

Net community production and hypolimnetic nutrient regeneration in a Michigan lake¹

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Abstract

Net community oxygen production in Third Sister Lake, Michigan, was calculated from concentration gradients, eddy diffusion, and gas flux at the lake surface. The trophogenic zone extended on average to 4.5 m from April to August. Vertical flux of dissolved P provided negligible support for the productivity during this time. Stoichiometries for biomass production from inorganic N and P were inferred from enclosure experiments and from vertical profiles. N and P accumulated in the hypolimnion at a ratio of 24:1 by atoms, whereas ratios in the algae averaged 9.5:1. On the basis of areal rates of nutrient remineralization and the oxygen budget, most of the net community production from April to August could be assigned to the open water rather than to the littoral region. Littoral production processes are relatively isolated from the open water in this small, sheltered lake during the time of thermal stratification.

The relationships between biological production and nutrient regeneration are of interest for both theoretical and practical reasons. The extent to which production is fueled by recycled nutrients rather than by allochthonous inputs provides an index of how tightly coupled the biological community may be and also of the relative importance of physical processes compared with biological ones (Eppley and Peterson 1979).

Primary production within a euphotic zone relies on nutrients from sources external to the lake, from shallow sediments, vertical water column fluxes, and in situ regeneration. Net community production, as used here, refers to the balance between oxygen-producing and oxygen-consuming processes at different depths in the lake. Net production thus depends on all of the nutrient sources identified above, with some of the processes being very interdependent. In situ catabolism of organic matter in the euphotic zone leads to both oxygen consumption and nutrient regeneration. Rates of nutrient return from sediments and hypolimnia rely in part on net production in the water over-

lying them. The nutrients may be returned, however, at different rates and in different proportions than they were deposited. Thus sediments of lakes on the Canadian Shield may retain much phosphate even when they become anoxic (Schindler et al. 1980), whereas those of the English Lake District release it (Mortimer 1941, 1942). These within-lake nutrient returns are sometimes as important as external loading (Nürnberg 1984), and they can confound efforts to control eutrophication (Lorenzen et al. 1976).

We studied the relationship between hypolimnetic metabolism of nutrients and net community production in Third Sister Lake, a moderately eutrophic lake in southeastern Michigan. We wished to discover how much of the production could be supported by nutrient fluxes through the water column, and conversely, how rates of accumulation of inorganic nutrients in the hypolimnion could be related to concurrent rates of production. We adopted an integrative approach based on water column chemistry and estimated vertical diffusive flux. The calculations are consequently restricted in time by the diffusivity estimates, but they apply to the conditions in Third Sister Lake shortly after ice-out to the onset of convective hypolimnetic entrainment in the fall. We sought to answer three questions with

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our investigation: How much nutrient must be supplied to the trophogenic zone to support net community production during the study period, and can the probable sources be quantified? Is the measured O_2 budget dominated by processes in the offshore community or the littoral region? Are rates of nutrient accumulation in the hypolimnion comparable in magnitude to the productivity of the overlying water?

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Methods

Third Sister Lake is a small kettle lake (3.85 ha) in southern Michigan that occupies a sheltered depression within the Saginaw Forest Reserve administered by the University of Michigan. The watershed covers 110 ha, of which 88.5 ha are fields lying outside the forest (from U.S. Geol. Survey topographic maps). The morphometry and benthos were described by Eggleton (1931). The littoral region of the lake covers 30% of its surface area and contains 6% of its volume (Ball 1948). Present maximum and mean depths are 16.5 and 7.2 m. The lake is moderately eutrophic, with 5–40 μg Chl *a* liter⁻¹ and 0.5–1.5 μM TP in the epilimnion for most of the ice-free period. Secchi disk transparencies are typically 1–3 m. The lake has no permanent inlets, and intermittent drainage is westward to the Huron River. Overland runoff provides conspicuous inputs to the lake during and after storms. Some groundwater input is likely.

We investigated physical and chemical properties from April to October 1981 at 2–3-week intervals. We measured temperatures with a Whitney TC-5C thermistor calibrated to $\pm 0.05^\circ\text{C}$ against an NBS-calibrated mercury thermometer and photosynthetically active radiation (400–700 nm) with a submersible LiCor LI-193S spheri-

cal-corrected sensor and LI-188 integrator. From plots of the natural logarithm of PAR against depth we calculated attenuation coefficients (m^{-1}) by linear regression.

