Internal phosphorus loading in Lake Mendota: response to external loads and weather

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Abstract: We quantified summer internal phosphorus (P) loads and all the major P fluxes in Lake Mendota, Wisconsin, a deep stratified eutrophic lake, during two summers of contrasting external loads to determine (*i*) whether internal loading by entrainment (mixing at the thermocline) is a significant part of the epilimnetic P budget and (*ii*) what factors lead to interannual variability in internal loading. We estimated variables for the P budget weekly (standing stock, sedimentation) or daily (outflow, inflow, and entrainment) during a summer of average runoff (1992) and one of higher than average runoff (1993). Entrainment, estimated by calculating the amount of P transported into the epilimnion after the thermocline deepened following storms, was about 10 times higher than external loading during 1992, but was about equal to external loading during 1993. When entrainment was included, the epilimnetic P budget balanced. Interannual variability in internal loading appears to be due to a combination of water column stability, weather, and the P levels accumulated in the metalimnion. External loads to the epilimnion during summer 1993 were much higher than in 1992 (7.0 and 0.9 mg $P \cdot m^{-2} \cdot day^{-1}$, respectively); however, total loads (internal + external) were more similar (12.5 and 7.8 mg $P \cdot m^{-2} \cdot day^{-1}$ in 1993 and 1992, respectively). Although summer chlorophyll concentrations were similar in the two summers, blue-green algal biomass in 1993 was about double that in 1992.

Résumé : Nous avons quantifié les charges internes estivales de phosphore (P) et tous les principaux flux du P dans le lac Mendota, Wisconsin, qui est un lac profond eutrophe stratifié, au cours de deux étés pendant lesquels les charges externes ont contrasté pour déterminer (*i*) si la charge interne par entraînement (mélange au niveau de la thermocline) constitue une partie substantielle du bilan épilimnétique du P et (*ii*) quels facteurs sont responsables de la variabilité interannuelle de la charge interne. Nous avons estimé les variables du bilan du P hebdomadairement (biomasse, sédimentation) ou quotidiennement (flux de sortie, flux d'entrée et entraînement) au cours d'un été où le ruissellement était moyen (1992) et d'un été où le ruissellement était supérieur à la moyenne (1993). L'entraînement, estimé en calculant la quantité de P transportée dans l'épilimnion après que la thermocline s'est enfoncée après des tempêtes, était environ 10 fois plus important que la charge externe en 1992, mais était à peu près égal à cette dernière en 1993. Lorsque l'entraînement était inclus, le bilan du P épilimnétique était équilibré. La variabilité interannuelle de la charge interne semble être due à une combinaison de stabilité de la colonne d'eau, de climat et des concentrations de P accumulées dans le métalimnion. Les charges externes de l'épilimnion au cours de l'été 1993 étaient beaucoup plus élevées qu'en 1992 (7,0 et 0,9 mg $P \cdot m^{-2} \cdot jour^{-1}$, respectivement); toutefois, les charges totales (internes + externes) se ressemblaient davantage (12,5 et 7,8 mg $P \cdot m^{-2} \cdot jour^{-1}$ en 1993 et 1992, respectivement). Bien que les concentrations de chlorophylle estivales étaient semblables au cours des deux étés, la biomasse des algues bleu-vert en 1993 était environ le double de celle de 1992.
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Introduction

Phosphorus (P) loading from diffuse or nonpoint sources continues to be a large source of nutrients to lakes (NRC 1992; Duda 1993). In culturally eutrophied lakes, many years of high nutrient loads may leave a legacy of stored nutrients in lake sediments (Sas 1989; Cooke et al.1993). This internal store of nutrients can take many years to decline, at rates which depend on the morphometry and hydrologic regime of a lake, sediment minerology, and pore water chemistry (Sas 1989). In both shallow and deep lakes, internal nutrient loading acts as a memory of past external loads and is the reason that lakes often fail to respond to nutrient reduction strategies (NRC 1992).

Internal nutrient loading can be especially high in shallow lakes where mixing at the sediment–water interface effectively maintains nutrients in the water; and depending on climate and external nutrient loading conditions, interannual variability of internal loads can be high (Jensen and Andersen 1992; Sondergaard et al. 1993; van der Molen and Boers 1994). In contrast, internal loading to the epilimnion in deep lakes during the summer can be low, because thermal stratification can effectively isolate much of the sediment area from the epilimnion even though nutrients accumulate in the hypolimnion during anoxia. Because hypolimnetic nutrients at the annual scale are mixed throughout the water column during fall and spring overturn, total internal loading in deep lakes can be quite large. In fact, nutrient dynamics in lakes with anoxic hypolimnia have been found to behave differently than lakes with oxic hypolimnia, partly as a result of this internal loading

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(Nürnberg 1984). However, the importance of internal loading that occurs within the summer stratified season alone is not well documented.

Internal loading in stratified lakes during the summer period is complex, difficult to measure, and has only occasionally been quantified directly (Stauffer and Lee 1973; Larsen et al. 1981; Kortmann et al. 1982; Effler et al. 1986; James et al. 1990). This internal loading occurs through two mechanisms: (*i*) release of P from sediments in contact with the epilimnion and (*ii*) turbulent vertical flux across the thermocline when P gradients between the hypolimnion and epilimnion are large (Stauffer and Lee 1973; Kortmann et al. 1982; Effler et al. 1986). In lakes where the epilimnetic volume is large relative to the area of epilimnetic sediments, the first mechanism is minor relative to other fluxes. In such lakes, the thermocline can be a highly dynamic boundary and fluxes across it are potentially large (Stauffer and Lee 1973). Mixing usually results from storms that cause the thermocline to deepen and entrain nutrients from the hypolimnion into the epilimnion. In some lakes, P entrainment into the epilimnion has been shown to be a significant input and has been suggested to exceed external inputs during the summer stratified season (Stauffer and Lee 1973; Larsen et al. 1981; Effler et al. 1986; Stauffer 1987).

At the annual scale, external nutrient loading can be the largest source of nutrients to lakes. In northern temperate climates, most of this loading occurs in winter–spring from a combination of snowmelt and spring runoff, which is strongly driven by weather conditions. In fact, spring runoff or its surrogate, in-lake spring total P (TP), is correlated to average summer algal biomass and in particular, blue-green algal biomass (Lathrop and Carpenter 1992). Nevertheless, variance around these relationships is large (Lathrop and Carpenter 1992; Stow et al. 1997), and consideration of internal loading during the summer may improve predictions. Because few studies have directly measured internal P loads in stratified lakes, it is not known if internal loads contribute a relatively constant source of nutrients year to year or if they vary as widely as external loads do in response to changing weather conditions.

Our objectives in this study were to quantify summer internal P loads and all the major P fluxes in Lake Mendota, a stratified eutrophic lake in Wisconsin, during 2 years of contrasting external loads. Specifically, we wanted to determine (*i*) whether internal loading by entrainment represents a significant part of the lake's epilimnetic P budget and (*ii*) what factors lead to interannual variability in internal loading to the lake.

