

Hypolimnetic metabolism in Lake Washington: Relative effects of nutrient load and food web structure on lake productivity¹

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Abstract

The general metabolism of carbon, oxygen, phosphate, nitrate, and silicate in the hypolimnion of Lake Washington is examined from 23 yr of record. Magnitudes of net consumptive and regenerative processes in the water column and sediments are identified and stoichiometries of regeneration in situ are calculated. Aerobic respiration appears to be almost equally divided between the water column and sediment surface. Net nitrification is more rapid in the water column, and silicate regeneration is confined to the sediment surface. Nutrients do not accumulate on average at the Redfield ratio.

Rates of hypolimnetic oxygen consumption are compared to production rates inferred independently from ¹⁴C and oxygen bottle assays. A third of all gross primary production is respired in the hypolimnion of Lake Washington during spring and summer, but the proportion was significantly lower during an episode of cultural eutrophication in the 1960s. Rates of primary production and hypolimnetic processes decreased in response to changes in nutrient income when effluents from waste treatment plants were diverted from the lake. After a period of recovery from eutrophication, Lake Washington experienced a second basinwide perturbation involving alteration of the planktonic herbivore community. The change in food web structure failed to produce a response comparable to that of altered nutrient loading. Despite inferred changes in algal growth rates and in species composition, total primary productivity and rates of hypolimnetic metabolism did not change.

The magnitudes and measurement of biological production in aquatic systems have been perennial themes in limnology and oceanography. The drive to answer questions about production rates has spawned a host of innovative techniques, from the light and dark bottle oxygen method of Gaarder and Gran (1927), to Steemann Nielsen's (1952) ¹⁴C method, to Atkins' (1922) direct pH change method, and to many modifications and refinements of these. Today, more than a half century after the first measurements the answers remain contested. Data on oxygen accumulation in situ (Schulenberg and Reid 1981) and isotope fractionation (Jenkins 1982) are sometimes at odds with inferences from assays conducted in bottles. Notwithstanding this need to improve measurements further, there has emerged a sense that rates of primary production in lakes can be manipulated, and managed, from two directions. First is by control of nutrient income, owing to the strong relation between nutrient load and

algal biomass (Sawyer 1947; Dillon and Rigler 1974; Vollenweider 1976; Jones and Bachmann 1976; Smith 1982). Others have argued that physical or ecological factors are as important as nutrient supply (e.g. Harris 1980) and, in particular, that rates of herbivory constrained by food web relations can control primary production (Carpenter and Kitchell 1984, 1987; Carpenter et al. 1985).

One powerful tool for deciphering the production biology of natural waters was suggested by Thienemann (1926, 1928) and Ohle (1934). Hypolimnia of lakes are seasonally isolated water masses in which biological processes can be studied by measuring changes in chemical concentrations. Ohle demonstrated the close stoichiometry between oxygen deficits and carbon dioxide accumulations in hypolimnia and their relations to trophic condition. The approach was refined by Hutchinson (1938, 1941) in his pioneering studies of hypolimnetic processes in Linsley Pond. Hutchinson noted that overall mass balance and stoichiometric relations depend not only on the content of material within a depth stratum, but also

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on the diffusive flux of material between strata. Although Hutchinson's method of calculating eddy diffusivities was criticized in later years (Jassby and Powell 1975), his pioneering approach stands as a quantitative investigative tool with which to assay basinwide production rates.

Oxygen deficits have subsequently been used as a correlate of production and particularly as a way to chart changes within single basins (e.g. Edmondson 1966; Bazin and Saunders 1971; Lind 1978; Cornett and Rigler 1979), although sometimes the relation between hypolimnetic oxygen deficits and primary production is not strong (Cornett and Rigler 1980). The deficits can be related to regeneration of nutrients, which is sometimes called "internal loading" (Nürnberg 1984), and thus to balances of nutrients in the water column.

Productivity and community metabolism involve more than the fluxes of C and O₂. The Redfield ratio (Redfield 1934) or some close variant (Vallentyne 1974) is often used to estimate the fluxes of N, P, Si, or other mineral elements which accompany organic production and catabolism. Redfield himself cautioned, however, that the ratios were composite figures and that broad variation exists with season, latitude, and basin. Now that the influence of nutrient ratios on plankton species success (Pearsall 1932) has been established both in cultures (e.g. Rhee and Gotham 1980) and in situ (Schindler 1977), the integrated study of primary production and biological community structure requires direct attention to fluxes of many elements simultaneously.

Nutrients are released during respiration, excretion, and decomposition. These processes occur both in the water column and at the sediment surface. Because hypolimnetic metabolism is integrative over entire seasons, comparable data from many years or many basins are needed to evaluate the patterns in nature. In this paper I examine the intermediary metabolism of inorganic carbon, phosphate, nitrate, and silicate in the hypolimnion of Lake Washington from 23 yr of record. The extents to which various net consumptive or regenerative processes occur in the water column or sediments are identified, as are the net

stoichiometries of regeneration in situ. Finally, I compare the hypolimnetic rates to production rates inferred independently from radiocarbon and oxygen bottle assays.

Edmondson and Lehman (1981) provided a detailed account of the changes in income of nitrogen and phosphorus to Lake Washington and the responses of the lake over 17 yr. Changes in sewerage arrangements brought about changes in the content of N and P and in the abundance and species composition of phytoplankton. The original paper dealt with nutrient loading from allochthonous sources: streams, the atmosphere, and waste treatment plants. In that paper we demonstrated that fluxes of P and N to the sediments were strongly seasonal and associated with times of maximal production of diatoms in the water column (*see also* Lehman and Edmondson 1983). We also showed that at times net flux of P occurred from the sediments to the water. By focusing on the hypolimnion it is possible to study these fluxes of P and other nutrients in great detail during different loading regimes and different trophic conditions.

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Methods

Hypolimnetic rates—Methods for sampling and chemical analyses have been described elsewhere (Edmondson 1977a; Edmondson and Lehman 1981). Rates of accumulation or removal of nutrients in the hypolimnion were computed from vertical profiles. Values at depths of 0, 5, 10, 12.5, 15, 17.5, 20, 25, 30, 35, 40, 45, 50, 55, and

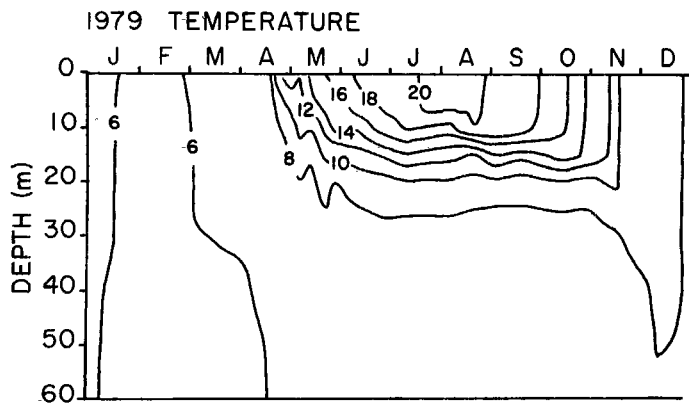


Fig. 1. Temperature isopleths for Lake Washington, 1979.

