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## Chlorophyll production, degradation, and sedimentation: Implications for paleolimnology<sup>1</sup>

*Stephen R. Carpenter, Monica M. Elser, and James J. Elser*

Department of Biology, University of Notre Dame, Notre Dame, Indiana 46556

### *Abstract*

Chlorophyll *a* production, degradation, and sedimentation were studied simultaneously during summer stratification in three lakes with contrasting plankton communities. Pigment budgets showed that chlorophyll production and pigment resuspension were both major sources of water column pigments. Photodegradation rates were rapid and indicated that detritus particles that remained in the epilimnion for periods longer than about 3 days lost nearly all detectable pigments. Therefore, only rapidly sinking detrital particles or those produced in deep layers at low light intensity could make appreciable contributions to sedimentary chlorophyll degradation products. Pheophorbide *a*, a grazing indicator, was the dominant chlorophyll *a* degradation product found in sediment traps. Pigment sedimentation increased significantly with mean size of cladocerans and omnivorous copepods. In contrast, sedimentation rates of chlorophyll degradation products did not increase with primary production. In these lakes, the deposition of chlorophyll degradation products in sediments depended primarily on the size and biomass of grazers.

The regulation of productivity during lake succession continues to stimulate controversy. The difficulty of interpreting the paleolimnological record and the apparent diversity of developmental pathways recorded in sediments allow much room for debate (Binford et al. 1983). Nutrient input frames lake ecosystem productivity, but within the framework there is enormous variability (Carpenter and Kitchell 1984). Development of littoral and marsh vegetation steadily alters lake succession over decades to centuries (Carpenter 1981) but can be catastrophically reversed by changes in water table or by fire. Shifts in food web structure cause variations in production on shorter time scales of months to years (Carpenter and Kitchell 1984). A better understanding of long term variability in lake productivity will provide perspectives on contemporary differences among lakes as well as a baseline for evaluating lake management issues (Likens 1983).

Among the many pigments used by paleolimnologists, chlorophyll *a* and its degradation products seem especially promising for reconstruction of past productivity

(Frey 1974; Wetzel 1983). Chlorophyll *a* is present in all major groups of freshwater photosynthetic organisms and forms several degradation products well preserved in sediments (Brown et al. 1977). In addition to chlorophyll *a*, we are concerned with three degradation products abundant in the lakes we studied: chlorophyll *a'*, a tautomer of chlorophyll *a*; pheophytin *a*, formed by removal of the magnesium atom from either chlorophyll; and pheophorbide *a*, which lacks both magnesium and the phytol chain of the chlorophyll molecule (Carpenter and Bergquist 1985). Daley (1973) noted that grazers were the principal source of pheophorbide and suggested that this compound was a paleolimnological grazing indicator.

The relationships between planktonic processes and sedimentary chlorophyll derivatives have not been established directly (Frey 1974; Binford et al. 1983). Epilimnetic chlorophyll concentration was well correlated with pigment: carbon ratios in the sediments of the English lakes (Gorham et al. 1974) but poorly correlated with primary production in regression analyses involving many lakes (Brylinsky and Mann 1973; Oglesby 1977). In an unusually detailed stratigraphic study, Daley et al. (1977) found few directional trends in pigment deposition or pigment ratios and indicated that relationships between plankton dynamics

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and pigment sedimentation were quite complex.

We present here simultaneous measurements of primary production, chlorophyll production and loss from the epilimnion, grazer assemblages, and sedimentation of chlorophyll derivatives. Pigment budgets for the water column including the magnitudes of chlorophyll production, nonplanktonic inputs of pigments, photodegradation, and sedimentation provided direct comparisons of pigment sedimentation rates and plankton dynamics. To obtain these data for systems differing in productivity and plankton community structure, we studied three lakes that were similar chemically and morphometrically but had contrasting food webs.

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#### *Pigment budget: Basic concepts*

Welschmeyer and Lorenzen (1985) developed pigment budgets for marine ecosystems in which allochthonous inputs and resuspension of pigments are negligible. These nonplanktonic pigment sources must be considered in pigment budgets for small lakes. A complete budget for Chl *a* in the photic zone of a lake (all quantities  $\mu\text{mol m}^{-2} \text{ week}^{-1}$ ) is

$$D_{\text{Chl}} = P_{\text{Chl}} + N_{\text{Chl}} - L \quad (1)$$

where  $D_{\text{Chl}}$  is the change in chlorophyll standing stock during a time interval,  $P_{\text{Chl}}$  is chlorophyll production,  $N_{\text{Chl}}$  is nonplanktonic input of chlorophyll, and  $L$  is the sum of loss processes. Nonplanktonic inputs of chlorophyll include resuspension, benthic chlorophyll production by macrophytes or attached algae, and terrestrial sources of pigments. We divide chlorophyll loss into three components:

$$L = P_{\text{CDP}} + X_{\text{Chl}} + S_{\text{Chl}}; \quad (2)$$

$P_{\text{CDP}}$  is degradation of Chl *a* to colored chlorophyll degradation products (CDP: chlorophyll *a'*, pheophytin *a*, and pheophorbide *a* in this study),  $X_{\text{Chl}}$  is degradation to colorless (therefore undetectable) com-

pounds, and  $S_{\text{Chl}}$  is sedimentation of Chl *a*. Several processes cause degradation to pheophytin *a* (Daley and Brown 1973; Daley 1973), but grazing is the major, perhaps exclusive, source of pheophorbide *a* (Daley 1973; Shuman and Lorenzen 1975; Carpenter and Bergquist 1985; Welschmeyer and Lorenzen 1985). Colorless degradation products are formed primarily by photodegradation of pigments in moribund algae and fecal particles (SooHoo and Kiefer 1982*a,b*).