Methods

Study site

Lake Mendota (3985 ha, 12.7 m mean depth, 25.3 m maximum depth) is a culturally eutrophic lake located in south-central Wisconsin, U.S.A. (43°6′N, 89°24′W). The lake's 600-km^2 watershed is 85% agriculture and 9% urban; the remainder is in forests and wetlands. Since the 1850s, nutrient loadings from the watershed have been high (average annual loading of 0.96 g $P \cdot m^{-2} \cdot year^{-1}$ during the 1970s; Lathrop 1979, 1990), and currently, nutrients deriving from nonpoint agriculture and urban land sources are the dominant external nutrient input to the lake (Lathrop 1979, 1990).

Lake sampling

We measured the following variables to calculate an epilimnetic budget of TP during the summer stratified season for 1992 and 1993 using a mass-balance equation:

$$(1) \qquad dSS_P = Ext + Atm + SedR + Entr - Out - Sed + Res$$

The change in P standing stock (dSS_P) is balanced by inputs from external loading (Ext), dry and wet atmospheric deposition (Atm), release of P from epilimnetic sediments (SedR), entrainment (Entr), and outputs from sedimentation (Sed) and outflow (Out). The residual (Res), representing P that is not accounted for, was calculated by difference. We assumed that entrainment was the dominant process by which P is transported from the hypolimnion to the epilimnion (see below). If other processes were operating, they would appear as the residual in the P-budget equation when entrainment is included (eq. 1). All variables were measured directly except for Atm and SedR, which were estimated from past studies conducted on nearby lakes. The stratified season for 1992 lasted from 9 June to 14 September and for 1993, from 21 June to 13 September.

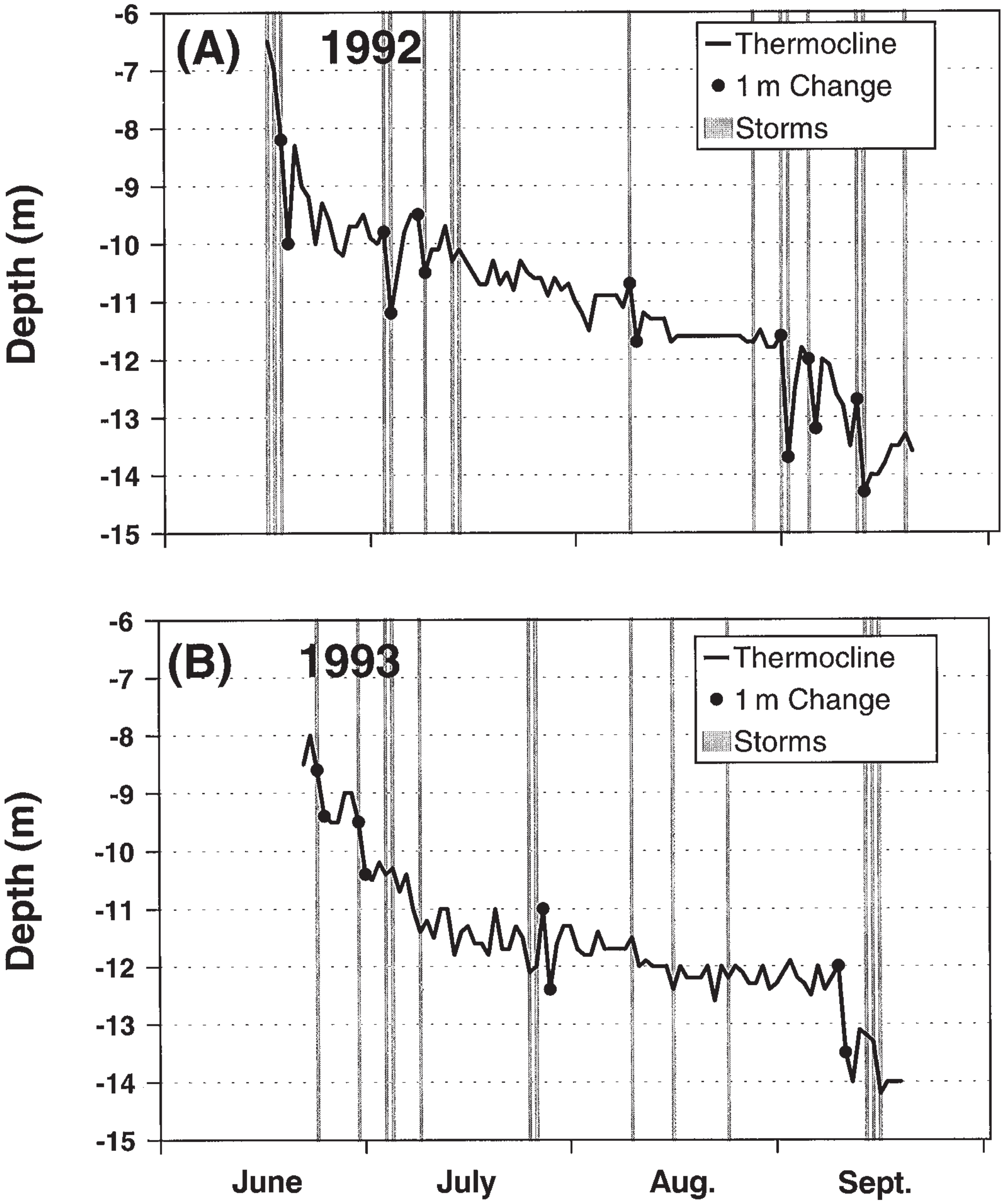
We sampled the lake weekly at the central sampling station located at the deepest part of the lake during the two summers. We collected samples for TP standing stock at six depths every 4 m between 1 and 20 m and also at 22 m. Duplicate sediment traps (three cylinders per trap) were suspended at 22 m and retrieved weekly. Traps were designed with a height to width ratio of 5, and an internal diameter of 5.1 cm (Blomqvist and Kofoed 1981). The three cylinders in each trap were pooled and TP content determined. Daily external loading was calculated from data obtained from continuous flow monitoring stations on two of the five major streams draining into the lake and one of the two main storm sewers connected to the lake (USGS 1994). Total phophous concentrations from storm events and occasionally base flow, were measured from discrete water samples collected using automatic samplers (USGS 1994). The three monitored inflows represent approximately 53% of the TP flowing into the lake (Lathrop 1979). Total phosphorus loading from unmonitored streams was estimated by calculating ratios of TP loading from monitored to unmonitored streams from data for 2 years of complete loading measurements of all the major streams draining into Lake Mendota (Lathrop 1979). Phosphorus loads from the gauged streams and the storm sewer were calculated by direct integration (USGS 1994). Concentrations of P from all inputs and the lake were measured spectrophotometrically by forming phosphomolybdate complexes after persulfate digestion (Strickland and Parsons 1968). Total phosphorus outflow from the Yahara River (the only outflow) was calculated by multiplying daily discharge values (computed from a program that uses the outlet operational records as input and USGS rating equations to calculate total daily discharge) by the average weekly epilimnetic TP concentration measured at the central lake station.

