> *Just how . . . lakes are able to support a crop of phyto-*
> *plankton from May to July or August without any appre-*
> *ciable decrease in the soluble phosphorus of the*
> *upper water or only a slight one, is not known—*
> Juday et al. 1927

New and recycled primary production in an oligotrophic lake: Insights for summer phosphorus dynamics

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Abstract

Primary production that is supported by new inputs of nutrients from outside the system is distinct from production that is supported by remineralization of nutrients within the system. We applied the concept of new production to Mirror Lake, New Hampshire, and our view of P dynamics in this lake was altered dramatically. New production during midsummer put a large demand on P in surface waters, removing 37 μmol P m^{-2} d^{-1}. Without new inputs of P, the P content of surface waters would drop to zero in <1 month. There is, however, a slight increase, not a decrease, in P content of surface waters during summer stratification. Inputs to surface waters during summer months must, therefore, be large. We now believe that higher than average P loading to the lake occurs in summer, despite low runoff inputs.

In temperate lakes, a large fraction of the annual primary production generally occurs in surface waters in summer (Jordan et al. 1985; Wetzel 1975). A variable, but appreciable fraction of this production sediments into bottom waters, removing nutrients such as P from the photic zone (Cole et al. 1989; Capblancq 1990). Despite this loss of P, many of these temperate lakes experience little decrease in P in the surface waters during summer stratification (Juday et al. 1927; Lawacz 1985).

The above observations indicate that there must be a substantial source of P which fuels primary production and replaces the P lost by settling of particles to bottom waters. Juday et al. recognized this concept over 60 yr ago, and Dugdale and Goering (1967) formalized this outcome of the mass balance law some 25 yr ago for nitrogen dynamics in the sea. In their analysis, Dugdale and Goering divided primary production into two components: that fueled by recycling of nutrients in surface waters, which they termed "recycled production" and that fueled by nutrient inputs from outside surface waters, which they termed "new production" (Fig. 1).

The concept of new and recycled production has shaped the way that oceanographers look at nutrient cycling, nutrient budgets, and carbon flux (Eppley and Peterson 1979; Pace et al. 1987). Limnologists have, however, to a large degree overlooked this concept (*but see* Hama et al. 1990) or have discussed it in a far less formal sense (e.g. Lehman and Naumoski 1986).

Adopting the concept of new vs. recycled production by limnologists would lead to new insights on nutrient and C cycling. The concept of new production was formulated

originally for N dynamics in the ocean (where NH_4 and NO_3 uptake can be used to differentiate recycled from new production). The implied general mass balances (Fig. 1) can, however, be applied to any important nutrient. Here, we apply the concept of new production to P dynamics during summer in a temperate lake.

Site description and background

Mirror Lake is a small oligotrophic lake in the White Mountains of New Hampshire. The lake is dimictic and summer stratification generally lasts from May to October, during which ~50% of the epilimnion is underlain by epilimnetic sediments and the remainder by hypolimnetic waters. The lake has been extensively studied as part of the Hubbard Brook Ecosystem Study (Likens 1985).

Algal P demand is the amount of P needed for phytoplankton production. We calculate this demand using the range of C production measured in the lake (Jordan et al. 1985; Cole et al. 1989; Ochs 1991) and a C:P uptake ratio of 106:1 (Redfield et al. 1963). Previous sediment trap studies in Mirror Lake suggested that a large part (>30%) of this total production is new production, because it is exported from the epilimnion by settling (Caraco et al. 1988; Moeller and Likens 1978).

New production must be supported by depletion of the P in surface waters or by new inputs of P to surface waters during the summer growing season (Fig. 1). Previous work at Mirror Lake has demonstrated, however, that many sources of P, which are traditionally studied and important on an annual basis, are not significant in fueling new production in the summer growing season. For example, fluvial inputs which provide ~50% of the annual P loading can support <2% of the summer new production (Caraco et al. 1988). Further, total P concentrations in surface waters are relatively low (~0.1–0.2 μM total P) with little apparent change during summer stratification (Likens et al. 1985). In this paper, we attempt to balance the new production of the lake with sources of P to surface waters during summer stratification (Fig. 1). Budgeting
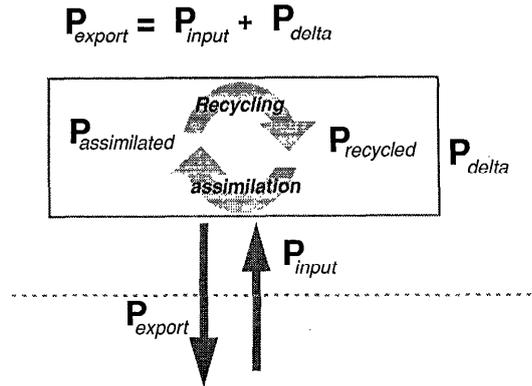
$$P_{export} = P_{input} + P_{delta}$$

Fig. 1. Diagram of the relation between recycled and new (or export) production in surface waters of aquatic systems. When phytoplankton grow they assimilate P. A certain amount of P taken up by phytoplankton escapes recycling and is exported by sinking to bottom waters and by outflow from the system. This term, P_{export}, is equivalent to the oceanographic term, new production (Eppley and Peterson 1979), and is the component of primary production that cannot be supported by P regeneration within the system. Particle sinking is the dominant loss term of P from surface waters (Lawacz 1985; Levine et al. 1986). Mass balance dictates that P_{export} be equal to the loading of P to surface waters (P_{input}) plus change in standing stock of P (P_{delta}; positive values of P_{delta} denote a decrease in P standing stocks and a negative value denotes an increase).

was done for epilimnetic waters (<6.5 m) from mid-July through the end of August for two consecutive years.

Methods

Particle flux from the epilimnion—Particle sinking from surface waters is a major export of nutrients in lakes. To measure particle flux in Mirror Lake, we deployed tall conical traps in 1986 and both tall conical and cylindrical traps in 1987. Conical traps were 1 m tall with a diameter of 20 cm at the mouth. The cylindrical traps were 30 cm tall and 10 cm in diameter. During both years, the traps were deployed every 3–4 d throughout the budgetary period at three (1986) or seven locations (1987) near the central part of the lake. The trap mouths were set at 6.5-m depth with a permanent mooring system. Because it was permanent, this mooring system did not resuspend bottom sediments. Further, the design has no obstructions above the trap mouth upon

which materials could collect and then fall into the trap.

