

Dynamics of Lake Michigan Phytoplankton: Relationship to Nitrogen and Silica Fluxes¹

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We describe rates of nitrogen and silica concentration change during May–August 1983 and 1984 in southeastern Lake Michigan and compare those rates with measured plankton processes. Epilimnetic dissolved inorganic nitrogen depletion, compared with total phytoplankton demand, suggests that about 44% of the nitrogen demand is recycled. Epilimnetic diatom production, calculated from soluble silica depletion, is a relatively small fraction (<20%) of total primary production, even when diatoms dominate. Sedimentation of epilimnetic diatom silica, compared with total silica depletion, suggests that a large portion (approximately 43%) of epilimnetic particulate silica sedimentation is due to nonliving diatoms.

Les auteurs décrivent la variation des concentrations d'azote et de silice notées de mai à août 1983 et 1984 dans la partie sud-est du lac Michigan et la comparent aux taux mesurés du processus planctonique. Le taux de disparition de l'azote inorganique dissous de l'épilimnion, comparé à la demande totale du phytoplancton, porte à croire que 44 % environ de l'azote est recyclé. La production de diatomées de l'épilimnion, calculée à partir de la disparition de la silice soluble, représente une fraction relativement faible (<20 %) de la production primaire totale, ceci même lorsque les diatomées dominent. La comparaison de la sédimentation de la silice des diatomées de l'épilimnion et de la disparition de la silice totale porte à croire qu'une grande partie (43 % environ) de la sédimentation de la silice particulaire de l'épilimnion est constituée de diatomées mortes.

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We have been studying the dynamics of southern Lake Michigan plankton with particular emphasis on assemblage growth rates, carbon (C) flow, and trophic interactions. Herein we report rates of change of silica (Si) and nitrogen (N) concentrations during 1983 and 1984 and use these rates to estimate diatom production and Si sedimentation. We also combine these and other data to attempt an epilimnetic Si balance for the period of May to early July and to evaluate the relative contribution of new versus recycled production with respect to N supply.

Other biological, chemical, and physical properties, determined in the region of the 100-m depth contour in southeastern Lake Michigan off Grand Haven, Michigan, between May and August 1983 and 1984, include phytoplankton and zooplankton species composition and vertical structure, primary production, phytoplankton and particulate organic C sedimentation, zooplankton grazing, effects of fish predation, bacteria production and dynamics, and water movements. These data have been evaluated and reported elsewhere (Scavia and Fahnenstiel 1987; Fahnenstiel and Scavia 1987a, 1987b, 1987c; Scavia et al. 1986a, 1986b, 1988; Laird et al. 1986, 1987; Gardner et al. 1986, 1987; Scavia and Laird 1987; McCormick et al. 1985; J. H. Saylor, unpubl. data). This collection of studies represents the most recent evaluation of plankton dynamics and controls in what has become a rather long but sparse history of such

studies of Lake Michigan (e.g. Bartone and Schelske 1982; Parker et al. 1977a, 1977b; Conway et al. 1977; Schelske et al. 1974, 1984; Schelske 1975, 1985; Stoermer et al. 1978; Glover 1982; Eadie et al. 1984). Our focus here, on N and Si dynamics, is designed to combine these *in vitro* observations with the primarily *in situ* information of the previous studies.

Methods

Water samples were taken from various depths in 5-L opaque Niskin bottles aboard the R/V *Shenoh* between May and August of 1983 and 1984. Sample locations were determined following a Lagrangian scheme in which parcels of water were tracked with a satellite-monitored drogue system (Pickett et al. 1983) deployed in the vicinity of the 100-m depth contour, 26 km west of Grand Haven, Michigan (43°1'11"N, 86°36'48"W). These windowshade drogues (Scavia and Fahnenstiel 1987) were 1 m wide and of variable length, set to the depth of the mixing layer (typically 10 m). The drifter buoy was tracked via the Argos satellite system (Pickett et al. 1983) and drifter location and hull temperature were captured, at best, every 4 h, but usually every 8–12 h. The drogue was retrieved and released four times in 1983 and seven times in 1984.

Biogenic Si was determined with material collected on 47-mm, 0.4- μ m Nuclepore filters following a wet alkaline extraction (Krausse et al. 1983). Soluble reactive Si was determined with an automated procedure (Technicon Method No.

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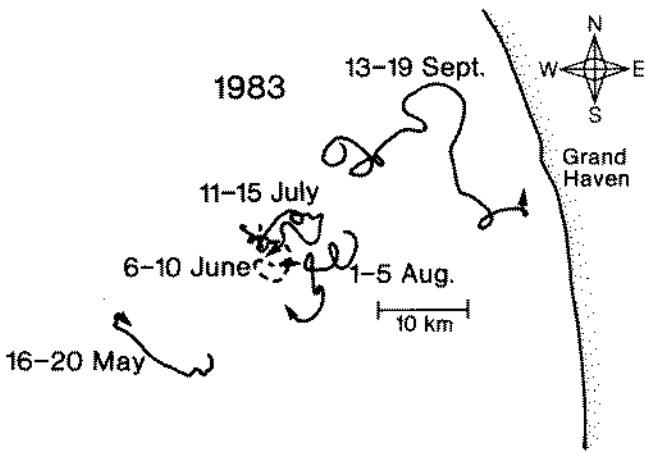


FIG. 1. Tracks of drogue locations recorded during 1983 deployments in the vicinity of the 100-m depth contour, 26 km west of Grand Haven, Michigan.

