Seasonal sedimentation trends in a mesotrophic lake: Influence of diatoms and implications for phosphorus dynamics

DAVID POISTER[1,*] and DAVID E. ARMSTRONG[2]
[1]*Departments of Chemistry and Environmental Science, St. Norbert College, 100 Grant St., De Pere, WI 54115, USA;* [2]*Environmental Chemistry and Technology Program and Department of Civil and Environmental Engineering, University of Wisconsin, 660 North Park Street, Madison, WI 53706, USA; *Author for correspondence (e-mail: david.poister@snc.edu; phone: (920)403-3185; fax: (920)403-4033)*

Abstract. To quantify the extent to which biomass and phosphorus in particular is removed from an aquatic system via sedimentation as well as to identify factors that influence sedimentation of nutrient elements, various characterizations of suspended and settling particulate matter were made in Trout Lake, Wisconsin, USA. The proportion of water column phosphorus reaching sediment traps showed a seasonal component with a minimum during late summer. Biogenic silicon analysis indicated that relatively high rates of phosphorus removal were associated with the sedimentation of siliceous algae (diatoms) from the water column. Estimates of the impact of nutrient removal through diatom sedimentation indicate that this process can reduce primary production by decreasing the amount of nutrient remineralization in the water column during the stratified period.

Introduction

Sedimentation is a key biogeochemical process in aquatic systems and has received attention from scientists studying both freshwater and marine environments. Sedimentation limits the supply of material available for regeneration of biologically available nutrient elements in the water column, the main source of nutrients to primary producers in many aquatic systems (Bloesch et al. 1977; Caraco et al. 1992; Poister et al. 1994). Thus, the sedimentation of nutrient elements such as phosphorus and nitrogen that limit production are of particular interest. Sedimentation also initiates the permanent removal of material from aquatic systems via sediment burial. Thus, sedimentation is important in marine systems where it plays a role in the global cycling of important elements such as carbon (Slengenthaler and Sarmiento 1993; Arrigo et al. 1999). In addition, sedimentation can play a role in the community composition of the food web by influencing phytoplankton succession (Reynolds et al. 1982; Reynolds and Wiseman 1982).

Researchers have examined various factors that can influence sedimentation. Variables shown to affect the nature and settling velocity of sedimenting particles

include: chemical conditions relating to precipitation and coagulation (Boehm and Grant 1998; Hodell and Schelske 1998; Shafer and Armstrong 1991), the vertical distribution of primary production (Hurley and Garrison 1993), the creation of discrete fecal pellets by zooplankton (Butler and Dam 1994; Elser et al. 1995; Sarnelle 1999), and the size distribution of water column particles (Guy et al. 1994; Larocque et al. 1996). Phytoplankton community composition may also influence sedimenting particles. In particular, diatoms have a greater density than most other phytoplankton and may contribute disproportionally to the pool of sedimenting particles (Reynolds and Wiseman 1982; Wassman et al. 1996; Tallberg and Heiskanen 1998). In addition, certain diatoms have the ability to respond rapidly to turbulence and repopulate the water column with actively growing cells from resting stages in sediments (Reynolds 1984). Thus, periods of overturn can coincide with diatom blooms and subsequent sedimentation events.

A variable of particular importance to understanding biogeochemical cycles is the amount of particles reaching sediments relative to the amount of particulate matter being created through photosynthesis, often referred to as the export coefficient. Studies of this aspect of sedimentation have led to conflicting conclusions. Many models that consider sedimentation calculate the export coefficient based on primary production and depth (Suess 1980; Pace et al. 1987). The assumption that sedimentation is a fixed proportion of primary production is supported by research using sediment traps in both marine and freshwater systems of varying trophic status (Baines and Pace 1994; Tartari and Biasci 1997; Heiskanen and Tallberg 1999). However, other studies indicate that sedimentation is not a constant proportion of primary production and that the nature of the particles being created and water column conditions should be considered (Boyd and Newton 1995; Larocque et al. 1996).

Poister et al. (1994) compared the rate of primary production to the sedimentation rate in three north temperate lakes. In one system, Trout Lake, seasonal changes in the sedimentation rate were the opposite of changes in the rate of primary production, yielding higher export coefficients in spring and fall with more rapid water column recycling of nutrients in the summer. This paper presents data that supports the hypothesis that such seasonal sedimentation trends in Trout Lake are due to the presence of rapidly sinking diatoms. These data suggest that the taxonomic composition of the phytoplankton community can have a significant impact on the cycling of nutrient elements in aquatic systems.