The collecting cup of the conical traps was sealed upon recovery and the overlying water drained off. This procedure left 125 ml of liquid plus settled particles in the collecting cup. The entire contents of the collecting cup were homogenized by vigorous shaking, and subsamples of the particulate material were taken for analyses by filtration through 25-mm Gelman AE filters. In the case of the cylindrical traps, the entire contents of the traps (~750 ml of water plus settled and suspended particles) were collected, homogenized, and subsampled as above. Reference blanks consisted of traps, deployed as above, but sealed with lake water collected from the depth of deployment.

Change in the mass of P—A decrease in the mass of P during the summer growing season could fuel a significant amount of new production (Fig. 1). To determine the amount of P in the lake, we measured depth profiles of total P (TP) at three locations in the lake at roughly biweekly intervals during the budgetary period (mid-July through the end of August). For each profile, samples were taken at 0, 2, 4, 6, 7, and 8 m, and, at the deepest station, 9 and 10 m as well. The mass of P in the epilimnion (MP) was calculated as

$$MP = {}_{z=0}\Sigma_{z=6.5}(TP_z \text{ volume}_z).$$

TP_z and volume$_z$ are the TP concentration and volume at each depth layer, z. The hypsographic curve for the lake (Likens et al. 1985) was used along with weekly information on lake level to calculate volume$_z$.

Surface water inflow and outflow—The three inlet streams of the lake are gauged and monitored continuously for waterflow (Winter et al. 1989). Samples for TP were taken from each inlet at weekly intervals. For the input of P, we used these measurements to derive a relationship between water discharge and TP concentration and used this relationship to calculate TP input for each of the three inlets.

The single outlet of the lake is gauged and monitored continuously. To estimate outflow of P, we multiplied the TP concentration in the surface water of the lake times the volume of water flowing over the dam at the outlet.

Net input from and through epilimnetic sediments—There are three ways in which epilimnetic sediments can be a source of P to the water column. First, dissolved P in epilimnetic pore water can be transported through the sediments and into the water by the flow of groundwater into the lake (groundwater input; Shaw et al. 1990; Asbury 1990). Second, when a sufficient concentration gradient exists between the water column and the pore water, dissolved P could be moved into the water by diffusion, even in the absence of advective flow (diffusive input). Third, materials deposited on the surface of the epilimnetic sediments can decompose and release P directly into the water. We used three different approaches to investigate each of these potential inputs.

We estimated groundwater P inputs as the product of the volume of groundwater that entered the lake and the concentration of TDP in pore water at the 10-cm depth in the epilimnetic sediments. This estimate is maximal because some of the pore-water P may be removed by sorption as groundwater is advected up through the surficial sediments.

To obtain samples of TDP in epilimnetic pore water, we deployed a series of minipiezometers at 61 sites in the lake. Most (50 sites) were chosen to be in areas which Asbury (1990) and Winter et al. (1989) reported be areas of inseepage. Each piezometer was sampled on three dates in 1986 and three dates in 1987. Details of the estimates of groundwater inputs and outputs are described elsewhere (Winter 1991). Briefly, a series of ~60 boreholes, water-table wells, and piezometer wells were drilled into the watershed and monitored continuously for hydraulic head. Using these data, measurements of soil and bedrock geology, and a complete water budget for the lake, we developed a model of seepage inflow that recognizes nine geographic sectors around the lake, each with an individual groundwater flow character. We matched our lake groundwater piezometer samples to these sectors and multiplied the average P concentration during the budgetary periods in each sector by the estimate of groundwater flow in each sector during the same periods to obtain an estimate for the entire lake.

For the output of P through groundwater,

we multiplied the volume of groundwater exiting the lake by the concentration of TDP in the surface water. We assumed that particles would not exit the lake in seepage flow.

To consider the magnitude of a possible diffusive input of dissolved P from pore water into the water column, we made several measurements of the pore-water profile of dissolved P in epilimnetic sediments with a system of micropiezometers. Samples were taken at 0.5–1-cm intervals from 0- to 8-cm depth; sites representative of the sediment types are identified in Table 1. From these data, we estimated the maximum concentration gradient between the pore water and overlying lake water and calculated Fickian diffusion with phi of 0.80 and D_s for phosphate of 3.6×10^{-6} cm^2 s^{-1}. This calculation provides a diffusive estimate for the three types of sediments. By proportioning the area of epilimnion to each type of sediment (Table 1), we estimated a diffusive flux for the entire lake.

To estimate the input of P from decomposition on the surface of the epilimnetic sediments, we deployed a series of chambers on various sites in the epilimnetic sediments. Details of chamber design and deployment are described elsewhere (Mattson 1989). The important features of these chambers are their relatively large size (0.155 m^2, enclosing 22 liters in volume), the minimal disturbance they caused, and that the mixing regime in the chambers was designed to match those outside the chambers (Mattson 1989). Further, the chambers were equipped with a reservoir that would expand when seepage inflow occurred and contract when outflow occurred. This reservoir would prevent unnatural flow conditions from occurring in the chamber due to seepage. Deployments were for 24 h, with samples taken at various intervals throughout the period. Deployments were made from dawn to dawn to avoid uptake of P released in the dark (Carlton and Wetzel 1988). Deployments were made in several sediment types, ranging from high organic muds to sand, and at various depths from 0.3 to 6 m. Nine sites were used (six in 1986 and three in 1987). There were three or four replicate chambers at each site and each site was sampled from 1 to 3 times during the summer.

Table 1. Loading of P from epilimnetic sediments (<6.5 m) of Mirror Lake as measured by benthic chambers. Measurements were made on four sediment types: sand to cobble area consisting of inorganic sediments of various grain sizes with little to sparse macrophyte growth; organic sand area made up of coarse organic debris <6 cm thick overlaying inorganic substrate; organic mud area consisting of organic sediments >6 cm thick; gyttja areas of fine sediment which is permanently accumulating in the deeper portion of the lake. In areas of extensive boulders, flux could not be directly measured. To calculate flux from these areas we used the average value for organic sand because boulders are often overlain by a thin layer of organic deposit.