105-71w/tentative 1972, Technicon Industrial Systems, Technicon Instruments Corporation, Tarrytown, NY) on water passing a 0.2- μm Nuclepore filter. Size-fractionated samples taken from the surface water at the same station in 1987 (D. J. Conley and D. Scavia, unpubl. data) indicate that the concentration of biogenic Si between 0.2 and 0.4 μm increased slowly over the season (mean = 0.34 μM , SE = 0.072) and constitutes a significant fraction (approximately 10–20%) of total biogenic Si only after the larger particles have sedimented from the epilimnion.

Si and C contained in living diatoms were calculated from cell counts and volume estimates converted with equations developed for diatom C (Strathmann 1966) and for freshwater diatom Si: $\log_{10}(\text{Si}) = (1.03 \pm 0.06) \cdot \log_{10}(V) - (2.45 \pm 0.19)$ with Si in picomoles per cell and V in cubic micrometres per cell ($R^2 = 0.82$, $p < 0.0001$, $N = 62$; Conley et al. 1988).

Nitrate was measured by copper-cadmium (Cu-Cd) reduction following an automated procedure (Technicon Method No. 158-71w, 1972, Technicon Industrial Systems, Technicon Instruments Corporation, Tarrytown, NY; Malczyk and Eadie 1980) and ammonium was determined by a microfluorometric method based on *o*-phthalaldehyde derivation (Gardner 1978; Gardner and Miller 1981).

Nutrient depletion rates were calculated from linear regression of depth-averaged concentration on time. Regression confidence is reported as standard errors of the determined slopes.

Results

Water Movements

The most persistent feature of our drogue tracks were inertial-period circles (17-h period, average diameter 2.8 km) and longer-term direction reversals (Fig. 1), like the "meandering flow" described for similar drogues in offshore autumn Lake Michigan water (Pickett et al. 1983). The net direction of drogue movement in our experiments varied throughout the summer, as well as during each deployment (Table 1). Drogue net speeds for each deployment ranged between 0.0023 and 0.061 $\text{m}\cdot\text{s}^{-1}$ between May and September 1983 and 1984 (mean \pm SD = $0.028 \pm 0.018 \text{ m}\cdot\text{s}^{-1}$) and were similar to those measured in 1984 in the same region with vector-averaging current meters (Table 1). These measurements indicate that in offshore surface waters during summer, advective transport was slow.

Short-Term Variability

To explore short-term (weekly) versus longer-term (monthly) changes in nutrient concentration, we sampled 4 d apart at drogue locations on each monthly cruise in 1983. Because the drogues track near-surface currents in the Great Lakes under moderate winds and waves (McCormick et al. 1985), changes in nutrient concentrations observed over this time period should be due to biological and chemical alterations and not to changes in water masses.

During the 4-d cruise in May, temperature remained uniform vertically and temporally and we detected no significant changes in N or Si concentrations. While diatoms were certainly growing during this period (Fahnenstiel and Scavia 1987a), vertical mixing apparently minimized their impact on water-column-averaged nutrient concentrations over the 4 d. However, with the onset of weak thermal stratification in June, soluble Si concentrations decreased measurably during the 4-d interval through the top 30 m (Fig. 2). Concentration change during this period was consistent with the longer-term depletion rate (see two June data points along regression line in Fig. 6a below). No notable changes occurred during each of the 4-d experiments in July and August, except that subthermocline ammonium concentrations increased (Fig. 2), consistent with the seasonal trend described below (Fig. 3b).

Seasonal Trends

The water column at our 100-m station stratified thermally in early June 1983 and late June 1984 and, once stratified, thermocline depths varied between 10 and 15 m (Laird et al. 1987).

TABLE 1. Drifter movement.

	1983			1984			1984	
	Speed ($\text{m}\cdot\text{s}^{-1}$)	Direction ($^{\circ}$)	Time (d)	Speed ($\text{m}\cdot\text{s}^{-1}$)	Direction ($^{\circ}$)	Time (d)	Speed ($\text{m}\cdot\text{s}^{-1}$) ^a	Time (d)
May	0.030	297	4	—	—	—	—	—
June	0.021	127	4	0.002	38	14	0.013 ± 0.007	16
July	0.020	82	4	0.009	90	3	0.005 ± 0.003	5
				0.019	7	2	0.015 ± 0.010	5
August	0.030	215	4	0.061	60	1	0.043 ± 0.017	5
				0.044	237	5	0.027 ± 0.025	5
September	0.044	86	6	—	—	—	—	—

^aG.S. Miller, GLERL/NOAA, unpubl. data; mean \pm SD of four current meters.

