanthes clevei* var. *rostrata* Hust., *Cyclotella michiganiana* Skv., *C. ocellata* Pant., and *Nitzschia recta* Hantz. all decreased between 2.5- and 11.0-fold on Si substrata relative to controls and were absent on N+P and Si+N+P substrata. *Amphora hemicycla* Stoerm. & Yang only occurred on CONT substrata, while the remaining species had variable occurrences on N+P and Si+N+P compared with CONT and Si treatments. These species each contributed between 1 and 4% to the total biovolume on CONT and Si substrata.

Discussion

Enrichment with Si alone did not stimulate benthic algal growth to any significant extent in the nearshore area of northern Lake Michigan. However, Si may become a limiting factor to benthic algal growth following enrichment with N+P, as evidenced by the greatest increase in algal chlorophyll, biovolume, and PSi following Si+N+P enrichment during the first 14 d of the study. Enrichment with Si relative to N+P had little effect during the days 14–31, when factors other than nutrients seem to have become important.

It is quite possible that benthic algal communities at 10 m (ambient light is 4.5% of surface irradiance) are jointly limited by nutrients and light (see Rhee and Gotham 1981). This would explain the relatively low growth rates exhibited by the assemblage, despite the abundant supply of nutrients (see below). Moreover, chlorophyll to biomass ratios (micrograms chlorophyll per milligram, assuming specific weight = 1.0) were high on all treatments (average = 3.3) but greatest for N+P and Si+N+P treatments (3.6 and 3.9, respectively), indicating that these algae were the most light-limited. Ratios calculated here are comparable with those determined for shade-adapted subsurface phytoplankton existing under a similar light regime in Lake Michigan (Fahnenstiel and Scavia 1987b). In fact, subsurface phytoplankton demonstrated the greatest growth response to enrichment with Si and P only when higher than in situ light was provided (Fahnenstiel et al. 1984). Unexpectedly higher chlorophyll concentrations on N+P over Si+N+P substrata on day 31 may also be related to the greater contribution of green algae and subsequent chlorophyll *a* to that assemblage (see Fig. 3). Because green algae have a lesser pigmentation diversity than do blue-green algae and diatoms (Round 1981), they may contribute more chlorophyll *a* per unit cell volume.

The nearshore of Lake Michigan is a dynamic zone subject to periodic nutrient enrichment attributable to common upwell-

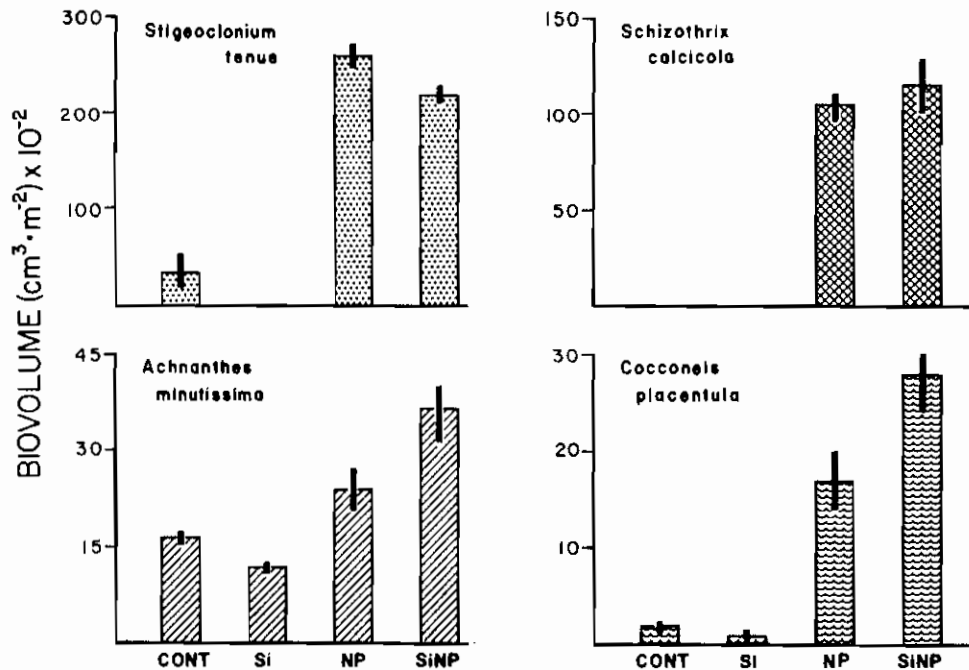


FIG. 4. Average biovolume of four dominant algal species among four nutrient treatment after 31 d of exposure. Vertical bars denote 1 SE from the mean.