60 m were either measured directly or interpolated from measured values at other depths. By combining these values with the morphometry of the lake (table 1: Edmondson and Lehman 1981) total masses of nutrients below selected depths were calculated by the formula (Hutchinson 1957, p. 166):

$$\frac{1}{3}[c_i A_i + c_{i+1} A_{i+1} + (c_i A_i c_{i+1} A_{i+1})^{1/2}] \cdot (z_{i+1} - z_i) \quad (1)$$

where c_i is concentration and A_i is area at depth z_i .

Total dissolved inorganic C (DIC) was calculated from measured pH and alkalinity. I used the Güntelberg approximation (Stumm and Morgan 1970) to calculate activity coefficients for HCO_3^- and CO_3^{2-} based on the ionic strength of Lake Washington water (0.0014; Edmondson 1972, table 1). The coefficients thus computed were 0.96 for monovalent ions and 0.85 for divalent ions. Because total alkalinities are $\sim 700 \mu\text{Eq}$ and pH occasionally exceeded 9.0 during the period of eutrophication, calculations were made under the assumption that total titration alkalinity (TA) is

$$\text{TA} = [\text{HCO}_3^-] + 2[\text{CO}_3^{2-}] + [\text{OH}^-] - [\text{H}^+]. \quad (2)$$

Concentrations of silicates, phosphates, ammonium, and other titratable conjugate bases of weak acids were not sufficient to warrant including them in the equation.

Heat contents and total masses of O_2 , DIC, SRP (soluble reactive phosphate), NO_3^- , and dissolved Si below 20 and 40 m were plotted against time. These depths were well within the hypolimnion in all years; the

thermocline in Lake Washington develops between 10 and 15 m (Fig. 1). For each year, data were displayed on a Hewlett-Packard 9845B graphics computer. The time intervals for calculations were selected interactively and were identical for all properties in a year. Intervals at each depth were selected to ensure that heat contents of underlying strata were increasing almost linearly, a procedure which facilitated the calculation of mean eddy diffusion (*see below*). The slopes of lines fit to the data consequently represent estimates of the rates at which the total mass of material changed within defined regions of the hypolimnion. Interannual analyses on decade scales were the subject of this study, and consequently a method was selected to provide estimates for mean rates during each year, rather than trying to interpret changes between individual sampling dates. Besides, simple inspection revealed that properties changed almost linearly during the summer in all years (Fig. 2), as originally recognized by Edmondson (1966: figure 2).

Estimates of fluxes across the 20- and 40-m contours were obtained by using heat as a tracer (Jassby and Powell 1975). Preliminary calculations by the method of Lehman (1979) showed that virtually no in situ heating from direct solar radiation occurred below 20 m, so all heating at greater depths could be ascribed to eddy diffusion or convection. The mechanical bathythermographs used in Lake Washington do not permit reliable estimates of the slight changes in temperature through the hypolimnion between profiles 1 or 2 weeks apart, and internal waves can obscure the representative nature of single profiles in any event. Rather than try to estimate diffusivities between sampling dates, I adopted a scheme that estimated a single mean value for eddy diffusivity for each year and depth during the selected calculation intervals. Heat content below a depth was plotted vs. time and a linear regression was fit to the period of stratification. The slopes represent mean heat flux. The fluxes were adjusted to include sediment heating by the method of Lehman and Naumoski (1986). The total heat flux ($\text{cal m}^{-2} \text{d}^{-1}$) was then divided by the mean heat gradient across the depth

contour (cal m^{-4}) to derive mean diffusivity (\bar{D}_z , $\text{m}^2 \text{d}^{-1}$). These figures could then be multiplied by mean gradients in chemical properties ($\overline{dc/dz}$, mmol m^{-4}) to compute vertical diffusive fluxes. Although the method is insensitive to short-term variations in vertical mixing, the fact that hypolimnetic contents of heat and nutrients changed linearly or nearly so in every instance endorses the approach.

Rates of metabolism in the hypolimnion were calculated as

$$R_z = \frac{\Delta \int_z^{z_m} C(z) \cdot A(z) dz}{\Delta t + A_z \cdot \bar{D}_z \cdot \overline{dc/dz}|_z} \quad (3)$$

where R_z is the rate of consumption or accumulation (mol d^{-1}) below depth z . Because each component of R_z is a mean or the slope of a regression, each has its own estimation error. Standard errors for calculated quantities like R_z were computed by first-order error propagation techniques (Meyer 1975; Edmondson and Lehman 1981).

Epilimnetic production rates—Primary production was estimated between sampling dates from daily insolation, vertical light attenuation, and empirical relations between photosynthesis and irradiance. In situ incubations with light and dark bottles have accompanied water column investigations of Lake Washington since 1957. Data are most extensive for O_2 production by Winkler titration, but ^{14}C productivity measurements are available after 1971; after 1979 only ^{14}C productivity was measured. Concentrations of dissolved oxygen were measured on replicate initial samples from each incubation depth as well as on replicate samples incubated under ambient conditions for 24 h, from solar noon to solar noon. Bottles were suspended at 0, 0.5, 1, 2, 3, 4, and 5 m in the 1960s and at additional depths in later years. Some of the primary production data for Lake Washington have been reported elsewhere in summary forms (e.g. Edmondson 1977b; Lehman 1980), and the present work incorporates and extends those results.