Sediment type	Areal flux (μmol P m^{-2} d^{-1})	Area (m$^2 \times 10^4$)	Flux (μmol P $\times$ 10^4 d^{-1})
Sand	0.64(1.88)	2.54	1.6
Organic sand	5.06(0.63)	1.09	5.5
Organic mud	20.50(9.50)	0.87	17.8
Gyttja	5.64(1.79)	1.45	8.2
Boulders	nd	1.45	7.3
Total			40.4
Whole lake avg/area	2.8		

Rainfall and atmospheric particles—Precipitation amounts and P concentrations are measured at the lake as part of the Hubbard Brook Ecosystem Study (Likens 1985). In addition, an intensive study was done in 1986 and 1987 as part of the present P budget to measure the particles derived terrestrially and transported through the atmosphere into the lake. This study and the methods are described by Cole et al. (1990).

Mixing with hypolimnetic water—Mixing across the thermocline can be a significant source of P to epilimnetic waters in some lakes when the rate of cross-thermocline mixing is rapid and when a sufficient concentration gradient in P exists between the epi- and hypolimnion. Profiles of TP and TDP were obtained as explained above. The rate of mixing was estimated with a modification of the heat-flux gradient method of Jassby and Powell (1975). Details are described by Mattson (1989).

Bathers—Because the lake is used recreationally, we considered the amount of P that could leach from typical bathers by conducting a series of experiments. In each of these trials, a 142-liter polyethylene tub was filled with water from the lake. After stirring, an initial sample was taken and a bather entered his/her entire body in the water
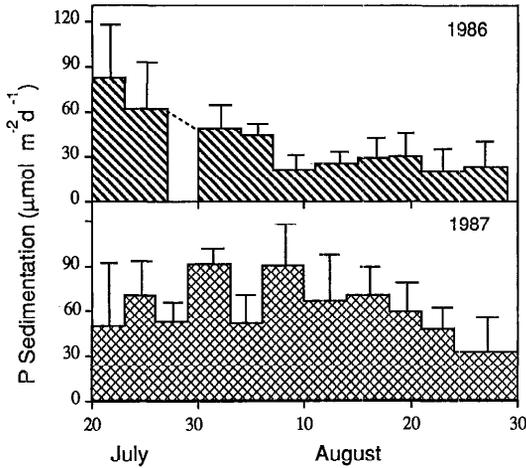
Fig. 2. Time series of the sedimentation of particulate P from the epilimnion for the budgetary periods in 1986 and 1987. Values shown are the average (with SD) for each time block. Time blocks were 2–4 d, denoted by the width of the bars. In 1986 tall conical traps were used; in 1987 both tall conical and cylindrical traps were used. Because the conical traps tended to underestimate sedimentation, we corrected the data from those traps according to the calibration experiment we ran in 1987 (*see text*). The open bar represents missing data.

for 10 min. During this simulated swim, samples were taken for TP at 0, 2, 5, and 10 min. Separate trials were conducted with three humans and one dog, each judged to be representative of the average swimmer in the lake. Two types of controls were also performed. We measured TP over time in the identical setup but without any bathers to determine whether the container contributed P. In addition, we spiked the water in the container with several levels of phosphate to determine if the container walls would remove P from the water column.

Chemical methods — Samples for dissolved P were combusted by persulfate digestion (Menzel and Corwin 1965). Samples for particulate P were collected by filtration through Gelman AE filters. Samples were dried and combusted (500°C, 4 h) and the resultant ash was extracted in acid (1 N HCl, autoclaved at 120°C for 1 h). The digested dissolved and particulate samples were analyzed as molybdate reactive P (Murphy and Riley 1962). Dissolved P analyses were calibrated with ATP as standards. Particulate

P analyses were calibrated with NBS orchard leaves and estuarine sediments.

Results

Particle flux from the epilimnion—During the budgetary period for 1987 we had 60 successful sediment trap deployments on 11 dates (Fig. 2). Of these, 28 were cylinders and 32 were cones, and both cones and cylinders were represented on each date. We compared the average catch by day for each type of trap and found that the cones consistently caught ~30% less particulate material than did the cylinders. For the budgetary period in 1987, and expressed per unit of collecting area for each sediment, the cones trapped 47 ± 8.7 (95% C.I.) μmol P m^{-2} d^{-1} and the cylinders trapped 61 ± 13.6. These differences, which are significant ($P < 0.05$, t-test), are consistent with the suggestion that a cone-shaped trap would tend to underestimate the true particulate flux (Gardner 1980). In 1986, we had 40 successful deployments on 10 dates during the budgetary period and all were cones. The mean daily flux (with 95% C.I.) was 29 ± 10.7 μmol m^{-2} d^{-1} and is, thus, considerably lower than the estimate for the identical cone traps in 1987. We assume that the estimates provided by the cone traps are too low by a factor of 1.29 based on the calibration in 1987. Thus, our best estimate of flux is 37 μmol P m^{-2} d^{-1} in 1986 and 61 in 1987. The average for the 2 yr would be 49 μmol P m^{-2} d^{-1}.

The above analysis assumes that particles sink evenly over the lake (e.g. no sediment focusing). In Mirror Lake the area below the 6.5-m isopleth is ~50% of the area of the lake. If particles were resuspended continuously from epilimnetic sediments and deposited into the hypolimnion below 6.5 m (complete focusing), the amount caught in a sediment trap at 6.5 m would overestimate sedimentation to the entire lake by a factor of ~2, and our estimate of sedimentation would be 25 μmol P m^{-2} d^{-1} rather than 49. Previous studies in the lake suggest that there is no long-term accumulation of gyttja in shallow sediments on an annual basis (Davis and Ford 1985). However, this annual pattern is likely caused by intense

resuspension and focusing during fall over-turn (Davis and Ford 1985) rather than by complete focusing during summer stratifi-cation. If we assume that half the material were focused during summer stratification, our best estimate for sedimentation would be 37 μmol P m^{-2} d^{-1}. This export of P represents a new production value of ~35% of total production, which is in rough agree-ment with values suggested for other shal-low systems (Hargrave 1973).