Total chlorophyll and algal biomass was sampled at the central lake station biweekly during both summers from an integrated sample taken from the surface to 8 m. Phytoplankton samples were preserved with glutaraldehyde, filtered, and mounted in a water-soluble methacrylic resin (Crumpton 1987). Biovolumes were calculated based on identification, enumeration, and individual measurements of a subsample of cells or colonies of each algal taxon. Chlorophyll *a* was determined after filtration through glass fibre filters and extraction in 90% acetone, using the trichromatic technique (Kopp and McKee 1979; Lathrop and Carpenter 1992).

Estimating thermocline depth

We measured temperature profiles continuously throughout the summer to examine the dynamics of thermocline migrations during the stratified periods of 1992 and 1993. A permanent buoy with a thermistor chain and datalogger was placed at the central lake station. Thermistors were placed at depths that would best characterize both the epilimnion and thermocline depths throughout the summer. (In 1992, depths were 1, 5, 6, 9, 10, 11, 12, and 16 m.) Based on an analysis of 47 years of temperature data for Lake Mendota, the average

Fig. 1. Daily thermocline depth (solid line) and days of thermocline migrations ≥1 m·day $^{-1}$ (circles) for 1992 (A) and 1993 (B). Days that were classified as storms (see text) are shown as gray vertical bars.

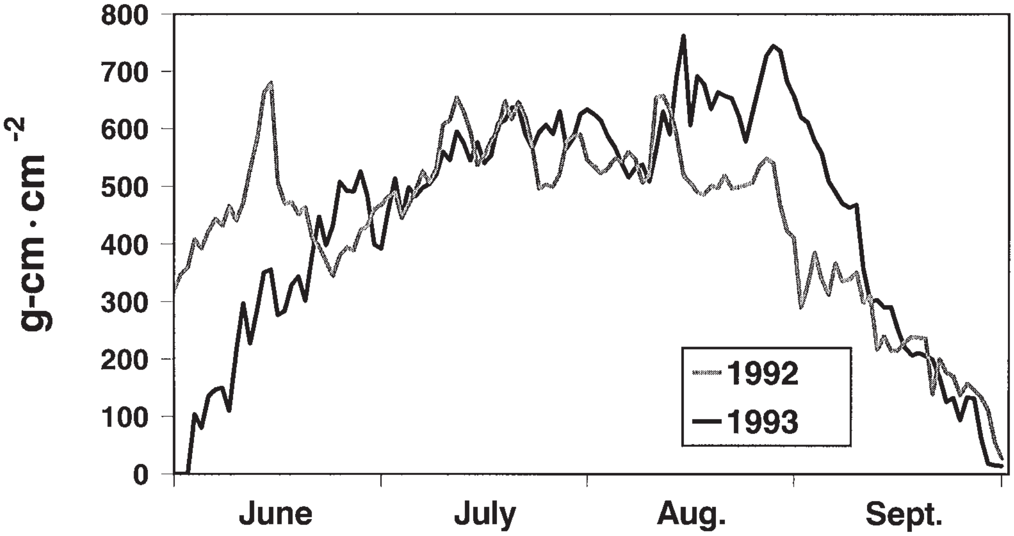


depth of the thermocline from 15 June to 31 August was 10.5 ± 1.7 m (mean ± SD); Robertson 1989). Therefore, we concentrated thermistors between 8 and 12 m. Thermistors placed at 7, 8, and 22 m stopped functioning after a week in the field and could not be replaced. We updated the temperature profiles weekly for the 22 m depth only using temperature profiles taken manually once a week with a portable YSI meter. Temperatures at 22 m changed little from week to week, and this substitution had no effect on thermocline estimates (Soranno 1995). Comparisons of epilimnion and thermocline depths calculated from the thermistor data agreed well with epilimnion and thermocline depths calculated from the temperature profiles taken from weekly YSI meter readings (Soranno 1995). In 1993, thermistors were placed at 1, 5, 6, 8, 9, 10, 11, 12, 14, 16, and 22 m. Thermistors from both years were calibrated in a water bath from 5 to 27.5°C. Temperatures were recorded every 2 min. To remove the effects of internal seiches (period 15.4 h. during July; Stewart 1965), mean daily profiles were computed from each days' 720 recorded profiles and used for all analyses. Also, because the central lake station is located at the node of the primary seiche, temperatures sampled there should be minimally affected by seiches.

Because the thermal structure of medium–large lakes such as Lake Mendota (>500 ha) can be quite dynamic and difficult to characterize (Robertson 1989; Fee et al. 1996), an automated search for thermocline as it is typically defined (the depth at which the maximum temperature change occurs) resulted in erratic and incorrect thermocline and epilimnetic depths (P.A. Soranno, unpublished data). Fee et al. (1996) reached the same conclusion when they consistently were unable to fit a simple exponential curve to temperature versus depth profiles in medium–large lakes in their study of Canadian Shield lakes (surface area ranging from 706 to 34 700 ha). Therefore, we estimated thermocline depth from visual inspection of the temperature profiles.

The actual definition of thermocline depth in larger lakes can also be difficult to characterize. Because of the complex thermal structure in these lakes as well as the presence of secondary or "breeze"

Fig. 2. Schmidt stability (g-cm·cm^{-2}) calculated from daily temperature profiles for 1992 (gray line) and 1993 (black line).



thermoclines that that are sharper than primary thermoclines, thermocline estimates defined as the maximum rate of temperature change per metre, as thermocline depth is commonly defined, resulted in inaccurate estimates of thermocline depth (Soranno 1995). Therefore, we used an alternate approach. We first estimated the temperature of the primary thermocline as the temperature that was midway between the temperatures of the maximum and minimum of the second derivative of the temperature versus depth profile (which are the boundaries for the epilimnion and hypolimnion, respectively). This temperature was determined by visual inspection of temperature profiles interpolated with a cubic spline for each day during the summer and then averaged across the entire summer. The temperature of the primary isotherm in 1992 was 15.8 ± 0.7°C, and in 1993 was 17.5 ± 1.0°C. Thermocline depth was then defined for each day as the depth of this primary thermocline isotherm. The isotherm method has been used in several studies in Lake Mendota, and the temperature of the primary thermocline has been previously identified to be between 17 and 18°C (Stauffer 1974; Robertson 1989). It was necessary to first identify the temperature of the primary thermocline, since there can be some interannual variation in water temperatures. The isotherm method has the advantage of being less sensitive to dynamics of the epilimnion (i.e., complex thermal patterns and breeze thermoclines) and being slightly less dynamic through time so that the large thermocline migrations can be identified more clearly (Soranno 1995).