Water samples were drawn from selected

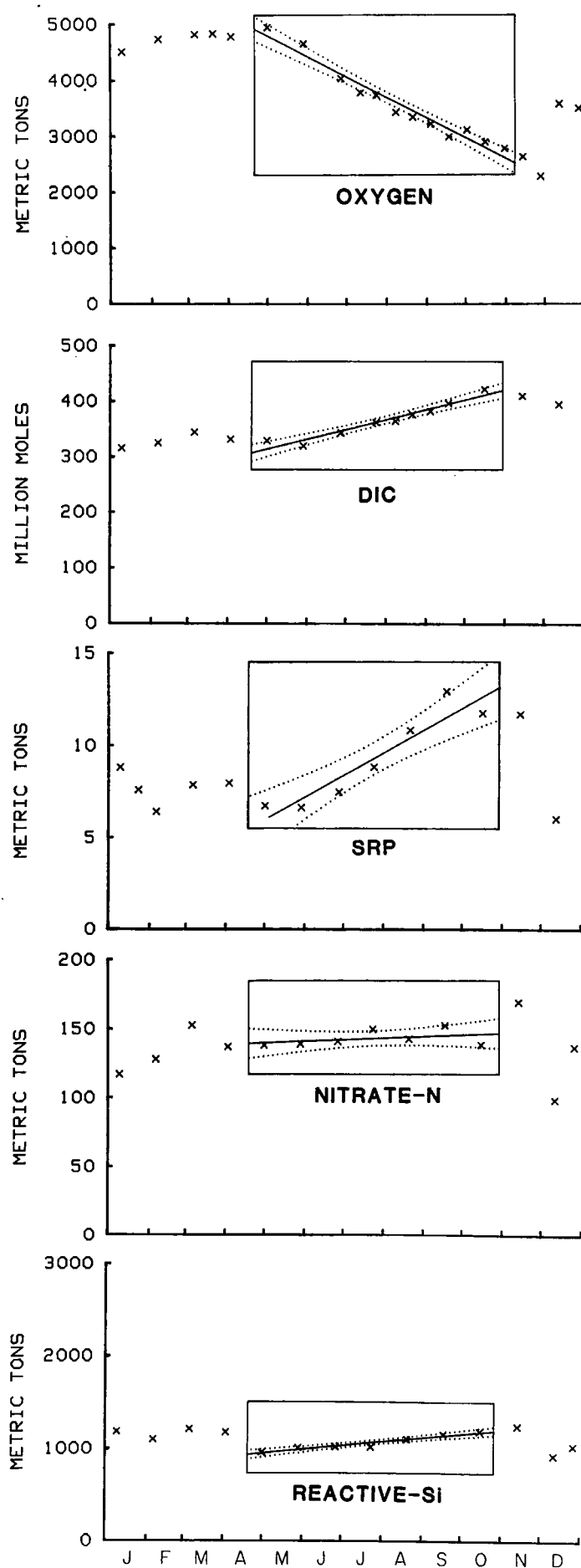


Fig. 2. Masses of chemical substances below 40 m in Lake Washington, 1979. The data interval selected for analysis is indicated by framing and the linear fit is plotted. Values for 95% C.I. for the regression lines are shown.

depths with an opaque Van Dorn bottle. Samples were incubated at the depth of collection inside 250-ml Pyrex-stoppered bottles. Incident solar radiation ($\text{cal cm}^{-2} \text{min}^{-1}$) was monitored at lakeside during each deployment and precise irradiance totals for each incubation were obtained. Total incident light was monitored constantly, moreover, by the University of Washington Department of Atmospheric Sciences at a site < 1 km from Lake Washington. Thus each incubation of ~ 24 h duration has a corresponding value for incident light (I_0 , cal cm^{-2}). The empirical data were also integrated to generate values for total daily incident light ($\text{cal cm}^{-2} \text{d}^{-1}$) for each day of the year. When instrument failures occurred, data were obtained from a federal installation at Seattle-Tacoma International Airport (Edmondson 1977b), and the values were adjusted by empirical correlation to account for the orographic differences between measurement sites.

Light penetration in Lake Washington has been measured principally by Secchi disk transparency. In 1964, 1968, 1970, and 1981, detailed investigations were mounted using a Whitney LMD-8 photometer equipped with narrow-band Corning filters. The investigations showed that green light at ~ 520 – 550 nm was the most penetrating spectral component in the lake water. Enough measurements were assembled to establish spectral attenuation coefficients during years of differing trophic condition. In particular, three wavelengths (420, 530, and 650 nm) proved representative of attenuation of PAR. The vertical attenuation coefficients for these wavelengths were predicted from Secchi disk visibility (Z_{sd} , m) as follows:

$$\begin{aligned} \epsilon_{420} &= 0.420 + 4.508/Z_{\text{sd}} \\ \epsilon_{530} &= 0.185 + 1.404/Z_{\text{sd}} \\ \epsilon_{650} &= 0.471 + 0.781/Z_{\text{sd}} \end{aligned} \quad (4)$$

where ϵ_{420} (m^{-1}) is representative of light attenuation from 400 to 450 nm, ϵ_{530} of attenuation from 450 to 600 nm, and ϵ_{650} of attenuation from 600 to 700 nm. The true extinction coefficients at 530 nm, for example, are estimated to within $< 15\%$ error for $Z_{\text{sd}} > 2$ m and to within $< 10\%$ for Z_{sd}

< 2 m. Secchi transparency readings accompany each incubation and thus the vertical light fields can be reconstructed for comparisons among dates. Incident quanta in each of the spectral windows are calculated as:

$$I_{0i} = I_{0\text{ total}}(1 - r)f_{\text{PAR}}E(\Delta\lambda_i)Q(\Delta\lambda_i) \quad (5)$$

where r is surface reflectance ($= 6\%$), f_{PAR} is fraction of incident radiation that is in the range 400–700 nm (41%: Lehman 1979), $E(\Delta\lambda_i)$ are fractions of PAR energy that are in the ranges 400–450, 450–600, and 600–700 nm (0.14, 0.55, 0.31 respectively: Wetzel 1983, figure 5-3), and $Q(\Delta\lambda_i)$ are mean quanta cal^{-1} in the three spectral bands (9.1×10^{18} , 1.2×10^{19} , 1.4×10^{19}).

For each incubation I constructed an empirical relation between net and gross photosynthesis and irradiance, $P_n(I)$ and $P_g(I)$, by reference to the oxygen determinations, I_0 , and light attenuation (Fee 1973). Gross photosynthesis was presumed to equal zero in the absence of light, and net photosynthesis was presumed to equal mean respiration (i.e. net photosynthesis at zero light = a negative number). These $P(I)$ relations formed a basis for estimating photosynthesis between dates of incubations. For all dates integral areal primary production (mmol O_2 or $\text{C m}^{-2} \text{d}^{-1}$) was calculated as

$$\sum P = \int_0^z P(I) dz \quad (6)$$

by numerical trapezoidal integration with $\Delta z = 0.1$ m. Smaller vertical spacing changed estimates $< 1\%$. PAR at depth z was calculated from

$$I(z) = \sum I_{0i} \exp(-\epsilon_i z). \quad (7)$$

Rates of photosynthesis ($\text{mmol m}^{-3} \text{d}^{-1}$) measured at specific irradiances in the profiles were interpolated between sample dates. The resulting estimates of areal production are more secure than would result from linear interpolation of individual measurements, because they incorporate daily information about light intensity and data for water transparency which are more frequent than productivity assays. The nonlinear nature of light attenuation and $P(I)$ relations guarantees that integral photosynthesis per unit area of lake surface cannot be a direct

Table 1. Summary data for rates of decrease of total mass of dissolved oxygen (10^3 mol d^{-1}) below 20 and 40 m in Lake Washington during periods of stable thermal stratification with net downward heat flux. Number of sample dates used for the regression— n ; in situ rate measured as in Fig. 2— ΔO_2 ; rates of O_2 consumption corrected for vertical flux— R_{20} and R_{40} ; area (20 m)— $61,585 \text{ m}^2$; area (40 m)— $34,770 \text{ m}^2$.