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axa among four nutrient treatment after 31 d of

TABLE 3. Results from one-way analysis of variance (ANOVA) comparing the biovolume of three algal divisions among nutrient treatments for each sampling date. Treatments joined by underlining were not significantly different from one another when assessed with the Student-Newman-Keuls (SNK) multiple means range test (at $P < 0.05$). *** $P < 0.0001$.

Date	Algal division	F (df = 3)	SNK range test
Day 7	Blue-green	3.17	<u>CONT N+P Si+N+P</u> Si
	Green	1.01	<u>N+P Si</u> <u>CONT Si+N+P</u>
	Diatom	2.32	<u>CONT N+P Si</u> <u>Si+N+P</u>
Day 14	Blue-green	1.81	<u>N+P Si+N+P</u> <u>CONT Si</u>
	Green	0.90	<u>CONT N+P Si+N+P</u> Si
	Diatom	13.95***	<u>CONT N+P Si</u> <u>Si+N+P</u>
Day 31	Blue-green	122.89***	<u>CONT Si</u> <u>Si+N+P N+P</u>
	Green	94.87***	<u>Si</u> <u>CONT Si+N+P N+P</u>
	Diatom	3.20	<u>Si</u> <u>CONT N+P Si+N+P</u>

ing events (Schelske et al. 1971), external perturbations (e.g. Auer et al. 1982), and inputs from tributaries (Schelske 1975). The release of both Si and P from substrata used here are comparable with Si and P concentrations in many Lake Michigan tributaries (Schelske 1975). Despite the relatively low atomic N:P provided by our substrata (3:1), it still is within the range of N:P measured from water entering Lake Michigan through the Grand River (Stephenson and Waybrant 1971). However, the supply of nutrients from nutrient-diffusing substrata can vary in time and space and potentially influence experimental results (Pringle 1987). Based upon nutrient-diffusion rates determined under laboratory conditions (Fairchild et al. 1985; this study), we assume that nutrients were supplied linearly throughout the experiment by our in situ substrata.

With this in mind, we feel that our results represent a realistic measure of the benthic algal response to nutrient perturbations

relevant to the Lake Michigan system. Chlorophyll and particulate (biogenic) Si estimates for algal communities on N+P and Si+N+P substrata on day 31 fall well within the range for summer chlorophyll ($11-77 \text{ mg}\cdot\text{m}^{-2}$) and biogenic concentrations ($60 \text{ g}\cdot\text{m}^{-2}$, assuming $1 \text{ cm}^3 = 1.1 \text{ g}$ dry weight of sediments) present in nearshore southern Lake Michigan sediments (Nalepa and Quigley 1987; Conley et al. 1986, respectively). Also, our chlorophyll estimates correspond well with chlorophyll levels common in several oligotrophic Canadian lakes (Cattaneo 1987). Furthermore, according to the relationship between total P and periphyton biovolume for the same suite of Canadian lakes (Cattaneo 1987), the level of biovolume production we observed here correlates with water column total P concentrations (approximately $15-20 \text{ }\mu\text{g}\cdot\text{L}^{-1}$) common for nearshore Lake Michigan (Schelske 1980).

Aspects of Algal Community Development

The growth response of Lake Michigan benthic algae to nutrient enrichment is dependent upon the specific pattern of enrichment and on the period at which the community is analyzed. This temporal interaction may reflect the operation of three components of algal community development: colonization, growth, and maturation. Collections on day 7 can be interpreted to represent a period of algal colonization and acclimation (average exponential growth rate, $r = 0.33\cdot\text{d}^{-1}$), where algal biomass differed little among treatments. Values for r during this period may be inflated because passive accumulation was not taken into account (Bothwell and Jasper 1983). Days 7-14 can be characterized as an initial growth phase ($r = 0.19\cdot\text{d}^{-1}$), where increases in biomass were highest on Si+N+P substrata and community composition was similar among treatments. Days 14-31 represent a period where algal biomass accumulation on N+P and Si+N+P treatments increased nearly ninefold over Si and control treatments and