A similar budget equation (also in  $\mu\text{mol m}^{-2} \text{ week}^{-1}$ ) can be written for changes in standing stock of chlorophyll degradation products ( $D_{\text{CDP}}$ ):

$$D_{\text{CDP}} = P_{\text{CDP}} + N_{\text{CDP}} - X_{\text{CDP}} - S_{\text{CDP}} \quad (3)$$

where  $N_{\text{CDP}}$  is nonplanktonic inputs,  $X_{\text{CDP}}$  is degradation to colorless compounds, and  $S_{\text{CDP}}$  is sedimentation.

Chlorophyll production ( $P_{\text{Chl}}$ ) was calculated from measurements of carbon fixation (PPR,  $\text{mmol C m}^{-2} \text{ week}^{-1}$ ) and the ratio of algal carbon to Chl *a* (C:Chl,  $\text{mmol C } \mu\text{mol}^{-1} \text{ Chl } a$ ):

$$P_{\text{Chl}} = \text{PPR}/(\text{C:Chl}); \quad (4)$$

C:Chl was determined by in situ chlorophyll-labeling experiments (Redalje and Laws 1981). Like other production estimates based on bottle experiments, this procedure assumes that the potential chlorophyll synthesis observed in the bottles was realized in nature. If  $P_{\text{Chl}}$  was overestimated, then nonplanktonic inputs were underestimated (Eq. 6, below).

Sedimentation was measured directly with sediment traps. Photodegradation rates were measured as a function of light intensity and used to calculate the amount of detrital pigment degraded to colorless compounds. Photodegradation of pigment *i* in a given depth layer on a given day is

$$X_i = P_i[1 - \exp(-kI)] \quad (5)$$

where  $X_i$  is the amount of pigment photodegraded ( $\mu\text{mol m}^{-3} \text{ d}^{-1}$ ),  $P_i$  is the concentration of pigment ( $\mu\text{mol m}^{-3}$ ),  $I$  is the daily photon flux to the depth layer ( $\text{Einst m}^{-2}$ ), and  $k$  ( $\text{m}^{-2} \text{ E}^{-1}$ ) is a photodegradation rate constant (SooHoo and Kiefer 1982*a,b*).

These data provided estimates of non-

planktonic pigment inputs, by rearrangement of budget Eq. 1–3:

$$N_{\text{Chl}} + N_{\text{CDP}} = D_{\text{Chl}} + D_{\text{CDP}} - P_{\text{Chl}} + X_{\text{Chl}} + X_{\text{CDP}} + S_{\text{Chl}} + S_{\text{CDP}} \quad (6)$$

The left side of Eq. 6 is nonplanktonic inputs of all pigments; all terms on the right side were measured. In calculating nonplanktonic inputs, we assumed that Chl *a* was converted to CDP before photodegradation, so that  $X_{\text{Chl}} = 0$ . Detrital Chl *a* cannot be distinguished from that in living cells. The pigments of living cells are protected from net photodegradation, even though intracellular turnover of chlorophyll may be rapid. If direct net photodegradation of Chl *a* was substantial, then we underestimated resuspension by an amount equal to  $X_{\text{Chl}}$ .

#### Lakes studied

Paul, Peter, and Tuesday Lakes have been the objects of numerous studies, including whole ecosystem experiments, since 1951 (Hasler 1964). This historical record enriches paleolimnological studies of their laminated sediments (Kitchell and Kitchell 1980). The three lakes lie less than 0.5 km apart in the same moraine in section 36, T45N R42W, Gogebic County, Michigan, within the boundaries of the University of Notre Dame Environmental Research Center. Bog mats are developed to some degree around all three lakes, which are acidic (pH 5.5–6.7), weakly buffered (alkalinity 40–240  $\mu\text{eq liter}^{-1}$ ), and lack surface inflows. Peter Lake (area = 2.4 ha,  $Z_m = 19.3$  m,  $\bar{Z} = 8.3$  m) is the largest and clearest (Secchi depth = 6.6 m), followed by Paul (area = 1.2 ha,  $Z_m = 12.2$  m,  $\bar{Z} = 5.0$  m, Secchi depth = 4.8 m) and Tuesday (area = 0.79 ha,  $Z_m = 18.5$  m,  $\bar{Z} = 10$  m, Secchi depth = 2.3 m). The annual laminations and high pigment concentrations of the sediments of all three lakes indicate stable depositional environments (J. F. Kitchell and S. R. Carpenter unpubl. data). Paul and Peter Lakes support dense populations of largemouth bass, but vertebrate planktivores are absent, in sharp contrast to Tuesday Lake which supports dense populations of minnows (J. R. Hodgson, D. M. Lodge, and J. F. Kitchell unpubl. data). Invertebrate planktivores include *Chaoborus punctipennis* in all three lakes

and *Chaoborus flavicans* in Paul and Peter (von Ende 1979). The very different plankton communities of the lakes are described below.

#### Methods

**Sampling**—To minimize nonplanktonic pigment inputs by resuspension and from terrestrial sources, we confined our study to a summer period of stable stratification. Data reported here were obtained from 4 June to 22 August 1984.

Solar radiation was monitored continuously with a Belfort pyrheliumeter. Pyrheliumeter traces were digitized and integrated by computer. Pyrheliumeter data in  $\text{cal cm}^{-2} \text{min}^{-1}$  (*A*) were converted to photosynthetically active radiation in  $\text{Einst m}^{-2} \text{s}^{-1}$  (*B*) by the empirically determined equation  $B = 1,629A - 8$  ( $R^2 = 0.982$ ,  $n = 7$ ).