Change in mass of P—The concentration of TP in the surface waters averaged 0.17±0.06 (SD) μM during mid-July through September in 1986 for 41 indepen-dent station-dates sampled. During the same period in 1987, 45 station-dates were sam-pled and TP averaged 0.18±0.09 μM (SD). The mass of TP in the epilimnion during the budgetary period (mid-July through September) averaged 818±178 μmol TP m^{-2} d^{-1} 1986 and 733±305 in 1987. To calcuate P_{delta} for both years, we used a linear re-gression of the mass of TP in the lake against time. The slope of this regression was -6.7 μmol TP m^{-2} d^{-1} ($r^2 = 0.55$) and $+15.4$ ($r^2 = 0.62$) for 1986 and 1987, respectively. The average P_{delta} for the 2 yr using this method is -4.3 μmol m^{-2} d^{-1}. Note that the sign of P_{delta} is defined so that a negative sign denotes an increase in the mass of P (Fig. 1).

Surface inflow and outflow—During the budgetary period, discharge from the three inlet streams ranged from nearly undetect-able (~10^{-6} m^3 s^{-1}) to peak discharges in the west and northwest inlets of 0.02 m^3 s^{-1}. TP concentrations varied from ~0.1 μM to peaks of ~0.6 μM and were generally lowest in the northwest inlet. TP concentration was poorly related to discharge in this low range of summer discharges, but the input of TP was strongly and linearly related to dis-charge, with a different relationship in each inlet. Using these relationships and the measured discharge for each inlet, we cal-culated the total P input over time. For the budgetary period the time-weighted average TP input was 0.39 μmol m^{-2} d^{-1} averaged over the entire surface area of the lake.

The flow of the surface outlet generally decreases during summer from ~0.014 m^3 s^{-1} in June to barely detectable values in August and September (<0.001 m^3 s^{-1}; Li-kens et al. 1985). The calculated loss of TP, then, through the outlet is the product of surface water TP and outlet volume. Ex-pressed per unit area of lake surface, this rate of loss of TP is ~0.3 μmol m^{-2} d^{-1} for the budgetary period in both years.

Inputs from and through epilimnetic sed-iments—According to the model and cal-culations of the USGS data (T. Winter pers. comm.), seepage into the lake was quite comparable in the summers of 1986 and 1987, averaging 121 and 116 m^3 d^{-1}. The nine geographic sectors identified by the USGS model, however, behave quite dif-ferently from each other (Fig. 3). TDP con-centrations in the pore water varied both through time and between the nine sectors, with generally lower TDP concentrations in the areas of outseepage. To get groundwater flux, we multiplied the appropriate TDP value for the time and sector by the estimate of groundwater inflow to obtain the values for the inseepage of P shown in Fig. 3. Dur-ing both years and for each period we sam-pled, the northwestern sector (DNW) con-tributed most of the groundwater and, consequently, most of the TDP. This large contribution is clearly controlled by the large flow, as the mean TDP concentration in this sector (2.9 μM) is not significantly different from the mean concentration in all areas of inseepage (2.4 μM; Fig. 3). Our best estimate of the integrated groundwater P input is 1.9 μmol m^{-2} d^{-1}. This estimate would translate to an annual seepage input of ~0.02 g P m^{-2} yr^{-1} which is comparable to estimates for eight lakes reviewed by Asbury (1990) and about half that (0.039 g P m^{-2} yr^{-1}) esti-mated for Narrow Lake by Shaw et al. (1990).

In 1986 and 1987, the mean values of outseepage for the budgetary periods were 673 and 647 m^3 d^{-1}. These values are some-what lower than the 1,000 m^3 d^{-1} calculated by Likens et al. (1985), based on the rate at which the lake volume declined during dry periods when inseepage was assumed to be negligible. We assumed that water seeping out of the lake had the TDP concentration of ambient lake water and that no particu-
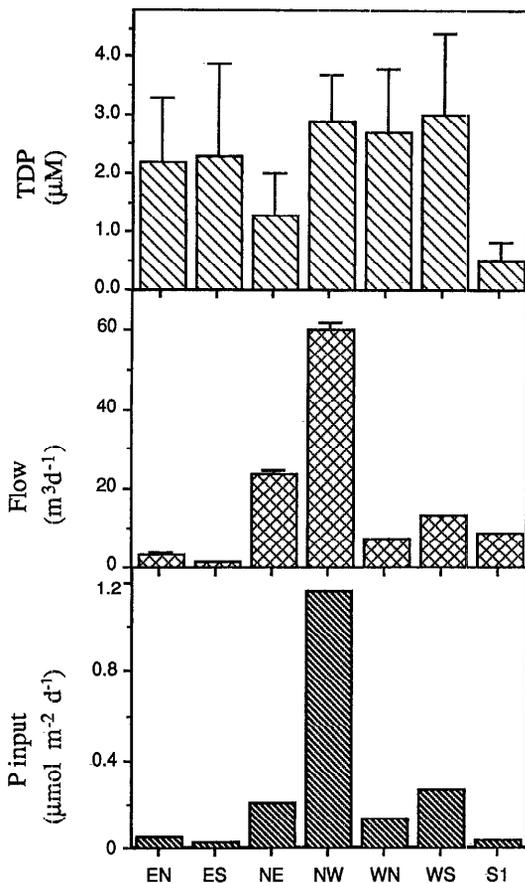
Fig. 3. Potential input of P by groundwater movement through epilimnetic sediments. The X-axis shows the name (by compass direction) of the seven sectors of the lake that experience inseepage (two sectors experience outseepage). The upper panel shows the mean (with SD) concentration of TDP at 10-cm depth in the pore water for each sector during the budgetary periods in 1986 and 1987, and the middle panel shows the mean (with SD) flow. The lower panel gives the P input to the lake expressed per unit area of the entire lake.

late P was lost by seepage. Our estimate of outseeping P is ~0.57 μmol m^{-2} d^{-1} in both 1986 and 1987. Our measurements of pore-water TDP in the outseepage sectors of the lake show values at 10-cm depth of 0.5–0.8 μM, severalfold higher than TDP in the water column. Had we used the average TDP concentration in pore water in the outseepage sectors of the lake for this calculation, our estimate would be ~2.7 μmol P m^{-2} d^{-1}. However, as much of this pore-water TDP is generated by decomposition of par-

ticles in the sediments, it would not be considered as an output of dissolved P from the water column.