Year	20 m					40 m				
	n	Dt (d)	ΔO_2	r^2	R_{20}	n	Dt (d)	ΔO_2	r^2	R_{40}
1933	8	171	818	0.94	781	9	191	271	0.93	326
1957	14	218	1,505	0.98	1,461	8	152	481	0.97	535
1963	11	164	1,191	0.99	NA*	11	164	431	0.98	NA
1964	13	178	1,672	0.98	1,778	14	196	517	0.95	718
1965	9	185	1,295	0.98	1,191	11	222	447	0.95	637
1966	11	138	1,488	0.82	1,467	11	138	411	0.70	469
1967	10	173	1,452	0.98	1,423	11	185	544	0.96	594
1968	16	199	1,272	0.94	1,151	17	217	377	0.92	466
1969	10	161	1,058	0.99	1,022	14	229	312	0.99	340
1970	12	160	1,123	0.95	1,039	14	177	393	0.93	473
1971	13	181	1,284	0.98	1,268	15	208	384	0.98	424
1972	14	197	1,081	0.98	1,073	14	197	343	0.97	349
1973	12	224	1,138	0.99	1,142	12	224	377	0.96	488
1974	14	206	1,195	0.98	1,020	13	194	368	0.98	530
1975	8	156	1,318	0.99	1,287	8	156	397	0.98	477
1976	8	145	1,166	0.97	1,156	8	145	398	0.97	423
1977	13	186	1,104	0.99	1,115	13	186	398	0.98	468
1978	13	182	928	0.98	934	12	168	300	0.92	365
1979	11	187	1,093	0.95	1,050	12	197	371	0.96	431
1980	7	191	1,054	0.99	1,004	8	221	322	0.97	329
1981	7	202	1,099	0.98	1,084	7	202	360	0.92	427
1982	6	160	963	0.98	883	6	160	271	0.93	324
1983	7	192	1,182	0.99	1,215	7	192	335	0.98	386

* Instrument failure precluded estimation of vertical heat flux.

linear function of I_0 . Thus the simple method of interpolating integral photosynthesis between sample dates by scaling values to I_0 would yield biased results. Beyond this logic, I found no satisfactory way to assign estimation errors to the integral production rates. The bulk of the error must come from unknown biases introduced by the bottle incubations directly, and from the presumption that $P(I)$ relations can be interpolated over intervals of ~ 14 d. The unknown magnitudes of error must be kept in mind when the primary production figures are compared with the more defined estimates of hypolimnetic metabolism.

Results

The values for mean eddy diffusivities in Lake Washington at 20 and 40 m, based on heat fluxes and gradients, were about two orders of magnitude greater than molecular heat conduction. Diffusivities have differing significance to each chemical property because relative gradients $[(1/c)(dc/dz)]$ vary considerably among chemical species. With

oxygen, for instance, vertical flux at 20 m corrected the consumption rates based on changes in situ (e.g. Fig. 2) $< 5\%$ on average. For SRP, however, the corrections were $> 100\%$.

Estimated rates of hypolimnetic oxygen consumption are listed in Table 1. Rates became elevated from 1933 to 1957, and they subsequently declined during the 1970s to values that were once again comparable to 1933. Based on the known limnological condition of Lake Washington, it is possible to identify three episodes suitable for statistical comparisons. The years 1957–1968 are designated the cultural eutrophication era because the lake was receiving nutrient income from waste treatment plants during the entire period; the last effluents were diverted in 1968 (Edmondson and Lehman 1981). The years 1969–1975 are called the recovery era because water transparency increased and algal biomass declined in response to nutrient diversion. The plankton community during the recovery era, however, contained many of the same species

Table 2. Changes in rates of hypolimnetic oxygen consumption (from Table 1) during three episodes: cultural eutrophication era (1957–1968), recovery era (1969–1975), and *Daphnia* era (1976–1983).

A priori episodes (AOV)	ΔO_2 (20 m)	R_{20}	ΔO_2 (40 m)	R_{40}
1957–1968 (eutrophication)				
1969–1975 (recovery)	$F = 14.92$	10.04	12.14	9.95
1976–1983 (<i>Daphnia</i>)	$P = 0.0001$	0.0012	0.0004	0.0012
Episode comparisons (<i>t</i> -test)				
1957–1968	mean = 1,411	1,412	458	570
vs. 1969–1975	mean = 1,171	1,122	368	440
	$t = 3.28$	2.99	3.60	2.72
	$P = 0.0037$	0.0068	0.0021	0.0107
1969–1975	mean = 1,171	1,122	368	440
vs. 1976–1983	mean = 1,074	1,055	344	394
	$t = 2.00$	1.14	1.14	1.43
	$P = 0.034$	0.139	0.138	0.089

common during eutrophication, particularly the dominant copepod herbivore *Diaptomus ashlandi*. The years 1976–1983 are called the *Daphnia* era (Edmondson and Litt 1982), because *Daphnia* species, particularly *Daphnia pulicaria*, first dominated the zooplankton in 1976 and produced further changes in water transparency and food web structure.

Results of statistical comparisons among the three episodes which were designated a priori are shown in Table 2, for both uncorrected rates (ΔO_2) and rates corrected for vertical eddy diffusion (R_{20} and R_{40}). ANOVA revealed that substantial differences existed among the episodes and therefore specific comparisons were investigated. Rates of hypolimnetic oxygen consumption decreased significantly ($\alpha = 0.05$), by about 20%, from the eutrophication era to the recovery era. Differences between the recovery era and the *Daphnia* era were much smaller, and not statistically significant for either R_{20} or R_{40} , which are the best estimates for total hypolimnetic respiration.

Based on the results with oxygen consumption, I examined a priori contrasts between eras to test the proposition that other metrics of hypolimnetic metabolism had declined from the eutrophication era to the recovery era, but not from the recovery to the *Daphnia* era. One-tailed *t*-tests revealed that mean rates of accumulation in the hypolimnion (R_{20}) for DIC, SRP, and NO_3^- decreased significantly from 1957–1968 to 1969–1975 ($P < 0.05$ in all cases), but not from 1969–1975 to 1976–1983 ($P > 0.3$ in all cases).

Rates of hypolimnetic metabolism expressed on an areal basis (R_z/A_z , where R_z is calculated from Eq. 3 and A_z is the area at depth z) are plotted in Fig. 3. The early 1960s were the time of greatest nutrient income from allochthonous sources (Edmondson and Lehman 1981), and rates of hypolimnetic metabolism were elevated during those years. In many cases the total mass of materials produced or consumed below the 20-m contour differed from rates calculated below the 40-m contour even when both were expressed per unit of sediment surface area. Similar rates for total mass flux per unit area for the two depths would be expected if decomposition and regeneration were occurring exclusively at the sediment surface, and if slight differences in water temperature through the hypolimnion did not affect the rates of the processes. Linear patterns of oxygen consumption (Fig. 2) despite slow progressive warming during summer suggest that the catalytic role of temperature was not the major reason for the differences.