Permanent stations for weekly sampling were established near the deepest spot of each lake. On each sampling date, profiles were taken of temperature and dissolved oxygen with a YSI meter and light penetration with a submersible spherical quantum sensor connected to a LiCor meter. Samples for pigment analysis and carbon fixation were taken at depths of 100, 50, 25, 10, and 1% of surface irradiance with an opaque Van Dorn bottle. Two additional pigment samples were taken, at the depth of the sediment traps and at 15% of surface irradiance. Phytoplankton samples were pooled from three depths in the mixed layer. Zooplankton was collected by vertical hauls of a 75- $\mu\text{m}$ -mesh Nitex net. Net calibrations for each taxon in each lake were calculated from samples taken at seven depths with a 28-liter Schindler-Patalas trap.

Contents of duplicate sediment traps were collected weekly from each lake. Traps were suspended in anoxic water with temperatures 4.2°–4.8°C at 10 m in Paul and Tuesday Lakes and at 12 m in Peter Lake. Eddy diffusivities at the trap depths were  $<0.02 \text{ cm}^2 \text{ s}^{-1}$ ; at such low eddy diffusivities, trap performance is not significantly affected by turbulence (Reynolds 1979). Sediment traps were modified from the design of White and Wetzel (1973) with three collection chambers and three inverted control chambers (for wall growth) per trap. All chambers were

made of PVC pipe, 5.08-cm i.d. and 25 cm long to satisfy the diameter and height: diameter recommendations of Gardner (1980) and Blomqvist and Kofoed (1981). Contents of collection, and control, chambers from each trap were pooled, mixed, and subsampled for dry mass, organic mass, and pigment content. Collection chamber contents were corrected for ambient seston at trap depth and for wall growth. Wall growth was always <0.001% of collection chamber contents.

*Limnological analyses*—Carbon fixation was determined in situ with two light bottles and a DCMU control (Legendre et al. 1983) at each depth in each lake, from about 1000 to 1600 hours on each sampling date. An additional dark bottle control was run at 1% light to correct for bacterial photosynthesis (Parkin and Brock 1980). Each 125-ml bottle contained 185 kBq of  $\text{NaH}^{14}\text{CO}_3$  (sp act  $1.1$  to  $5.3 \times 10^9$  dpm  $\text{mmol}^{-1}$  C). Initial dissolved inorganic carbon was calculated from total inflection point alkalinity (Gran 1952) using table 8-1 of Wetzel and Likens (1979). Incubations were ended by filtering the bottle contents in the field onto Whatman GF/F filters which were rinsed with 1 N HCl, dried overnight, and placed in a dioxane-based fluor for liquid scintillation counting. Counting efficiencies were determined with internal standards.

Routine pigment analysis was by fluorometry. Samples collected on Whatman GF/F filters were frozen, sonicated and homogenized in methanol (Marker et al. 1980), centrifuged to remove debris, and analyzed (Strickland and Parsons 1968).

High-pressure liquid chromatography (HPLC) was used for one or two water column samples from each lake each week, all sediment trap samples, and samples from chlorophyll-labeling and degradation experiments. The HPLC method (Carpenter and Bergquist 1985) was used with minor modifications. Frozen filters were sonicated in methanol-acetone (15:85) and centrifuged. Supernatant was filtered through 0.2- $\mu\text{m}$  porosity Acropore filters into vials, from which the solvent was then evaporated under a nitrogen stream. Dried samples were lyophilized and kept frozen in the dark until they were chromatographed, always within

4 weeks of collection. Normal phase chromatography used a dual-pump Beckman system and two solvents, first 15% acetone in petroleum ether, and second a 50-50 mixture of the first solvent with methanol, petroleum ether, and acetone in the ratio 27:30:43. Absorbance peaks (660 nm) were integrated electronically. Calibration standards were purified by preparative paper chromatography of spinach and sediment extracts (Brown et al. 1977). We do not report data on chlorophyllide *a* and several unidentified degradation products because they were rarely detected and always minor pigments. The results here are based on Chl *a* and its three major degradation products in these lakes: chlorophyll *a'*, pheophytin *a*, and pheophorbide *a*. To test for artifacts in our extraction procedure, we purified Chl *a* by HPLC, dried it under  $\text{N}_2$ , and then re-extracted and re-chromatographed the pigment. No detectable chlorophyll isomers or pheopigments were produced.

Primary production was calculated from weekly profiles of chlorophyll-specific photosynthesis (CSP) and light extinction, coupled with continuous measurements of surface irradiance. Preliminary analyses of variance indicated that log transformation was necessary to stabilize the variance and normalize residuals in analyses of CSP (Box et al. 1978). For each lake, an orthogonal polynomial surface was fit to predict log CSP from number of days since the beginning of the study and mean hourly photon flux density at each bottle (Draper and Smith 1981). Residuals from these regressions satisfied the criteria of Draper and Smith (1981) and were generally small (Paul,  $R^2 = 0.79$ ; Peter,  $R^2 = 0.86$ ; Tuesday,  $R^2 = 0.94$ ). The orthogonal polynomials were used to calculate daily production above the 1% incident light depth from measured surface irradiance and interpolated profiles of chlorophyll concentration and light extinction.

Phytoplankton was preserved with Lugol's iodine, settled, and counted with an inverted microscope. Zooplankton was preserved in Formalin, counted, and measured under a Wild dissecting microscope. Crustacean lengths were converted to mass with the equations in table 7.2 of Downing and Rigler (1984); for species not included, we

used an equation for a closely related species of similar shape. Where several equations were presented, we selected the equation calculated for the range of animal lengths and life stages that most closely matched our data. Because we wanted to use zooplankton biomass as an index of grazing intensity, we excluded the sheath of *Holopedium gibberum* by calculating its mass from the general zooplankton equation of Peters and Downing (1984). Rotifer masses were calculated from the formulae in table 7.5 of Downing and Rigler (1984). We assumed dry mass/wet mass = 0.1 (Downing and Rigler 1984).