The regeneration, measured in benthic chambers, of TDP from epilimnetic sediments was variable across different sites (Table 1) but was quite low throughout the lake. Release rates generally were related across sites to the organic content of sediments (Table 1), with sand sites having an average flux of 0.7 μmol P m^{-2} d^{-1} and organic mud sites having an average flux of 10. The lakewide average release (2.8 μmol P m^{-2} d^{-1}) was calculated by summing the products of area of sediment type by the average flux from that sediment type.

As a check on the low estimates of input from groundwater advection, we attempted to calculate a diffusional input from pore water. The concentration of TDP in epilimnetic interstitial water increased with increasing depth in the sediments for all of the sediment types we investigated. Concentration gradients were steepest at the organic sand and organic mud sites with values of 0.50 and 0.57 μmol liter^{-1} cm^{-1}. The estimated diffusive flux expressed per unit area for each type of site was 0.15 μmol m^{-2} d^{-1} for sand to cobble areas, 1.2 for organic sand, and 1.4 for organic mud sites. Integrating for the entire lake and for the percent of area represented by each type of site, the total diffusive flux of P to the epilimnion would be ~0.4 μmol m^{-2} d^{-1}.

The three different measurements of P input from epilimnetic sediments include different input terms. The chambers should provide the best estimate of input and would include advection, diffusion, and decomposition at the sediment–water interface. The major difficulty with our chamber study is the limited number of sites that we were able to cover and sites of high groundwater input may have been missed. We have much greater aerial coverage of the lake for the groundwater input. This measurement, however, does not include input from material decomposition at the sediment–water interface. The diffusional input is the least relevant since the epilimnetic water is far from still; it serves, however, as a useful lower bound for the input. If we were to add the groundwater input to that measured in

the benthic chambers, we could be double-accounting, as the chambers may include the advective input. However, by doing the calculation this way, we can be fairly certain that we are not underestimating the input from and through epilimnetic sediments. We, therefore, consider these two inputs separately.

Mixing with the hypolimnion—Neither the rate of mixing across the thermocline nor the gradient in TP concentration were large in Mirror Lake. Values of K' (the coefficient of eddy diffusion) were quite low near the top of the thermocline. During the budgetary periods of 1986 and 1987 these K' values ranged from ~0.007 to 0.008 m^2 d^{-1} (Mattson 1989). In the region of the thermocline, the gradients of TP were on average only 0.07 mmol m^{-4} in both years. Thus, the P flux across the thermocline, expressed per unit area of hypolimnion, would be only ~0.5 μmol m^{-2} d^{-1} for 1986 and 1987. The hypolimnion underlies only 50% of the area of the lake. Expressed per unit surface area of the entire lake, then, our values could be 0.25 μmol P m^{-2} d^{-1}. This flux is higher than we previously estimated (0.1 μmol P m^{-2} d^{-1}; Caraco et al. 1988) but quite low in comparison to the P required to fuel new production in the lake (~37 μmol P m^{-2} d^{-1}).

Bathers—Human bathers have been reported to contribute significant amounts of P to lakes (Schulz 1981). Our experimental data suggest, however, that neither human nor canine bathers leach a significant amount of P. The average of three human and one canine bather, each for a 10-min simulated swim, gave a mean P release of 11 ± 33 μmol. In fact, only one of the bathers, a human male, released P at all; the others sorbed it slightly. Our values of P release are far lower than release rates reported by Schulz (1981; ~3 mmol bather^{-1} d^{-1}). Additions of PO_4 to the experimental tub clearly demonstrated that the tub walls did not remove significant P by sorption. Thus, this potential artifact did not account for our low measured values. Schulz (1981) suggested that most of the leakage of P from human bathers is from urination, a vector we did not include in our experiment. This input can, however, be calculated. A typical human

will excrete in urine between 9.7 and 42 mmol of inorganic P (Gaudin and Jones 1989) for an average of 26 mmol d^{-1}. If we assume that half the bathers at Mirror Lake urinate in the lake (there are no toilet facilities at the lake), and excrete a fifth of their daily discharge this way, the average bather input would be 2.6 mmol, a value close to the number reported by Schulz (1981). Adding our measured average leaching input we get a total input of 2.61 mmol per bather per day.

During summer, the lake is used for some recreational swimming and we estimate ~25 swims on a typical weekday and ~150 on a typical 2-d weekend for an average of ~61 swims per day during the study period. At the mean P release rate we measured, these swims would represent only ~0.004 ± 0.01 μmol m^{-2} d^{-1}. If, on the other hand, we were to use the P input value (reported by Schulz 1981), we calculate an input by bathers of 1.5 μmol P m^{-2} d^{-1}. Thus, we have an uncertainty of several orders of magnitude for this input. Our best estimate is based on an average input per bather of ~2.6 mmol d^{-1} (above). This value gives a P input to the entire lake of ~1 μmol m^{-2} d^{-1}.

Discussion

Primary production measurements in lakes indicate that phytoplankton require a substantial nutrient supply in summer (Wetzel 1975). During this same time period, nutrient supply to the lake by surface runoff and precipitation inputs is often quite low (Juday et al. 1927; Lawacz 1985; Caraco et al. 1988). In the case of P inputs in Mirror Lake, runoff plus precipitation accounts for <1% of calculated algal demand. One possible explanation for this phenomenon is that recycling of nutrients in surface waters provides essentially the entire requirement for phytoplankton growth.

