SILICA REGENERATION PROCESSES IN NEARSHORE SOUTHERN LAKE MICHIGAN

Michael A. Quigley and John A. Robbins

U.S. Department of Commerce
National Oceanic and Atmospheric Administration
Great Lakes Environmental Research Laboratory
2300 Washtenaw Avenue
Ann Arbor, Michigan 48104

ABSTRACT. The seasonal depletion of dissolved silica to levels that limit diatom production is particularly critical in Lake Michigan's nearshore zone where diatom biomass is greatest, and where silica regeneration from sediments is not well-understood. In our study, intact, medium-fine sand cores, collected from an 11 m deep site in nearshore Lake Michigan during July-August 1980, released soluble reactive silica (SRS) at a mean rate of 2,707 ± 122 (SE) µg Si cm^{-2} yr^{-1} when incubated in darkness and at 12°C. This measured SRS release was greater than a diffusive flux (270 ± 49 (90% C.I.) µg Si cm^{-2} yr^{-1}) estimated from SRS pore water profiles and physical sediment properties. SRS release from individual cores was not correlated with abundance of most macroinvertebrates (chironomids, pisidiid clams, or oligochaetes). However, a significant (P < 0.05) and inverse relationship between SRS release and Pontoporeia hoyi *densities implied that amphipods suppressed SRS release through mixing and burial of a surficial floc layer, where most dissolution of biogenic silica occurs. Moreover, SRS release rates measured from our coarse-grained nearshore sediments were comparable to rates reported for fine-grained offshore material and further implicate dissolution of surficial biogenic silica as the source of remineralized SRS. Because nearshore areas of Lake Michigan undergo strong seasonal variations in temperature and diatom production, and because significant riverine silica inputs exist, we cannot extrapolate our results on a lakewide, or season-long basis. The data, however, strongly imply that nearshore sediments are an important participant in the Lake Michigan silica cycle.*
ADDITIONAL INDEX WORDS: Diatoms, lake sediments, sediment-water interface, cores, coastal waters.

INTRODUCTION

Recent changes in Lake Michigan phytoplankton communities include a decline in the overall dominance of diatom species and a concomitant increase in populations of green and blue-green algae (Schelske and Stoermer 1971). This species shift has been attributed to elevated phosphorus loading, which triggered an initial increase in diatom abundance. Thereafter, supplies of dissolved silica in the trophogenic zone were depleted to a level that limited further diatom growth. This, coupled with greater availability of phosphorus, led to increases in green and blue-green algal populations (Schelske and Stoermer 1972, Schelske et al. 1983). This observed shift in the Lake Michi-

gan phytoplankton community, from one limited entirely by phosphorus to one now partially limited by silica availability, underscores the need for a more thorough understanding of lakewide silica cycling processes.

To date, studies examining silica flux between sediments and overlying waters of the Great Lakes have been generally confined to profundal areas (Robbins 1980, Parker *et al.* 1977, Nriagu 1978, Johnson and Eisenreich 1979, Robbins *et al.* 1975). The present study examined dissolved (soluble reactive) silica (SRS) flux from nearshore sediments into overlying waters. Our objectives included (1) measurement of SRS flux across the sediment-water interface in the nearshore of south-

eastern Lake Michigan; (2) estimation of vertical concentration profiles of SRS in sediment pore waters; (3) evaluation of the importance of Fickian diffusion in overall SRS release from sediments; (4) assessment of the relative importance of SRS flux from nearshore sediments within a lakewide silica budget; and (5) examination of possible roles of animal-sediment interactions in SRS release. Previous work (Tessenow 1964, Ferrante and Parker 1977, Graneli 1979, Rippey 1983) has implicated benthic macroinvertebrates in enhanced SRS release from sediments.

METHODS

The Study Site

Samples were collected during July 1980 at an 11-m-deep site located 1.0 km offshore and 5.5 km NNW of the mouth of the Grand River in southeastern Lake Michigan (86°17′00″ W Long., 43°06′18″ N Lat., Fig. 1). Sediments consisted of well-sorted medium-fine beach sand having a median particle size of 1.90 ϕ (270 μm). Seasonal
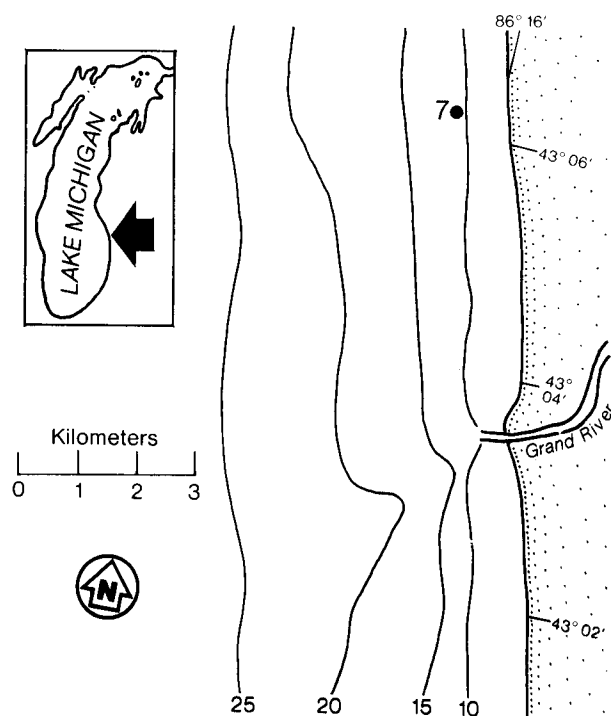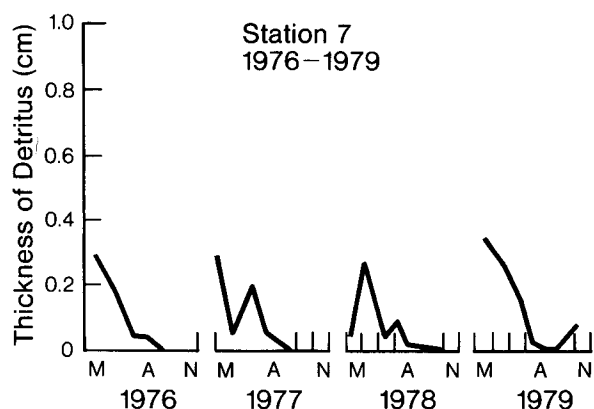