TABLE 4. Species showing significant biovolume ($\text{cm}^3 \cdot \text{m}^{-2} \times 10^{-3}$) responses to specific nutrient additions on day 31 ($\bar{X} \pm \text{SE}$), as determined by one-way analysis of variance. Species responses were classified into groups using the Student–Newman–Keuls (SNK) range test ($P < 0.05$). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Species	CONT	Si	N + P	Si + N + P
<i>A. Species responding to Si enrichment</i>				
<i>Achnanthes exigua</i> *	0	0.5 ± 0.5	0	0
<i>Amphora ovalis</i> ***	2.0 ± 2.0	7.5 ± 0.9	0	0
<i>Cocconeis diminuta</i> *	1.0 ± 0.6	1.2 ± 0.4	0	0
<i>Cymbella hustedtii</i> *	0	1.6 ± 0.7	0	0
<i>C. minuta</i> ***	1.0 ± 0.6	2.7 ± 0.7	0	0
<i>Diploneis oculata</i> **	0	1.1 ± 0.4	0	0
<i>Gomphonema gracile</i> *	0	1.3 ± 0.8	0	0
<i>Navicula cryptocephala</i> var. <i>veneta</i> ***	1.8 ± 0.3	1.8 ± 0.2	2.1 ± 2.1	0
<i>Nitzschia acicularis</i> ***	0	1.3 ± 0.6	0	0
<i>N. bacta</i> *	1.3 ± 0.8	1.7 ± 0.6	0	0
<i>Synedra rumpens</i> *	0.7 ± 0.4	0.7 ± 0.2	0	0
<i>B. Species responding to N + P enrichment</i>				
<i>Schizothrix calcicola</i> ***	0.4 ± 0.4	0	1043.6 ± 129.1	1130.9 ± 367
<i>Stigeoclonium tenue</i> ***	3.5 ± 3.5	0	2578.5 ± 251.6	2201.7 ± 164
<i>C. Species responding to Si + N + P enrichment</i>				
<i>Achnanthes minutissima</i> *	161.8 ± 26.5	120.1 ± 16.9	243.6 ± 60.9	283.1 ± 63
<i>Cocconeis placentula</i> ***	20.1 ± 3.6	11.9 ± 3.3	169.4 ± 59.1	376.1 ± 108
<i>D. Species responding negatively to enrichment</i>				
<i>Achnanthes clevei</i> var. <i>rostrata</i> *	1.4 ± 0.7	0.1 ± 0.1	0	0
<i>Amphora hemicycla</i> **	8.0 ± 3.8	0	0	0
<i>Cyclotella comensis</i> ***	4.9 ± 1.5	1.1 ± 0.3	0.5 ± 0.5	0
<i>C. michiganiana</i> ***	1.2 ± 0.4	0.5 ± 0.5	0	0
<i>C. ocellata</i> ***	1.5 ± 0.7	0.4 ± 0.1	0	0
<i>Fragilaria construens</i> **	10.4 ± 5.9	5.5 ± 2.9	0	0
<i>F. construens</i> var. <i>pumila</i> *	3.9 ± 2.1	0.4 ± 0.4	0	0
<i>F. crotonensis</i> ***	19.0 ± 3.3	10.4 ± 4.3	53.8 ± 53.8	0
<i>F. intermedia</i> *	4.8 ± 2.8	2.1 ± 1.3	0	0
<i>Nitzschia palea</i> ***	7.2 ± 2.5	2.5 ± 1.2	0	1.9 ± 1.9
<i>N. recta</i> *	8.8 ± 3.1	2.6 ± 1.5	0	0

consisted mainly of four species. Exponential growth rates were highest for N + P and Si + N + P treatments ($r = 0.11$ and $0.04 \cdot \text{d}^{-1}$), but decreased on all treatments compared with days 7–14 (average $r = 0.05 \cdot \text{d}^{-1}$). This decline in growth rate for all treatments suggests that each assemblage reached some abundance plateau (Rodriguez 1987). Overall, the algal growth rates following enrichment in this study are very low compared with those obtained for Lakes Huron and Michigan phytoplankton assemblages enriched with Si, N, and P (average r for 23 July 1975 = $0.44 \cdot \text{d}^{-1}$; Lin and Schelske 1981) and with Si and P (average $r = 0.40 \cdot \text{d}^{-1}$; Schelske et al. 1975), respectively. Furthermore, lotic periphyton exposed to various concentrations of effluent high in N and P experienced increases in intrinsic growth rates (average r for all concentrations = $0.35 \cdot \text{d}^{-1}$) over controls (average $r = 0.16 \cdot \text{d}^{-1}$) (Bothwell and Stockner 1980).