One possibility for the differences in area-based estimates of metabolism between hypolimnetic strata is that substantial amounts of respiration and decomposition are occurring in the water column of the hypolimnion rather than at the sediment surface. The ratios between rates of consumption or accumulation below 20 and 40 m ($R_{20} : R_{40}$) are shown in Fig. 4. The ratio of the area of sediment surface below 20 m to the area below 40 m is 1.77. The ratio of water volume below 20 m to that below 40 m is 3.26. By plotting the ratio $R_{20} : R_{40}$ for each prop-

erty and examining its magnitude, it is possible to infer the spatial distribution of metabolism. If processes were occurring exclusively at the sediment surface, ratios should approach 1.77; if processes occur exclusively in the water column, values should approach 3.26. The fact that most of the values for oxygen consumption and DIC accumulation fall between 1.77 and 3.26 implies that neither the sediments nor the water column are dominant sites of respiration. Accumulation of SRP followed the volume distribution of the hypolimnion during the years of cultural eutrophication, but more closely approximated the distribution of surface area in other years. Nitrate accumulation consistently followed the volume distribution (mean ratio = 4.28, SE = 0.56) whereas accumulation of silicon conformed to the surface area (mean = 1.89, SE = 0.24). Regeneration of dissolved Si, presumably by dissolution of diatom frustules, thus appears to occur at the sediments, whereas net nitrification may be occurring substantially in the water column. The spatial distribution of denitrification cannot be inferred unambiguously from the data, because the pattern of NO_3^- accumulation is consistent with denitrification fluxes either at the sediments or in the water column, but the sediments are the more likely site of the process. Neither nitrite nor ammonium accumulated in the hypolimnion. Perennial oxygenation of the hypolimnion probably contributed to low levels of NH_4^+ , often $< 1 \mu\text{M}$, even during the eutrophicated years, and NO_2^- rarely exceeded $0.5 \mu\text{M}$ in the deepest strata.

Net stoichiometric relations between DIC, SRP, NO_3^- , Si, and oxygen are plotted in Fig. 5. For each year the ratio of DIC accumulation to oxygen consumption is almost identical for calculations based at 20 and at 40 m. Overall mean DIC: O_2 below 20 m is 1.24 (SE = 0.14) by moles vs. 1.29 (SE = 0.14) below 40 m. In most cases the ratios of DIC to O_2 are not significantly different from 1.0, but in 1976 and 1981 the ratios exceeded 2.0. Similarly, Si: O_2 ratios are consistent between hypolimnetic strata although some interannual variation exists. The mean ratio at 20 m is 0.174 (SE = 0.033) by moles compared to 0.236 (SE = 0.024) at 40 m. Nitrate: O_2 ratios (excluding 1933) are on average 50% higher below 20

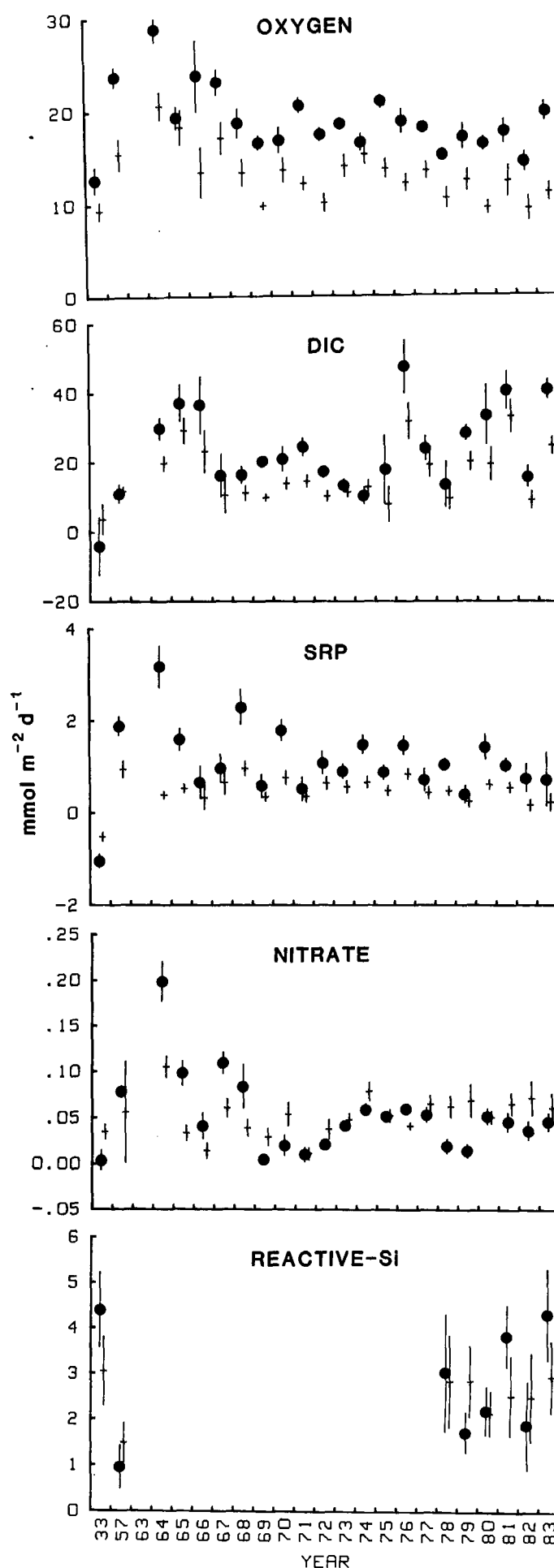


Fig. 3. Rates of O_2 consumption and accumulation of chemical substances in the hypolimnion (R_{20} and R_{40} , Eq. 3) divided by area at the 20-m (●) and 40-m (+) contours. Means ± 1 SE.