We collected water samples from discrete depths with an 8.2-liter Van Dorn sampler, transported them to the laboratory within 1 h, and filtered them through GF/F filters. The filters were stored frozen until analysis. Pigments were measured spectrophotometrically after grinding the filters in ice-cold 90% acetone for 2 min inside a borosilicate tissue-grinder with a motor-driven Teflon pestle. The resulting slurry was filtered to remove glass fibers and cell fragments. We used Lorenzen's correction for pheopigments (Strickland and Parsons 1972). Nutrient determinations followed Stickland and Parsons (1972) for soluble reactive P, nitrate, and nitrite; Solórzano (1969) for ammonium; Menzel and Corwin (1965) for total P and dissolved P; and Golterman (1969) for soluble reactive Si. Ca, Mg, Na, K, Fe, and Mn were measured by flame atomic absorption spectrometry with a Perkin-Elmer model 403 with an oxygen-acetylene flame; lanthanum was added to samples for Ca and Mg determinations. Alkalinity and chloride were measured by potentiometric titration followed by Gran's plot analysis (Stumm and Morgan 1970). Sulfate was measured turbidometrically (Golterman 1969). Oxygen, pH, and conductivity were measured either *in situ* with a Whitney-Montedoro Mark V submersible instrument cluster or in the laboratory (Orion O_2 electrode) from samples collected in 250-ml glass-stoppered reagent bottles.

We obtained daily integrated measurements of incident solar radiation ($\text{kJ m}^{-2} \text{d}^{-1}$) from a site in Ann Arbor, 5 km from the lake, maintained by the University of Michigan, Department of Atmospheric and Oceanic Science. We reduced the values by 6% to account for reflection at the air-water interface at this latitude (R. Stauffer pers. comm.). For wavelengths other than those of measured PAR, spectral attenuation coefficients were obtained as described by Lehman (1979). Rates of eddy diffusion in the metalimnion were calculated by the heat flux-gradient method of Jassby and Powell (1975). Temperatures were measured at 1-m

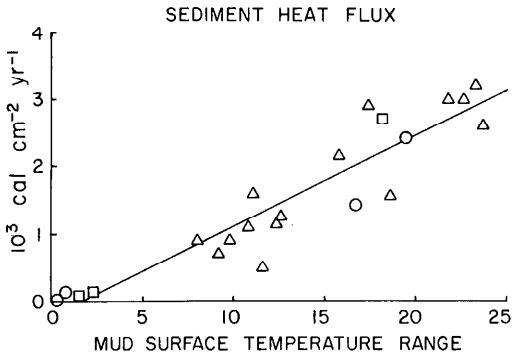


Fig. 1. Sediment heat budgets vs. annual temperature range at the sediment-water interface reported by Birge et al. (1927) for Lake Mendota (Δ), and by Likens and Johnson (1969) for Tub Lake (\square) and Stewart's Dark Lake (\circ). The sediment heat budget is calculated as the integral quantity of heat gained by a sediment profile during a heating period (i.e. maximum heat content less minimum heat content). Data represent heat gain over single heating periods at depths of 8, 12, 18, and 23.5 m in Lake Mendota; 0.3, 0.9, 5.7, and 6.8 m in Stewart's Dark Lake; and 0.8, 5.5, and 8.0 m in Tub Lake.

intervals and we used 1-m strata in our calculations. We included heat exchange with the sediments in our estimates of heat flux. From the data of Birge et al. (1927) and Likens and Johnson (1969) we discovered a linear relation between the heat budget of the sediments and the annual range of temperatures experienced at the mud-water interface at measured depths (Fig. 1). The data were obtained from three lakes at similar latitude to Third Sister, all in Wisconsin. For purposes of budget calculations we assumed that the heat flux was distributed uniformly over a 6-month heating period.

Rates of oxygen flux across the lake surface were calculated from

$$\text{Flux} = -D/\tau([O_2]_{0\text{ m}} - [O_2]_{\text{sat}}) \quad (1)$$

where $[O_2]_{0\text{ m}}$ is the measured concentration of O_2 in surface water and $[O_2]_{\text{sat}}$ is the saturation value predicted by equation 7 of Mortimer (1981), applied at the surface elevation of the lake (275 m). We used a boundary layer thickness (τ) of 200 μm , consistent with that of other small lakes (Peng and Broecker 1980), so that $D/\tau = 0.4\text{ m d}^{-1}$. We computed fluxes between sampling dates by linear interpolation of the fluxes.