Alterations in Community Composition

Following an increase in diatom biovolume for the first 14 d of the experiment, the community composition on substrata enriched with N + P and Si + N + P shifted to one dominated by green and blue-green algae. This shift in algal community structure is similar to changes observed from in situ bag experiments involving Lake Michigan phytoplankton assemblages exposed to a similar pattern of nutrient enrichment (Schelske and Stoermer 1971, 1972). Such alterations in phytoplankton community structure were attributed to depletion of soluble Si within the phytoplankton enclosures.

Mechanisms prompting taxonomic shifts in the present study are difficult to ascribe. Low N:P like those supplied by our substrata have been shown to favor the growth of green and blue-green benthic algae in another lake enrichment study (Schindler 1975). Also, the ability of filamentous green and

blue-green algae to take up large stores of nutrients (Rosemarin 1982; Stewart et al. 1978, respectively), suffer minimal grazing losses (Canale and Auer 1982), and reduce shading effects (Cattaneo 1987) cannot be discounted as factors contributing to their relative success on N + P and Si + N + P treatments.

Enrichment of plant communities in restricted growing space often escalates the importance of resources other than nutrients (i.e. light and space) and the interactions among species utilizing these resources (Tilman 1982). Given the low light conditions and high algal standing crop on N + P and Si + N + P substrata by day 31, comparable development of biomass and community composition on N + P and Si + N + P substrata at the end of the experiment may have been mediated, in part, by the relative success of a few dominant species.

Communities on N + P and Si + N + P substrata consisted primarily of four species. *Schizothrix calcicola* (Cyanophyta) and *Stigeoclonium tenue* (Chlorophyta) formed extensive mats covering most of the surface of N + P and Si + N + P substrata. In addition, Fairchild et al. (1985) also identified *S. tenue* as a dominant following enrichment with N + P in Douglas Lake, Michigan, and commented on the possibility of habitat modification by this species. The other two dominant taxa on these treatments (*Achnanthes minutissima* and *Cocconeis placentula*) are adnate diatoms of very limited motility (Patrick and Reimer 1966) which thrive in habitats of limited space (Pringle 1985; Krejci and Lowe 1986) and light (Stockner and Shortreed 1978; McIntire 1968, respectively). Hence, we feel that secondary limitation of light and space were pertinent forces under these two nutrient regimes by day 31. Many algal species on these treatments appeared to vary as a function of the relative success of *Schizothrix* and *Stigeoclonium*, and only species with low requirements for light and space coexisted (primarily *Achnanthes* and *Cocconeis*).

Population Responses to Nutrient Enrichment

The observed growth enhancement of 11 diatom species following Si enrichment suggests that these species were Si limited. Of these, *Cocconeis diminuta*, *Nitzschia bacata*, and *Nitzschia acicularis* are known to thrive in nutrient-enriched habitats (Lowe 1974). Also, *Nitzschia acicularis* grows best in cultures with high Si concentrations (approximately 30 mg·L⁻¹; Chu 1942). No specific data pertaining to the nutrient requirements of the other eight diatom species are available. Because some Si is liberated from the CONT substrata, estimates of algal response to Si enrichment are probably conservative.

In addition to ambient dissolved Si concentrations, benthic diatoms may be able to use other sources of Si. Diatoms may be able to sequester Si by modifying the biogeochemical decomposition of silicate minerals (Hutchinson 1957). Studies by Vernadsky (1922) have documented the breakdown of silicate materials (i.e. kaolinite and nacrite) by species of the diatom genera *Nitzschia* and *Navicula*. Also, significant release of Si from nearshore sediments in Lake Michigan (Quigley and Robbins 1984) may be another potential Si source. Third, the high annual sedimentation of remnants from the spring diatom bloom in Lake Michigan (Fahnenstiel and Scavia 1987a) settles in some nearshore zones (Nalepa and Quigley 1987) and deposits diatom frustules and fragments which can dissolve swiftly (80–100% annually; Conway et al. 1977), providing another potential Si source. Thus, benthic diatoms may have a mode of maintaining populations in Si-poor waters by using an additional source(s) of Si present in the sediments (Cheng and Tyler 1973).