Direct estimates of the nutrient supply by zooplankton grazers and microbial mineralization have been made in several aquatic systems. The results of these studies show generally that, given the uncertainties in both nutrient demand and zooplankton supply, the supply by regeneration is essentially in balance with the demand by phytoplankton (e.g. Barlow and Bishop 1965; Fisher et al.
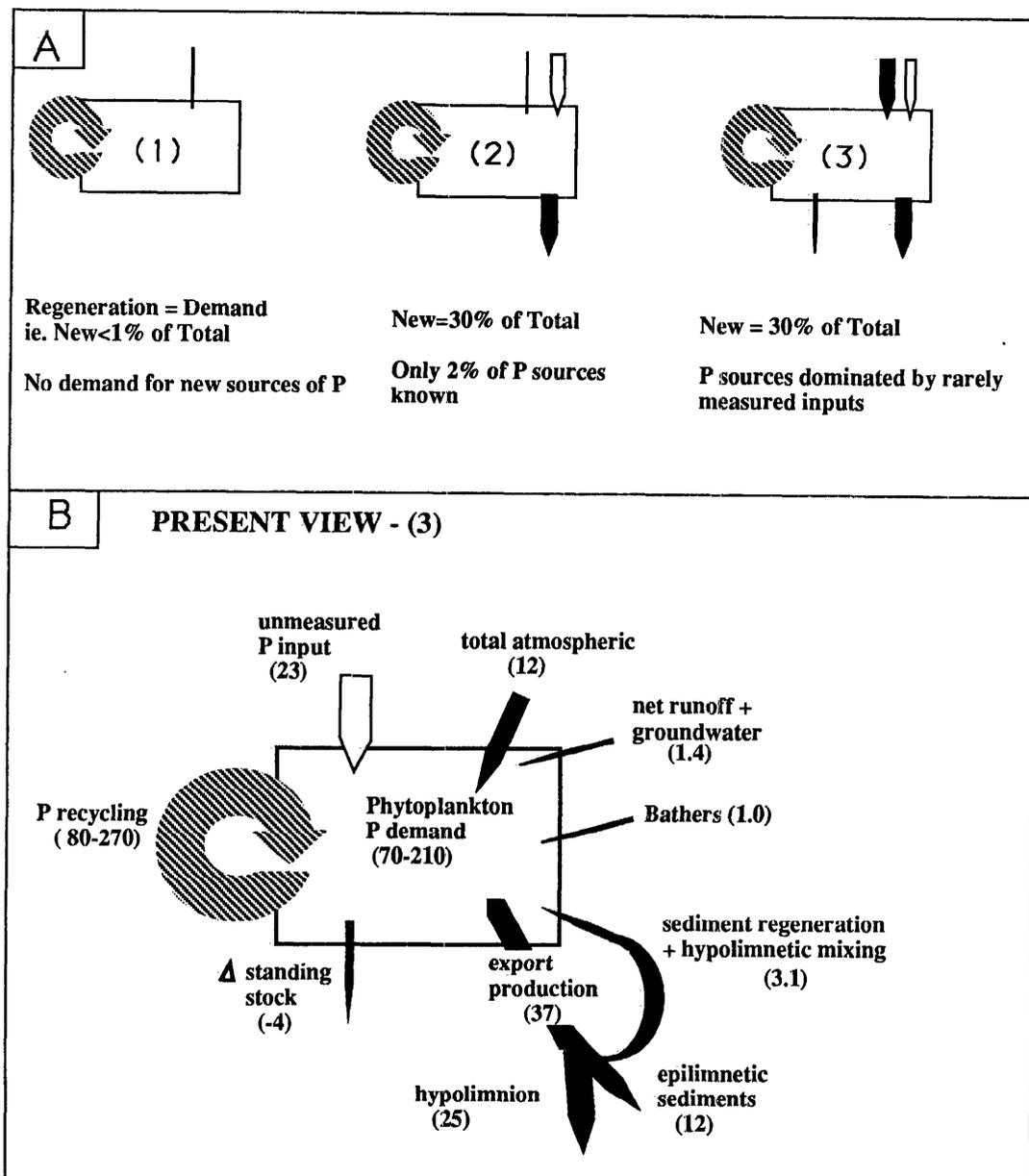
Fig. 4. A. Changing views of P dynamics in the epilimnion of Mirror Lake. 1—Prior to the direct estimate of new production our view was that P inputs to surface waters were low in summer and that algal P demand was almost entirely met by recycling. 2—The direct estimate of new production demonstrated an extreme imbalance in the epilimnetic P budget, measured inputs of P accounted for < 1% of P outputs. 3—The imbalance has been lowered by the measurements reported here. In all three cases, the hatched arrow represents P recycled by zooplankton and bacterial mineralization, the black arrows represent the measured P inputs and outputs to-from surface waters and the clear arrow is unmeasured input needed to balance the P export. These arrows are labeled in panel B.

B. Details of panel A. Present view of P dynamics in epilimnion of the lake. Our measurements suggest that the export of particles by sinking puts a substantial demand on P, which must be met by new inputs to the epilimnion. Measurements made during this study have increased our estimate of P loading from <1 to ~18 μmol P m^{-2} d^{-1}. The present P budget is dominated by inputs of P that are rarely measured. Phytoplankton P demand is calculated as measured primary production in the lake (in C units; Jordan et al. 1985; Cole et al.

Table 2. Phosphorus budget of the epilimnion of Mirror Lake in midsummer. Units, μmol P m^{-2} (of lake surface area) d^{-1}; measurements and ranges are explained in the text. All values are from the present study except precipitation and atmospheric particles, which are from Likens et al. 1985 and Cole et al. 1990, respectively. The columns provide three estimates for the budget: A—our best estimates of all inputs and outputs; B—an estimate using the lowest estimates for all outputs and the highest estimates for all inputs, providing a most balanced case; C—a value using the highest estimates for all outputs and the lowest estimates for all inputs, providing a least balanced case. Note, the negative sign for change in standing stock (P_{delta}) means that the mass of P in the epilimnion increased during the budgetary period. *See text.* The inputs are grouped by frequency in which terms are measured in limnological studies of nutrient loading: frequent (used in essentially all P budgets), occasional (used in some P budgets), and rare (used rarely).

	A Best	B Lowest	C Highest	Frequency of measurement
Outputs				
Sedimentation	37.0	25.0	49.0	
Seepage	0.6	0.6	2.7	
Surface outflow	0.3	0.3	0.3	
Total output	37.9	25.9	52.0	
Inputs				
Precipitation	0.2	0.2	0.2	frequent
Surface inflow	0.4	0.4	0.4	frequent
Hypolimnetic mixing	0.3	0.3	0.3	occasional
Seepage	1.9	1.9	1.9	occasional
Benthic regeneration	2.8	2.8	2.8	occasional
Bathers	1.0	1.5	0.0	rare
Atmospheric particles	12.0	13.0	11.0	rare
Total input	18.6	20.1	16.6	
Change in mass	−4.3	−4.3	−4.3	
Imbalance (export − input − P_{delta})	23.6	10.1	39.8	

1988; Sterner 1989). If we compare an estimate of P supply by regeneration to phytoplankton P demand for Mirror Lake, the same conclusion could be reached (Fig. 4A, case 1). This apparent balance between phytoplankton demand and supply by zooplankton could imply that there is no need to explore further any other aspects of P supply.