We estimated net rates of oxygen pro-

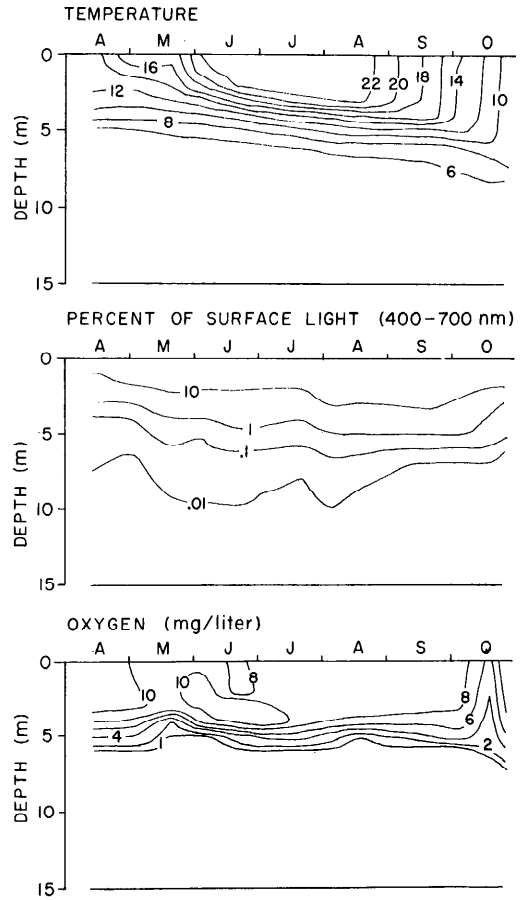


Fig. 2. Isopleth diagrams for temperature, light, and O_2 in Third Sister Lake, 1981. Light is %PAR at depth with respect to reading just below lake surface.

duction as a function of depth by mass balance: measured change in O_2 concentrations = change resulting from concentration gradients, eddy diffusion, and basin morphology + biological reactions (e.g. photosynthesis and respiration), or,

$$\frac{\partial S(Z)}{\partial t} = \frac{\partial}{\partial [A(Z) \times Z]} \times \left[A(Z) \times K(Z) \frac{\partial S(Z)}{\partial Z} \right] + R(Z) \quad (2)$$

where $A(Z)$ = area at depth Z (m^2), $K(Z)$ = eddy diffusivity at depth Z ($\text{m}^2\text{ d}^{-1}$), $S(Z)$ = concentration at depth Z (mmol m^{-3}), and $R(Z)$ = reaction rate ($\text{mmol m}^{-3}\text{ d}^{-1}$).

Table 1. Mean coefficients of vertical eddy diffusion (K_z , $m^2 d^{-1}$), with estimated standard errors, corrected for molecular heat conduction for Third Sister Lake, 14 April–17 August 1981.

Depth (m)	K_z	(SE)
2.5	0.0328*	0.0027
3.5	0.0141	0.0017
4.5	0.0132	0.0018
5.5	0.0162	0.0033
6.5	0.0319	0.0111
7.5	0.0470	0.0191
8.5	0.3390	0.2112

* Calculated for 4 May–17 August.

Boundary constraints were the estimated O_2 fluxes across the lake surface together with an assumption that the epilimnion was well mixed. We solved Eq. 2 for $R(Z)$ in discrete strata between successive sampling dates. The depth interval for calculations was set to 1 m below 2.5 m to correspond with the estimates of $K(Z)$. Values for O_2 concentrations were interpolated where necessary to conform with the calculation scheme.

To estimate the stoichiometry of N and P in algal biomass we plotted the relationships among chlorophyll increases and uptake of PO_4^{3-} and inorganic N ($NH_4^+ + NO_2^- + NO_3^-$) from in situ enclosures (Lehman and Sandgren 1982; Naumoski and Lehman 1984). Enclosures containing from 100 liters to 3 m^3 , closed to the sediments, were enriched with inorganic salts of P and N and changes in Chl *a* and nutrients followed through time. For estimates of stoichiometry, we used only measurements after the first 4 days to eliminate anomalies introduced by rapid initial uptake and storage of P (Lehman and Sandgren 1982).

Rates of nutrient supply to Third Sister Lake from its watershed were estimated from export coefficients proposed by Reckhow (1980) in conjunction with our measurements of watershed area and land use. We used median values of 0.206 kg P $ha^{-1} yr^{-1}$, 2.46 kg N $ha^{-1} yr^{-1}$ for the forested land and 0.81 kg P $ha^{-1} yr^{-1}$, 5.19 kg N $ha^{-1} yr^{-1}$ for the fields, which are planted mainly in grass and hay.

Errors were propagated through all calculations by first-order uncertainty analysis (Meyer 1975).

Table 2. Vertical distribution of major dissolved chemical ionic species on 14 April 1981. All values μM except as noted. In situ densities were computed according to Chen and Millero (1977) as functions of dissolved salts, temperature, and pressure, $d(S,T,P)$.