Phosphorus-entrainment calculations

We calculated daily entrainment of P from the hypolimnion to the epilimnion following deepening of the thermocline. Total P mass transported into the epilimnion was calculated by multiplying the volume of water added to the epilimnion (caused by the deepened thermocline depth) by the average P concentration in the thermocline region (Stauffer 1987). At the daily scale the thermocline is highly variable, so we assumed that only large thermocline movements would entrain significant net amounts of P. Based on visual inspection of the daily thermocline changes, major events always exceeded 1 m in magnitude, which is near the vertical resolution of our temperature record. Therefore, we calculated entrainment using all events in which the thermocline deepened by ≥1 m. Other methods to determine the occurrence of migration events such as identifying thermocline depth immediately before and after storm events (as is commonly done) or using all thermocline migrations resulted in either implausibly low or high estimates of P entrainment, respectively (Soranno 1995). We checked our method for calculating P entrainment by estimating internal loading by difference. Equation 1 was rearranged and a residual (Res) of 0 was assumed:

$$\text{(2)} \qquad \text{Entr}_{\text{diff}} = \text{dSS}_{\text{P}} + \text{Out} + \text{Sed} - \text{Ext} - \text{Atm} - \text{SedR}$$

where $\text{Entr}_{\text{diff}}$ is entrainment calculated by difference, and all other terms are as in eq. 1.

Other calculations

Water column stability, S (g cm·cm^{-2}), was calculated from the daily temperature profiles using the Schmidt stability index (Likens 1985):

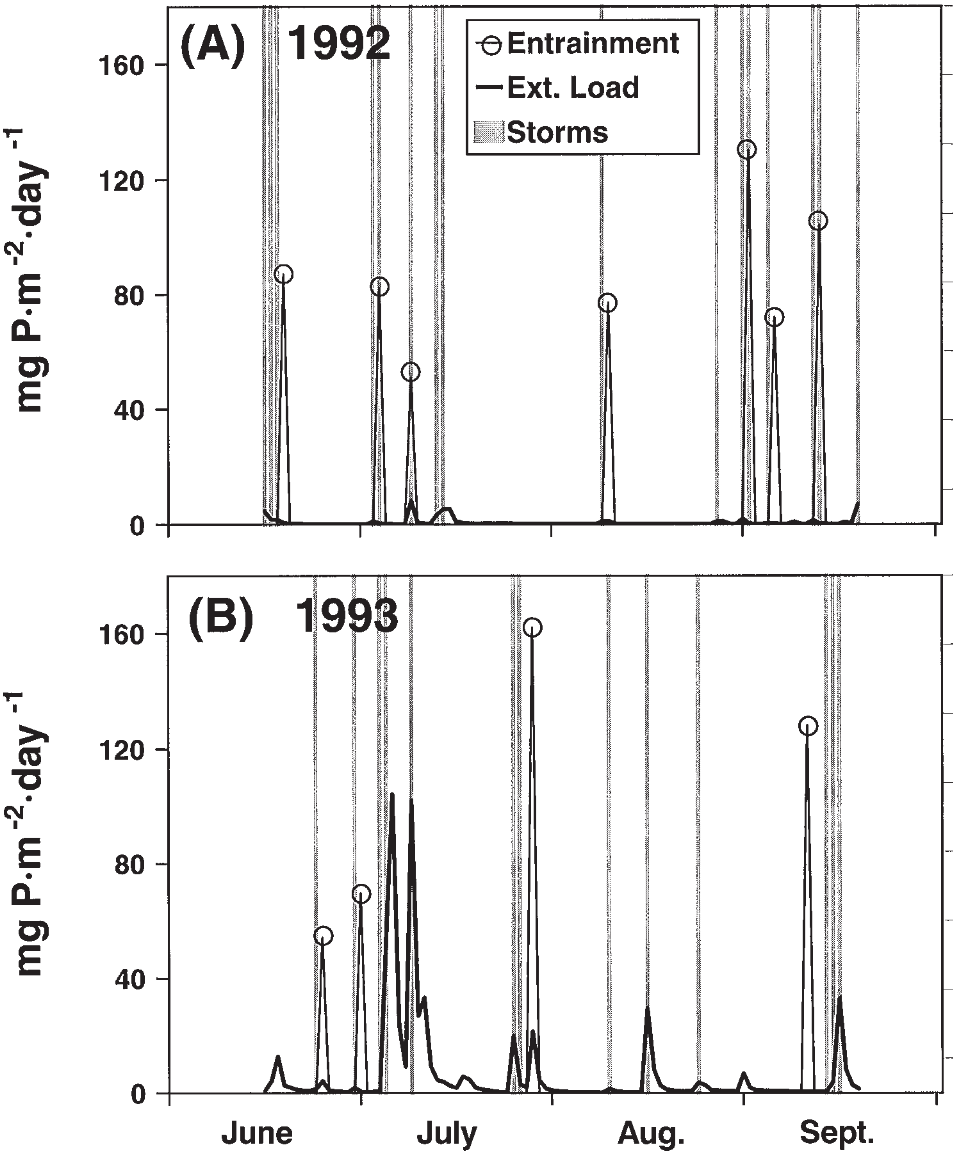
$$S = A_0^{-1}\,\Sigma(z - z^*)(\rho_z - \rho^*)A_z\,\mathrm{d}z$$

where A_0 is surface area of the lake, A_z is the lake area at depth z, ρ_z is density as calculated from the temperature at depth z, ρ^* is the lake's mean density, and z^* is the depth where the mean density occurs. The summation is taken over all depths (z) at an interval dz = 1 m. Schmidt stability is the amount of work required to mix the lake to an isothermal temperature (Likens 1985). It is zero when the lake is isothermal and maximal when the lake is most strongly stratified.

Storm events were estimated from daily precipitation and wind velocity data obtained from the Madison weather station. Storms were defined to be days when daily precipitation was >20 mm, and wind velocity was greater than the summer average wind speed (3.8 m·s^{-1}). Days were also included when wind speed was well above the summer average (>5.0 m·s^{-1}) and where there was at least some precipitation, which usually occurred on days immediately preceding or following storm events as defined above. Although this definition of storms is somewhat arbitrary, our method for calculating P entrainment does not depend on the identification of storms, and we use the storms only to check our identification of migration events.

The only P inputs to the lake that were not directly measured were dry deposition, precipitation, and P release from epilimnetic sediments. Because previous budgets developed for Lake Mendota showed that dry deposition and precipitation were an extremely small portion of the P budget, we did not feel that it was necessary to measure these directly (Lathrop 1979). In developing a P budget for Lake Mendota, Lathrop (1979) determined the best estimate for dry deposition to be based on annual measurements of dry fallout solids sampled by the City of Madison from 1972 to 1977 (630 kg·ha^{-1}·year^{-1}) multiplied by a mean annual total P per unit weight of dry fallout solids measured from urban areas across the country (0.98 mg P·g^{-1} dry solids; Amy et al. 1974). Dry deposition of TP across the summer for Lake Mendota was estimated to be 0.17 mg·m^{-2}·day^{-1}. Total phophorus in precipitation was calculated

Fig. 3. Daily P entrainment (open circles) and P loads from stream inputs (thick lines; mg P·m^{-2}·day^{-1}) for 1992 (A) and 1993 (B). Days that were classified as storms (see text) are shown as gray vertical bars.



by multiplying daily precipitation volume (obtained from the Madison weather station at the Dane County Truax airport about 7 km northeast of the lake) falling over the lake area by an average TP concentration of precipitation that was measured for nearby Lake Wingra (0.032 mg·L^{-1}; Kleusner 1972).