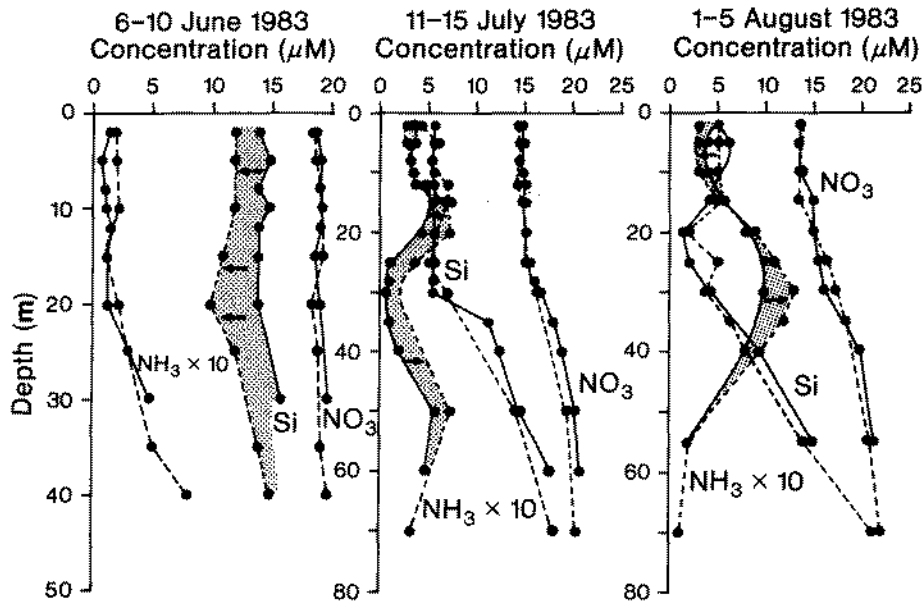


FIG. 2. Vertical profiles of ammonium, soluble Si, and nitrate plus nitrite concentrations at the beginning and end of 4-d periods at drogue locations during June, July, and August 1983. Solid line represents the first day and the broken line represents the last day of each 4-d sequence.

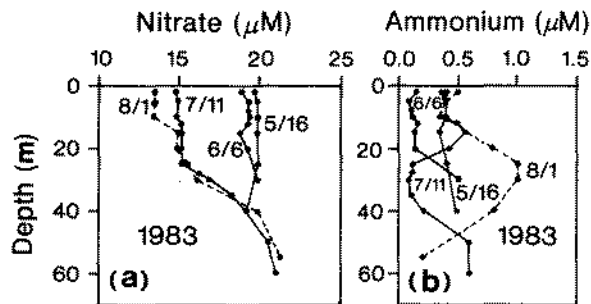


FIG. 3. (a) Nitrate plus nitrite and (b) ammonium concentration vertical profiles for 1983.

Prior to stratification, ammonium and nitrate plus nitrite (referred to here as nitrate) concentrations were uniform with depth. Surface nitrate concentration (Fig. 3a) decreased between 6 June and 11 July 1983 and thereafter remained low in the epilimnion, increased with depth through the region of the deep chlorophyll layer (DCL) (25–50 m; Fahnenstiel and Scavia 1987c), and increased slowly with time deeper in the hypolimnion. Ammonium concentrations (Fig. 3b) decreased in the epilimnion and DCL regions (20–35 m) between 16 May and 6 June 1983, increased in the epilimnion and decreased in the DCL (25–50 m) between 6 June and 11 July, and then increased in the upper portion of the DCL between 11 July and 1 August. Epilimnetic total inorganic N depletion rate for the period of late May to early August 1983 was $0.088 \mu\text{M}\cdot\text{d}^{-1}$ (SE = 0.0063 , $R^2 = 0.97$, $p < 0.00001$; Fig. 4).

Soluble Si concentrations initially were similar in both years (Fig. 5). Concentrations in the surface waters decreased between 16 May and 11 July 1983 at a rate of $0.21 \pm 0.014 \mu\text{M}\cdot\text{d}^{-1}$ ($R^2 = 0.98$, $p < 0.0001$; Fig. 6a) and between 21 May and 5 July 1984 at $0.25 \pm 0.013 \mu\text{M}\cdot\text{d}^{-1}$ ($R^2 = 0.96$, $p < 0.001$; Fig. 6b). Concentrations in deeper water decreased prior to the onset of thermal stratification and then remained fairly constant through the remainder of the season. While initial concentrations and seasonal depletion rates were similar for both

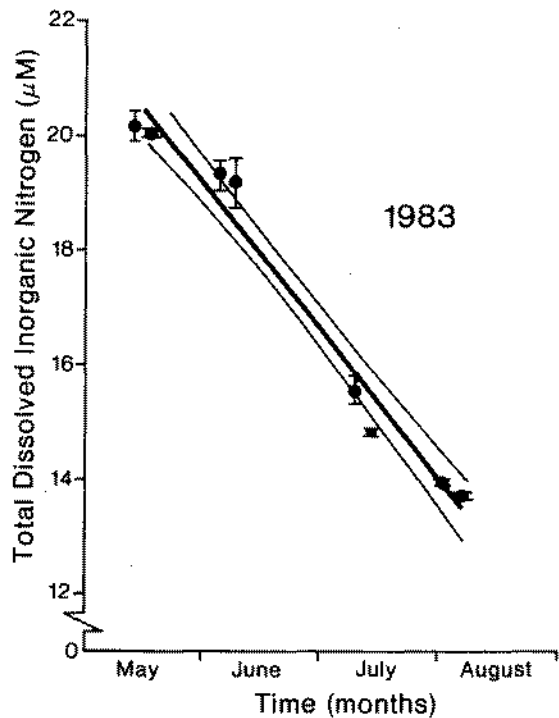


FIG. 4. Epilimnetic total dissolved inorganic N concentration versus time in 1983. Vertical bars represent ± 1 SD of data from two to five depths within the epilimnion on each date. Lines represent regression results with 95% confidence intervals.