Depth (m)	Ca ²⁺	Mg ²⁺	Na ⁺	K ⁺	NH ₄ ⁺	Mn ²⁺	SO ₄ ²⁻	Cl ⁻	HCO ₃ ⁻	Conductivity ($\mu S cm^{-1}$)	Diss. salts (mg cm^{-3})	T (°C)	$d(S,T,P)$ (g cm^{-3})
0	681	338	478	141	0.9	0.9	93	502	1,837	285	0.191	13.04	0.999520
3	708	337	477	141	1.1	0.8	94	551	1,952	280	0.201	11.71	0.999701
6	800	348	453	159	21.0	1.9	88	*	2,079	300	0.213	4.43	1.000171
9	776	361	473	156	60.8	14.1	101	554	2,272	315	0.227	4.00	1.000198
12	812	363	469	153	104.3	33.8	79	534	2,401	327	0.235	3.98	1.000220
15	826	375	476	167	161.5	53.5	71	545	2,621	345	0.252	4.10	1.000248

* No data.

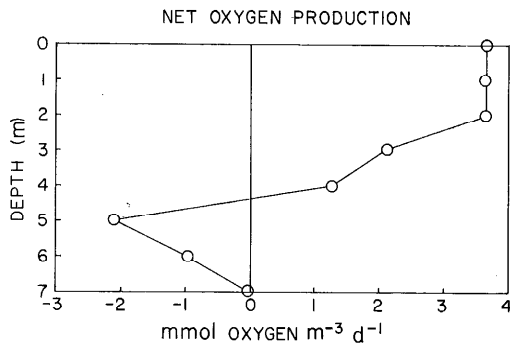


Fig. 3. Calculated net community O_2 production for 14 April–17 August 1981, from Eq. 3.

Results

Oxygen production rates—Heat content of the lake increased uniformly from 14 April to 17 August (Fig. 2), so we confined our estimates of eddy diffusion to that period, which included eight sampling dates. In situ heating by solar radiation contributed little to measured rates of heating below 4 m. Average rates of eddy diffusion in the metalimnion are listed in Table 1. Temperature gradients were usually too slight in the surface 3 m to apply the flux-gradient model validly. The profiles suggested that the water was well mixed to 2.5 m on a daily basis after 4 May and that mixing extended to 3.5 m before that date.

Like many other small sheltered lakes in southern Michigan, Third Sister Lake did not turn over when its ice cover melted in 1981, but instead stratified with its hypolimnion already anoxic (Fig. 2). Fe was not detectable throughout the water column, and hypolimnetic sulfate was progressively reduced to sulfide through summer. The gradient in dissolved chemical species in April (Table 2) contributed to density differences below 6 m that were from 1.47 to 1.87 times as large as those caused by temperature and pressure alone. Persistent temperature inversions of as much as $0.03^\circ\text{C m}^{-1}$ at depth were rendered stable by this chemical stratification. Maximum surface temperature of 25°C was recorded on 22 July; the epilimnion remained warmer than 23°C from 23 June to 17 August. Surface oxygen concentrations equaled or exceeded saturation by up to 19% from April to August (mean =

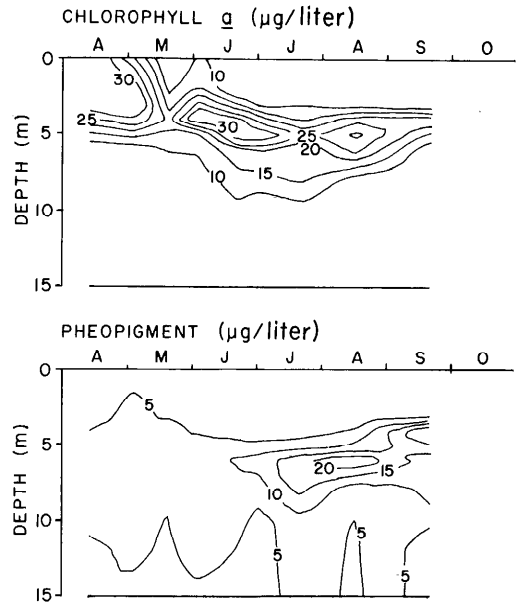


Fig. 4. Isopleth diagrams for Chl *a* and pheopigment in Third Sister Lake, 1981.

8.9%, SE = 3.4%), except on 23 June when concentrations were only 92% of saturation.

Average net rates of oxygen production from April to August are plotted in Fig. 3. The averages represent total net O_2 production divided by the time interval (125 d). The lake was anoxic below 8 m and so calculations based on oxygen gradients yield zero flux below that depth. As judged from net O_2 production the trophogenic zone extends to 4.5 m on average, a depth to which slightly $<1\%$ of surface PAR penetrates (Fig. 2). By the nature of the analysis the values in Fig. 3 represent net community production rates, and they include processes at the sediment surface as well as in the adjacent water.