FIG. 2. *Seasonal occurrence of detrital floc layer depth (cm) at study site, 1976–1979 (redrawn from Nalepa and Robertson 1981).*

occurrence of a thin surficial detrital floc layer of clay-silt sized particles (Fig. 2) at the site has been previously described (Nalepa and Robertson 1981). Ripple marks and irregular bottom contours were noted during sediment sampling operations.

Sediment Porosity

Porosity data were obtained from 18 hand-collected, intact (5.0-cm diameter) sediment cores taken during May-October 1979. Cores were immediately frozen and later extruded and sectioned at 1-cm intervals. Wet weight and dry weight following 24 hours of drying at 60°C were used to calculate porosity (modified method of Berner 1971). Percent water by weight was converted to percent water by volume (porosity) by assuming a sediment particle density of 2.6 g mL^{-1} for quartz grains.

Soluble Reactive Silica Determinations

SRS concentrations were measured colormetrically with the silico-molybdate method (American Public Health Association 1979) after passing water samples through pre-rinsed 0.45-μm (Millipore HA) membrane filters. SRS concentrations are expressed as μg silicon (Si) per unit volume.

Vertical SRS Profiles in Pore Water

Profiles of SRS concentrations in pore waters over a 0 to 6-cm sediment depth range were obtained through on-site deployment of two sediment peepers (after Hesslein 1976). Each sampler had a series of five compartments containing filtered lake water separated from surrounding sediments by a

FIG. 1. *Location of study site (Station 7) in nearshore southeastern Lake Michigan. Depth contours are in meters.*

0.45 μm polycarbonate filter membrane. Peepers were installed on 18 July and recovered on 8 September 1980 (53-day deployment interval). The SRS concentration in water above the sediment-water interface was determined from water collected 2 to 3 cm above sediments with a 50-mL syringe immediately before core collection and/or peeper deployment/retrieval operations on 18 and 27 July and 8 September (two replicates per date).

Core Collection and Incubation

On 18 and 27 July, 16 intact cores were collected by divers and transported to a dockside laboratory where they were maintained in a dark environmental chamber at a temperature of 12°C. Core tubes were 4.5 cm in diameter with an overall 30-cm length. During coring, tubes were inserted to a 10-cm depth and then stoppered at both ends. Air was bubbled through overlying water to promote mixing and to prevent any vertical SRS gradient from forming. The turbulence created by air emerging from the tube orifice 2 to 3 cm above the sediment surface did not result in sediment resuspension. The presumption of this experimental arrangement is that turbulent regimes in the nearshore environment do not allow a stagnant layer to exist. Aeration also maintained dissolved oxygen in overlying water at levels greater than 90% saturation. Cores showing evidence of water leakage were not included in SRS flux determinations.

SRS Flux Determination

SRS flux from sediments to overlying water was determined by periodic monitoring of SRS accumulation in overlying water. Water was sampled at 0, 4, 8, 16, 24, 48, and 168 hours following core collection.

Macroinvertebrate Enumeration

After completion of SRS flux determinations, cores were preserved in 10% buffered formalin. Animals and detritus were later separated by flotation in sugar solution and sieving (250-μm pore size; method of Nalepa and Quigley 1980). Major macroinvertebrate groups were separated and counted in a white enamel pan without magnification. Biomass of resident oligochaete worm communities was determined by extrapolating overall length to weight (T. F. Nalepa, personal communication, Great Lakes Environmental Research Laboratory, 1983).

RESULTS

Sediment Porosity

Figure 3 shows an exponential decline in sediment porosity with depth. Mean porosities ranged from 50.21 ± (SD) 19.35% in the uppermost (0 to 1 cm) layer to a constant value of 31.45 ± (SD) 2.86% at depths of 6.5 cm and below.
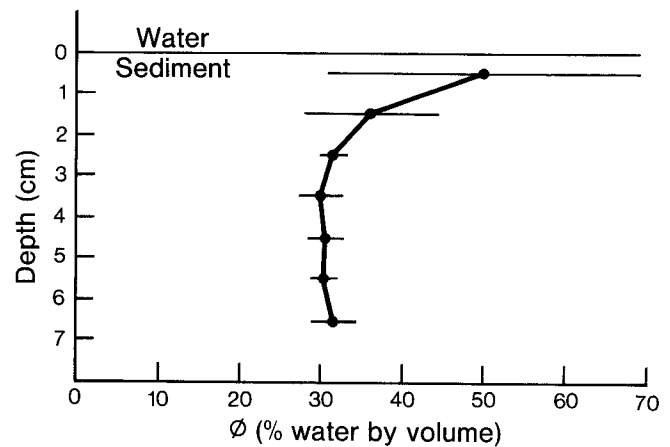

FIG. 3. Mean sediment porosity (ϕ) (±SD) versus depth (cm) below sediment-water interface from 18 cores collected at study site from May-October 1979 (six sampling dates, three cores per date).