Methods

All samples were collected during the 1993 ice-free season at Trout Lake, a mesotrophic, softwater lake located in Vilas County, Wisconsin, USA. The lake has an average annual mid-lake production based on ^{14}C uptake measurements of 569 mg C $\times$ m^{-2} $\times$ day^{-1} (Adams et al. 1993), a surface area of 11 km^2, a total volume of 0.16 km^3, and a maximum depth of 35.7 m. Trout Lake receives surface water in-
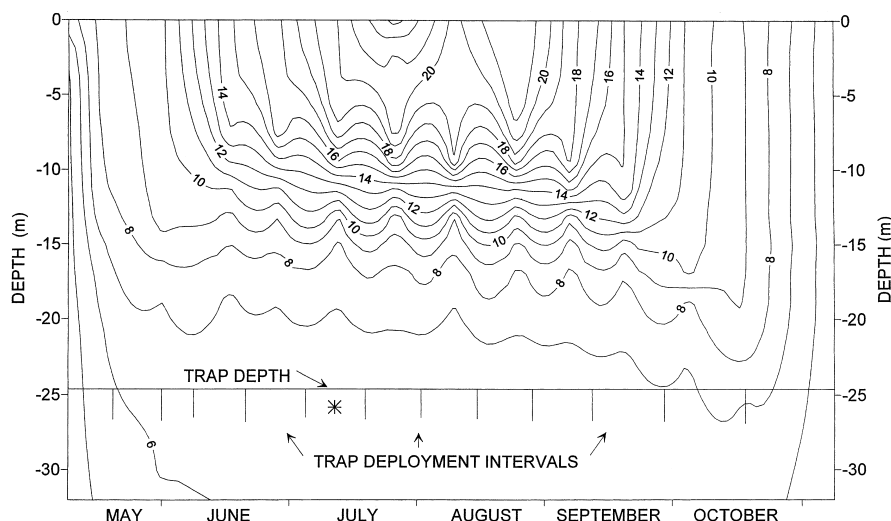
Figure 1. Water column temperature (Celsius) during the 1993 ice-free season. Based on temperature profiles collected every two weeks at 1 m intervals. Also shown, location and duration of sediment trap deployment. (* = traps not recovered from this interval).

put from four small tributaries and is drained by one outflowing stream. The lake is divided into two basins. All samples were collected at the deepest point in the southern basin, the larger and deeper of the two. In 1993, Trout Lake had a completely mixed water column starting at ice-out in early May until the onset of stratification at the beginning of June (Figure 1). The lake remained stratified until fall mixis at the end of October.

Water column samples were collected from 4 depths throughout the water column at approximately 2 week intervals during the ice-free season. Samples for total particulate P (PP), particulate biogenic Si (PBSi), and total particulate matter (TPM) where pumped directly from the lake through opaque tubing onto filters contained in opaque filter holders to minimize exposure to light and air. TPM and PBSi samples were collected on a preweighed 0.4 μm pore size, 47 mm diameter polycarbonate filters. PP samples were collected on 0.45 μm pore size, 47 mm cellulose acetate filters that had been acid washed in 1 N HCl. The filtrate was collected in preweighed plastic bottles to determine the volume of lake water filtered. Whole water samples were also preserved in Lugol's solution for future microscopic examination.

Duplicate sediment traps were deployed at the sampling location for approximately two week intervals to collect sedimenting particles. Each cylindrical trap was constructed of a clear acrylic tube with a conical bottom which funneled particles into a detachable plastic bottle. Traps had a collection area of 165 cm^2 and an aspect ratio of 4:1. Each trap contained an ampule of 0.2 g NaN$_3$ poison to retard microbial decomposition during sample collection while minimizing swimmer poisoning (Lee et al. 1992). Traps were deployed on an anchored line and held up-

right by attachment to a buoy positioned 1 m below the water surface. Traps were deployed approximately 12 m above the sediment surface to minimize the effect of resuspended benthic sediments on material collected.

Sediment trap samples consisted of all the solid material funneled into the detachable bottle during the deployment interval. Subsamples of material from each trap were filtered onto a preweighed 0.4 μm pore size polycarbonate filter and subsequently used to determine mass and PBSi. A subsample from each size fraction was preserved in Lugol's solution for visual examination. The remaining trap material was freeze-dried and used for total P analysis.

The rate of particle sedimentation ($mg \times m^{-2} \times day^{-1}$) was calculated by dividing the total mass of particles collected in a given trap by the collection area (165 cm^2) and the duration of trap deployment. The rate of PBSi and PP sedimentation were calculated by multiplying the concentration of these components in sediment trap particles (e.g., mg P/mg particles) by the mass sedimentation rate. The determination of PBSi and PP concentration in sediment trap material and water column particles is described below.

PBSi analysis was based on the method of DeMaster (1981). Sediment trap and water column particles collected on polycarbonate filters were digested in 10% ultrapure Na_2CO_3 at 85 °C for two hours. Digested samples were cooled, neutralized with 2 N HCl, and filtered through a 0.4 μm pore size nylon syringe filter. Reactive silicon concentration was then measured in an appropriate subsample of the filtrate (Strickland and Parsons 1972). Samples from duplicate sediment traps were on average 16% different with respect to PBSi concentration (μg Si/mg particles).