*Chlorophyll-labeling experiments*—The C:Chl ratio was determined monthly at five depths in each lake using chlorophyll-labeling experiments. The theory of these experiments (Welschmeyer and Lorenzen 1984; Laws 1984) will be recounted briefly here.

Lake water was incubated in situ at depths corresponding to 100, 50, 25, 10, and 1% of surface irradiance. Three bottles were deployed at each depth from about 1000 to 1600 hours: two 300-ml experimental bottles, each containing 740 kBq  $\text{NaH}^{14}\text{CO}_3$  (sp act  $1.7\text{--}8.1 \times 10^9$  dpm  $\text{mmol}^{-1}$  C), and a 125-ml control bottle containing DCMU and 185 kBq  $\text{NaH}^{14}\text{CO}_3$ . Initial samples were analyzed for alkalinity, dissolved inorganic carbon, and pigments. At the end of each incubation, the contents of the control bottle and a measured aliquot (50–100 ml) from each experimental bottle were filtered (Whatman GF/F) for counting to determine dpm in algae  $\text{liter}^{-1}$  ( $A^*$ ) and calculate carbon fixation ( $F$ ). The remaining contents of the experimental bottles were pooled, filtered (Whatman GF/F) in the field, and returned immediately to the laboratory for extraction. During HPLC analysis, the Chl *a* in the column effluent was collected in a scintillation vial and dried under a nitrogen stream. Fluor was added for counting to determine dpm  $\mu\text{mol}^{-1}$  chlorophyll C ( $R^*$ ). At least 1,000 counts were collected for each pigment sample, and efficiencies were determined individually by internal standards. In our chromatographic system, coelution of radioactive non-Chl *a* material with Chl *a* is negligible (S. Carpenter un-

publ. data). Initial and final algal carbon ( $C_i$  and  $C_f$ ) were calculated from formulae 6 and 8 of Welschmeyer and Lorenzen (1984):

$$C_f = A^*/R^*$$

$$C_i = C_f - F.$$

C:Chl ratios were then calculated for the beginning and end of each experiment.

We present results only of experiments in which recovered Chl *a* activity was >50 dpm above background and Chl *a* concentration was >0.1 nM. Like Welschmeyer and Lorenzen (1984), we found that C:Chl often increased during experiments. In some cases chlorophyll concentrations decreased, even though chlorophyll that contained radiocarbon was being synthesized. Such chlorophyll bleaching may be a bottle effect (Welschmeyer and Lorenzen 1984). Incorporation of labeled C into bacteria and grazers is another source of error (Laws 1984). To minimize these artifacts, we calculated chlorophyll production (Eq. 4) from initial C:Chl.

*Photodegradation experiments*—Photodegradation of pigments was measured from 1115 on 14 August to 1430 on 15 August 1984. During this period surface irradiance was 51.7  $\text{Einst m}^{-2}$ . In a preliminary experiment on 10–11 August we determined that this light dose was sufficient to reduce pigment concentrations to near the detection limit. Daily irradiance from June to August ranged from 14 to 69  $\text{Einst m}^{-2}$ .

Pigment-rich water was obtained from the deep chlorophyll maximum of Paul Lake. We added DCMU (10  $\mu\text{M}$ ),  $\text{NaN}_3$  (100  $\mu\text{M}$ ), and NaOH (0.01 N) to poison both autotrophs and heterotrophs and retard acid hydrolysis of pigments. Two light bottles and two dark bottles (each 125 ml) were incubated at each of three depths (100, 33, and 10% of surface irradiance) in each lake. Initial and final pigment concentrations were determined by HPLC. Photodegradation rate constants ( $k$ ) were calculated for each pigment by linear regression of  $\ln(P_f/P_0)$  vs.  $I$ , where  $P_0$  and  $P_f$  are initial and final pigment concentrations and  $I$  is photon flux ( $\text{Einst m}^{-2}$ ) at the depth of the bottle during the incubation (SooHoo and Kiefer 1982a,b). Values of  $k$  and interpolated pro-

files of light and pigments were used to calculate daily photodegradation ( $X$ : Eq. 5). Weekly photodegradation of each pigment was calculated by integrating over depth layers and time.

*Error propagation*—We used first-order error propagation (Meyer 1975) to estimate the confidence intervals of calculated quantities such as primary production, chlorophyll production, and total sedimentation. If a calculated quantity  $Y = F(X_i)$  and the variances and covariances of the  $X_i$  have been estimated, then the error of  $Y$  is estimated by

$$\begin{aligned} \text{var}(Y) \approx & \sum_{i=1}^n (\partial F/\partial X_i)^2 \text{var}(X_i) \\ & + 2 \sum_{j=i+1}^n (\partial F/\partial X_i)(\partial F/\partial X_j) \\ & \cdot \text{cov}(X_i, X_j). \end{aligned} \quad (7)$$

These propagated errors are minimal estimates because they only include sources of variance that were actually measured (Box et al. 1978).

### Results and discussion

All three lakes were stratified throughout the study. The depth range of the metalimnion was 3–5 m in Paul Lake, 3–6 m in Peter Lake, and 1–2 m in Tuesday Lake. All three lakes had positive heterograde oxygen profiles at the beginning of the study and anaerobic hypolimnia throughout the study. The metalimnetic oxygen maximum of Peter Lake persisted throughout the study, while those of Paul and Tuesday Lakes disappeared by 2 July and 20 June. The depths at which light intensity reached 10% of surface irradiance were 2.2–3.5 m in Paul Lake, 3.0–4.8 m in Peter Lake, and 1.1–1.5 m in Tuesday Lake. Mean chlorophyll concentrations above 1% surface irradiance were 4.7 nM in Paul, 2.6 nM in Peter, and 3.6 nM in Tuesday. Both Paul and Peter Lakes had deep chlorophyll layers (20–100 nM Chl  $a$ ) in anoxic water below 1% surface irradiance.