Vertical SRS Profiles in Pore Water

SRS concentrations in pore water exhibited an initial exponential increase with depth and then approached a constant value below 3 cm (Fig. 4). The overall shape of the profile was similar to curves described elsewhere for SRS profiles in Great Lakes sediments (Robbins 1980, Nriagu 1978).

SRS Flux from Sediments

Because test cores had a closed volume of overlying water, an increase in SRS concentration was expected to lead eventually to a reduced SRS gradient across the sediment-water interface and to a decline in SRS flux out of sediments. Given this potential increase in SRS concentration of overlying water to artificially high levels, we chose to use flux values calculated over a 24-hour interval to obtain the least biased estimates of actual SRS release in the nearshore zone, where water movement and mixing would prevent accumulation of
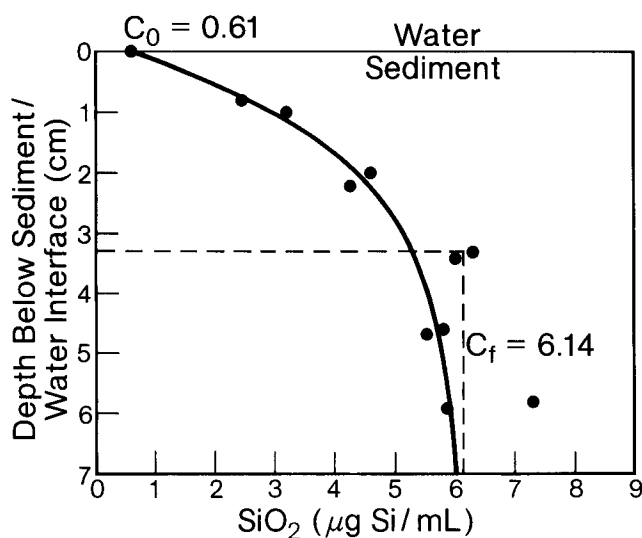
FIG. 4. SRS concentration (μg Si cm^{-2} yr^{-1}) versus depth (cm) below the sediment-water interface for pore waters at the study site. The curve represents a regression fitted to data by least squares method (Zar 1974).

SRS levels approaching those noted during prolonged core incubation. Andrews (1980) also used and recommended a 24-hour incubation interval in determining dissolved silica flux from marine sediments.

During the first 24 hours of core incubation, SRS concentrations in overlying water of cores increased by an average of 0.43 mg Si L^{-1} in experiments on 18 July (from an initial 0.45 mg Si L^{-1} to 0.88). In tests on 27 July, mean increase in SRS concentration was 0.41 mg Si L^{-1} (from an initial 0.76 mg Si L^{-1} to 1.17 mg Si L^{-1} 24 hours later).

Our (24-hour) SRS flux measurements in samples collected on 18 and 27 July produced means of 2,718 $\pm$ (SE) 150 (n = 13) and 2,698 $\pm$ (SE) 89 (n = 16) μg Si cm^{-2} yr^{-1}, respectively. Because these two SRS flux estimates were not significantly different [T test (P < 0.05), Zar 1974], flux values from the two dates were pooled, giving a grand mean of 2,707 $\pm$ (SE) 122 (n = 29).

Calculation of Diffusive SRS Flux

The expected diffusive SRS flux from pore waters into overlying water, F, was calculated by including porosity and SRS vertical concentration profile data within a simple diffusion equation (Fick 1855, Lerman 1979) in which

$$F(\mu g\ cm^{-2}\ yr^{-1}) = -\phi\ \frac{D}{\theta^2}\ \frac{\partial C}{\partial z}\bigg|_{z=0} \quad (1)$$

where D (217 cm^{-2} yr^{-1}) is the diffusion coefficient of SiO_2 in free (freshwater) solution corrected for temperature (12°C) (Robbins 1980, Li and Gregory 1974),

ϕ (0.50) is the porosity of the uppermost 1-cm sediment layer, and

θ is a tortuosity term that depends on size, shape, and packing of sediment particles, although its relations to porosity are not well understood. Tortuosity is mathematically defined by Berner (1980) as: $\theta = dL/dx$, where dL is the actual sinuous diffusion path over a depth interval dx. Since L $\geq$ x, $\theta \leq 1$. Moreover:

$$\theta^2 = \phi F$$

where F = ϕ^{-n}.

For sands, Archie (1942) empirically determined an n of 1.3 and thus, $\theta = 1.11$

$\frac{\partial C}{\partial z}\big|_{z=0}$ is the SRS concentration gradient at the sediment-water interface (z = 0).

The SRS gradient was estimated through a least squares fit of an exponential decay equation, Eq. (2) (Fig. 4) to the vertical concentration profile (Tzur 1971, Robbins 1980).

$$C_z = [C_o - C_f]e^{-\beta z} + C_f \quad (2)$$

where C_z is the SRS concentration (μg Si mL^{-1}) in pore water at depth z and

C_o is the mean SRS concentration (0.61 $\pm$ (SE) 0.16 mg Si L^{-1}) measured in overlying water collected at the sediment-water interface on 18 and 27 July and 8 September.