Total P was determined by digestion of 10–20 mg of solid trap material (or the cellulose acetate filter for water column PP) with perchloric/nitric acid (Sommers and Nelson 1972). The cellulose acetate filter completely dissolved during the digestion. Phosphate concentration in the digest was determined by molybdate blue determination of phosphate concentration (Murphy and Riley 1962). The precision and accuracy of this procedure is described elsewhere (Poister 1992).

Results

Water column particulates

Trends in the concentration of total particulate matter (TPM) are typical for mesotrophic lakes in the region (Figure 2). An initial peak in particulate matter in mid-May reflects the spring bloom of phytoplankton, typically indicating the response of primary producers to increased light and nutrient levels in the recently thawed and mixed lake. The spring TPM maximum consists largely of autochthonous particles as reflected by a corresponding peak in chlorophyll concentration at the same time and depth (Poister et al. 1999). A second increase in particulate matter occurs in the epilimnion of the lake in August. These two periods of high TPM concentration are separated by a minimum in June, a period when zooplankton
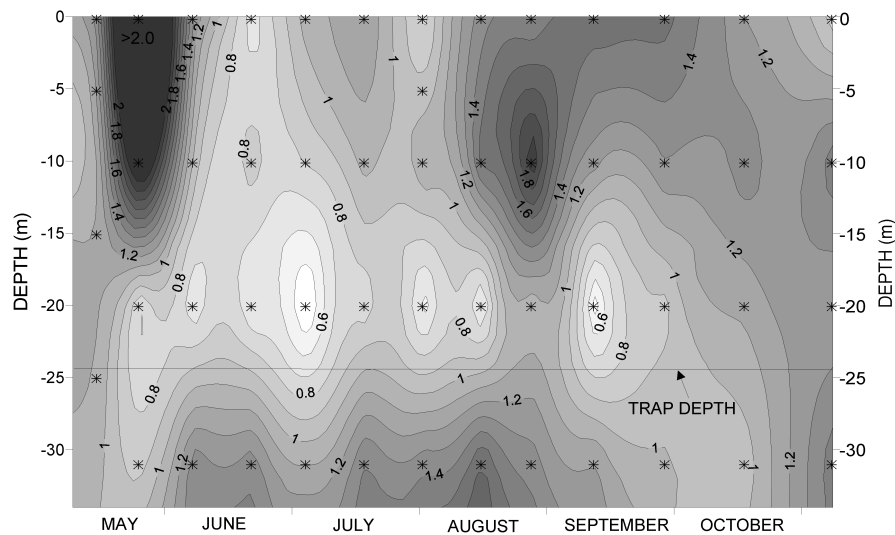
Figure 2. Total particulate matter (TPM) concentration (mg/L) in Trout Lake during the 1993 ice-free season. * = sampling point.

grazing likely diminished the standing stock of particulate matter. Pigment concentrations indicate that water column particles in the spring maximum consisted mostly of chrysophytes while the particles formed during the stratified period contained more cryptophytes and chlorophytes (Poister 1995).

PBSi analysis was performed to assess the relative abundance and distribution of siliceous algae such as diatoms in the water column (Figure 3). With the exception of the clear-water phase in June, PBSi concentrations were highest in the spring and first half of the summer. Again, this result is typical for lakes of this type where diatoms tend to flourish in the nutrient rich and turbulent environment early in the season. A comparison of Figures 2 and 3 indicates that the May TPM peak had a higher proportion of diatoms relative to the summer TPM peak in August and September. This interpretation is confirmed by similar trends in the concentration of the diatom pigment fucoxanthin measured at the same time (Poister 1995). Interestingly, PBSi concentrations return to spring levels during the final sampling day in November following the fall mixis that occurred at the end of October (Figure 1). Increased diatom production at fall overturn may be related to resuspension and subsequent rejuvenation of previously sedimented meroplanktonic diatom cells from near the sediment – water interface (Schelske et al. 1995).