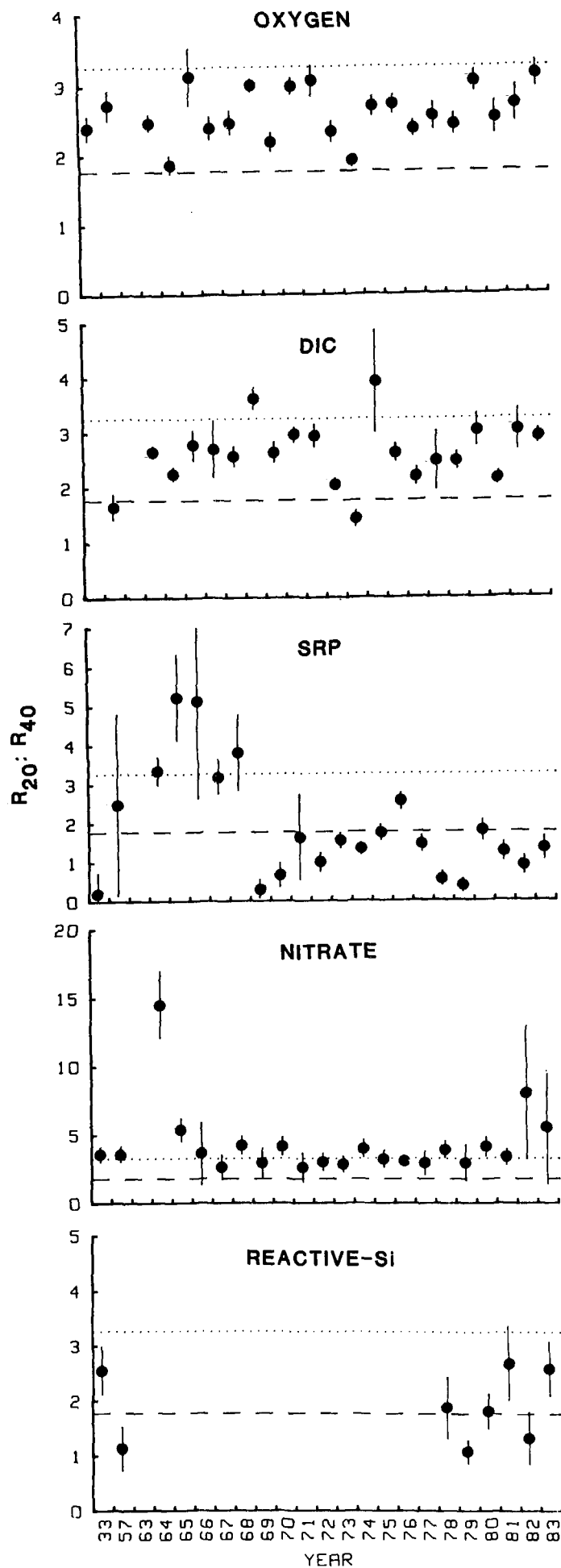


Fig. 4. Ratios of O_2 consumption and chemical accumulation below 20 m (R_{20} , Eq. 3) to rates below 40 m (R_{40}). Dotted line represents ratio of basin volumes

m (0.0630, SE = 0.0064) than below 40 m (0.0410, SE = 0.0038). Net rates of nitrification (i.e. nitrification less denitrification) are evidently higher in the shallower hypolimnetic strata, possibly because rates of denitrification increase with depth. The nitrate measurements in 1933 were methodologically unique and probably not directly comparable with later analyses. Reported concentrations during midwinter were only $\sim 10 \mu\text{M}$, compared to 20–30 μM in recent years.

SRP behaves oppositely from nitrate (Fig. 5). On average the SRP: O_2 stoichiometry computed below 40 m (mean = 0.00408, SE = 0.00035) exceeds the values below 20 m (0.00260, SE = 0.00036) by a factor of 1.5. Thus the mean SRP: O_2 between 20 and 40 m was only 0.0017. The years from 1964 to 1968 are an exception to this rule, and they are the same years that show high ratios of SRP accumulation in Fig. 4.

The changes in mean rates of oxygen depletion and DIC accumulation reported in Fig. 3 are paralleled by magnitudes of areal-based annual primary production (Fig. 6). The estimates based on ^{14}C equal about half the rates calculated as gross oxygen production from light and dark bottles incubated under identical conditions. Productivity changed by a maximum factor of three over the years, with the major decrease occurring in the period 1966–1971. When rates of hypolimnetic oxygen consumption are compared with productivity rates from 1 March to 1 September of each year (Fig. 7), the data suggest that different proportions of gross productivity were catabolized in the hypolimnion before and after 1970. From 1964 to 1970 the ratios averaged 0.228 (SE = 0.025); after 1970 the mean was 0.357 (SE = 0.029). The means are significantly different (t -test, $P = 0.0033$).

Discussion

Changes in algal abundance and primary production in Lake Washington were trig-

[vol(20 m) : vol(40 m) = 3.26]; dashed line represents ratio of sediment surface areas [area(20 m) : area(40 m) = 1.77]. Values are mean \pm 1 SE. Estimation errors include the covariance of chemical contents between strata.

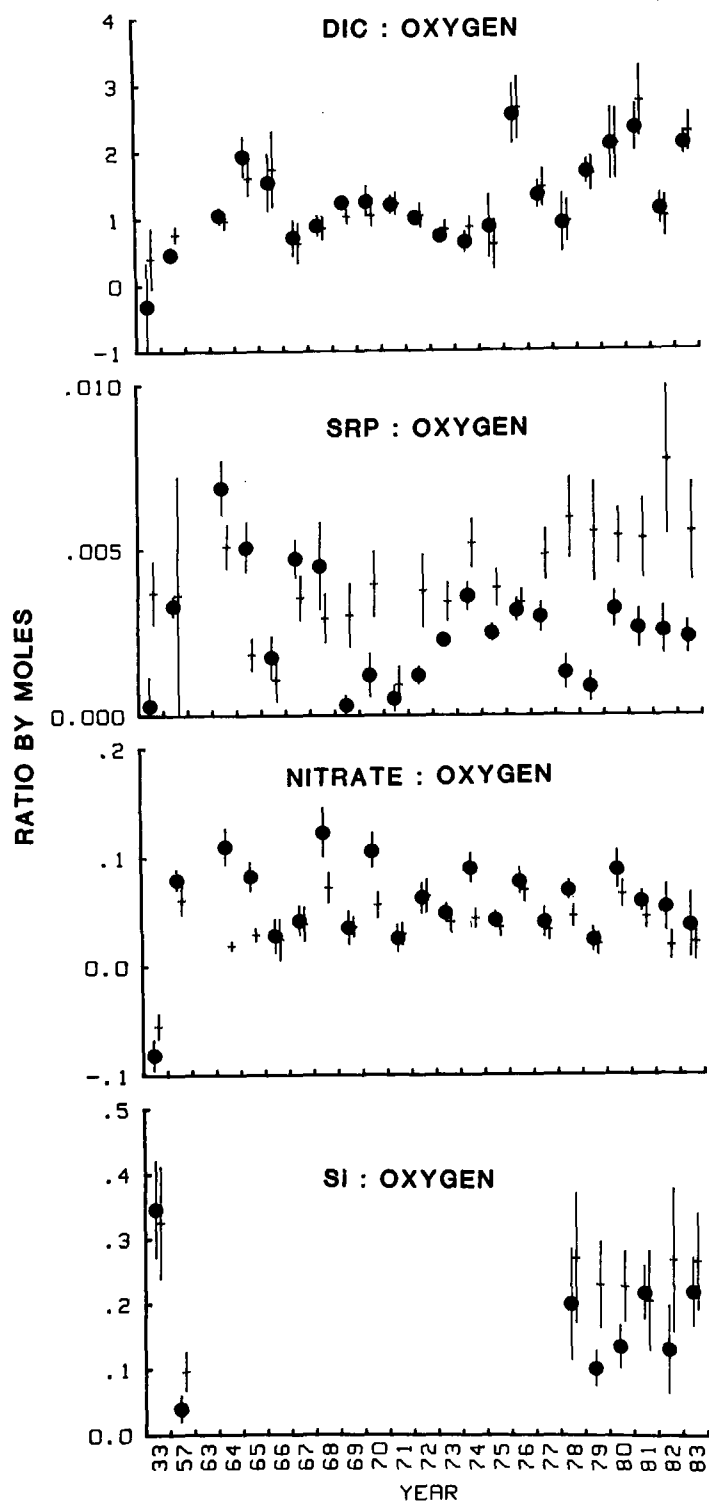


Fig. 5. Stoichiometries of accumulation of DIC, SRP, NO_3^- , and Si to oxygen consumption (means \pm SE), by moles, below 20 (●) and 40 m (+).