Although release of P from epilimnetic sediments is a potentially important component in summer P budgets, it is difficult to estimate directly across the entire summer (Stauffer 1987). Based on laboratory and field studies from hardwater Wisconsin lakes, including Lake Mendota (Lee et al. 1977; Gallepp 1979; Holdren and Armstrong 1980; Erickson 1980), Stauffer (1987) determined the average sediment release of P from sediments in contact with the epilimnion in Lake Mendota to range from 1.2 to 3.5 mg P·m^{-2}·day^{-1}. We used the average of this range, 2.4 mg P·m^{-2}·day^{-1} and assumed that the average depth of the epilimnion was 9 m across the summer (average depth from both years) to derive an aerial loading estimate.

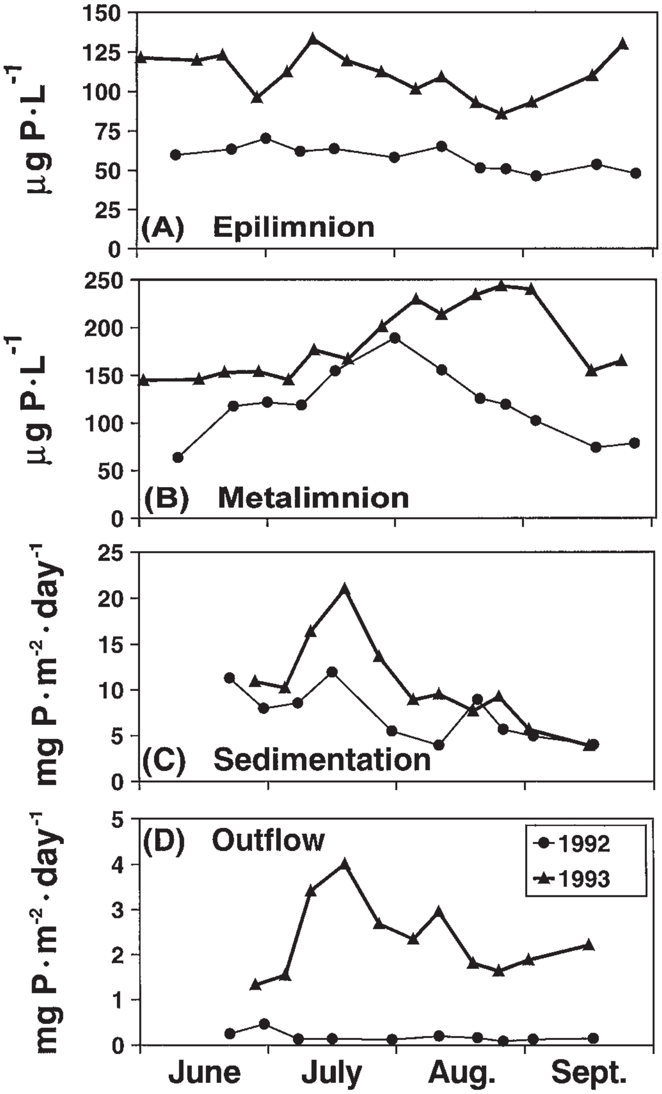
Error analysis

In budget studies, errors will depend on the identification of error for each component. Because most of the errors in our budget are poorly known, we have attempted only a rough estimate of the error in our budget by propagating estimated and measured errors through all terms of the above equation (Reckhow and Chapra 1983). Errors were measured directly for sedimentation rates through duplicate sediment traps. Phosphorus profiles measured at the deep lake station in Lake Mendota by Stauffer (1985) were found to underestimate total lake phosphorus by 3%, which is the error term we use. For all other components we assume an arbitrarily chosen coefficient of variation for each variable of 50%.

Results

Weather was substantially different between the two summers. Total precipitation in 1993 during the summer stratified season was the highest of the past 100 years (64 cm in 1993 vs. 40 cm in 1992, an average year), resulting in unusually high runoff in 1993 compared with 1992. But, the number of storms in 1992 was slightly more than in 1993 (16 vs. 13) (Fig. 1). During both years, storms were concentrated in early and late summer,

Fig. 4. Daily TP concentrations in the epilimnion (A) and in the metalimnion (depth between 9 and 14 m) (B) in µg P·L^{-1} and measured sedimentation rate (C) and stream outflow (D) in mg P·m^{-2}·day^{-1} for 1992 (circles) and 1993 (triangles). Note the difference in the *Y*-axis scale.



although there were also five storms in midsummer in 1993 compared with only 1 in 1992. Daily thermocline depth was highly variable both years (Fig. 1); and although thermocline migrations ≥1 m·day $^{-1}$ usually coincided with storm events, thermocline migrations did not always occur on the day immediately following the storms. Also, not all storm events resulted in thermocline migrations due in part to differences in water column stability. During midsummer, when the lake is very stable, it is unlikely that storms will result in major thermocline migration. For example, when stability was at a maximum during August 1993 (Fig. 2), three storms had little effect on the thermocline. In contrast, in 1992, stability was especially low in September, and the many storms that occurred at that time resulted in migration events. Also, a major thermocline migration occurred in mid-September when stability was low on a day that we did not classify as a storm. During these 2 days, average wind velocity was 7.2 and 4.9 m·s^{-1} with 0.3 mm precipitation.

Phosphorus entrainment calculated from these thermocline migrations resulted in pulsed nutrient inputs throughout both summers (Fig. 3). There were more entrainment events in 1992 compared with 1993, most likely resulting from a combination of more storms and weaker stratification, especially during late summer. Storms also coincided with stream runoff events (Fig. 3). Both stream and entrainment inputs occurred in relatively discrete pulses with little input during the time period between events.

Total phosphorus concentrations during both years followed typical patterns for eutrophic lakes in that TP built up below the epilimnion during the stratified season (Figs. 4A and 4B). However, there were distinct differences between the 2 years. In 1992, TP concentrations in the metalimnion did not increase beyond early August; but in 1993, metalimnetic TP concentrations continued to increase through the end of September. In addition, TP concentrations in both the epilimnion and metalimnion were substantially higher in 1993 than in 1992, often by a factor of two. Much of the difference in TP standing stock can be attributed to the unusually high external loads to Lake Mendota that occurred in both spring and summer 1993 (Fig. 3; P.A. Soranno, unpublished data). Both sedimentation and outflow of TP increased in response to the elevated external loading and were higher in 1993 than 1992 (Figs. 4C and 4D).