Sedimentation

Figure 4 shows the rate of particle deposition into sediment traps deployed in Trout Lake. The mass sedimentation rate gradually decreases from a spring high and reaches a minimum prior to the fall overturn of the water column. The final sedi-
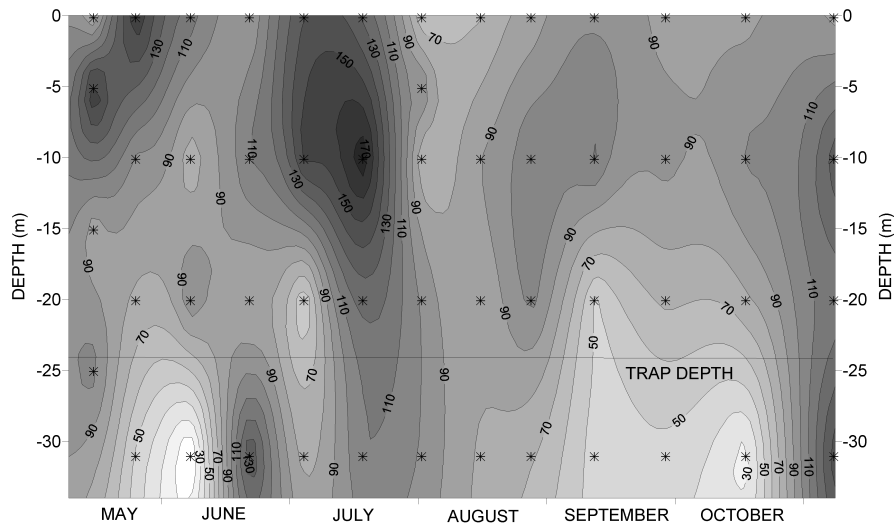
Figure 3. Particulate biogenic silica (PBSi) concentration (μg/L) in Trout Lake during the 1993 ice-free season. * = sampling point.
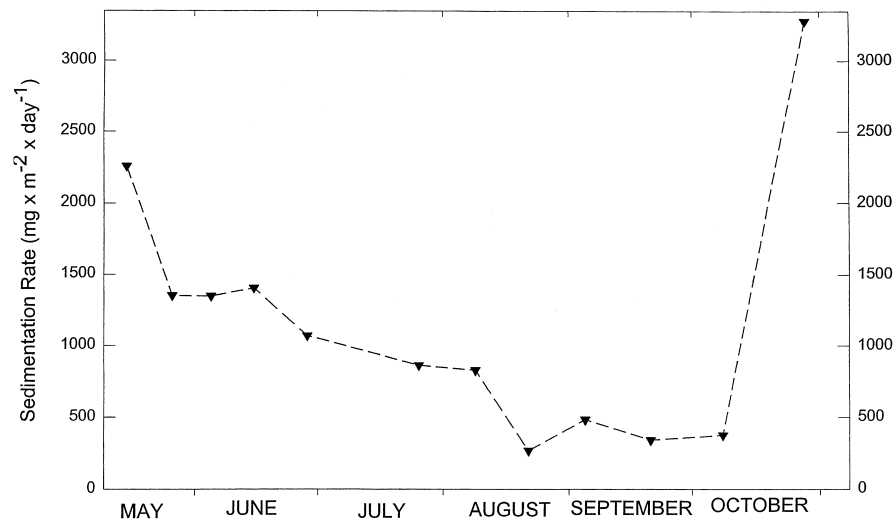

Figure 4. Mass sedimentation rate in Trout Lake during the 1993 ice-free season. Average of duplicate sediment traps.

ment trap deployment interval showed a marked increase in the sedimentation rate and corresponds to the fall overturn of the water column (Figure 1).

Various factors influence the sedimentation rate as measured by sediment traps under certain conditions. These factors can compromise the use of sediment traps as a tool for measuring the sedimentation of autochthonous particles. Resuspension of deposited sediments and the influx of allochthonous particles into the water col-

umn have been shown to increase the sedimentation rate in lakes (Bloesch 1995; Effler et al. 2001). In Trout Lake, these processes may influence sediment trap measurements when the water column is mixed and in the spring when surface water input is greatest. Since water column TPM concentrations did not increase uniformly throughout the water column or preferentially closer to the sediment water interface during spring mixis (Figure 2) it is unlikely that these processes had a significant impact on sediment trap measurements in the spring. However, given the gradual increase in TPM concentration throughout the stratified period at the 31 m sampling point relative to other depths and the increase in TPM and PBSi throughout the water column during fall mixis, it is possible that the increase in sedimentation during the final trap deployment interval in the fall is partially attributable to redeposition of previously deposited sediments.

Sediment traps can overestimate the sedimentation rate when deployed in turbulent environments (Kozerski 1994). If energy from wind-induced turbulence was transferred from the lake surface to the depth of trap deployment, sediment traps in Trout Lake could have overtrapped particles. Since this scenario is most likely during the spring and fall mixed periods, the influence of overtrapping may have increased estimates on the sedimentation rates during the initial and final trap deployment intervals.

A comparison of the mass sedimentation rate (Figure 4) to the concentration of particles available for sedimentation in the water column (Figure 2) indicates that sedimentation is not a constant proportion of water column particles in Trout Lake. In fact, the minimum in the rate of particle sedimentation (August through October) corresponds to a period of relatively high concentration of particles in the water column.

A temporal trend similar to that observed for TPM exists when the concentration of particulate water column P is compared to the P sedimentation rate. Figure 5 shows seasonal trends in P flux to sediment traps similar to trends in the mass sedimentation rate. P sedimentation does not vary in concert with the amount of P available for sedimentation from the water column expressed as areal particulate P (PP) concentration. Areal PP concentration is calculated by averaging PP concentrations determined at the three water column sampling points above the depth of trap deployment (see Figure 2). The concentration of PP in the water column rises in August and September while the sedimentation rate of P is at the lowest point of the season.

Differential sedimentation of material on a seasonal basis has implications for the internal nutrient cycles of lakes. Delivering nutrient elements to the sediments in spring and early summer to some extent limits their availability to phytoplankton in the photic zone during the stratified period, thus limiting productivity.