C_f, the maximum asymptotic SRS concentration approached in pore waters of deeper sediment layers, was obtained by averaging all SRS concentrations for pore water below a 3.3-cm depth (Fig. 4) where SRS concentrations in pore waters approached an upper limit. The resulting C_f was 6.14 $\pm$ (SE) 0.60 μg Si mL^{-1}.

β is the slope of a regression of ln $[C_z - C_f]$ versus depth z. The two terms in the regression were derived from a natural log transformation of both sides of Eq. (2). The regression produced an estimate of β equal to 0.554 cm^{-1}. A significant (P <

0.05) correlation coefficient (r) of 0.98 showed a good fit of the regression equation to the data (Fig. 4). Through differentiation;

$$\frac{\partial C}{\partial z}\bigg|_{z=0} = \beta(C_f - C_o) = 3.06 \ \mu g \ Si \ cm^{-4}$$

Calculation of a 90% confidence interval (Meyer 1975) indicated that β varied by ± 0.10. Consequently, $\partial C/\partial z$ can be expected to vary by ± 0.56 μg Si cm^{-4}. Combining this estimate of the SRS concentration gradient with other terms in Eq. (1) yielded a predicted SRS diffusive flux of 270 $\pm$ 49 (90% C.I.) μg Si cm^{-2} yr^{-1}.

Macroinvertebrate Abundance and SRS Flux

Results of comparisons of macroinvertebrate abundance with measured SRS release from sediment cores are shown in Table 1. Numbers of the amphipod *Pontoporeia hoyi* were inversely related to magnitude of SRS flux in cores collected on both July dates. Because the regression lines from the two dates were not significantly different, data from both were pooled within an overall regression (Fig. 5).

DISCUSSION

Predicted Versus Measured SRS Flux Values

The SRS flux predicted by our Fickian diffusion equation (270 $\pm$ 49 μg Si cm^{-2} yr^{-1}) was far smaller than the fluxes we measured during core incubation [2,707 $\pm$ (SE) 122 μg Si cm^{-2} yr^{-1}]. Large differences between predicted and measured SRS release rates from Great Lake sediments have been attributed previously to silica dissolution reactions at the sediment-water interface (Table 2) (Robbins
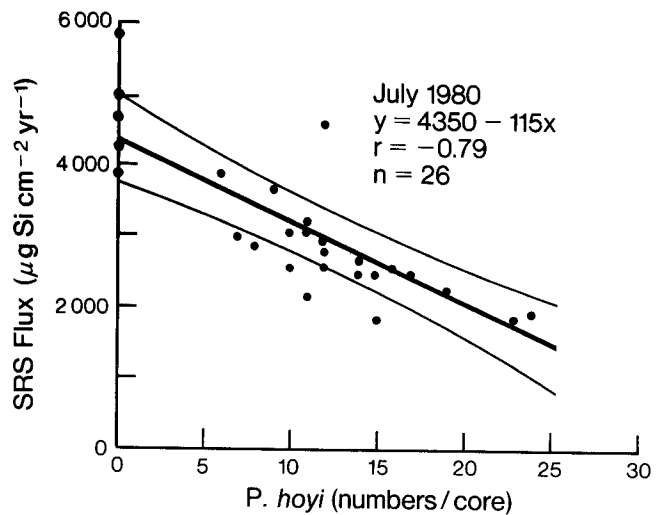

FIG. 5. Pontoporeia hoyi *abundance plotted against SRS flux* (μg Si cm^{-2} yr^{-1}) *measured in individual test cores. Regression line includes 95% confidence limits.*

1980, 1984). Because Fickian diffusion equations used in these studies did not account for surficial reactions, the models should underestimate SRS flux if surficial reactions are extensive.

In the Lake Michigan nearshore, a surficial floc layer of silt/clay-sized particles may constitute a major source of SRS regenerated from sediment. At our sampling site, a 1 to 2-mm layer of this material was noted in cores during July sampling. Floc is also abundant in the nearshore during spring and summer (Nalepa and Robertson 1981, Fig. 2). It is easily resuspended, forming a high-turbidity zone that extends 5 or more meters above the bottom (Chambers and Eadie 1980). Recent sediment trap data (Schelske *et al.* 1984) have also shown the floc to be rich in biogenic silica (6.5% Si by dry weight). Moreover, data on biogenic silica

TABLE 1. Linear correlation coefficients (r) from comparison of macroinvertebrate abundance and/or biomass with SRS measured in individual test cores after 24 hours of incubation. Abundance and biomass means are listed at lower end of table.

Date	n	Amphipods (P. hoyi)	Chironomids	Pisidiid clams	Oligochaetes Abundance	Oligochaetes Biomass
18 July 1980	10	-0.78*	0.06	0.57	-0.01	-0.04
27 July 1980	16	-0.75*	-0.09	-0.36	-0.20	-0.15
18, 27 July 1980	26	-0.79*	-0.12	0.18	-0.15	-0.31
Mean abundance or biomass (pooled)		5,476 m^{-2}	661 m^{-2}	569 m^{-2}	5,370 m^{-2}	0.66 g m^{-2}
(SE) (pooled)		(641)	(110)	(118)	(651)	(0.7)

*Linear correlation coefficient (r) was significant (P < 0.05).

TABLE 2. SRS fluxes measured from Great Lakes sediments. Left side of table contains values measured by monitoring direct SRS release from cores. Right side lists flux values predicted from SRS porewater gradients using Fickian diffusion equation.