Phytoplankton assemblages of the three lakes were quite different. Paul Lake supported a bloom of *Synura* from 11 to 15

June. From 18 June through the end of the study, *Rhodomonas minutum* and other small flagellates dominated the algal counts; however, large colonies of *Merismopedia tenuissima* bloomed from 2 to 30 July, and *Anabaena circinalis* colonies were common after 9 July. In Peter Lake *Synura* disappeared from the plankton by 3 July and was replaced by *Oocystis*, *R. minutum*, and small flagellates such as *Chlamydomonas*; from 31 July to 21 August, *Dinobryon cylindricum* was prominent in the phytoplankton. Tuesday Lake was dominated by *R. minutum*, *Peridinium pulillum*, and other small flagellates through 8 August. The phytoplankton changed markedly from 2 to 22 August as *Peridinium limbatum*, other large dinoflagellates, and *Chryso-sphaerella longispina* became dominant.

*Production of chlorophyll*—Like other investigators who have compared chromatographic and fluorometric determinations of Chl  $a$  in natural waters (Jacobson 1978, 1982; Abaychi and Riley 1979; Gieskes and Kraay 1983), we found that chromatography gave consistently lower concentrations than fluorometry. Fluorometric readings are increased by interfering fluorescent compounds (other chlorophylls and pheopigments and their isomers) and matrix effects which are largely eliminated in chromatography (Jacobsen 1982; Gieskes and Kraay 1983).

We measured ratios of pigments determined by HPLC to fluorometric determinations of chlorophyll and pheophytin (Table 1). These empirical ratios were based on at least one mixed layer sample from each lake on each sampling date. To facilitate comparisons of water column and sediment data, we converted all fluorometric measurements of Chl  $a$  and pheopigment to HPLC equivalents using the tabulated ratios.

Weekly profiles of carbon fixation per unit chlorophyll showed similar values in the three lakes (Fig. 1). Productivities, however, were different because of differences in chlorophyll concentration and light penetration. Total primary production during the study, with 95% confidence intervals estimated by first-order error analysis, was  $2,411 \pm 136$  mmol C m<sup>-2</sup> in Paul,  $2,637 \pm 135$  in Peter,

Table 1. Molar ratios of pigments determined by HPLC to pigments determined fluorometrically; 95% confidence intervals based on 13–20 replicates are presented. For both chlorophyll *a* and *a'*, the denominator is fluorometric “chlorophyll *a*.” For both pheophytin *a* and pheophorbide *a*, the denominator is fluorometric “pheophytin *a*.” Molecular weights (Daltons) are from Daley et al. (1973).

Phorbin	Mol wt	HPLC:Fluorometry		
		Paul	Peter	Tuesday
Chlorophyll <i>a</i>	893.5	0.528±0.141	0.405±0.142	0.334±0.071
Chlorophyll <i>a'</i>	893.5	0.354±0.083	0.282±0.076	0.140±0.018
Pheophytin <i>a</i>	871.2	0.765±0.221	1.412±0.258	0.483±0.075
Pheophorbide <i>a</i>	592.7	1.509±0.760	2.339±0.872	1.400±0.441

and  $3,528 \pm 119$  in Tuesday Lake. Daily mean rates ( $\text{mmol C m}^{-2} \text{d}^{-1}$ ) were: Paul, 30.9; Peter, 33.8; Tuesday 45.2.

C:Chl *a* ratios ranged from 0.4 to  $79 \mu\text{mol C nmol}^{-1}$  Chl *a* (Fig. 2). Ratios of 0.5–20  $\mu\text{mol C nmol}^{-1}$  Chl in marine studies (Redalje and Laws 1981; Welschmeyer and Lorenzen 1984) and 1.5–40 in laboratory cultures (Hunter and Laws 1981; Laws et al. 1983) are based on fluorometric chlorophyll data; on the basis of uncorrected

fluorometric chlorophyll measurements, our ratios ranged from 0.2 to 32.

Weekly chlorophyll production rates spanned a 10-fold range (Fig. 3). The 95% confidence intervals for mean C:Chl ratios used to calculate chlorophyll production (Eq. 4) were: Paul,  $10.5 \pm 4.4$ ; Peter,  $36.9 \pm 19.4$ ; and Tuesday,  $24.8 \pm 9.5$ . Weekly turnover rates for chlorophyll in the whole water column ranged from 0.2 to 1.2 in Paul, 0.1 to 0.6 in Peter, and 0.1 to 2.0 in Tuesday. Metalimnetic chlorophyll cycled more slowly than epilimnetic chlorophyll. Weekly chlorophyll turnover rates in the epilim-

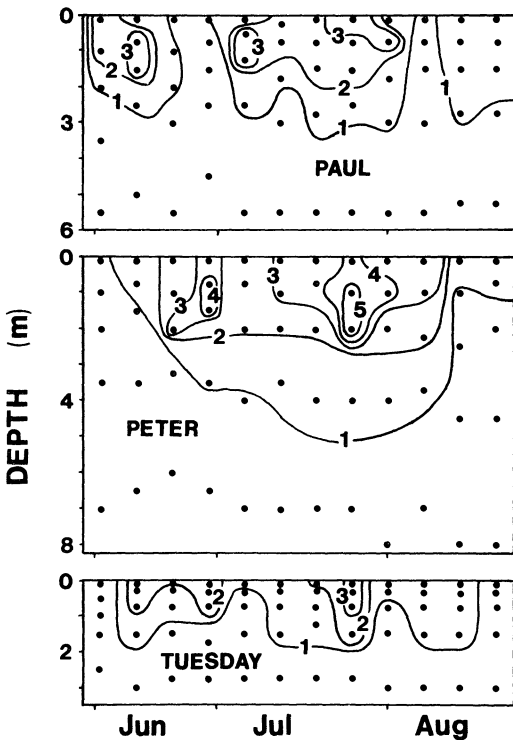


Fig. 1. Isopleths of carbon fixation per unit chlorophyll ( $10^2 \mu\text{mol C } \mu\text{mol}^{-1} \text{Chl h}^{-1}$ ) during the study in Paul, Peter, and Tuesday Lakes. Dots denote location of two light bottles and a DCMU control.