To examine the impact of seasonal P sedimentation, a P export ratio was calculated for each trap deployment interval. The export ratio was calculated by dividing the rate of P sedimentation by the areal concentration of particulate phosphorus above the trap on the first day of the deployment interval then multiplying this ratio by 100. In several instances, PP was not measured on the same day the trap deployment interval began. In these cases, the water column concentration of PP
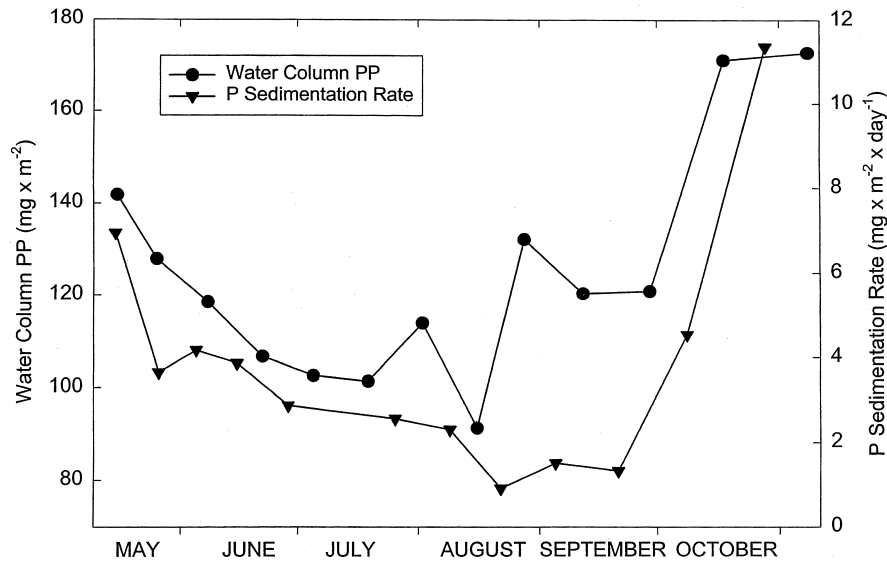
Figure 5. Areal PP concentration in the water column above the depth of trap deployment (24 meters) and the P sedimentation rate in Trout Lake.

was estimated for that day assuming a linear change from the two closest data points. Calculated in this manner, the P export ratio can be used to assess seasonal trends in the proportion of water column P available for sedimentation that is actually removed from the water column.

Figure 6 displays the seasonal aspect of nutrient removal in Trout Lake as indicated by the P export ratio. In spring and early summer, when diatoms are abundant, the proportion of P removed via sedimentation is greater than during the remainder of the stratified period. This proportion increases during fall mixis when diatoms become more abundant once again as evidence by increases in the concentration of PBSi (Figure 2) and fucoxanthin (Poister 1995). Figure 6 also displays the sedimentation rate of PBSi. The fact that the sedimentation rate of PBSi (an indicator of diatom abundance) varies in concert with the export coefficient of phosphorus supports the contention that the sedimentation of siliceous algae can affect the rate of nutrient sedimentation in lakes. In 1993 the P export ratio and the PBSi sedimentation rate were positively correlated ($r^2 = 0.73$, $p = 0.0004$). Visual examination confirmed that diatoms, particularly a species of *Aulacoseira*, were a major component of trap material early in the ice-free season (Poister et al. 1999). Sediment trap material did not contain any discernable zooplankton fecal pellets, a component of sedimenting particles that can contribute to seasonal sedimentation trends.
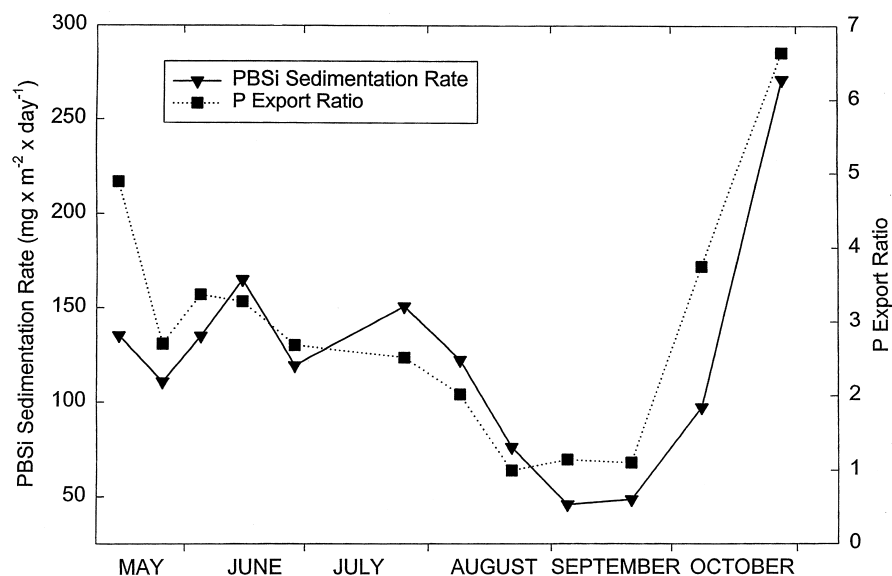
Figure 6. PBSi sedimentation rate and P export ratio (P sedimentation: water column PP × 100) in Trout Lake.