The increase in algal biomass on N + P and Si + N + P substrata was primarily due to the growth of *Stigeoclonium tenue* and *Schizothrix calcicola*. *Stigeoclonium tenue* grows well in organically enriched habitats (Palmer 1969). In addition, culture studies have demonstrated increased growth response of *S. tenue* to enrichment with combinations of NO₃⁻ and PO₄³⁻ (DeVries et al. 1985) and a capacity for high P-uptake kinetics and growth rates (2.0·d⁻¹) (Rosemarin 1982). *Schizothrix calcicola* is also associated with organic pollution (Van Landingham 1983), and is one of the more pollution tolerant members of the Oscillatoriaceae (Drouet 1968). Because green and blue-green algae have little to no requirement for Si (Hutchinson 1957), we deduce that *Schizothrix* and *Stigeoclonium* responded to supplies of N and P (and/or other unknown ions) liberated from N + P and Si + N + P substrata.

The diatoms *Achnanthes minutissima* and *Cocconeis placentula* experienced increased growth on N + P substrata and reached the greatest abundance on substrata enriched with Si + N + P. Although *A. minutissima* is found in a variety of freshwater habitats (Lowe 1974), it responds to nitrate addition (Stockner and Shortreed 1978; Fairchild and Lowe 1984; Pringle and Bowers 1984), as does *Cocconeis* (Pringle and Bowers 1984; Fairchild et al. 1985). Our results indicate that both species respond positively to N + P addition and that greatest growth is obtained when Si is also provided.

The negative response to nutrient enrichment exhibited by 11 diatom species was expected given what is known about their autecology. The three *Cyclotella* species encountered here have been characterized as pollution-intolerant species (Stoermer 1978) which decline in abundance under increasing eutrophic conditions (Stoermer et al. 1985). Of the four sensitive species of *Fragilaria*, *F. construens* and *F. construens* var. *pumila* are intolerant to eutrophication (Engstrom et al. 1985). *Fragilaria crotonensis* is a more tolerant "weed" species that occurs under a wide range of conditions and declines under more advanced stages of nutrient perturbation (Stoermer et al. 1985). *Nitzschia palea* is also regarded as a "weed" species (Lowe 1974) and perhaps responds to nutrient enrichment much like *F. crotonensis*. The cosmopolitan nature of *F. crotonensis* and *N. palea* may account for their variable response to nutrient enrichment in this study. Information concerning the autecology of the other sensitive species is scarce.

Concluding Remarks

In summary, enrichment with Si + N + P led to the greatest increase in total algal chlorophyll, biovolume, and P_{Si} between treatments during the first 14 d of the study when diatoms dominated the assemblage. Additions of Si alone affected a limited number of poorly represented species. Thus, Si appears to be a secondarily limiting nutrient, becoming important to benthic algae following N + P addition. Although the observed shift from diatom to green and blue-green dominance following N + P enrichment in this study coincides with findings for Lake Michigan phytoplankton exposed to the same pattern of enrichment (Schelske and Stoermer 1971, 1972), the mechanism driving these changes may differ. Taxonomic shifts observed here were attributed to the low N:P supplied and to species-level interactions. Low growth rates and high chlorophyll to biomass ratios for algae across treatments is indicative of light limitation, which was apparently accentuated by the extensive growth of *Schizothrix* and *Stigeoclonium* on N + P and Si + N + P substrata. This implies that the trade-off between nutrients and other potentially limiting resources (i.e. light and space) cannot be

ignored and may manifest themselves readily within communities restricted to substrata.