	SRS Flux (μg Si cm^{-2} yr^{-1})						
	Direct Measurement (Release from Cores)			Indirect Measurement (From Pore Water Gradients)			
Lake	n	Value	Range	n	Value	Range	Reference
Erie	13	2,500 ($\bar{x}$)	(700–4,800)				K. M. Remmert[1], J. A. Robbins, and D. N. Edgington[2] (pers. comm. 1977)
Central Basin					875 ± 87	(SD)	J. B. Fisher[3] (pers. comm. 1982)
Central Basin		2,500					Robbins and Edgington (1979)
Eastern Basin		1,600					
Western Basin		4,800					
Huron	9	1,200 ($\bar{x}$)	(580–2,030)				K.M. Remmert[1], J. A. Robbins, and D. N. Edgington[2] (pers. comm. 1977)
Saginaw Bay	48	3,013 ($\bar{x}$)	(1,463–5,335)	1	660		Robbins (1984)
Southern				4	1,065 ± 217	(SE)	Robbins (1980)
Michigan	4	1,630 ($\bar{x}$)	(1,180–2,300)				K. M. Remmert[1], J. A. Robbins, and D. N. Edgington[2] (pers. comm. 1977)
				2	1,120 ± 180	(SE)	Robbins (unpubl.)
	29	2,707 ± 122	(SE)		270 ± 49	(90% C.I.)	Present Study
Ontario				4	173 ± 23	(SE) (121–229)	Nriagu (1978)
Superior				6	276 ± 161	(SD) (115–437)	Johnson and Eisenreich (1979)

[1]Great Lakes Research Division, The University of Michigan, Ann Arbor, Michigan 48109.

[2]Center for Great Lakes Studies, University of Wisconsin-Milwaukee, Milwaukee, Wisconsin 53217.

[3]Research Center, Amoco Production Company, Tulsa, Oklahoma 74102.

distribution in sediments at our study site indicate that the floc's presence within the uppermost 0 to 1-cm layer may contribute to higher amounts of biogenic silica for this region (Fig. 6). In summary, the dissolution of the biogenic silica fraction of a surficial floc layer appears to be the primary route of SRS release from nearshore sediments. Although some diffusion of SRS from deeper sediment layers probably occurs, our data indicate that only about 10% of the measured SRS flux can be attributed to this process.

The importance of surficial reactions has also been demonstrated for silty clay sediments of Lake Huron's Saginaw Bay (Robbins 1984). For these sediments, SRS release rate varied strongly with temperature according to the Arrhenius equation (Tinoco *et al.* 1978). Rippey (1983) observed a similar relationship between temperature and SRS release from sediments of Lough Neagh, Northern Ireland.

Experimental Artifacts

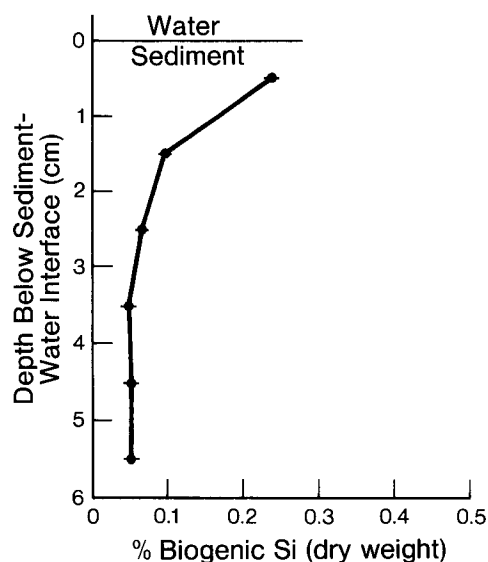There is much uncertainty as to the degree to which laboratory flux measurements reflect actual *in situ*

FIG. 6. Percent biogenic silica (dry weight as Si) versus depth (cm) below the sediment-water inteface. Means ± SD are shown. Biogenic silica was determined by method of DeMaster (1981).

fluxes at the sediment-water interface. Unfortunately, few investigations have compared laboratory and *in situ* flux values. For dissolved silica, Andrews (1980) found close agreement between laboratory and *in situ* fluxes out of marine sediments.

Although we did not determine *in situ* fluxes in our study, we did take precautions to ensure that flux values from our core incubation studies validly represented *in situ* release rates from nearshore Lake Michigan sediments. The use of a short-term (24-hour) incubation period for intact cores prevented excessive SRS accumulation in overlying water and guaranteed that the SRS gradient across the sediment-water interface was comparable to that actually existing in the nearshore (see Results).

Ripple marks and irregular contours at our study site indicated that wave and current activity was an important process in the nearshore region. Although the nearshore is largely a nondepositional area, the presence of detrital floc at the sediment-water interface in cores collected during spring and summer demonstrates that this material is temporarily deposited on the nearshore bottom before subsequent erosion and transport down the shelf later in the year (Nalepa and Robertson 1981, Eadie *et al.* 1979). Certainly the confinement and incubation of intact sediment within core tubes eliminated the physical effects of wave and current action, except for gentle aeration and mixing of overlying water in cores. However, we believe that the direct effects of wave and current stirring on SRS flux are important only during storm events, when water movement is sufficient to resuspend most of the floc layer. The persistent presence of the floc layer and the fact that this material is easily resuspended (Chambers and Eadie 1980) are evidence that wave and current activity is generally low and that the current regime at the sediment-water interface is probably similar to conditions in our test cores.