Discussion

Possible implications of diatom associated P sedimentation

Diatom sedimentation may reduce primary production in P limited lakes. The potential impact of diatom-associated P sedimentation is elucidated using Trout Lake data. The average P sedimentation rate in Trout Lake in September, 1993 was 1.2 mg × m^{-2} × day^{-1}. PBSi sedimentation data suggest that during this period, diatom sedimentation is at a minimum. Thus, September P sedimentation represents P sedimentation minimally affected by diatoms. Subtracting non-diatom associated P sedimentation from the sedimentation rate throughout the remainder of the ice-free season yields an estimate of diatom associated P sedimentation. Assuming non-diatom associated P sedimentation estimated from September data remains constant throughout the ice-free season, estimated diatom associated P sedimentation accounts for the removal of 470 mg P × m^{-2}, 72% of the total P flux to sediment traps during the ice-free season.

Poister (1992) estimated that P incorporation by primary producers occurred at a rate of 10.6 mg P × m^{-2} × day^{-1} during the stratified period and that new soluble reactive phosphorus added to Trout Lake would be used approximately 7 times before permanent loss from the system. Thus, if the diatom-associated P had not sedimented out of the photic zone of Trout Lake, P reuse would give an effective increase in P available to primary producers of 3100 mg P/m^2. If this extra P were completely taken up by phytoplankton during the 190 day ice-free season, average

P incorporation by primary producers would increase by 16 mg P $\times$ m^{-2} $\times$ day^{-1} to nearly 27 mg P $\times$ m^{-2} $\times$ day^{-1}. If diatom-associated P had not been removed via sedimentation in Trout Lake 1993, these estimates predict that primary production could have more than doubled.

It is important to note that sedimentation as assessed by sediment trap deployment does not represent permanent removal of nutrient elements from the system. P can be remobilized into the water column by recycling at the sediment surface throughout the stratified period and by resuspension of previously deposited particles during spring and fall overturn (Roden and Edmonds 1997; Shafer and Armstrong 1994). Ultimately, only a percentage of the total P deposited onto sediments throughout the year is buried. However, any factor that increases the rate of P sedimentation will decrease nutrient availability to primary producers by decreasing the amount of P available for nutrient regeneration in the water column. This is particularly true for diatom sedimentation which is most likely to occur in the spring and early summer and will thus limit P availability to epilemnetic phytoplankton throughout the stratified period.

Diatom associated P sedimentation may represent an important feedback mechanism to buffer the response of a lake to increased phosphorus input. If diatom production and consequently, diatom sedimentation, increases with increased nutrient input, diatoms may mitigate the effects of nutrient input on primary production by increasing nutrient sedimentation seasonally. Lake Michigan is an example of a system that may have been influenced by this feedback loop. Silica analysis of sediment cores from southern Lake Michigan revealed that diatom sedimentation has been increasing since the 1940s, possibly as a result of increased P loading (Schelske et al. 1983). Data from Trout Lake suggest that diatom sedimentation can decrease the availability of nutrients to the photic zone of aquatic systems. Thus, in Lake Michigan, the increase in production due to nutrient loading was likely lessened by increased diatom sedimentation. However, as diatoms became more abundant, dissolved reactive silica became depleted (Schelske and Stoermer 1971) which limited the duration of the summer bloom of diatoms (Conway et al. 1977; Parker et al. 1977). Once Si rather than P limited the growth of diatoms in Lake Michigan, increased P loading would not have resulted in increased diatom sedimentation. At that point, the importance of diatom sedimentation in mitigating effects of increased P loading on primary production would decrease. The point at which a resource other than P limits diatom production is the break point for the feedback loop between increased diatom sedimentation and increased P loading. It is likely that a similar break point has also been reached in the lower Great Lakes where diatoms are even more severly Si limited those in than Lake Michigan (Schelske et al. 1986).

Lake Michigan also illustrates the importance of the seasonal aspect of diatom associated nutrient sedimentation as it relates to nutrient availability and primary productivity in aquatic systems. In Lake Michigan, much of the nutrient material removed from the water column via sedimentation is eventually regenerated at the sediment-water interface (Shafer and Armstrong 1994). However, P released from sediments is isolated in both space and time from summer nutrient demand created

by primary production. Availability to the photic zone of P released from the sediment is limited during the summer months due to thermal stratification of the water column. In Lake Michigan, regeneration of previously sedimented P is most important during the winter and spring months when the water column is mixed (Eadie et al. 1984; Brooks and Edgington 1994). Similar to other freshwater systems, Lake Michigan experiences diatom blooms and subsequent sedimentation in spring and early summer (Scavia and Fahnenstiel 1987; Shafer and Armstrong 1991). Thus, by removing P from the water column early in the season in Lake Michigan, diatom sedimentation limits the amount of P available to primary producers from water column regeneration during the remainder of the stratified period.