years, soluble Si concentration decreased to values lower in 1984 compared with 1983.

Epilimnetic biogenic Si concentration in 1984 was highest on 21 May ($8.0 \mu\text{M}$) and decreased steadily at a rate of $0.100 \pm 0.016 \mu\text{M}\cdot\text{d}^{-1}$ ($R^2 = 0.95$, $p < 0.03$) to $0.36 \mu\text{M}$ on 24 August. Concentrations in the region below the thermocline (20–30 m) first increased and then decreased as summer progressed. The epilimnetic total Si (soluble reactive plus bio-

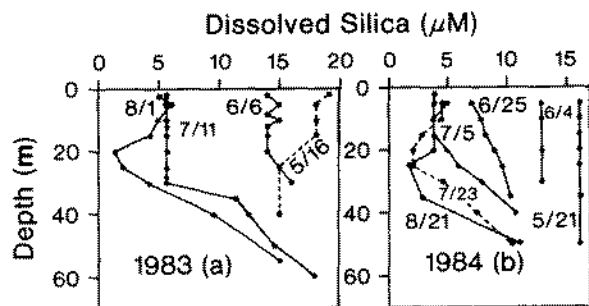


FIG. 5. Dissolved Si concentration vertical profiles for (a) 1983 and (b) 1984.

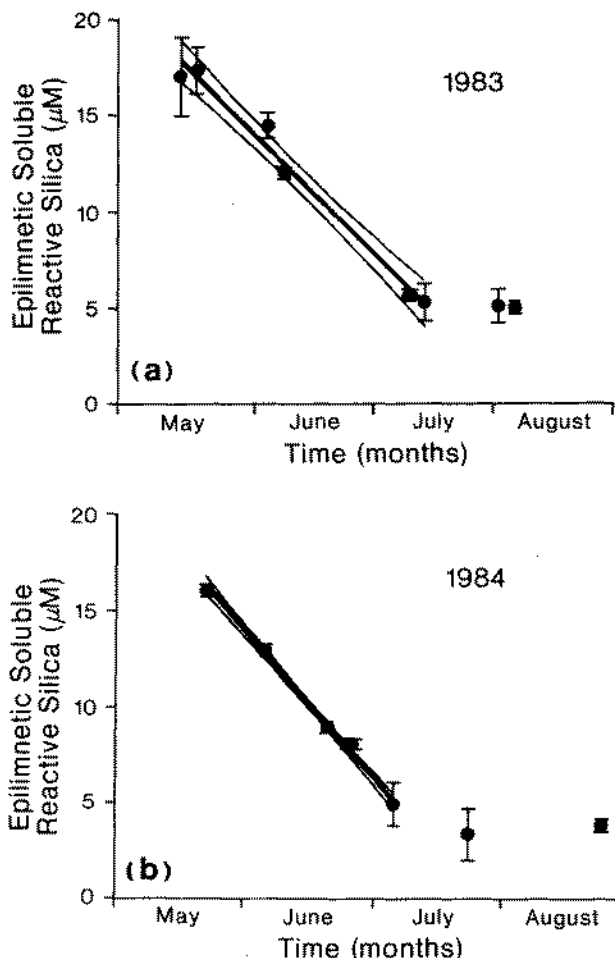


FIG. 6. Epilimnetic soluble Si concentration versus time in (a) 1983 and (b) 1984. See legend to Fig. 4 for details.

genic) depletion rate was $0.35 \pm 0.02 \mu\text{M}\cdot\text{d}^{-1}$ ($R^2 = 0.99$, $p < 0.004$; Fig. 7) between 21 May and 4 July.

Discussion

Abiotic Factors

Because there was little concentration change during each of the 4-d experiments in 1983 and because those changes were consistent with long-term dynamics, we conclude that our observed concentration changes were driven by seasonal processes. However, before proceeding with analysis of seasonal trends, we must determine whether concentration

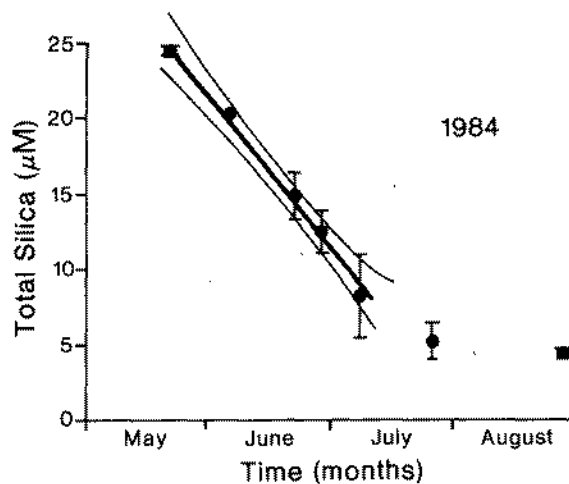


FIG. 7. Total epilimnetic Si concentration versus time in 1984. See legend to Fig. 4 for details.

changes due to abiotic factors are subordinate to biotic processes on that time scale.