gered by alterations of the nutrient income (Edmondson 1972). The elevated nutrient supplies of the 1960s led to higher biomass accumulation, rather than faster growth rates of the phytoplankton in situ. Rates of gross oxygen production from 1 March to 1 September, for instance, were $0.36 \text{ mmol O}_2 (\text{mg Chl } a)^{-1} \text{ d}^{-1}$ in 1964 compared with 0.84 in 1975. The species assemblage present during the eutrophic years was less pro-

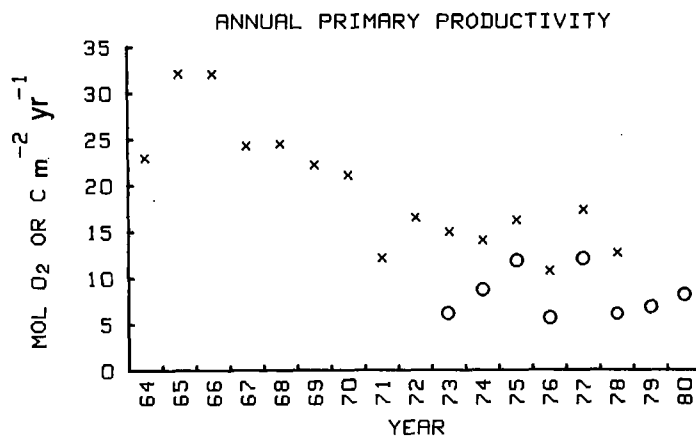


Fig. 6. Areal-based annual primary production, calculated from gross O_2 production (x) and ^{14}C fixation (o). Values were calculated from daily irradiances and summed for each year.

ductive per unit chlorophyll than more recent populations. Some differences in C:Chl ratios may have occurred, but plankton biomass ($\mu\text{m}^3 \text{ liter}^{-1}$) has changed in parallel with chlorophyll concentrations (Edmondson and Lehman 1981: figure 7; Edmondson and Litt 1982: figure 8). Algal specific production was lower during the richest years, a finding which is consonant with the general inverse relationship between total algal biomass and productivity per unit algal biomass (Wetzel 1983).

Large changes in primary production and hypolimnetic processes accompanied nutrient diversion but not a later, major trophic alteration of the lake. Edmondson and Litt (1982) have described changes in the herbivorous zooplankton of Lake Washington that accompanied a second episode of improved water transparency and reduced

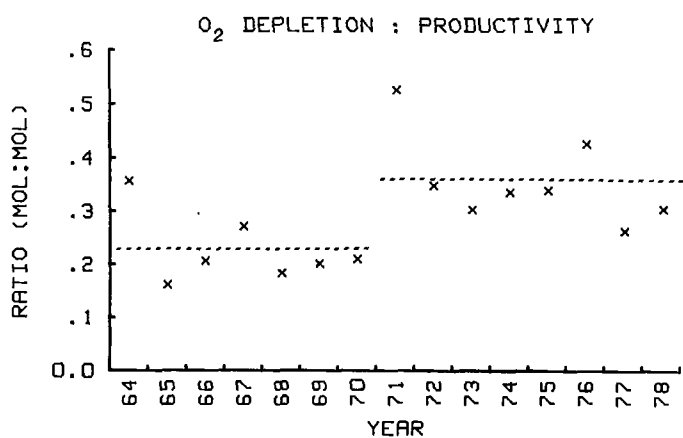


Fig. 7. Annual ratios of the rates of oxygen consumption below 20 m ($\text{mol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) to the mean water column estimated gross O_2 productivity ($\text{mol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) from 1 March to 1 September of successive years.

algal abundances in the 1970s. *Daphnia* species replaced *Diaptomus* as the major herbivores during summer months. The species composition of the phytoplankton community changed as well, but primary productivity and hypolimnetic oxygen consumption were unaltered by these fundamental changes in food web relations. Neither the production of new biomass nor its transport downward changed quantitatively. Such a response means that the production rate per unit mass, or growth rate, of the phytoplankton became elevated.

When Lake Washington was administered large and continual doses of nutrients before 1968, the plankton community present then had lower intrinsic growth rates than the assemblage present under more oligotrophic conditions. The increased nutrient loads were manifested as biomass, not as increased rates of cell division. In sufficient abundance, some of the algae may have been able to inhibit successful colonization of the lake by *Daphnia* (Infante and Abella 1985). Not until manipulations of the nutrient base excluded *Oscillatoria*, in particular, did *Daphnia* come to dominate. In turn, intense herbivory by *Daphnia* in recent years may have selected for species with higher division rates, presumably by improving the light climate, cycling nutrients rapidly, and by inflicting direct mortalities which might exclude some slow-growing species. *Daphnia* does not produce compacted fecal pellets as does *Diaptomus*, and its ability to account for nutrient regeneration in Lake Washington is already known (Lehman 1980).

A major portion of material fluxes, particularly fluxes of P and Si, to the hypolimnion of Lake Washington probably comes with the spring diatom bloom (Lehman and Edmondson 1983). The pattern of accumulation of dissolved reactive Si suggests that dissolution occurs only at the sediments, and P generally obeys the same rule (Fig. 4). The volume-dependent pattern of P accumulation from 1964 to 1968 arose from the fact that SRP-rich effluent from the Lake City waste treatment plant discharged to the hypolimnion before its diversion, contributing about half of the annual P income to the lake (Edmondson and

Lehman 1981). Other chemical species did not mimic P and Si, however, which underscores the point that detrital matter may not decompose simultaneously or uniformly with respect to all nutrient elements. Nondiatom algae, especially the species common during summer, sink more slowly than diatoms. Some nutrients may be lost from the particles before they cross the 20-m contour and thus hypolimnetic heterotrophs may consume relatively C-rich substrates in the water column. Overall metabolic stoichiometries of DIC:O₂:Si:NO₃⁻:PO₄³⁻ were 477:385:67:22:1 by moles below 20 m, but logic argues against thinking that these rates arise from simultaneous decay of a single substrate. Stoichiometries below 40 m were 316:245:59:9:1 owing to the greater influence of sediment processes in deeper strata (Stauffer 1985). The ratios depart substantially from mean values constructed by Redfield et al. (1963) for ocean waters. Nitrogen losses via denitrification are included indirectly in these estimates, because NO₃⁻ accumulation represents the net excess of nitrification over denitrification. Denitrification is analogous to permanent sediment burial, in that the element is lost to water column processes. The same cannot be said for methanogenesis. Some methane produced by anaerobic processes in the sediments could be oxidized in the oxic hypolimnion, thereby increasing the changes in both C and O₂ but not biasing the stoichiometry. The overall C:O₂ ratio of ~1.25 probably owes to CO₂ released by glycolysis or other anaerobic oxidative processes in the sediments. There is little carbonate material present in the sediments. Some of the chemically reduced species which account for the unbalanced stoichiometry of DIC and O₂ may be buried permanently, but others may be oxidized when the lake mixes. Detailed investigations of oxygen budgets during fall and winter might therefore prove revealing.