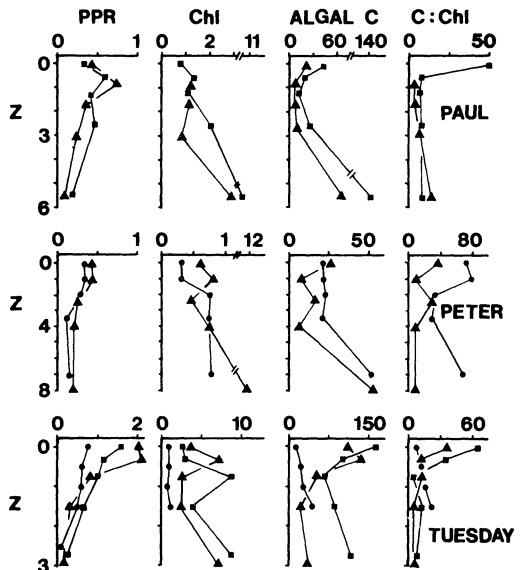


Fig. 2. Results of chlorophyll-labeling experiments. In all panels the ordinate is depth (m). First column shows primary production (PPR,  $\text{mmol C m}^{-3} \text{h}^{-1}$ ); second column shows initial Chl *a* ( $\mu\text{M}$ ); third column shows initial C ( $\mu\text{M}$ ); fourth column shows initial C:Chl ratios. ●—4–6 June 1984; ■—2–4 July 1984; ▲—30 July–2 August 1984.

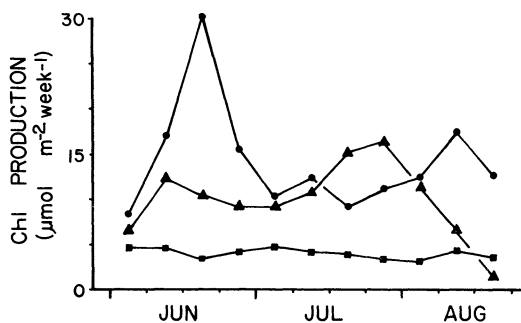


Fig. 3. Chlorophyll *a* production above depth of 1% surface irradiance ( $\mu\text{mol m}^{-2} \text{week}^{-1}$ ) vs. time during the study in Paul (●), Peter (■), and Tuesday (▲) Lakes.

nion were 2.2–3.6 in Paul, 0.5–2.2 in Peter, and 1.1–4.4 in Tuesday.

**Chlorophyll loss processes**—Biomass of zooplankton which could have contributed to chlorophyll loss was calculated excluding taxa such as *Chaoborus*, *Mesocyclops edax*, *Epischura*, and *Asplanchna* which are primarily carnivorous (Balcer et al. 1984). However, smaller copepods which are counted as potential grazers probably feed on both phytoplankton and zooplankton (Balcer et al. 1984), and many of the rotifers feed on detritus, algae, and smaller rotifers (Reynolds 1984).

Paul Lake had the largest grazer biomass during most of the study because of high densities of *Daphnia pulex*, *Daphnia rosea*, and *H. gibberum*. *Orthocyclops modestus* accounts for most of the copepod biomass shown in Fig. 4. Dominant rotifers were *Conochilus* colonies, *Filinia terminalis*, *Gastropus*, *Keratella cochlearis*, and *Polyarthra vulgaris*.

Grazer biomass declined in Peter Lake from 5 to 26 July and then stabilized for the rest of the study. Most of the decline is due to attrition of *Diaptomus oregonensis*, which nevertheless persisted through July and August with the codominant *Cyclops varicans rubellus*. The biomass of the codominant cladocerans *D. pulex* and *H. gibberum* declined steadily during the study. The rotifer assemblage was similar to that of Paul Lake.

Grazer biomass in Tuesday Lake was lower than that of Peter Lake in June and Paul Lake throughout the study and similar to that of Peter Lake in July and August.

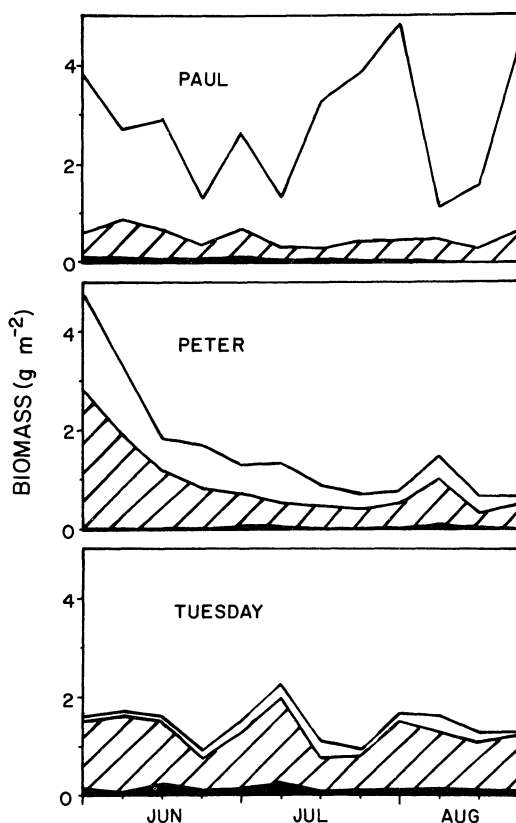


Fig. 4. Biomass ( $\text{g dry mass m}^{-2}$ ) vs. time during the study of omnivorous rotifers (solid), omnivorous copepods (hatched), and cladocerans (open) in the three lakes.