Rather than examining the nutrient demand of phytoplankton as a single entity, however, this demand can be considered as two distinct components: recycled and new P demand. When the new P demand is considered independently, the interpretation of P dynamics changes dramatically. In Mirror Lake, for example, our view changed from an essentially balanced P demand, despite extremely small measured new inputs of P to surface waters (Fig. 4A, case 1), to a P budget that was highly imbalanced (Fig. 4A, case 2). The overwhelming imbalance led us to re-evaluate inputs of P to surface water and export of P from surface waters in the present study. In our present view new production accounts for ~35% of total primary production and requires an input of P of some 37 μmol P m^{-2} d^{-1}, which can only be accounted for by external (not recycled) inputs and P_{delta} (Fig. 4A, case 3, and B).

Our best representation of the P budget of the epilimnion in the lake is provided in Table 2. The inputs of P clearly are dominated by sources that rarely are measured in traditional element budget studies for lakes. Benthic remineralization plus atmo-

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1989; Ochs 1991) times a P:C ratio of 1:100. Zooplankton recycling is calculated in two ways. First, from estimates of zooplankton and microflagellate respiration (Cole et al. 1989) and a P:C of 1:100 (giving 80 μmol P m^{-2} d^{-1}). Second, using an empirical approach and predictors measured in the lake (giving a value of 270 μmol P m^{-2} d^{-1}; outlined by Makarewicz et al. 1985). The measurements of inputs and outputs of P to-from surface waters are explained in the text.

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spheric particles (two rarely measured P sources) together account for ~80% of the measured P income to the lake, while surface water flow (the term measured most often as the primary P input) accounts for only 2% of measured P income. In fact, the potential input from human bathers is as large or larger than the fluvial input. Outputs are dominated by the sinking of particulate matter out of the epilimnion.

By measuring some P inputs that are not measured commonly, we have improved greatly the P budget for the epilimnion of the lake since we first analyzed it (Caraco et al. 1988), and our new view of epilimnetic P cycling in Mirror Lake has been changed dramatically by this re-evaluation. Previously, it was considered that summer P inputs to the lake were extremely low (<0.5 μmol m^{-2} d^{-1}), due to the low runoff. By considering some sources of P normally ignored, we have increased our measurement of P inputs by >30-fold (from 0.6 to 19 μmol m^{-2} d^{-1}). We now realize that despite low stream flows summer is actually a period of enhanced P loading and that daily loading during this period exceeds the annual average measured daily loading (Likens et al. 1985).

In our previous P budget, we reported that the outputs of P exceeded the inputs by some 50-fold (Fig. 4B; Caraco et al. 1988). The present P budget for the epilimnion of the lake reduces this imbalance significantly. Our best estimate is the sum of all estimated outputs (including here the change in standing stock). This estimate exceeds the sum of estimated inputs by ~23 μmol P m^{-2} d^{-1}. All of the terms that were evaluated have uncertainties; the term in the present budget with the largest uncertainty is sedimentation (Table 2). If we were to use the range in estimated values that would achieve the closest mass balance, measured outputs would exceed inputs by only 10.1 μmol P m^{-2} d^{-1}. Calculating for the other extreme, however, we get an apparent imbalance of ~39.8 μmol P m^{-2} d^{-1}. We can say only that we still are likely missing a P source and this P source could be extremely important.

It is interesting to speculate on the nature of this P input. Possibilities that we have considered, but have no estimates for, are desorption of P from chaoborids (or other invertebrates) that migrate at night from sediments to the water column and dissolution and oxidation in surface waters of reduced P compounds, such as phosphine, which might be transported from anoxic sediments by methane ebullition (Dévai et al. 1988). Although the suggestion that these inputs will prove important may seem far-fetched, the results of this study have already demonstrated that new production in the lake is supported primarily by P sources that are measured rarely (Table 2).

Conclusions

Although we have some uncertainty about both the absolute magnitude of new production, as well as the degree to which our epilimnetic P budget is in imbalance, several firm conclusions about P cycling can be drawn. During midsummer, new production in Mirror Lake is equal to ~35% of total phytoplankton production. Without new inputs of P to surface waters P content would be depleted rapidly (being completely exhausted in <1 month) and all phytoplankton production would cease. Despite low stream flows, summer is actually a period of enhanced P loading; daily loading to the lake during this period exceeds the annual average measured daily loading. Important P sources during summer such as atmospheric particulates and benthic regeneration are sources that rarely are measured and may be of general importance. For most lakes, it is not known what nutrient sources support new production during summer and the original question of Juday et al. (1927) has not been answered satisfactorily.

References

ASBURY, C. E. 1990. The role of groundwater seepage in sediment chemistry and nutrient budgets in Mirror Lake, New Hampshire. Ph.D. thesis, Cornell Univ. 275 p.

BARLOW, J. P., AND J. W. BISHOP. 1965. Phosphate regeneration by zooplankton in Cayuga Lake. Limnol. Oceanogr. 10: R15–R25.

CAPBLANCQ, J. 1990. Nutrient dynamics and pelagic food web interactions in oligotrophic and eutrophic environments: An overview. Hydrobiologia 207: 1–14.

CARACO, N. F., J. J. COLE, G. E. LIKENS, M. D. MATTSON, AND S. NOLAN. 1988. A very imbalanced nutrient budget for Mirror Lake, New Hampshire, U.S.A. Int. Ver. Theor. Angew. Limnol. Verh. 23: 170–175.

CARLTON, R. G., AND R. G. WETZEL. 1988. Phosphorus flux from lake sediments: Effect of epipelic algal oxygen production. Limnol. Oceanogr. 33: 562–570.

COLE, J. J., N. F. CARACO, AND G. E. LIKENS. 1990. Short-range atmospheric transport: A significant source of phosphorus to an oligotrophic lake. Limnol. Oceanogr. 35: 1230–1237.