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References

- ALEXANDER, V., D. W. STANLEY, R. J. DALEY, AND C. P. MCROY. 1982. Primary producers, p. 179–250. *In* J. E. Hobbie [ed.] *The limnology of tundra ponds*. Dowden, Hutchinson, and Ross Publ., Stroudsburg, PA.
- AUER, M. T., R. P. CANALE, H. C. GRUNDLER, AND Y. MATSUOKA. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 1. Program description and field monitoring of growth dynamics. *J. Great Lakes Res.* 8: 73–83.
- BOTHWELL, M. L., AND S. JASPER. 1983. A light and dark trough methodology for measuring rates of lotic periphyton settlement and net growth: an evaluation through intersite comparison, p. 253–265. *In* R. G. Wetzel [ed.] *Periphyton of freshwater ecosystems*. Dr. W. Junk Publ., Boston, MA.
- BOTHWELL, M. L., AND J. G. STOCKNER. 1980. Influence of secondarily treated kraft mill effluent on the accumulation rate of attached algae in experimental continuous-flow troughs. *Can. J. Fish. Aquat. Sci.* 37: 248–254.
- CANALE, R. P., AND M. T. AUER. 1982. Ecological studies and mathematical modelling of *Cladophora* in Lake Huron: 5. Model development and calibration. *J. Great Lakes Res.* 8: 112–125.
- CARRICK, H. J. JR. 1985. The response of Lake Michigan benthic algae to an *in situ* nutrient manipulation. Masters thesis, Bowling Green State University, Bowling Green, OH. 86 p.
- CATTANEO, A. 1987. Periphyton in lakes of different trophic. *Can. J. Fish. Aquat. Sci.* 44: 296–303.
- CHENG, D. M. H., AND P. A. TYLER. 1973. The effects of diatom populations on silica concentrations of lakes Sorell and Crescent, Tasmania, and the utilization of tripton as a source of silica. *Br. Phycol. J.* 8: 249–256.
- CHU, S. P. 1942. The influence of the mineral composition of the medium on the growth of planktonic diatoms. Part I. Methods and culture media. *J. Ecol.* 30: 284–325.
- CONLEY, D. J., C. L. SCHELSKE, B. G. DEMPSEY, C. D. CAMPBELL, AND T. L. NEWBERRY. 1986. Distribution of biogenic silica in the surficial sediments of Lake Michigan. *Can. J. Earth Sci.* 23: 1442–1449.
- CONWAY, H. L., J. I. PARKER, E. M. YAGUCHI, AND D. L. MELLINGER. 1977. Biological utilization and regeneration of silicon in Lake Michigan. *J. Fish. Res. Board Can.* 34: 537–544.
- DAVIS, C. O., AND M. S. SIMMONS. 1979. Water chemistry and phytoplankton field and laboratory procedures. Univ. Mich. Great Lakes Res. Div. Spec. Rep. No. 70.
- DEVRIES, P. J. R., S. J. M. DESMET, AND J. VAN DERHEIDE. 1985. Effects of phosphorus and nitrogen enrichment on the yield of some strains of *Stigeoclonium* Kütz. (Chlorophyceae). *Freshwater Biol.* 15: 95–103.
- DILLON, P. J., AND F. H. RIGLER. 1974. The phosphorus–chlorophyll relationship in lakes. *Limnol. Oceanogr.* 19: 767–773.
- DROUET, F. 1968. Revision of the Oscillatoriaceae. *Acad. Nat. Sci. Philadelphia Monogr.* 15: 370 p.
- ENGSTROM, D. R., E. B. SWAIN, AND J. C. KINGSTON. 1985. A paleolimnological record of human disturbance from Harvey's Lake, Vermont: geochemistry, pigments, and diatoms. *Freshwater Biol.* 15: 261–288.
- FAHNENSTIEL, G. L., AND D. SCAVIA. 1987a. Dynamics of Lake Michigan phytoplankton: recent changes in surface and deep communities. *Can. J. Fish. Aquat. Sci.* 44: 509–514.
- 1987b. Dynamics of Lake Michigan phytoplankton: the deep chlorophyll layer. *J. Great Lakes Res.* 13: 285–295.
- FAHNENSTIEL, G. L., D. SCAVIA, AND C. L. SCHELSKE. 1984. Nutrient–light interactions in the Lake Michigan subsurface chlorophyll layer. *Verh. Int. Ver. Limnol.* 22: 440–444.
- FAIRCHILD, G. W., AND R. L. LOWE. 1984. Artificial substrates which release nutrients: effects on periphyton and invertebrate succession. *Hydrobiologia* 114: 29–37.
- FAIRCHILD, G. W., R. L. LOWE, AND W. B. RICHARDSON. 1985. Algal periphyton growth on nutrient-diffusing substrates: an *in situ* bioassay. *Ecology* 66: 465–472.
- GRIMM, N. B., AND S. G. FISHER. 1986. Nitrogen limitation in a Sonoran Desert stream. *J. N. Am. Benthol. Soc.* 5: 2–15.