Data presented by Edmondson and Lehman (1981: figure 8) show that ~42 μmol P m⁻² d⁻¹ were buried from 1970 to 1978 based on a P budget for the lake, and sediment traps yielded flux rates of 81 μmol P m⁻² d⁻¹ to the sediment surface. Mean hypolimnion accumulation of SRP from 1970

to 1978, corrected for vertical flux, was $44 \mu\text{mol P m}^{-2} \text{ d}^{-1}$. This estimate is identical to two significant figures with the calculated flux from sediments based on the intercept of a regression between sediment trap collections and net inputs of P from the watershed, $42 \text{ mg m}^{-2} \text{ month}^{-1}$ ($=44 \mu\text{mol m}^{-2} \text{ d}^{-1}$; Edmondson and Lehman 1981). These values define the efficiency with which P is retained in the sediments, once it arrives there, as being about 50%. This figure is different from the term "retention" that usually connotes the fraction of P added to an entire lake basin that remains there and should not be confused with it. The calculation is undoubtedly influenced by the fact that mineral particles brought into the lake with fluvial discharges are quickly sedimented and poorly regenerated. If the fluvial particulate loads are called "mineral P" and are discounted from the annual fluxes to sediment traps, and rates of SRP regeneration cited above are compared with the residual "nonmineral" fluxes of P to sediment traps, then only 13% of the nonmineral P that reaches the sediments stays there permanently. Little of the P that is sedimented during diatom blooms (Edmondson and Lehman 1981; figure 7) is thus fated to remain in the sediments.

Considering that so much of the P that falls to the sediments in organic form is remineralized, it may be worth reconsidering why Lake Washington responded so quickly to reduced allochthonous nutrient loads. The key characteristic of the lake seems to be its monomictic regime and the extensive hydrologic discharges during its winter mixing period. Even though the remineralized P is mixed into the surface waters each autumn, it is then flushed from the basin by low-nutrient water draining from the Cascade Range. As much as a third of the lake's volume is renewed each winter. This makes the lake an ideal candidate for predicting response from flushing rate and was the cornerstone for Edmondson's extremely precise forecasts (Lehman 1986).

Given the results shown in Fig. 7, there is doubt that hypolimnetic rates of oxygen consumption or DIC accumulation yield a precise measure of integral water column productivity. Hypolimnetic oxygen con-

sumption represented a lower fraction of total gross production before 1970, probably because the photic zone was shallower then, the region of positive net productivity was constrained well above 20 m, and much decomposition may have taken place above the hypolimnion. The phytoplankton community in those rich years included many nondiatoms which sink slowly or in some cases float. What the figures show, nonetheless, is that substantial amounts of the organic matter produced in the euphotic zone are catabolized in the hypolimnion. The values in Fig. 7 rival the high proportions of P regenerated from sediments. The comparison is between two fundamentally different processes which together govern the patterns of material cycling in the lake. P is lost rapidly, but not permanently, when it sediments with diatoms in the spring. During summer, however, the nutrient is recycled in the photic zone where as much as 95% of the algal "demand" for P is met from regenerated material in situ (Lehman 1980). Throughout the year much of the organic products of photosynthesis find their way to the hypolimnion, but in summer the material has been largely scavenged of its P. It appears that on average a significant fraction of the products of gross primary production—about a third—is exported to the hypolimnion. This estimate closely parallels the findings of Quay et al. (1986), who concluded that 70–80% of the primary production of Lake Washington in 1980 was recycled in the epilimnion, based on changes in the ratios of stable carbon isotopes. As Quay et al. pointed out, DOC in Lake Washington remains almost constant, and river inputs of POC approximately equal POC outflow both on an annual basis and during summer, so analysis can be focused securely on net changes in the lake basin. Cycling of materials in the euphotic zone is more rapid for the nutrients N and P than for biomass (cf. Lehman 1980). Algal biomass produced *de novo* in the photic zone is about half as likely to fall to the hypolimnion in Lake Washington as to be completely respired in situ.

Metrics like areal oxygen consumption can be relatively insensitive to volumetric changes in plankton abundance. Their ap-

peal stems from their properties as integrators over time and thus from their ability to census episodic events or fluxes that might escape conventional sampling programs. These features are especially important given the vagaries that face estimation of primary productivity. All of the primary production data presented in this paper have been derived from in situ exposures of 24-h duration. The protocol for productivity incubations was established in 1957 and was maintained consistently through the study. For the bulk of the data, obtained by the oxygen method, a 24-h incubation was logical because the 24-h cycle of day and night is the ecological unit of interest. Occasional tests at alternative incubation intervals had established 24 h as a reliable and consistent time period. Standard procedures for measuring ^{14}C productivity, however, usually call for incubations of only 4 h or less (Vollenweider 1969), in order to minimize respiration of incorporated radiocarbon. Extrapolation of such short incubations to 24-h estimates of production involve additional classes of assumptions and calculations not treated here. Data from 24-h ^{14}C incubations have been presented in Fig. 6 for purposes of comparison with oxygen data. They represent an internally consistent set of measurements that show no trend of increase or decrease during years when the planktonic food web of Lake Washington was in a state of flux.

The findings reported here have relevance to the study of food web manipulations and their role vis-à-vis nutrient loading in setting the trophic condition of lake waters. Some investigators have argued, based on model calculations, that food web relations can control rates of primary production in aquatic environments (Carpenter and Kitchell 1984). Data from Lake Washington show that this claim is doubtful. Primary production under one square meter of the lake surface was a function of nutrient loading, but not of changing fields of herbivory. Changes to nutrient income or food web structure produce fundamentally different patterns of response in lakes, which can be identified readily when the lake is treated as an ecological unit. Both types of manipulation have important effects on lakes, but

they cannot be regarded as equivalent for control of trophic condition. Reduction of the nutrient income to Lake Washington in the 1960s, for instance, led to reduced rates of oxygen depletion in the hypolimnion, but later food web changes had no such effect. Culturally eutrophicated lakes that experience seasonal hypolimnetic anoxia will thus respond more securely to restricted nutrient loading than to food web manipulations.

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