*Bosmina longirostris* was the dominant cladoceran, with *D. pulex* subdominant in June and *Diaphanosoma brachyurum* in July and August. Dominant copepods were *Orthocyclops modestus* from 6 to 20 June and *Tropocyclops prasinus* after 20 June. Tuesday had the highest rotifer biomass of the lakes. Rotifer assemblages of the three lakes were similar in composition, except for the notable absence of *Conochilus* from Tuesday Lake.

Size distributions of crustacean zooplankton were quite different among the lakes. In Paul Lake, weekly mean lengths ranged from 0.84 to 1.45 mm for cladocerans and 0.27 to 0.37 mm for copepods. In Peter Lake, cladocerans were similar in size to those of Paul (0.94–1.35 mm) but copepods were larger than those of the other lakes (0.42–0.56 mm). Tuesday Lake har-

Table 2. Photodegradation constants ( $k$ ,  $m^2 \text{Einst}^{-1}$ ),  $R^2$ , and  $n$  for four pigments in the three lakes.

	Paul	Peter	Tuesday
<b>Chlorophyll <math>a</math></b>			
$k$	0.0741	0.0307	0.0959
$R^2$	0.939	0.754	0.956
$n$	9	10	6
<b>Chlorophyll <math>a'</math></b>			
$k$	0.0716	0.0572	0.0707
$R^2$	0.973	0.980	0.967
$n$	9	10	11
<b>Pheophytin <math>a</math></b>			
$k$	0.0229	0.0107	0.0285
$R^2$	0.970	0.778	0.928
$n$	10	13	11
<b>Pheophorbide <math>a</math></b>			
$k$	0.0392	0.012	0.0268
$R^2$	0.952	0.984	0.946
$n$	6	8	10

bored smaller cladocerans than either of the other lakes (0.22–0.50 mm). Copepods from Tuesday Lake (0.19–0.34 mm) were distinctly smaller than those from Peter and somewhat smaller than those from Paul. Body sizes of rotifers, excluding *Conochilus* colonies, were similar in all three lakes (weekly mean lengths 0.11–0.16 mm); colonies of *Conochilus* (weekly mean diam 1.8–2.9 mm) occurred only in Paul and Peter.

Photodegradation of detrital Chl  $a$  was rapid (Table 2). Chlorophylls  $a$  and  $a'$  (mean  $k = 0.0665$ ,  $SE = 0.009$ ) photodegraded faster than the pheopigments (mean  $k = 0.0235$ ,  $SE = 0.004$ ). The rapidity of photodegradation can be appreciated from daily percentages and the half-lives in days of the pigments. Mean daily photodegradation (with 95% C.I.) was  $75 \pm 3\%$  for Chl  $a'$  and  $40 \pm 2\%$  pheopigments. Mean pigment half-lives (with 95% C.I.) were  $0.52 \pm 0.05$  for Chl  $a'$  and  $1.5 \pm 0.1$  days for pheopigments. Evidently, detrital pigments suspended in the epilimnion for more than a few days will be largely destroyed and make only a minor contribution to sedimentary pigments. Since residence times of moribund algae are as long as 100 days (Reynolds et al. 1982), it is clear that photodegradation can substantially reduce the flux of pigments to the sediments. Photodegradation rates of pheophorbide in the sea are similar to those

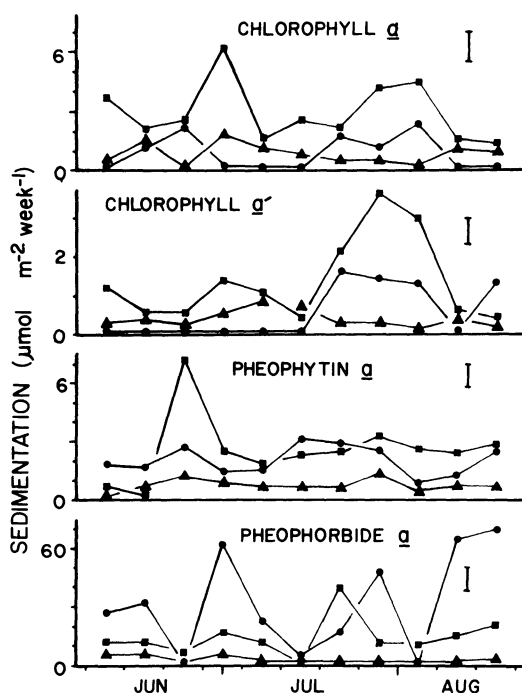


Fig. 5. Pigment sedimentation ( $\mu\text{mol m}^{-2} \text{week}^{-1}$ ) vs. time during the study in Paul (●), Peter (■), and Tuesday (▲) Lakes. Each point is the mean of two traps. Vertical bar in each panel is the pooled standard error from ANOVA.

we measured (SooHoo and Kiefer 1982a,b; Welschmeyer and Lorenzen 1985).

Sedimentation was highly variable among weeks, among compounds, and among lakes (Fig. 5). However, duplicate traps in each lake gave similar results each week. Ratios of the standard error to the mean total phorbins sedimentation were  $<20\%$  for 27 of 33 samples and  $<10\%$  for 18 of them. Pheophorbide  $a$  was the dominant pigment in sediment traps in all three lakes. Paul Lake had the highest sedimentation rates of pheophorbide and total phorbins, Peter the highest of Chl  $a$  and  $a'$ , and Tuesday the lowest for all pigments.