Influence of the Grand River

Because our sampling site was close to the mouth of the Grand River, the river's potential influence on SRS flux from sediments in the nearshore zone must be considered. The Grand River, the largest tributary flowing directly into Lake Michigan, has a noticeable plume at its mouth that is generally 10 km² or less in area, with a spatial configuration that is determined largely by prevailing winds

(Chambers and Eadie 1980, Eadie *et al.* 1979). The average prevailing winds of the region are from the southwest and tend to drive the plume north. The major southern Lake Michigan gyre produces strong northward currents along the eastern shore and increased movement of both water and suspended matter (Pickett *et al.* 1983). Moreover, high loading rates of biogenic and total silica have been noted for the Grand River and several other large tributaries that empty into southeastern Lake Michigan (Schelske *et al.* 1980). Such loading may cause higher abundance of biogenic silica in southeastern Lake Michigan than in other areas of the Lake (Schelske *et al.* 1984). The greater abundance of biogenic silica could, in turn, produce a higher SRS flux from nearshore sediments along the eastern shore as riverborne silica is carried into the lake. However, our measured SRS flux from the Lake Michigan nearshore zone was comparable to rates measured elsewhere in the Great Lakes (Table 2). Also, fluxes based on pore water silica gradients were generally lower at this nearshore site than at offshore sites.

In light of the wide seasonal variation of both temperature and diatom production in nearshore areas (Schelske *et al.* 197), and given silica loading by the Grand River and other tributaries on southeastern Lake Michigan (Schelske *et al.* 1980), we are uncertain about how well our data represent SRS flux from sediments throughout the nearshore zone. In spite of this uncertainty, it is useful to view our nearshore results within the context of an overall silica budget.

Depth contour and sediment mapping by Cahill (1981) indicate that sand sediments at depths of 40 m or less compose 29.4% (1.7×10^4 km²) of the overall Lake Michigan bottom (5.8×10^4 cm²). Multiplication of the above area of the nearshore zone by our mean flux of 2,707 μg Si cm^{-2} yr^{-1} produces an annual SRS input of 4.6×10^8 kg Si, or 8.0 g Si m^{-2} yr^{-1}. Calculations by Parker *et al.* (1977) relied upon data from several sources for estimating that offshore diatom production required 53 g Si m^{-2} yr^{-1}. Annual watershed input was estimated to be 1.7 g Si m^{-2} yr^{-1} (or 3% of the annual silica requirement). By comparison, our estimated 8.0 g Si m^{-2} yr^{-1} value for the nearshore zone represents 15% of the total annual silica requirement of offshore diatom production. The proportion of SRS derived from nearshore sediments that reaches offshore diatom communities is unknown. The bulk of nearshore SRS flux is probably bound up in this region where diatom biomass

is greater (Vollenweider et al. 1974, Nalewajko 1967).

Although a portion of the SRS released from nearshore sediments is derived from tributary-supplied silica sources, the magnitude of this flux and the size of the nearshore zone indicate that silica cycling processes within this zone warrant inclusion in lakewide silica budgets. Furthermore, nearshore areas represent the sole source of SRS released from sediments during summer months because thermal stratification often prevents SRS released from deepwater sediments from entering the epilimnion and most of the euphotic zone. Only during periods of overturn or upwelling can SRS derived from profundal sediments cross the thermocline and replenish depleted silica supplies in the epilimnion (Schelske and Stoermer 1971, Schelske et al. 1971).

Macroinvertebrate Abundance and SRS Flux

Correlation analysis (Table 1) revealed that abundance of one of the most common invertebrates (Pontoporeia hoyi, Amphipoda) was significantly and inversely related to SRS flux. The regression of P. hoyi abundance and SRS flux from sediments was closely linked to the density of amphipods in individual test cores by a linear inverse relationship (Fig. 5). These results were unexpected because benthic invertebrates have been found to frequently enhance the release of solutes from pore waters into overlying water (Tessenow 1964, Wood 1975, Robbins 1980, Krezoski et al. 1984). Although our results initially appeared to conflict with this previous evidence, examination of P. hoyi habits that modify nearshore sediment properties indicated an explanation of the difference.

Pontoporeia hoyi are surface deposit-feeding scavengers that frequently migrate across the sediment-water interface (Pennak 1978, Mundie 1959) and mix particles to depths of 1.5 to 2.0 cm in a simple eddy-diffusive manner while feeding and burrowing (Robbins et al. 1979). In studies using radiolabeled material, such mixing has resulted in the partial dispersion of a surficial sediment layer to a maximum (1.5 cm) depth with an eddy-diffusive coefficient (D_B) of 1.24×10^{-7} cm^2 sec^{-1} (Krezoski et al. 1984). At our study site, 88.4% of the P. hoyi population was located in the upper 1-cm layer of sediment (Nalepa and Robertson 1981). Concentration of amphipods in this

layer further implies that burrowing and mixing is greatest in this region.

In addition, we would expect rates of eddy-diffusive mixing to be greater than, or equal to, rates reported by Krezoski et al. (1984) because P. hoyi densities in our test cores were 17% greater than their densities and because we did not directly handle individual Pontoporeia. Smith (1972) observed subsequent mortality of Pontoporeia following handling and Krezoski et al. (1984) noted a decline in sediment mixing at 250 hours that may have been related to such mortality. They recommended that handling of Pontoporeia be avoided as much as possible prior to any microcosm research. Because we used intact cores, individual amphipods were never handled and we observed no mortality during the 24-hour incubation period. In situations where solute concentrations in pore waters are high, enhanced diffusion caused by Pontoporeia burrowing can increase the flux of solute out of sediment by as much as 70% (Krezoski et al. 1984). In our study, low porosity of sand and low SRS concentration in pore water greatly reduced the role of diffusion as a pathway of SRS release.