Of the potential abiotic factors, horizontal advection is a major concern. Water mass movements, inferred from drogoue trajectories and current meters (Table 1), were relatively slow during the period of stratification in offshore waters. These relatively slow speeds become even less important if concentrations show small horizontal gradients because it is the product of these two properties that influences concentration changes at one location. We suggest that this was true for our study. Specific rates of change of chlorophyll concentrations, based on water-mass movements and measured horizontal chlorophyll gradients, were typically $\pm 0.01\cdot\text{d}^{-1}$ during this study (Scavia and Fahnenstiel 1987). Because these values are over an order of magnitude smaller than measured algal growth, grazing, and sinking rates ($0.1\text{--}0.4\cdot\text{d}^{-1}$; Fahnenstiel and Scavia 1987a, 1987b, 1987c; Scavia and Fahnenstiel 1987), biological process rates are far greater than horizontal physical transport of algal chlorophyll. Analogously, we conclude that changes in nutrient concentration due to horizontal water movement are not a major concern in summer offshore Lake Michigan waters.

Two other abiotic factors that can influence nutrient dynamics are vertical flux and external loads. Throughout late spring and summer, the presence of an actively growing subthermocline algal assemblage (Fahnenstiel and Scavia 1987c) assures that nutrients from the hypolimnion do not reach the epilimnion. This is reflected in the vertical profiles of nitrate and dissolved Si (Fig. 3a, 5) that show depletion well below the depth of the thermocline (10–15 m), indicating that nutrients from the hypolimnion are sequestered by the subthermocline assemblage. Nutrient budget and model analyses (e.g. Scavia 1980; Stadelmann and Fraser 1974) have shown that dilution by these massive water bodies lends significance to external nutrient loads only on annual time scales; internal cycling drives seasonal dynamics.

Seasonal Dynamics

Because abiotic factors are minimized and short-term variation is small compared with seasonal changes, we now focus on seasonal biotic factors. In 1983, nitrate (Fig. 3a) and soluble reactive Si (Fig. 5a) concentrations were highest early in the year and epilimnion values decreased after the onset of stratification. Nitrate and soluble Si depletion was not confined to

the epilimnion, but rather extended through the metalimnion into the DCL region (20–35 m; Fahnenstiel and Scavia 1987c). Later in summer, when the DCL broadened and deepened (25–50 m), the zone of nutrient depletion extended only into the upper portion of the DCL. This finding is consistent with reports of relatively fast algal growth in the upper portions of the DCL and light-limited slower rates in the lower portions (Fahnenstiel et al. 1984; Fahnenstiel and Scavia 1987a, 1987b) and with the fact that nitrate and Si are only slowly regenerated in the water column.

Ammonium is the primary form of recycled N and therefore its dynamics closely reflect the interaction of plankton demand and community regeneration. Decreasing ammonium concentration between 16 May and 6 June 1983 suggests that, during that time, demand exceeded supply rates. As epilimnetic phytoplankton production and abundance decreased later in the season (Scavia and Fahnenstiel 1987), ammonium concentration increased, indicating that regeneration rate was greater than assimilation. However, during that time, ammonium concentrations associated with the upper portion of the DCL (25–35 m) continued to decrease (Fig. 3b) and the balance was still shifted toward demand. In August, as the DCL deepened further (30–60 m), the zone of ammonium increase above the DCL deepened and broadened, indicating a region of dynamic nutrient regeneration. The fact that highest concentrations of crustacean zooplankton were also found in that same region (J. T. Lehman and D. Scavia, unpubl. data) suggests that these crustaceans may be the primary source of regenerated N on weekly to monthly time scales (see below).

Si depletion, while proceeding at similar epilimnetic rates in 1983 and 1984, resulted in slightly different vertical concentration profiles in those years (Fig. 5). While concentrations in the top 20 m were initially similar in both years, they were lower in July and August 1984 ($3.96 \pm 0.22 \mu\text{M}$, $N = 13$) compared with 1983 ($5.21 \pm 0.29 \mu\text{M}$, $N = 22$). Concentrations were similar in the upper region of the DCL in both years, but lower at 40 m (7.5 vs. 11.0 μM) and 50 m (10.7 vs. 14.8 μM) in 1984 compared with 1983. We suggest that the difference between the two midsummer vertical profiles is linked to the delayed thermal stratification in 1984 (Scavia and Fahnenstiel 1987) that prolonged effective mixing of diatom production and subsequent Si depletion throughout the water column. Shortly after the onset of thermal stratification, the Si-limited diatoms cannot combat sedimentation losses and are selectively removed from the epilimnion (Scavia and Fahnenstiel 1987; Fahnenstiel and Scavia 1987b), thus reducing the Si demand and depletion rates there. While production below the thermocline can be significant (approximately 50% of the water column rate; Fahnenstiel and Scavia 1987b, 1987c), its rate is lower than in spring and is confined to the 15- to 25-m depth range. Thus, the onset of thermal stratification reduces Si depletion throughout the water column and it is likely that delayed stratification in 1984 allowed total water column Si depletion to proceed longer into the season resulting in lower summer concentrations.