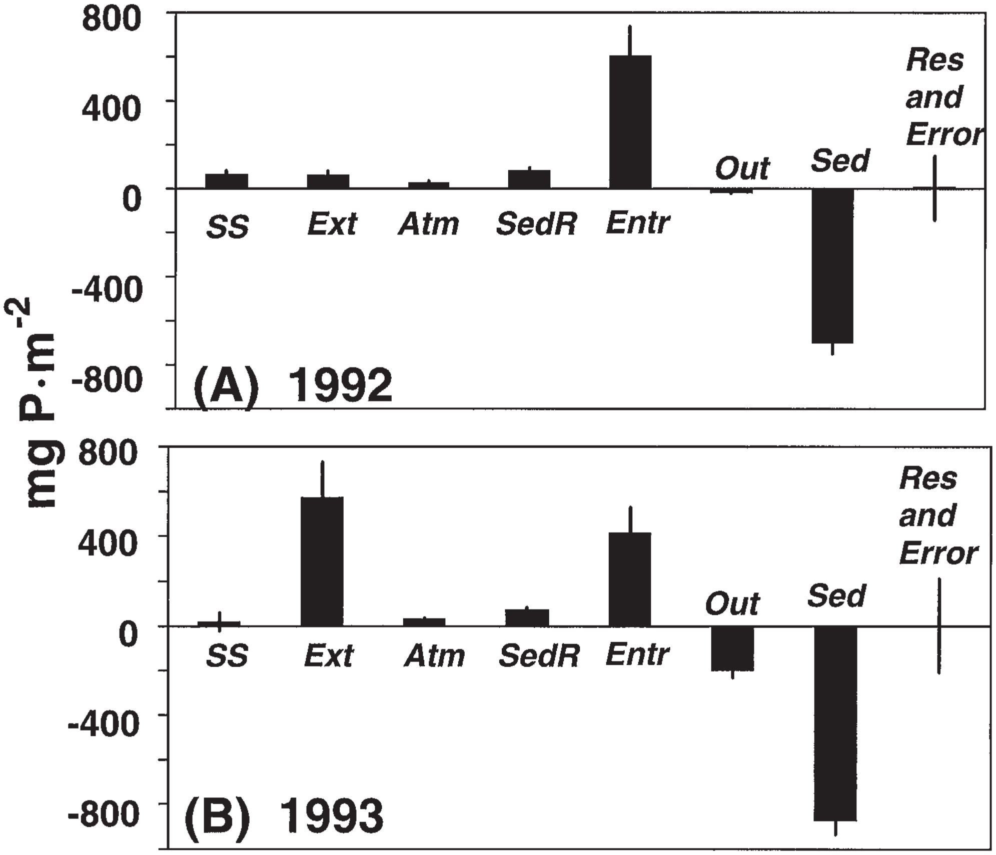
Major P fluxes during the summer differed between the 2 years. During 1992, external loading was lower than the combined loading from epilimnetic sediment release and atmospheric deposition, and all were relatively minor fluxes (Fig. 5A). Internal loading from entrainment was the largest input into the epilimnion. However, during 1993, external loading was about equal to all other inputs (Fig. 5B). Internal loading due to P entrainment was about 10 times higher than external loading during the average runoff year (1992), but was similar to external loading during the high runoff year (1993).

Summer budgets for epilimnetic TP balanced for both years. The residual terms for the mass balance, representing unaccounted-for P, were close to zero for both years (Figs. 5A and 5B). Thus, summer P entrainment calculated by difference using eq. 2 and assuming a residual of zero (0.61 and 0.42 g·m^{-2} for 1992 and 1993, respectively) agreed well with our direct estimate of entrainment (0.60 and 0.42 g·m^{-2} for 1992 and 1993, respectively). Also, both entrainment estimates and sedimentation rates were large relative to the estimated error term for the mass-balance equation, which lends confidence to our budget, since the budget is strongly driven by these two factors. Although the true error for the budget is poorly known, we assumed quite a large error for those parameters with no measured error (CV = 50%), so it is likely that the estimated error is an overestimate.

Discussion

This study confirms the relative importance of internal loading to the summer epilimnetic P budget in a stratified eutrophic lake. During normal rainfall conditions, P entrainment is the dominant source of P to the epilimnion of Lake Mendota. Only during highly unusual weather conditions did external inputs

Fig. 5. Epilimnetic TP budgets in mg P·m^{-2} across the summer stratified season for 1992 (A) and 1993 (B). Positive and negative values represent epilimnetic inputs and outputs, respectively. The residual term for both years (Res) is close to zero. The error term propagated for the entire budget is shown as an error bar on the residual term; otherwise, estimated or measured SDs (see text) for each variable are shown on each individual bar. SS is the change in TP standing stock across the summer, Ext is external loading, Atm is atmospheric loading (dry and wet deposition), SedR is release of P from epilimnetic sediments, Out is outflow, Sed is sedimentation from the epilimnion, and Entr is entrainment calculated from temperature profiles.



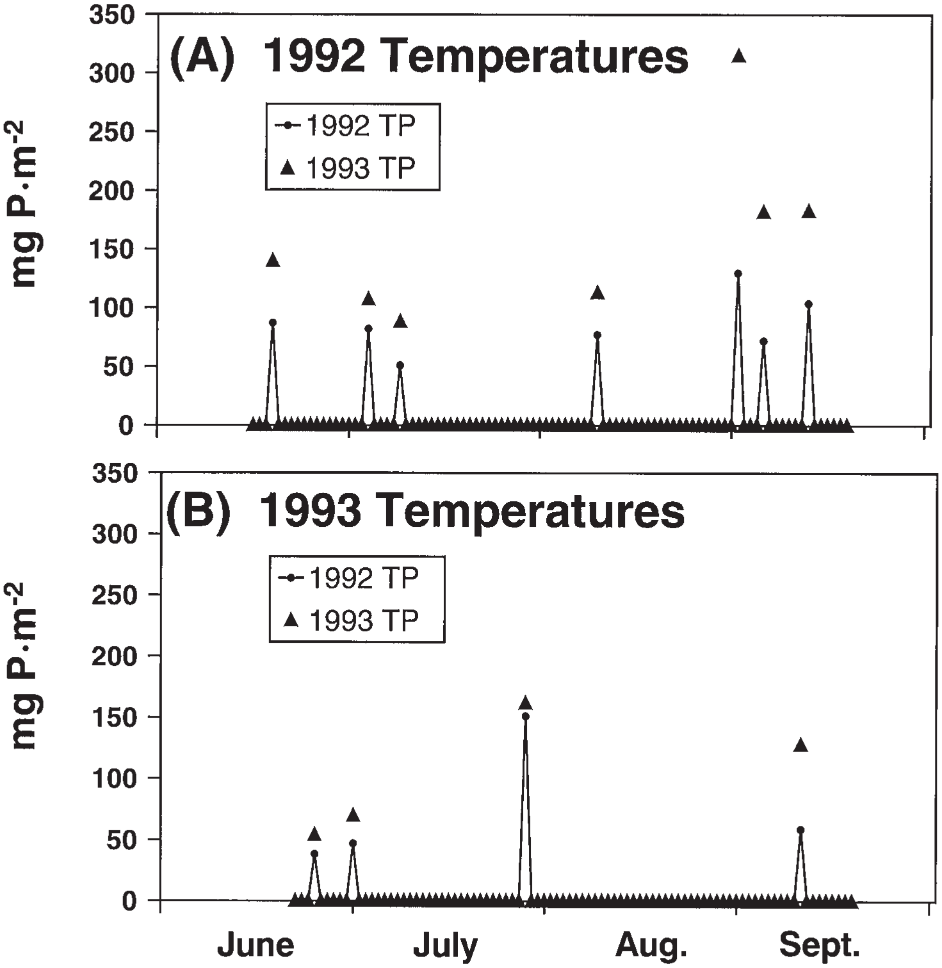
exceed internal inputs. In addition, we show that P entrainment and sedimentation are the dominant fluxes into and out of the epilimnion, and they appear to balance each other across the summer stratified season as suggested by Stauffer (1987). This is one of the few studies that has measured all of the major fluxes concurrently with estimates of P entrainment and also documented interannual variability in internal P loading in stratified lakes (but see Effler et al. 1986).