- HOOPER-REID, N. M., AND G. G. C. ROBINSON. 1978. Seasonal dynamics of epiphytic algal growth in a marsh pond: composition, metabolism, and nutrient availability. *Can. J. Bot.* 56: 2441–2448.
- HUTCHINSON, G. E. 1957. *A treatise on limnology, Volume I: Geography, physics, and chemistry*. John Wiley & Sons, Inc., New York, NY. 1015 p.
- KILHAM, P. 1971. A hypothesis concerning silica and the freshwater planktonic diatoms. *Limnol. Oceanogr.* 16: 10–18.
- KILHAM, S. S., AND P. KILHAM. 1978. Natural community bioassays: predictions of results based on nutrient physiology and competition. *Int. Ver. Theor. Angew. Limnol. Verh.* 20: 68–74.
- KINGSTON, J. C., R. L. LOWE, E. F. STOERMER, AND T. B. LADEWSKI. 1983. Spatial and temporal distribution of benthic diatoms in northern Lake Michigan. *Ecology* 64: 1566–1580.
- KRAUSSE, G. L., C. L. SCHELSKE, AND C. O. DAVIS. 1983. Comparison of three wet-alkaline methods of digestion of biogenic silica in water. *Freshwater Biol.* 13: 73–81.
- KREJCI, M. E., AND R. L. LOWE. 1986. The importance of sand grain mineralogy and topography in determining micro-spatial distribution of epipsammic diatoms. *J. N. Am. Benthol. Soc.* 5: 221–229.
- KREWER, J. A., AND H. W. HOLM. 1982. The phosphorus–chlorophyll *a* relationship in periphytic communities in a controlled ecosystem. *Hydrobiologia* 94: 173–176.
- LIN, C. K., AND C. L. SCHELSKE. 1981. Seasonal variation of potential nutrient limitation to chlorophyll production in southern Lake Huron. *Can. J. Fish. Aquat. Sci.* 38: 1–9.
- LOWE, R. L. 1974. Environmental requirements and pollution tolerances of freshwater diatoms. U.S. Environmental Protection Agency, Environmental Monitoring Series 670/4-74-005.
- MCINTIRE, C. D. 1968. Structural characteristics of benthic algal communities in laboratory streams. *Ecology* 49: 520–537.
- NALEPA, T., AND M. A. QUIGLEY. 1987. Distribution of photosynthetic pigments in nearshore sediments of Lake Michigan. *J. Great Lakes Res.* 13: 37–42.
- PALMER, C. M. 1969. A composite rating of algae tolerating organic pollution. *J. Phycol.* 5: 78–82.
- PATRICK, R., AND C. W. REIMER. 1966. *The diatoms of the United States, Volume I*. Academy of Natural Sciences, Philadelphia, PA. 688 p.
- PRINGLE, C. M. 1985. Effects of Chironomid (Insecta: Diptera) tube-building activities on stream diatom communities. *J. Phycol.* 21: 185–194.
1987. Effects of water and substratum nutrient supplies on lotic periphyton growth: an integrated bioassay. *Can. J. Fish. Aquat. Sci.* 44: 619–629.
- PRINGLE, C. M., AND J. A. BOWERS. 1984. An *in situ* substratum fertilization technique: diatom colonization on nutrient enriched substrata. *Can. J. Fish. Aquat. Sci.* 41: 1247–1251.
- QUIGLEY, M. A., AND J. A. ROBBINS. 1984. Silica regeneration processes in nearshore southern Lake Michigan. *J. Great Lakes Res.* 10: 383–392.
- REA, D. K., AND J. D. PIQUOLA. 1979. Mineralogy and distribution of fine-grained sediments in Little Traverse Bay, Lake Michigan. *J. Great Lakes Res.* 5: 170–176.
- RHEE, G-YULL, AND I. J. GOTHAM. 1981. The effects of environmental factors on phytoplankton growth: light and the interactions of light with nitrate limitation. *Limnol. Oceanogr.* 26: 649–659.
- RODRIGUEZ, M. A. 1987. Estimating periphyton growth parameters using simple models. *Limnol. Oceanogr.* 32: 458–464.
- ROSEMARIN, A. S. 1982. Phosphorus nutrition of two potentially competing filamentous algae, *Cladophora glomerata* (L.) Kütz and *Stigeoclonium tenue* (Agardh) Kütz. from Lake Ontario. *J. Great Lakes Res.* 8: 66–72.
- ROUND, F. E. 1981. *The ecology of algae*. Cambridge University Press, London. 653 p.
- SCHELSKE, C. L. 1975. Silica and nitrate depletion as related to the rate of eutrophication in Lakes Michigan, Huron, and Superior, p. 277–298. *In* A. D. Hasler [ed.] *Coupling of land and water systems. Ecological studies*. Vol. 10. Springer-Verlag, New York Inc., New York, NY.
1980. Dynamics of nutrient enrichment in large lakes: the Lake Michigan case, p. 41–46. *In* *Restoration of lakes and inland waters*. U.S. Environmental Protection Agency, Office of Regulations and Standards Rep. No. EPA 440/5-81-010.