——, ——, D. L. STRAYER, C. OCHS, AND S. NOLAN. 1989. A detailed organic carbon budget as an ecosystem-level calibration of bacterial respiration in an oligotrophic lake during midsummer. Limnol. Oceanogr. 34: 286–296.

DAVIS, M. B., AND M. S. FORD. 1985. Late-glacial and Holocene sedimentation, p. 346–355. In G. E. Likens [ed.], An ecosystem approach to aquatic ecology: Mirror Lake and its environment. Springer.

DÉVAI, I., L. FELFÖLDY, I. WITTNER, AND S. PLÓSZ. 1988. Detection of phosphine: New aspects of the phosphorus cycle in the hydrosphere. Nature 333: 343–345.

DUGDALE, R. C., AND J. J. GOERING. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. Limnol. Oceanogr. 12: 196–206.

EPPLEY, R. W., AND B. J. PETERSON. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature 282: 677–680.

FISHER, T. R., K. M. MORRISSEY, P. R. CARLSON, AND L. F. ALVES. 1988. Nitrate and ammonium uptake by plankton in an Amazon River floodplain lake. J. Plankton Res. 10: 7–29.

GARDNER, W. D. 1980. Sediment trap dynamics and calibration. A. Laboratory evaluation. J. Mar. Res. 38: 17–39.

GAUDIN, A. J., AND K. C. JONES. 1989. Human anatomy and physiology. Harcourt Brace.

HAMA, T., K. MATSUNAGA, N. HANDA, AND M. TAKAHASHI. 1990. Nitrogen budget in the euphotic zone of Lake Biwa from spring to summer, 1986. J. Plankton Res. 12: 125–131.

HARGRAVE, B. T. 1973. Coupling carbon flow through some pelagic and benthic communities. J . Fish. Res . Bd. Can. 30: 1317–1326.

JASSBY, A., AND T. POWELL. 1975. Vertical patterns of eddy diffusion during stratification in Castle Lake, California. Limnol. Oceanogr. 20: 530–543.

JORDAN, M. J., G. E. LIKENS, AND B. J. PETERSON. 1985. Organic carbon budget, p. 292–301. In G. E. Likens [ed.], An ecosystem approach to aquatic ecology: Mirror Lake and its environment. Springer.

JUDAY, C., E. A. BIRGE, G. I . KEMMERER, AND R. J. ROBINSON. 1927. Phosphorus content of lake waters of northeastern Wisconsin. Trans. Wis. Acad. Sci. 23: 233–248.

LAWACZ, W. 1985. Factors affecting nutrient budget in lakes of the Jorka River watershed Masurian

Lakeland Poland 11. Nutrient budget with special consideration to phosphorus retention. Ekol. Pol. 33: 357–382.

LEHMAN, J. T., AND T. NAUMOSKI. 1986. Net community production and hypolimnetic nutrient regeneration in a Michigan lake. Limnol. Oceanogr. 31: 788–797.

LEVINE, S. N., M. P. STAINTON, AND D. W. SCHINDLER. 1986. A radiotracer study of phosphorus cycling in a eutrophic Canadian Shield lake, Lake 227. Can. J. Fish. Aquat. Sci. 43: 366–378.

LIKENS, G. E. [ED.]. 1985. An ecosystem approach to aquatic ecology: Mirror Lake and its environment. Springer.

——, J. S. EATON, N. M. JOHNSON, AND R. S. PIERCE. 1985. Flux and balance of water and chemicals, p. 135–155. In G. E. Likens [ed.], An ecosystem approach to aquatic ecology: Mirror Lake and its environment. Springer.

MAKAREWICZ, J. C., G. E. LIKENS, AND M. J. JORDAN. 1985. The pelagic region, p. 322–337. In G. E. Likens [ed.], An ecosystem approach to aquatic ecology: Mirror Lake and its environment. Springer.

MATTSON, M. D. 1989. A metabolic electron budget for the sediments of Mirror Lake, New Hampshire. Ph.D. thesis, Cornell Univ. 326 p.

MENZEL, D. W., AND N. CORWIN. 1965. The measurement of total phosphorus in seawater based on the liberation of the organically bound fraction by persulfate oxidation. Limnol. Oceanogr. 10: 280–282.

MOELLER, R. E., AND G. E. LIKENS. 1978. Seston sedimentation in Mirror Lake, New Hampshire and its relationship to long-term sediment accumulation. Int. Ver. Theor. Angew. Limnol. Verh. 20: 525–530.

MURPHY, J., AND J. P. RILEY. 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta 27: 31–36.

OCHS, C. A. 1991. Population ecology of the bacterioplankton of Mirror Lake, New Hampshire. Ph.D. thesis, Cornell Univ. 307 p.

PACE, M. L., G. A. KNAUER, D. M. KARL, AND J. H. MARTIN. 1987. Primary production, new production and vertical flux in the eastern Pacific Ocean. Nature 325: 803–804.

REDFIELD, A. C., B. H. KETCHUM, AND F. A. RICHARDS. 1963. The influence of organisms on the composition of sea-water, p. 26–77. In M. N. Hill [ed.], The sea. V.2. Interscience.

SCHULZ, L. 1981. Nutrient input in lakes by bathers. Zentralbl. Bakteriol. Mikrobiol. Hyg. Ser. B Umwelthyg. Krankenhaushyg. Arbeitshyg. Praev. Med. 173: 528–548.

SHAW, R. D., J. F. H. SHAW, H. FICKER, AND E. E. PREPAS. 1990. An integrated approach to quantifying groundwater transport of phosphorus to Narrow Lake, Alberta. Limnol. Oceanogr. 35: 870–886.

STERNER, R. W. 1989. The role of grazers in phytoplankton succession, p. 107–170. In U. Sommer

Caraco et al.

[ed.], Plankton ecology: Succession in plankton communities. Springer.

WETZEL, R. G. 1975. Limnology. Saunders.

WINTER, T. C. 1991. Geohydrologic setting of Mirror Lake, West Thornton. U.S. Geol. Surv. Invest. Rep. 89-4266.

———, J. S. EATON, AND G. E. LIKENS. 1989. Eval-uation of inflow to Mirror Lake, New Hampshire. Water Res. Bull. 25: 991–1008.