If dissolution of biogenic silica in the detrital floc at the sediment-water interface accounts for most of the SRS flux, SRS release should be greatest when the floc remains at the sediment-water interface, where direct contact with overlying water is maximized. Eddy-diffusive mixing of topmost sediments by P. hoyi, however, will result in partial burial of the floc and an expected overall decline in SRS flux. Because a portion of the floc has been transported deeper into sediments, lowered diffusion and a reduced gradient between SRS concentration of pore water and biogenic silica will retard further silica dissolution. Such activity would explain the inverse relationship between P. hoyi density and measured SRS flux in individual test cores.

In addition to mixing of sediment, Pontoporeia may alter sediment texture through selective particle feeding. Substrate preference experiments (Marzolf 1965) have shown that Pontoporeia selected substrates having a surficial layer of organic matter. Gut analysis also revealed that the amphipods ingested diatom frustules that passed through the gut without being destroyed. Moreover, Ankar (1977) noted that Pontoporeia affinis ingested particles smaller than 60 μm.

In the upper 1 to 2-cm layer of our nearshore sediment, Pontoporeia feeding habits may consti-

tute a sorting mechanism that selectively concentrates material (including frustules) within fecal pellets. Packaging of frustules in this manner, combined with eddy-diffusive burial, should slow dissolution of frustules at the sediment-water interface and reduce SRS release from sediments. If these mechanisms operate throughout Lake Michigan's nearshore zone, they should slow overall SRS flux from this region. We further expect that biogenic silica buried in the upper layers of sediment (where *Pontoporeia* are most numerous and active) will eventually dissolve and diffuse out of sediments. The overall effect of amphipod activity may be to reduce the rate of SRS release, but it may also extend this release over a longer period. This extended pattern of release may be particularly significant in late summer and fall when most or all of the surficial floc layer has been eroded from the nearshore zone and transported offshore. In Lake Michigan, where seasonal SRS depletion limits diatom growth, a dampening of SRS release from sediments may have an important impact on primary production, particularly in nearshore regions.

REFERENCES

American Public Health Association. 1979. *Standard methods for the examination of water and wastewater, including bottom sediment and sludges*. Washington, D.C.: American Public Health Association.

Andrews, D. 1980. The prediction and measurement of dissolved silicate flux across marine sediments. Ph.D. dissertation, Dalhousie University, Halifax, Nova Scotia.

Ankar, S. 1977. *The soft bottom ecosystem of the northern Baltic proper with special reference to the macrofauna*. University of Stockholm, Asko Laboratory, Contribution number 19, Stockholm, Sweden.

Archie, G. E. 1942. The electrical resistivity log as an aid in determining some reservoir characteristics. *Am. Inst. Mech. Eng. Trans.* 146:54–61.

Berner, R. A. 1971. *Principles of Chemical Sedimentology*. New York: McGraw-Hill.

————. 1980. *Early Diagenesis*. Princeton, New Jersey: Princeton University Press.

Cahill, R. A. 1981. *Geochemistry of Lake Michigan Sediments*. Illinois State Geol. Survey., Circular number 517, Champaign, Illinois.

Chambers, R. L., and Eadie, B. J. 1980. *Nearshore chemistry in the vicinity of the Grand River, Michigan*. U.S. Department of Commerce, NOAA Technical Memorandum ERL GLERL-28, Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan.

DeMaster, D.J. 1981. The supply and accumulation of silica in the marine environment. *Geochim. Cosmochim. Acta* 45:1715–1732.

Eadie, B. J., Chambers, R. L. Malczyk, J. M., and Langston, A. 1979. *The effect of the Grand River spring runoff on Lake Michigan*. Pollution From Land Use Activities Group Task D, Subactivity 3-1, Special International Joint Commission PLUARG Report, International Joint Commission.

Ferrante, J. G., and Parker, J. I. 1977. Transport of diatom frustules by copepod fecal pellets to the sediments of Lake Michigan. *Limnol. Oceanogr.* 22:92–97.

Fick, A. 1855. Ueber Diffusion. *Ann. Phys.* (Leipzig) 170:59–86.

Graneli, W. 1979. The influence of *Chironomus plumosus* on the exchange of dissolved substances between sediment and water. *Hydrobiologia* 66:149–159.

Hesslein, R. H. 1976. An *in situ* sampler for close interval pore water studies. *Limnol. Oceanogr.* 21:912–914.

Johnson, T. C., and Eisenreich, S. J. 1979. Silica in Lake Superior: Mass balance considerations and a model for dynamic response to eutrophication. *Geochim. Cosmochim. Acta* 43:77–91.

Krezoski, J. R., Robbins, J. A., and White, D. S. 1984. Dual radiotracer measurement of zoobenthos-mediated solute and particle transport in freshwater sediments. *J. Geophys. Res.* 89:7937–7947.

Lerman, A. 1979. *Geochemical Processes: Water and Sediment Environments*. New York: John Wiley and & Sons.

Li, Y. H. and Gregory, S. 1974. Diffusion of ions in sea water and in deep sea sediments. *Geochim. Cosmochim. Acta* 38:703–714.