Conclusion

In Trout Lake in 1993, seasonal changes in the phytoplankton community structure were related to seasonal trends in nutrient cycles with the potential to significantly influence the rate of primary production. Specifically, the presence of siliceous diatoms in the phytoplankton community increased the proportion of particulate P being delivered out of the photic zone. Diatom associated P sedimentation removed the limiting nutrient from the water column and may have effectively cut the rate of primary production in half. In addition, diatom associated P sedimentation may serve as a natural feedback loop to mitigate the effects of increased P loading to aquatic systems on the primary production of that system.

References

Adams M.S., Meinke T.W. and Kratz T.K. 1993. Primary productivity of three Northern Wisconsin Lakes, 1985–1990. Verh. Internat. Verein. Limnol. 25: 406–410.

Arrigo K.R., Robinson D.H., Worthen D.L., Dunbar R.B., Ditullio G.R., VanWoert M. et al. 1999. Phytoplankton community structure and the drawdown of nutrients and CO_2 in the southern ocean. Science 283: 365–367.

Baines S.B. and Pace M.L. 1994. Relationships between suspended particulate matter and sinking flux along a trophic gradient and implications for the fate of planktonic primary production. Can. J. Fish. Aquat. Sci. 51: 25–36.

Bloesch J. 1995. Mechanisms, measurement and importance of sediment resuspension in lakes. Mar. Freshwater Res. 46: 295–304.

Bloesch J., Stadelmann P. and Bührer H. 1977. Primary production, mineralization, and sedimentation in the euphotic zone of two Swiss lakes. Limnol. Oceanogr. 22: 511–526.

Boehm A.B. and Grant S.B. 1998. Influence of coagulation, sedimentation, and grazing by zooplankton on phytoplankton aggregate distributions in aquatic systems. J. of Geophys. Res. 103: 15,601–15,612.

Boyd P. and Newton P. 1995. Evidence of the potiential influence of planktonic community structure on the interannual variability of particulate organic carbon flux. Deep-Sea Res. 42: 619–639.

Brooks A.S. and Edgington D.N. 1994. Biogeochemical control of phosphorus cycling and primary production in Lake Michigan. Limnol. Oceanogr. 39: 961–968.

Butler M. and Dam H.G. 1994. Production rates and characteristics of fecal pellets of the copepod *Arcatia tonsa* under simulated phytoplankton bloom conditions: implications for vertical flux. Mar. Ecol. Prog. Ser. 114: 81–91.

Caraco N.F., Cole J.J. and Likens G.E. 1992. New and recycled primary production in an oligotrophic lake: Insights for summer phosphorus dynamics. Limnol. Oceanogr. 37: 590–602.

Conway H.L., Parker J.I., Yaguchi E.M. and Mellinger D.L. 1977. Biological utilization and regeneration of silicon in Lake Michigan. J. Fish. Res. Board Can. 34: 537–544.

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., Gardner W.S. and Bell G.L. 1984. Sediment trap studies in Lake Michigan: Resuspension and chemical fluxes in the southern basin. J. Great Lakes Res. 10: 307–321.

Effler S.W., Matthews C.M. and Mathews D.A. 2001. Patterns of gross deposition in reservoirs enriched in inorganic tription. Can. J. Fish. Aquat. Sci. 58: 2177–2188.

Elser J.J., Foster D.K. and Hecky R.E. 1995. Effects of zooplankton on sedimentation in pelagic ecosystems: Theory and test in two lakes of the Canadian sheild. Biogeochem. 30: 143–170.

Guy M., Taylor W.D. and Carter J.C.H. 1994. Decline in total phosphorus in the surface waters of lakes during summer stratification, and its relationship to size distribution of particles and sedimentation. Can. J. Fish. Aquat. Sci. 51: 1331–1337.

Heiskanen A. and Tallberg P. 1999. Sedimentation and particulate nutrient dynamics along a coastal gradient from a fjord-like bay to the open sea. Hydrobiol. 393: 127–140.

Hodell D.A. and Schelske C.L. 1998. Production, sedimentation, and isotopic composition of organic matter in Lake Ontario. Limnol. Oceanogr. 43: 200–214.

Hurley J.P. and Garrison P.J. 1993. Composition and sedimentation of aquatic pigments associated with deep plankton in lakes. Can. J. Fish. Aquat. Sci. 50: 2713–2722.

Kozerski H.P. 1994. Possibilities and limitation of sediment traps to measure sedimentation and resuspension. Hydrobiol. 284: 93–100.

Larocque I., Muzumder A., Prouix M., Lean D.R.S. and Pick F.R. 1996. Sedimentation of algae: relationships with biomass and size distribution. Can. J. Fish. Aquat. Sci. 53: 1133–1142.

Lee C., Hedges J.I., Wakeham S.G. and Zhu N. 1992. Effectiveness of various treatments in retarding microbial activity in sediment trap material and their effects on the collection of swimmers. Limnol. Oceanogr. 37: 117–130.