Areal rates of production were calculated by trapezoidal approximation with attention to basin morphometry as

$$P = 1/A_0 \times \sum_i [\bar{R}(Z_i) \times A(Z_i) + \bar{R}(Z_{i+1}) \times A(Z_{i+1})] \times \Delta Z/2; \quad (3)$$

rates were $9.28 \text{ mmol } O_2 \text{ m}^{-2} \text{ d}^{-1}$ from 0 to 4.5 m, the approximate depth of the trophogenic zone, and $7.43 \text{ mmol } O_2 \text{ m}^{-2} \text{ d}^{-1}$ from 0 to 7 m ($A_0 = 38,500 \text{ m}^2$).

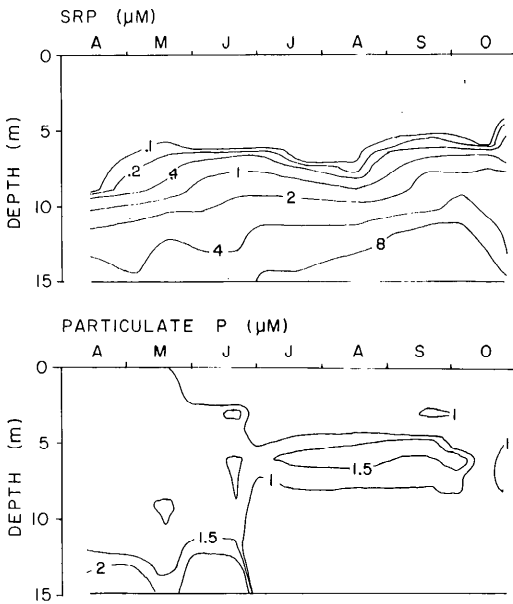


Fig. 5. Isopleths for SRP and particulate P, 1981.

Nutrient dynamics—The vertical distribution of net O₂ production (Fig. 3) differs from the pattern of algal biomass measured as Chl *a* (Fig. 4). Concentrations of phytoplankton are maximal at the lower limit of the trophogenic zone, where net oxygen production by the entire plankton and benthos is close to zero. The chlorophyll maxima occur near strong gradients in SRP and NH₄⁺ (Figs. 5 and 6). Mass balance calculations like those for O₂ show that uptake of upward-diffusing SRP is greatest at 6 m and of NH₄⁺ at 5 m. We made these calculations without allochthonous N and P loading to find out whether vertical fluxes could possibly support the productivity of the trophogenic zone (see below). Upward flux at 4.5 m was only 0.018 µmol m⁻² d⁻¹ for SRP and 121 µmol m⁻² d⁻¹ for DIN (NH₄⁺ + NO₂⁻ + NO₃⁻).

The relevance of these nutrient fluxes to measured net rates of oxygen production depends on the stoichiometries between nutrients and plankton biomass. We have two ways of estimating these relations. One is to compare increments in chlorophyll that accompanied uptake of nutrients added to enclosures in the lake (Lehman and Sandgren 1982; Naumoski and Lehman 1984).

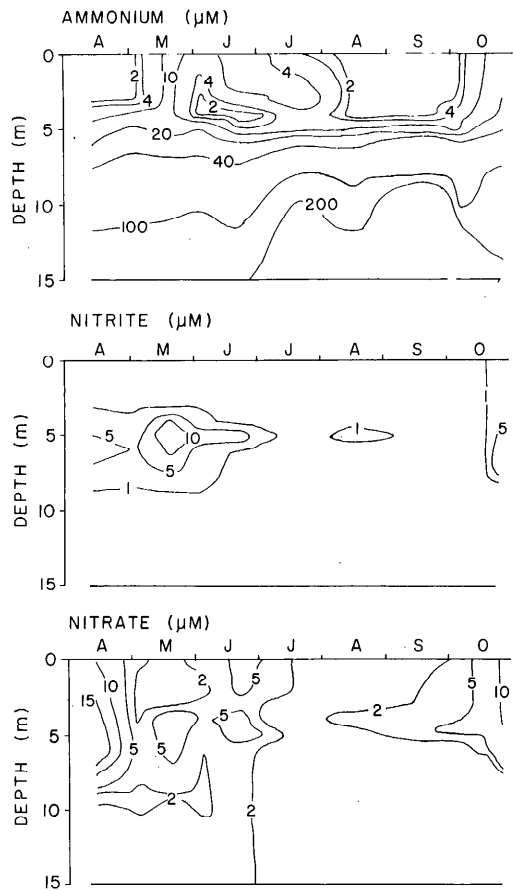


Fig. 6. Isopleths for dissolved inorganic N chemical species, 1981.