Marzolf, G. R. 1965. Substrate relations of the burrowing amphipod *Pontoporeia affinis* in Lake Michigan. *Ecolog* 46:579–591.

Meyer, S. L. 1975. *Data Analysis of Scientists and Engineers*. John Wiley and Sons, New York.

Mundie, J. H. 1959. The diurnal activity of the larger invertebrates at the surface of Lac la Ronge, Sas-

katchewan. *Can. J. Zool.* 37:945-956.

Nalepa, T. F., and Quigley, M. A. 1980. *The macro- and meiobenthos of southeastern Lake Michigan near the mouth of the Grand River 1976-77.* U.S. Department of Commerce, NOAA Data Report ERL GLERL17, Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan.

_____ , and Robertson, A. 1981. Vertical distribution of the zoobenthos in southeastern Lake Michigan with evidence of seasonal variation. *Freshwater Biol.* 11:87-96.

Nalewajko, C. 1967. Phytoplankton distribution in Lake Ontario. In *Proceedings of the 19th Conf. Great Lakes Res.,* pp. 63-69. Internat. Assoc. Great Lakes Res.

Nriagu, J. O. 1978. Dissolved silica in pore waters of Lake Ontario, Erie, and Superior sediments. *Limnol. Oceanogr.* 23:53-67.

Parker, J. I., Conway, H. L., and Yaguchi, E. M. 1977. Dissolution of diatom frustules and recycling of amorphous silicon in Lake Michigan. *J. Fish. Res. Board Can.* 34:545-551.

Pennak, R. W. 1978. *Freshwater Invertebrates of the United States.* New York: John Wiley and Sons.

Pickett, R. L., Campbell, J. E., and Clites, A. H. 1983. Satellite-tracked current drifters in Lake Michigan. *J. Great Lakes Res.* 9:106-108.

Rippey, B. 1983. A laboratory study of the silicon release process from a lake sediment (Lough Neagh, Northern Ireland). *Arch. Hydrobiol.* 96:417-433.

Robbins, J. A. 1980. *Sediments of southern Lake Huron: Elemental composition and accumulation rates.* U.S. Environmental Protection Agency, Report number 600/3-80-080, Environmental Research Laboratory, Duluth, Minnesota.

_____ . 1984. *Sediments of Saginaw Bay, Lake Huron: Elemental composition and accumulation rates.* Special Report No. 102, Univ. of Michigan, Great Lakes Research Div., Ann Arbor, Michigan.

_____ , and Edgington, D. N. 1979. Release of dissolved silica from sediments of Lake Erie. Abstracts, p. 19, *22nd Conf. Great Lakes Res.,* Internat. Assoc. Great Lakes Res.

_____ , McCall, P.L.,Fisher, J. B., and Krezoski, J. R. 1979. Effects of deposit feeding on migration of ^{137}Cs in lake sediments. *Earth Planet. Sci. Lett.* 42:277-287.

Schelske, C. L., and Stoermer, E. F. 1971. Eutrophication, silica depletion, and predicted changes in algal quality of Lake Michigan. *Science* 173:423-424.

_____ . 1972. Phosphorus, silica, and eutrophication in Lake Michigan. In *Nutrients and Eutrophication: The Limiting Nutrient Controversy.* Ed. G. E. Likens, Spec. Symp. ASLO 1:157-171.

_____ , Stoermer, E. F., and Feldt, L. E. 1971. Nutrients, phytoplankton productivity, and species composition as influenced by upwelling in Lake Michigan. In *Proceedings of the 14th Conf. Great Lakes Res.,* pp. 102-113. Internat. Assoc. Great Lakes Res.

_____ , Feldt,L. E., and Simmons, M. S. 1980. *Phytoplankton and physical-chemical conditions in selected rivers and the coastal zone of Lake Michigan 1972.* University of Michigan, Great Lakes Research Division Publication number 19, Ann Arbor, Michigan.

_____ , Stoermer, E. F., Conley, D. J., Robbins, J. A., and Glover, R. M. 1983. Early eutrophication of the lower Great Lakes: New evidence from biogenic silica in sediments. *Science* 22:320-322.

Smith, W. E. 1972. Culture, reproduction, and temperature tolerance of *Pontoporeia affinis* in the laboratory. *Trans. Am. Fish. Soc.* 101:253-256.

Tessenow, U. 1964. Experimentaluntersuchungen zur Kieselsaureruckfuhrung aus dem schlamm der see durch chironomidenlarven (*Plumosus*-Gruppe). *Arch. Hydrobiol.* 60:497-504.

Tinoco, I., Jr. Saver, K., and Wang, J. C. 1978. *Physical Chemistry; Principles and Applications in Biological Sciences.* Prentice-Hall Inc., Englewood Cliffs, New Jersey.

Tzur, Y. 1971. Interstitial diffusion and advection of solute in accumulating sediments. *J. Geophys. Res.* 76:4208-4211.

Vollenweider, R. A., Munawar, M., and Stadelmann, P. 1974. A comparative review of phytoplankton and primary production in the Laurentian Great Lakes. *J. Fish. Res. Board Can.* 31:79-762.

Wood, L. W. 1975. Role of oligochaetes in the circulation of water and solutes across the mud-water interface. *Verh. Internat. Verein. Limnol.* 19:1530-1538.

Zar, J. H. 1974. *Biostatistical Analysis.* Englewood Cliffs: Prentice-Hall, New Jersey.