Murphy J. and Riley J.P. 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta. 27: 31–36.

Pace M.L., Knauer G.A., Karl D.M. and Martin J.H. 1987. Primary production, new production and vertical flux in the eastern Pacific Ocean. Nature 325: 803–804.

Parker J.I., Conway H.L. and Yaguchi E.M. 1977. Seasonal periodicity of diatoms and silicon limitation in offshore Lake Michigan, 1975. J. Fish. Res. Board Can. 34: 552–558.

Poister D. 1992. Nutrient Sedimentation and Recycling in Three Northern Temperate Lakes. MSc Thesis, University of Wisconsin, Madison.

Poister D. 1995. Effects of the Community Composition and Vertical Distribution of Phytoplankton on Pigment and Phosphorus Sedimentation in Three Wisconsin Lakes. PhD Thesis, University of Wisconsin, Madison.

Poister D., Armstrong D.E. and Hurley J.P. 1994. A six year record of nutrient element sedimentation and recycling in three north temperate lakes. Can. J. Fish. Aquat. Sci. 51: 2457–2466.

Poister D., Armstrong D.E. and Hurley J.P. 1999. Influences of grazing on temporal patterns of algal pigments in suspended and sedimenting algae in a north temperate lake. Can. J. Fish. Aquat. Sci. 56: 60–69.

Reynolds C.S. 1984. The Ecology of Freshwater Phytoplankton. Cambridge University Press, Cambridge.

Reynolds C.S., Thompson J.M., Ferguson A.J.D. and Wiseman S.W. 1982. Loss processes in the population dynamics of phytoplankton maintained in closed system. J. Plankton Res. 4: 561–600.

Reynolds C.S. and Wiseman S.W. 1982. Sinking losses of phytoplankton in closed limnetic systems. J. Plankton Res. 4: 489–522.

Roden E.E. and Edmonds J.W. 1997. Phosphate mobilization in iron-rich anaerobic sediments: microbial Fe(III) oxide reduction versus iron-sulfide formation. Arch. Hydrobiol. 139: 347–378.

Sarnelle O. 1999. Zooplankton effects on vertical particulate flux: Testable models and experimental results. Limnol. Oceanogr. 44: 357–370.

Scavia D. and Fahnenstiel G.L. 1987. Dynamics of Lake Michigan phytoplankton: Mechanisms controlling epilimnetic communities. J. Great Lakes Res. 13: 103–120.

Schelske C.L., Carrick H.J. and Aldridge F.J. 1995. Can wind-induced resuspension of meroplankton affect phytoplankton dynamics? J. N. Am. Benthol. Soc. 14: 616–630.

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

Schelske C.L., Stoermer E.F., Conley D.J., Robbins J.A. and Glover R.M. 1983. Early eutrophication in the lower Great Lakes: New evidence from biogenic silica in sediments. Science 222: 320–322.

Schelske C.L., Stoermer E.F., Fahnenstiel G.L. and Haiback M. 1986. Phosphorus enrichment, silica utilization, and biogeochemical silica depletion in the Great Lakes. Can. J. Fish. Aquat. Sci. 43: 407–415.

Shafer M.M. and Armstrong D.E. 1991. Trace element cycling in southern Lake Michigan: Role of water column particle components. In: Baker R.A. (ed.), Organic Substances and Sediments in Water. Vol. 2. CRC Press, Boca Raton, Florida, USA.

Shafer M.M. and Armstrong D.E. 1994. Mass fluxes and recycling of phosphorus in Lake Michigan: Role of major particle phases in regulating the annual cycle. In: Baker R.A. (ed.), Environmental Chemistry of Lakes and Reservoirs. Adv. in Chem. Series. American Chemical Society, Washington, DC, USA.

Slengenthaler U. and Sarmiento J.L. 1993. Atmospheric carbon dioxide and the ocean. Nature 365: 119–125.

Sommers L.E. and Nelson D.W. 1972. Determination of total phosphorus in soils: a rapid perchloric acid digestion procedure. Soil Sci. Soc. Amer. Proc. 36: 902–904.

Strickland J.D.H. and Parsons T.R. 1972. A Practical Handbook of Seawater Analysis. Bull. Fish Res. Bd. Can. No. 167. 2nd edn., pp. 65–70.

Suess E. 1980. Particulate organic carbon flux in the oceans – surface productivity and oxygen utilization. Nature 288: 260–263.

Tallberg P. and Heiskanen A. 1998. Species-specific phytoplankton sedimentation in relation to primary production along and inshore-offshore gradient in the Baltic Sea. J. Plankton Res. 20: 2053–2070.

Tartari G. and Biasci G. 1997. Trophic status and lake sedimentaion fluxes. Water, Air and Soil Poll. 99: 523–531.

Wassman P., Egge J.K., Reigstad M. and Aksnes D.L. 1996. Influence of dissolved silicate on vertical flux of particulate biogenic matter. Mar. Poll. Bull. 33: 10–21.