Implications for Plankton Fluxes

Because the dominant nutrient concentration changes during our study were due to biological processes acting on seasonal time scales, it is possible to relate those observed rates of change to estimates of plankton processes. Specifically, we make comparisons of soluble inorganic N depletion with phytoplankton N demand, soluble Si depletion with diatom Si demand, and

total (soluble plus biogenic) Si depletion with diatom sedimentation.

N cycling

Here, we compare the rate of change of epilimnetic dissolved inorganic N (nitrate + nitrite + ammonium) with phytoplankton demand, calculated from net phytoplankton carbon production. If net inorganic N depletion is due to phytoplankton assimilation only, then phytoplankton N demand, predicted from algal C production and a C:N ratio, will be similar to the observed N depletion rate; any difference between measured and predicted rates should estimate the N supply rate.

Total inorganic N depletion rate for the period from late May to early August 1983 was $0.088 \pm 0.006 \mu\text{M}\cdot\text{d}^{-1}$ (Fig. 4). Autotrophic C production, measured by 24-h in situ ^{14}C incubations in 2-L bottles (Fahnenstiel and Scavia 1987a) integrated over the same depth and time period, was $1.13 \mu\text{M C}\cdot\text{d}^{-1}$ (Scavia and Fahnenstiel 1987). Assuming a C:N atom ratio of 7.2 (mean of 8.1, Brzezinski 1985; 6.6 "Redfield ratio"; 7.2, Parsons et al. 1961; 7.0, Strickland 1960) yields a N demand of $0.157 \mu\text{M}\cdot\text{d}^{-1}$ and a required N supply rate of $0.069 \mu\text{M}\cdot\text{d}^{-1}$. This represents 44% of the algal demand, illustrating that, like in other systems (e.g. Stadelmann and Fraser 1974; Eppley and Peterson 1979), much of the N assimilated by phytoplankton is recycled.

Crustacean zooplankton are one source of this recycled N (Lehman 1980; Bidigare 1983). Normalizing our calculated N supply rate by average epilimnetic crustacean zooplankton biomass (J. T. Lehman and D. Scavia, unpubl. data; Scavia and Fahnenstiel 1987) yields a weight-specific rate of $16.4 \mu\text{g N}\cdot\text{mg dry weight}^{-1}\cdot\text{d}^{-1}$, a rate similar to those determined directly in other field and laboratory experiments with crustaceans (5.1–27.9, mean = 15.5, SE = 3.2, $N = 6$; Wetzel 1983).

The above analysis considers only Lake Michigan's traditional food web (nano- and microplanktonic autotrophs and crustacean zooplankton) as major mediators of N flux on weekly to monthly time scales. We have recently documented Lake Michigan heterotrophic bacterioplankton production that rivals autotrophic production (Scavia et al. 1986b; Scavia and Laird 1987) and micrograzer bacterivory that apparently often keeps pace with the rapid bacterial growth rates (Gardner et al. 1986, Scavia and Laird 1987), yielding little change in bacteria biomass over the season. The microbial food web also has the apparent capability of processing added amino acids and altering N fluxes in relatively long incubations (Gardner et al. 1987); however, the actual roles of bacteria and their grazers in controlling inorganic N concentration over days to months in nature are not clear. We assume here that N–bacteria–micrograzer dynamics (driven by typical bacterial turnover times of 5–25 h; Scavia and Laird 1987) are in dynamic equilibrium with respect to the longer time frame of the traditional web (driven by typical phytoplankton turnover times of 2–10 d; Fahnenstiel and Scavia 1987a) and therefore they do not strongly influence our conclusions. Work will have to be done to further test this assumption.

Diatom production

Our epilimnetic dissolved Si depletion rates ($0.21 \mu\text{M}\cdot\text{d}^{-1}$ for 16 May to 14 July 1983 and $0.25 \mu\text{M}\cdot\text{d}^{-1}$ for 21 May to 5 July 1984; Fig. 6) are similar to others ($0.19 \mu\text{M}\cdot\text{d}^{-1}$, assuming 60 d between the beginning of the spring diatom bloom and stratification, Conway et al. 1977; $0.3 \mu\text{M}\cdot\text{d}^{-1}$, Bartone and Schelske 1982) and can be used to estimate average epilimnetic diatom production during the period from late May to late July