Measuring P entrainment in lakes

Average daily temperature profiles showed the thermocline to be a highly dynamic boundary with large daily changes in thermocline depth (Fig. 1). We assumed that the large thermocline migrations (≥1 m·day^{-1}) would capture most of the vertical nutrient flux in a large lake with a dynamic thermal structure. Phosphorus entrainment calculated using such migrations appeared to identify the major migration events and agreed well with the P-entrainment estimate calculated by difference from the mass-balance P budget. Maximum thermocline displacement usually was concurrent with storms (Fig. 1) but did not necessarily occur immediately following a storm. This result suggests that daily sampling of temperature profiles may improve entrainment estimates. If upward vertical fluxes due to less turbulent processes such as eddy diffusion were important, they would have added to the residual term of the mass-balance equation. Although eddy diffusion coefficients can be calculated from temperature profiles and P gradients, the calculation requires many assumptions and usually uses temperature profiles that are more finely spaced vertically (Jassby and Powell 1975). Consequently, we did not attempt to calculate eddy diffusion. It is likely that our estimate of entrainment includes other transport processes but that the flux caused by major storm events is the dominant process by which P is transported from the hypolimnion to the epilimnion in medium–large lakes such as Lake Mendota.

To determine the potential importance of P entrainment of epilimnetic budgets to lakes in general, it would be useful to compare our entrainment results with other lakes. One of the few lakes where a total summer entrainment estimate is presented is Onondaga Lake (12.0 m mean depth and 1170 ha total area), a stratified, eutrophic lake in New York (Effler et al. 1986). Effler et al. (1986) estimated the average entrainment across two summers to be 2.5 mg P·m^{-2}·day^{-1}, which is of similar magnitude to our average estimate of P entrainment for both summers (5.5 mg P·m^{-2}·day^{-1}). However, our estimate differs from a previous entrainment estimate for Lake Mendota (Stauffer 1987), where summer entrainment in 1972 was calculated to be about 0.3 mg P·m^{-2}·day^{-1}. Epilimnetic TP

Fig. 6. Phosphorus entrainment calculated for 1992 temperature data with TP concentration data from 1992 (circles) and 1993 (triangles) (A) and P entrainment calculated for 1993 temperature data with TP concentration data from 1993 (triangles) and 1992 (circles) (B).



concentrations in 1972 were similar to those of 1992 (Stauffer 1987), so it is unlikely that there were major differences in nutrient dynamics in the lake during 1972 that would explain this large difference between the two entrainment estimates. Although we used similar methods to calculate entrainment, Stauffer (1987) used a sampling frequency that was roughly weekly, compared with our daily sampling. Entrainment may be underestimated using weekly sampling, because major migration events occur at finer temporal scales and because thermocline depth returns to prestorm levels soon after the storm passes (Fig. 1).

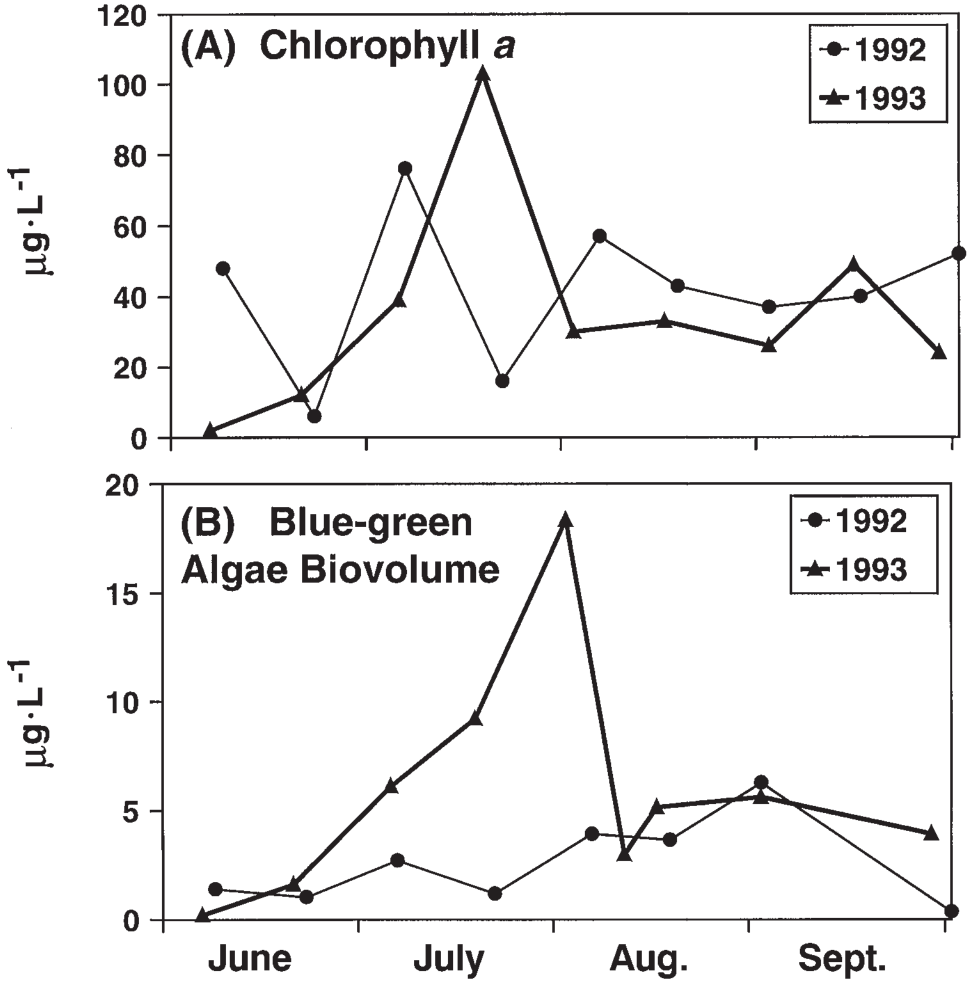
Phosporus entrainment in Lake Mendota

Estimates of P entrainment to the epilimnion in Lake Mendota during both summers were large relative to other terms of the P budget. Even though external loading to Lake Mendota was high because of increased precipitation and flooding throughout the summer of 1993, these conditions did not lead to large thermocline migrations as we had expected from the high number and intensity of storms. In studying the effect of wind stress on thermal structure in Lake Mendota, Stauffer (1992) found that the highest wind velocity events did not necessarily lead to the highest thermocline migrations, in part because of different initial water column stabilities at the time of the storm. External and internal loading are coupled with weather and thermal stratification in complex ways.