In Fig. 7 we plot changes in chlorophyll that accompanied uptake of added inorganic P and N from three experiments: 9–20 June 1980, 24–30 June 1980 (Lehman and Sandgren 1982), and 5–18 August 1981 (Naumoski and Lehman 1984). The data were pooled because there are no systematic differences among the slopes for each experiment singly. From Fig. 7 we determine that 1 µmol P yields 11.7 (SE = 1.4) µg of Chl *a* and that 1 µmol N yields 1.23 (SE = 0.16) µg of Chl *a*. Because there are no nonlinearities in the plots we think that the slopes provide good estimates of stoichiometries from the surface to 3 m, which is the range of depths where the enclosures were deployed.

The second way to determine the stoi-

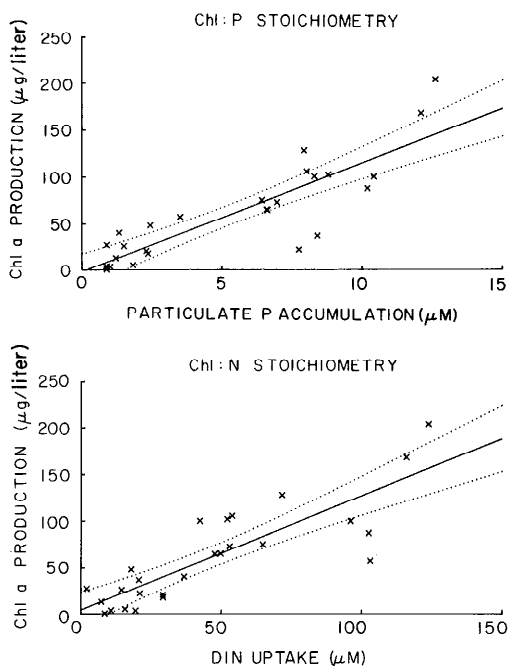


Fig. 7. Changes in concentrations of Chl *a* + pheopigments in enclosures compared to accumulation of particulate P (upper) and removal of inorganic N ($\text{NH}_4^+ + \text{NO}_2^- + \text{NO}_3^-$, lower). The 95% confidence regions for the regression lines are shown.

chiotries is to examine relationships between chlorophyll and particulate P in vertical profiles (Fig. 8). From July to August there was considerable vertical variation in concentrations of Chl (Fig. 4) and particulate P (Fig. 5) within the epilimnion and metalimnion. That circumstance allowed us to estimate stoichiometries directly. We used the sum of both Chl *a* and pheopigment for these comparisons because the measured particulate P exists not only in living cells but also in dead algae and algal fragments.

Stoichiometries derived from vertical profiles suggest that much more pigment is produced per unit mass of P in the metalimnion than we measured in the epilimnetic enclosures. We summarize the results in Table 3. The ratios differed significantly from date to date; for the three profiles in Table 3 the average value is 34.9 (SE = 9.9) $\mu\text{g Chl} : \mu\text{mol P}$. As is evident from the positive *x*-intercept in Fig. 8, not all the particulate P is present as algae or chlorophyll-containing algal fragments; some is bound

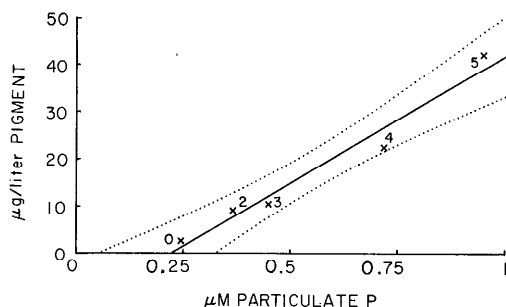


Fig. 8. Relation between Chl *a* + pheopigment and particulate P in the epilimnion of Third Sister Lake, 3 July 1981. Sample depths are identified by numerals next to the symbols. The 95% confidence region for the regression line is shown.

in zooplankton, bacteria, and detritus. These components probably contribute to the variability that we find. For our stoichiometric conversions we consequently used 11.7 (SE = 1.4) $\mu\text{g Chl} : \mu\text{mol P}$ from the surface to 3 m and 34.9 (SE = 9.9) below that; the requirement for N is tenfold greater. Based on the changes in Chl + pheopigments that accompanied uptake of DIC for algal growth in August 1981 (Naumoski and Lehman 1984) we compute a C:Chl ratio of 4.60 $\mu\text{mol} \mu\text{g}^{-1}$ (SE = 0.42, $n = 6$). We have no way to use the vertical profiles of measured properties to investigate variability of this ratio with depth or with time, but we note that 4.6 $\mu\text{mol C} (\mu\text{g Chl})^{-1} = 55 \mu\text{g C} (\mu\text{g Chl})^{-1}$, which is close to a conventional conversion factor of 50.