- SCHELSKE, C. L., AND E. CALLENDER. 1970. Survey of phytoplankton productivity and nutrients in Lake Michigan and Lake Superior, p. 93-105. *In* Proc. 13th Conf. Great Lakes Res. International Association for Great Lakes Research, Toronto, Ont.
- SCHELSKE, C. L., M. S. SIMMONS, AND L. E. FELDT. 1975. Phytoplankton responses to phosphorus and silica enrichment in Lake Michigan. *Verh. Int. Ver. Limnol.* 19: 911-921.
- SCHELSKE, C. L., AND E. F. STOERMER. 1971. Eutrophication, silica depletion, and predicted changes in algal quality in Lake Michigan. *Science (Wash., DC)* 173: 423-424.
1972. Phosphorus, silica, and eutrophication of Lake Michigan. *Nutrients and Eutrophication Spec. Symp. Vol. I:* 157-171.
- SCHELSKE, C. L., E. F. STOERMER, G. L. FAHNENSTIEL, AND M. HAIBACH. 1986. Phosphorus enrichment, silica utilization, and biogeochemical silica depletion in the Great Lakes. *Can. J. Fish Aquat. Sci.* 43: 407-415.
- SCHELSKE, C. L., E. F. STOERMER, AND L. E. FELDT. 1971. Nutrients, phytoplankton productivity and species composition as influenced by upwelling in Lake Michigan, p. 120-123. *In* Proc. 14th Conf. Great Lakes Res. International Association for Great Lakes Research, Toronto, Ont.
- SCHINDLER, D. W. 1975. Whole-lake eutrophication experiments with phosphorus, nitrogen, and carbon. *Verh. Int. Ver. Limnol.* 19: 3221-3231.
1977. Evolution of phosphorus limitation in lakes. *Science (Wash., DC)* 195: 260-262.
- STEPHENSON, M. E., AND J. R. WAYBRANT. 1971. Watershed analysis relating to eutrophication of Lake Michigan. *Mich. State Univ. Inst. Water Res. Tech. Rep.* 11.
- STEVENSON, R. J., AND E. F. STOERMER. 1981. Quantitative differences between benthic algal communities along a depth gradient in Lake Michigan. *J. Phycol.* 17: 29-36.
- STEWART, W. D. P., M. PEMBLE, AND L. AL-UGAILY. 1978. Nitrogen and phosphorus storage and utilization in blue-green algae. *Mitt. Int. Ver. Limnol.* 21: 224-247.
- STOCKNER, J. G., AND F. A. J. ARMSTRONG. 1971. Periphyton of the Experimental Lakes Area (ELA), northwestern Ontario. *J. Fish. Res. Board Can.* 28: 215-229.
- STOCKNER, J. G., AND K. R. S. SHORTREED. 1978. Enhancement of autotrophic production by nutrient addition in a coastal rainforest stream on Vancouver Island. *J. Fish. Res. Board Can.* 35: 28-34.
- STOERMER, E. F. 1978. Phytoplankton assemblages as indicators of water quality in the Laurentian Great Lakes. *Trans. Am. Microsc. Soc.* 97: 2-16.
- STOERMER, E. F., AND R. G. KREIS, JR. 1980. Phytoplankton composition and abundance in southern Lake Huron. E.P.A. Rep. EPA-600/3-8-161.
- STOERMER, E. F., J. A. WGLIN, C. L. SCHELSKE, AND D. J. CONLEY. 1985. An assessment of ecological changes during the recent history of Lake Ontario based upon siliceous algal microfossils preserved in the sediments. *J. Phycol.* 21: 257-276.
- STRICKLAND, J. D., AND T. R. PARSONS. 1968. A practical handbook of seawater analysis. *Bull. Fish. Res. Board Can.* 167: 311 p.
- TILMAN, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ. 296 p.
- VAN LANDINGHAM, S. L. 1982. Guide to the identification, environmental requirements and pollution tolerance of freshwater blue-green algae (Cyanophyta). U.S. Environmental Protection Agency 600/3-82-072.
- VERNADSKY, W. 1922. Sur la probleme de la decomposition du kaolin par les organismes. *C.R. Acad. Sci., Paris, France* 175: 450-452.
- ZAR, J. H. 1983. Biostatistical analysis. 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, NJ. 718 p.