Entrainment potential

The potential for P to be entrained into the epilimnion should depend on two things: (*i*) the mixing potential and (*ii*) the nutrient loading potential. First, mixing potential will depend on water column stability coupled with the number and strength of storm fronts that cause the thermocline to migrate (Stauffer and Lee 1973; Effler et al. 1986). Like Effler et al. (1986), we found that entrainment events were concentrated during early and late summer when stratification is weaker and the lake more subject to mixing, although some events did occur midsummer (Fig. 3). Although there were more storms that led to thermocline migrations of 1 m or more in 1992 than in 1993 (Fig. 1), this was most likely due to a combination of a greater number of major storms and weaker stratification late in the summer. Thus, total P entrainment was higher in 1992. The other factor determining P entrainment is the nutrient loading potential. In 1993, P concentrations in the metalimnion were higher than in 1992, increasing the potential internal load (Fig. 6). To compare the roles of these two mechanisms, we recalculated entrainment for each year using each year's temperature data with TP data from the other year (Fig. 6). In

Fig. 7. Chlorophyll *a* concentration in µg·L^{-1} (A) and blue-green algae biovolume in µL·L^{-1} (B) during summer for 1992 (circles) and 1993 (triangles).



1992, total summer entrainment calculated using TP data from 1993 was about 11.5 mg P·m^{-2}·day^{-1}, almost two times higher than that calculated with 1992 TP data (6.1 mg P·m^{-2}·day^{-1}). In contrast, total summer entrainment calculated for 1993 using TP data from 1992 was about 3.5 mg P·m^{-2}·day^{-1}, almost 1.5 times lower than that calculated using TP data from 1993 (4.9 mg P·m^{-2}·day^{-1}). These values may bracket high and low entrainment values possible in Lake Mendota. Daily entrainment calculated using TP data from 1993 was always higher than that calculated using TP data from 1992. There also appears to be a seasonal difference in this contrast. The largest discrepancies between the two entrainment calculations during both years were in late summer when metalimnetic TP concentrations were maximum in 1993, but were declining in 1992 (Fig. 4B).

Consideration of internal loads from entrainment may help explain some of the observed interannual variability in epilimnetic TP dynamics in stratified lakes such as Lake Mendota. For example, when spring and summer external loads are low, metalimnetic TP will be relatively low. In addition, if summer conditions are such that stratification is stable with few storm fronts, P entrainment should be relatively low. Such conditions occurred in Lake Mendota in 1988 during a regional drought and very warm summer resulting in a very stable water column and unusually low summer TP concentrations (Lathrop 1992). Conversely, with high winter and spring TP loads, low stability, and frequent storm fronts, internal loading can be large. This extreme situation was simulated by using TP data from 1993 and stratification data from 1992 (Fig. 6) and may represent the upper bound on P entrainment currently in Lake Mendota, although the full range of possibilities could not be addressed without data from a wider range of weather conditions.

Nutrient loading to the epilimnion

Our assessment of P loads to the epilimnion during these 2 years would be quite different had we not accounted for internal loading. External loads to the epilimnion during summer 1993 (7.0 mg P·m^{-2}·day^{-1}) were much higher than in 1992 (0.9 mg P·m^{-2}·day^{-1}). However, total loads (internal + external) during the 2 years were more similar: 12.5 mg P·m^{-2}·day^{-1} in 1993 and 7.8 mg P·m^{-2}·day^{-1} in 1992. In fact, our data suggests that the total range in internal loading may be smaller than the observed range in external loads, which is important because internal loading represents from 38% (during a high runoff year) to 78% (during an average runoff year) of the total loads to the epilimnion in Lake Mendota. Consequently, internal P loading may act to buffer large interannual fluctuations in external inputs to the lake. Adding factors related to internal loading from P entrainment to summer nutrient models may help predictions of lake response to changes in external nutrient inputs.

Ultimately, the ecological significance of these interannual fluctuations in internal loading will depend on the fate of P in the water column and its effect on the algal community. Algae in Lake Mendota appeared to respond to the observed yearly differences in total P loads. Although chlorophyll concentrations during the 2 years were similar (Fig. 7A), during both summers, blue-green algae dominated the algal biomass and represented on average 85% and 96% of the total algal biomass in 1992 and 1993 respectively. In addition, blue-green algal biomass was above nuisance levels (2 $\mu L \cdot L^{-1}$; Lathrop and Carpenter 1992) most of the study period and was, on average, about two times higher in 1993 than 1992 (Fig. 7B).

Another factor that may determine the ecological relevance of internal loading from P entrainment is the relative proportion of internal and external loads to the total loads. Phosphorus entrainment contributed 78% of the total loading in 1992 but only 38% in 1993. Internal loading has been shown to have higher levels of biologically available P than external sources (Nürnberg 1988). In fact, in a July and August sample taken from the metalimnion in 1992, 89 and 78% of the TP, respectively (R.C. Lathrop, unpublished data) was dissolved reactive phosphorus (DRP), a form of P that is available for algal uptake. These high levels of DRP from internal sources are important because typically in Lake Mendota, epilimnetic DRP concentrations are below analytical detection (Lathrop and Carpenter 1992) and hence most likely growth limiting to algae (Brownlee and Murphy 1983; Prepas 1983). In summers where entrainment events are large, more P is supplied to the epilimnion leading to higher algal biomass. Only when runoff is unusually high is DRP above analytical detection, as occurred in 1993, and probably not growth limiting to algae. In addition, dissolved N:P ratios of both sources may differ and influence the response of blue-green algae in particular. The relative importance of internal versus external sources of nutrients in explaining interannual variability in algal dynamics remains an important question.

Within lakes such as Lake Mendota, variation in internal loading from P entrainment can be explained in part by external loads, which determine nutrient gradients, and seasonal weather patterns (i.e., storm frequency), which influence stratification and thermocline dynamics. The highest internal loads should occur when metalimnetic P concentrations are high because of high spring and summer external loads and stratification is weak and variable because of storm fronts during the summer. The lowest entrainment should occur when external loads are low and the water column is stable with few storm fronts.

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