Using these conversion ratios together with the observed vertical distributions of chlorophyll in the lake during the study period, we conclude that C:P ratios (by atoms) were 73 (SE = 8.1) and that C:N ratios were 7.7 (SE = 1.6) for the phytoplankton of the trophogenic zone. The calculated vertical flux of P at 4.5 m could thus support an O_2 production rate (figuring $\text{O}_2 : \text{C} = 1.0$ in the trophogenic zone) of only 0.0013 (SE = 0.0001) $\text{mmol m}^{-2} \text{d}^{-1}$ and NH_4^+ flux could support 0.93 (SE = 0.19) $\text{mmol m}^{-2} \text{d}^{-1}$, both far short of the required 9.3 $\text{mmol m}^{-2} \text{d}^{-1}$.

Remineralization at the sediments—We measured the accumulation of both SRP and NH_4^+ below 8 m (Fig. 9) in order to assess the extent to which production in the tro-

Table 3. Stoichiometries derived from in situ enclosure experiments and from vertical profiles. Ratios are $\mu\text{g Chl}$ to $\mu\text{mol P}$ or N .

	Chl:P	(SE)	Chl:N	(SE)
Enclosure exp.	11.69	(1.41)	1.23	(0.16)
3 Jul 1981	53.88	(5.94)		
22 Jul 1981	20.67	(1.79)		
17 Aug 1981	30.13	(4.11)		

phogenic zone is coupled to simultaneous release rates in the hypolimnion. We computed average accumulation rates from April to August by linear regression. To these measured rates of accumulation we added estimates of the vertical flux of both SRP and NH_4^+ at 8 m. The resulting figures, 1.90 (SE = 0.33) mol SRP d^{-1} and 45.3 (SE = 7.8) mol NH_4^+ d^{-1} , represent net release of these substances from the hypolimnetic sediments. After these rates were divided by the area of sediment below 8 m (17,100 m^2), the average rates of release were 0.111 mmol SRP $\text{m}^{-2} \text{d}^{-1}$ and 2.65 mmol NH_4^+ $\text{m}^{-2} \text{d}^{-1}$. The value for NH_4^+ may be slightly inflated because of the possibility that downward-diffusing oxidized species of N (Fig. 5) are eventually reduced to NH_4^+ . If all the net downward flux of NO_2^- and NO_3^- is subtracted, however, the estimate of NH_4^+ remineralization is reduced by only 5%.

Allochthonous nutrients—Nutrient export coefficients tabulated by Reckhow (1980) suggest that the watershed supplied about 2,600 mol P yr^{-1} and 36,000 mol N yr^{-1} to Third Sister Lake. Distributed over the 8-month ice-free period this represents about 0.26 mmol P d^{-1} and 3.82 mmol N d^{-1} per m^2 of lake surface. These estimates may be subject to considerable error of unknown magnitude, but they are included as our only estimate to date of watershed loading of nutrients to the lake.

Discussion

Our analysis of metabolism in Third Sister Lake is based on mass balance rather than on a series of incubation assays. The mass balance approach integrates all physiological processes in the basin and is not subject to experimental artifacts or enclosure effects. It relies, however, on accurate

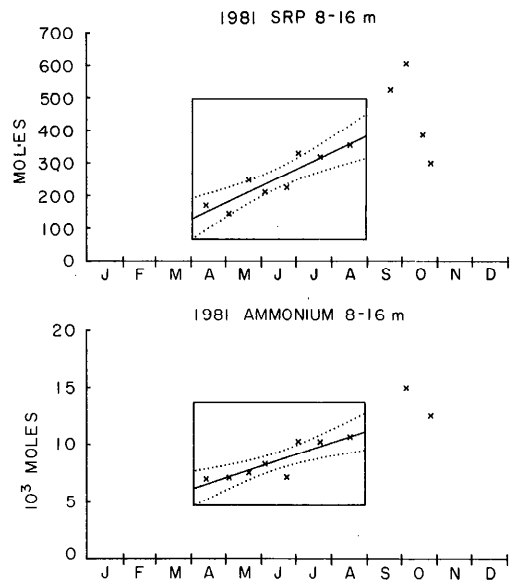


Fig. 9. Total masses of SRP and NH_4^+ from 8 m to the bottom of Third Sister Lake, 1981. Regression lines are fit to the data from April to August, the period when hypolimnetic heat content was increasing uniformly and before any entrainment of hypolimnion water had begun with fall turnover. Slopes are 1.67 mol SRP d^{-1} (SE = 0.33) and 33.1 mol NH_4^+ d^{-1} (SE = 7.8). The 95% confidence regions for the regression lines are shown.

assessments of nutrient concentrations and fluxes. Our analyses demonstrated that vertical flux of P upward to the trophogenic zone was smaller by four orders of magnitude than either watershed loading or the flux necessary to account for net rates of O_2 production. We used heat to trace the vertical mixing processes and we constructed water column budgets for O, P, and N. Incorporation of sediment heating in our budget had a noticeable effect. At 4.5 m, for instance, estimates of vertical eddy diffusion were elevated almost 20% over estimates that ignore the sediments. The heat budgets from Wisconsin lake sediments (Fig. 1) also help explain the slight temperature inversion in the chemically stabilized hypolimnion (Table 2). The deep sediments are warmer than 4°C and act as a weak source of heat.