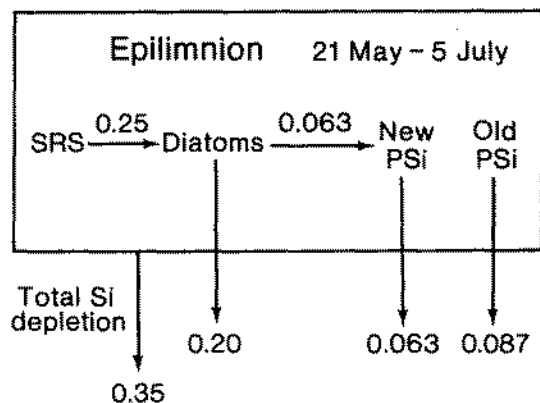


FIG. 8. Epilimnetic Si balance for the spring-summer period in 1984. SRS = soluble reactive Si; PSi = particulate Si of biogenic origin. All rates are micromoles per litre per day. Diatom Si decreased at a rate of $0.013 \mu\text{M}\cdot\text{d}^{-1}$.

1983 and 1984. We estimated Si:C ratios for diatoms in epilimnetic water samples collected between May and July of 1983 and 1984 by calculating for each date and depth the ratio of total diatom Si to total diatom C, each determined by conversion from cell counts and measured cell volumes using the equations of Strathmann (1966) for C and Conley et al. (1988) for Si. The mean atom ratio was 0.75 (SE = 0.08, $N = 24$). Dividing this ratio into the dissolved Si depletion rate yields diatom C production estimates of $0.28 \mu\text{M}\cdot\text{d}^{-1}$ for 1983 and $0.33 \mu\text{M}\cdot\text{d}^{-1}$ for 1984. Epilimnetic total phytoplankton production during the same time period ranged between 0.81 and $1.76 \mu\text{M}\cdot\text{d}^{-1}$ (integrated mean = 1.33) in 1983 and between 1.13 and $3.32 \mu\text{M}\cdot\text{d}^{-1}$ (integrated mean = 2.31) in 1984 (Scavia and Fahnenstiel 1987). The Si-based rate estimates suggest that even when diatoms make up most of the phytoplankton mass, their lower growth rates result in a disproportionately lower fraction of total epilimnetic C production (21% in 1983, 14% in 1984).

This conclusion is supported by comparison of N demand by the entire algal assemblage with that of diatoms only. The diatom Si:N atom ratio, estimated from our Si:C estimate (0.75) and a C:N estimate of 7.2 (see above), is 5.4. Dividing this ratio into the 1983 soluble Si depletion rate yields diatom N demand of $0.039 \mu\text{M}\cdot\text{d}^{-1}$. Because net N depletion ($0.088 \pm 0.006 \mu\text{M}\cdot\text{d}^{-1}$; Fig. 4) includes both assimilation and regeneration, $0.088 \mu\text{M}\cdot\text{d}^{-1}$ is clearly an underestimate of the total demand; yet the calculated diatom demand is only 44% of even that rate.

These estimates of low diatom production require a slight modification of the interpretation of sedimentation and grazing fluxes determined from the same study but reported earlier. Scavia and Fahnenstiel (1987) suggested that sedimentation is important in controlling diatom spring abundance and that summer epilimnetic production rates are within 30% of measured sinking and grazing loss rates. That analysis suggested further that grazing was not important during spring when diatoms dominate. However, in light of the present analysis, it seems that while the slower growing diatoms were not grazed (diatom production = $0.28\text{--}0.33 \mu\text{M}\cdot\text{d}^{-1}$; diatom sedimentation = $0.25 \mu\text{M}\cdot\text{d}^{-1}$, from integrated sequential trap deployments 23 May to 5 July 1984; Scavia and Fahnenstiel 1987), nondiatom production likely was grazed. If true, grazing could explain the large discrepancy between early spring (May to early June) total algal production ($2\text{--}3 \mu\text{M}\cdot\text{d}^{-1}$; Fahnenstiel and Scavia 1987b)

and measured loss rates ($0.4\text{--}0.8 \mu\text{M}\cdot\text{d}^{-1}$; Scavia and Fahnenstiel 1987), the latter attributed almost exclusively to sedimentation. The method of determining grazing loss rates in those experiments was based on measuring chlorophyll concentration changes in experimental enclosures (Scavia and Fahnenstiel 1987), and during spring, the high abundance of relatively ungrazed diatoms may have masked the effects of zooplankton on the cooccurring flagellate community. Analysis of changes in species abundances from June 1984 grazing experiments confirms that, while diatoms were not grazed significantly at that time, phytoflagellates were (D. Scavia and G. L. Fahnenstiel, unpubl. data).

Diatom sedimentation

The epilimnetic total Si depletion rate ($0.35 \pm 0.02 \mu\text{M}\cdot\text{d}^{-1}$ between 23 May and 5 July 1984; Fig. 7) estimates downward flux of epilimnetic diatom production. Diatom Si flux, determined from counts of trap-collected viable cells and cell size measurements converted to Si, integrated over the same period is $0.20 \mu\text{M}\cdot\text{d}^{-1}$. Comparison with total Si loss rate suggests that a substantial portion (43%) of the flux was due to nonliving diatoms. This is consistent with the fact that our calculated diatom Si concentration from epilimnetic samples accounts for only 23–37% of measured biogenic Si. Flux of nonliving diatoms and diatom fragments also contributed substantially to biogenic Si flux in Grand Traverse Bay in northern Lake Michigan (Glover 1982). Nonliving cells and fragments in the surface waters (0–40 m) there accounted for 45.5% of biogenic Si.