On the basis of ratios of C:P and C:N in the plankton and the presumption that $\text{O}_2 : \text{C} = 1.0$ in photosynthesis we computed

oxygen equivalents for the rates of release of P and N in the hypolimnion. In this way we could relate the nutrient remineralization to net production. Direct comparison of hypolimnetic nutrient accumulation with O_2 consumption is not possible because all remineralization below 8 m occurred through anaerobic processes. The fact that the data in Fig. 8 and from similar profiles plot as straight lines demonstrates that stoichiometries do not change markedly through the metalimnion. We thus see no evidence of differential loss of P from particles above the hypolimnion. Equation 3 applied to SRP in fact suggests that phosphate is being taken up at 6 and 7 m at about $5.4 \mu\text{mol m}^{-2} \text{d}^{-1}$, whereas these depths are well into the tropholytic zone on the basis of O_2 balance (Fig. 3). This uptake accounts for the accumulation of algal pigments and particulate P (Figs. 4 and 5) at depths below 5 m. Logic dictates that heterotrophic activity must dominate in the accumulating biomass. Net nutrient remineralization probably occurs only when particles sink into the anoxic hypolimnion. The SRP release thus corresponds to an original net O_2 production of 8.10 ($SE = 1.71$) $\text{mmol m}^{-2} \text{d}^{-1}$ and NH_4^+ corresponds to a production of 20.4 ($SE = 5.9$) $\text{mmol m}^{-2} \text{d}^{-1}$. The actual net O_2 production directly above the 8-m contour was $9.5 \text{ mmol m}^{-2} \text{d}^{-1}$ (Fig. 3). Net production in the part of the trophogenic zone lying over the 8-m contour was $12.2 \text{ mmol O}_2 \text{ m}^{-2} \text{d}^{-1}$.

Comparing these estimates from remineralization with actual net O_2 production helps us decipher patterns of productivity in Third Sister Lake. As we already noted, the O_2 budget alone does not discriminate between O_2 changes caused by processes in the open water and those at the interfacing sediments. In particular, net O_2 production in the trophogenic zone could be dominated by macrophytes and periphyton in the littoral region as suggested by Wetzel et al. (1972). Given the time scales that we selected for our calculations (April–August), the undisturbed pattern of thermal stratification, and the fact that the lake did not turn over in the spring, it is most unlikely that substantial redeposition of material occurred from the littoral to the deep water

(Davis 1968, 1973) during that time. The accumulation of SRP and NH_4^+ in the hypolimnion, therefore, represents remineralization of material deposited from the water directly above.

An alternate interpretation is that littoral production and horizontal dispersion of O_2 is responsible for the O_2 budget. The P and N remineralized in the hypolimnion would then have to come from particulate material produced terrestrially or littorally and transported to the benthic sediments. If this were the case the hypolimnion would appear to be a source, rather than a sink for nutrients with respect to the upper water. Instead, the rate of accumulation of nutrients in the hypolimnion appears closely tied to net oxygen production. The accumulation rates of SRP below 8 m correspond, for instance, to $1\% \text{ d}^{-1}$ of the mass of particulate P suspended in the water column above the 8-m contour. In other words, a sinking loss of only $1\% \text{ d}^{-1}$ could fuel the remineralization rates and correspondingly account for net production in the surface waters.

The nutrients needed to support this net production were necessarily allochthonous. No ambient reservoirs of inorganic nutrients existed in the epilimnion (Figs. 5 and 6), and vertical flux to the trophogenic zone was inadequate. The depth distribution of anoxia was roughly constant through our study (Fig. 2), making it unlikely that progressive chemical reduction of previously oxidized sediments could account for the nutrient release. Estimated nutrient loading from the watershed is well able to account for the requisite nutrients. Nutrient release from littoral sediments is discounted because oxygen could be used in decomposition at these shallow depths and hence the nutrients cannot be counted toward net production as we compute it.

On the basis of the preceding line of reasoning we conclude that despite the small surface area of the lake, metabolism deduced from the oxygen budget is dominated by planktonic rather than littoral processes during spring and summer. Most of the N and P necessary to support the net production during that time is supplied from sources outside the lake. Nutrient accumulation in the hypolimnion parallels the

magnitude of net production in the trophogenic zone. It appears that hypolimnetic metabolism is very strongly coupled temporally with net community production in this eutrophic lake.

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