Spring-summer Si balance

Compared with sedimentation and production rates, allochthonous Si load is low (approximately $0.002 \mu\text{M}\cdot\text{d}^{-1}$; Parker et al. 1977a). Biogenic Si dissolution rate is also slow (approximately $0.007 \mu\text{M}\cdot\text{d}^{-1}$), assuming a recycle rate of $90\%\cdot\text{yr}^{-1}$ (Conway et al. 1977) and mean particulate Si concentration of $3.0 \mu\text{M}$. This means that on a seasonal time scale we can represent epilimnetic Si dynamics as a balance among diatom production, sedimentation, and grazing losses (Fig. 8).

Epilimnetic diatom Si (DSi) dynamics can be represented by the following simple model:

$$(1) \quad \Delta\text{DSi}/\Delta t = \text{Production} - \text{sedimentation} - \text{grazing}.$$

Comparison of diatom sedimentation ($0.20 \mu\text{M}\cdot\text{d}^{-1}$) and production ($0.25 \mu\text{M}\cdot\text{d}^{-1}$) rates demonstrates that over 80% of particulate Si formation rate is accounted for by sediment trap collection of viable cells over the period 21 May to 5 July 1984, a conclusion we came to previously (Scavia and Fahnenstiel 1987). Net rate of change of DSi (left-hand side of equation 1), calculated from the rate of change in diatom concentration between 21 May and 5 July, is $-0.013 \mu\text{M}\cdot\text{d}^{-1}$. Grazing loss, estimated from the first three terms in equation 1, represents Si flux from diatoms to zooplankton of $0.063 \mu\text{M}\cdot\text{d}^{-1}$.

The difference between total Si depletion ($0.35 \mu\text{M}\cdot\text{d}^{-1}$) and diatom Si sedimentation ($0.20 \mu\text{M}\cdot\text{d}^{-1}$) represents sedimentation of nonliving diatoms and cell fragments ($0.15 \mu\text{M}\cdot\text{d}^{-1}$). Because only about $0.063 \mu\text{M}\cdot\text{d}^{-1}$ can be accounted for by contemporary production of Si in feces, the remaining $0.087 \mu\text{M}\cdot\text{d}^{-1}$ comes from dead cells. One source of these dead cells may be concurrent nonpredatory mortality. The flux of nonliving Si represents approximately 35% of the production rate. While crude, this estimate of nonpredatory diatom mortality is similar to that suggested from a C balance for the entire algal community (Scavia and Fahnenstiel 1987); however, in that pre-

vious balance we were also unable to make a statistically significant argument for the process. It is also likely that the sedimenting material is older Si resuspended during winter and early spring, as Eadie et al. (1984) and Chambers and Eadie (1981) have suggested for other particulate material. The mechanism could be similar to that described for plutonium and its association with autogenetically produced particles (Wahlgren et al. 1980). To see if this is reasonable, we compare the required mass of resuspended Si with that determined from full water column balances calculated by Conway et al. (1977) for the same region. Our estimated epilimnetic flux of nonliving Si is $0.087 \mu\text{M}\cdot\text{d}^{-1}$. That flux rate maintained over the 45-d period of our analysis indicates a total concentration initially available for sedimentation of $3.92 \mu\text{M}$. If that represents the concentration of resuspended material spread uniformly throughout the 100-m water column prior to stratification, then $392 \text{ mmol}\cdot\text{m}^{-2}$ would have to have been resuspended. Conway et al. (1977) estimated the winter maximum of reactive plus amorphous Si to be approximately $1.3 \text{ mol}\cdot\text{m}^{-2}$. That value decreases dramatically during spring and summer due to diatom production and sedimentation, but then increases in fall due to dissolution and resuspension. By November, 90% of the original Si has been returned to the water column, with 15% of it still in particulate form. That 15% represents $195 \text{ mmol}\cdot\text{m}^{-2}$. If we assume that the rest of the material is resuspended between November and the following spring (total 25%), then the resuspended particulate Si would be $325 \text{ mmol}\cdot\text{m}^{-2}$, a value not unlike our calculated requirement of $392 \text{ mmol}\cdot\text{m}^{-2}$; however, nonpredatory mortality may play a role as well.

Conclusion

We have combined nutrient fluxes estimated from changes in concentration to various plankton processes determined in vitro during the same study and come to the following conclusions regarding plankton-nutrient processes in southern Lake Michigan. Epilimnetic dissolved inorganic N depletion, compared with total phytoplankton demand, suggests that about 44% of the N demand is recycled. Epilimnetic diatom production, calculated from soluble Si depletion, is a relatively small fraction (<20%) of total primary production, even when diatoms dominate. Sedimentation of epilimnetic diatom Si, compared with total Si depletion, suggests that a large portion (approximately 43%) of epilimnetic particulate Si sedimentation is due to nonliving diatoms. Some simple budgets suggest further that a large portion of that dead Si is resuspended.

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