All three lakes had some large phytoplankters (e.g. *Anabaena*, *Dinobryon*, *Merismopedia*, *Peridinium*, *Synura*) comparable to taxa commonly recovered from sediment traps (Livingstone and Reynolds 1981; Reynolds et al. 1982). Sinking of living algae, or algae that died after reaching the hypolimnion, probably accounts for the

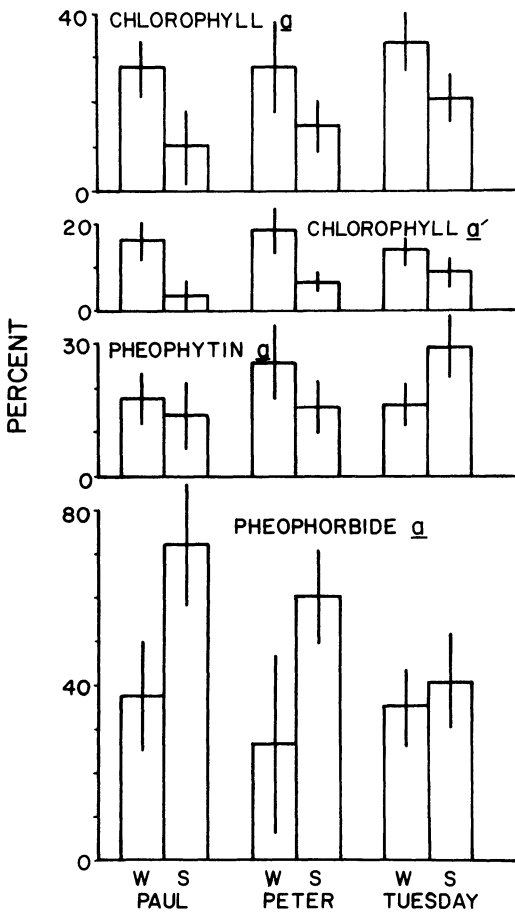


Fig. 6. Percentage of pigments derived from Chl *a* present as four compounds in the water of the epilimnion (W) and sediment traps (S) of the three lakes. Vertical bars denote 95% C.I. of the mean percentage.

chlorophylls in the sediment traps. However, in comparison with the seston, the sediment trap contents were deficient in Chl *a* and *a'* (Fig. 6). In Paul and Peter Lakes, sediment trap contents were enriched with pheophorbide *a*, in comparison with seston. In Tuesday Lake, sediment trap contents were enriched with pheophytin *a*, in comparison with seston. Tuesday Lake, with smaller grazers and lower grazer biomass than Paul and Peter, had the lowest deposition rates of pheophorbide *a*.

*Pigment budgets*—Budgets for Chl *a* and its derivatives showed that production, nonplanktonic inputs, photodegradation, and sedimentation each accounted for major pigment fluxes (Table 3). The differences between total inputs and total outputs for each lake represent net accumulation of pigments in the water column during the study.

Because of differences in C:Chl, the lakes' ranks in chlorophyll production (Paul, Tuesday, Peter) differ from their ranks in carbon fixation (Tuesday, Peter, Paul). The major source of uncertainty in the chlorophyll production estimates was the C:Chl ratio, which can vary with nutritional status of algae, among algal taxa, and with cell size (Hunter and Laws 1981; Carpenter and Kitchell 1984). By spacing our samples with depth and throughout the study period, we adequately estimated the lakewide mean and variance of the C:Chl ratio. However, more intensive sampling might have revealed trends with depth or time that could have

Table 3. Cumulative inputs and outputs of pigments from the water column above 1% surface irradiance during 11 weeks. 95% confidence limits calculated by first-order error propagation. All units  $\mu\text{mol m}^{-2}$ .

	Paul	Peter	Tuesday
<b>Inputs</b>			
Chlorophyll production	229±97	72±43	142±55
Nonplanktonic inputs	606±176	394±67	216±69
Total input	835±147	466±61	358±43
<b>Outputs</b>			
Photodegradation	367±57	212±32	268±42
<b>Sedimentation</b>			
Chlorophyll <i>a</i>	9±23	33±8	10±2
Chlorophyll <i>a'</i>	6±8	15±5	4±1
Pheophytin <i>a</i>	22±11	29±6	9±1
Pheophorbide <i>a</i>	352±133	159±39	26±5
Total	389±136	236±41	49±6
Total output	756±147	448±52	317±42

Table 4. Correlations of selected water column variables with ratios of pigment sedimentation to total herbivore biomass, based on weekly data from all three lakes.

	Sedimentation : herbivore biomass				
	Chlorophyll <i>a</i>	Chlorophyll <i>a'</i>	Pheophytin <i>a</i>	Pheophorbide <i>a</i>	Total
Primary production	-0.005	-0.235	-0.179	-0.423*	-0.427*
Chlorophyll standing crop	-0.062	-0.342	-0.198	-0.025	-0.020
Cladoceran mass	0.204	0.220	0.378*	0.552†	0.625†
Copepod mass	0.572†	0.514†	0.596†	0.450‡	0.578†
Rotifer mass	-0.170	-0.049	0.096	0.295	0.304

\*  $P < 0.05$ .

†  $P < 0.001$ .

‡  $P < 0.01$ .

narrowed the confidence intervals of chlorophyll production estimates.

Nonplanktonic inputs of pigments exceeded production in all three lakes. Since our study was restricted to summer periods of stable stratification in lakes that lacked surface inflows, allochthonous inputs were not a major source of pigments. The most likely sources of nonplanktonic pigments in these lakes are chlorophyll degradation products resuspended from littoral sediments and littoral chlorophyll production by epiphytic and epipelagic algae. Our results show that pigment dynamics in the water columns of small lakes depend heavily on suspension and lateral transport of benthic pigments. Davis et al. (1984) also noted substantial resuspension and focusing of sediments during summer stratification in Mirror Lake, N.H. Since most resuspension and focusing occur at lake overturn (Reynolds et al. 1982; Davis et al. 1984) and allochthonous pigment inputs are primarily autumnal, our data underestimate the annual importance of nonplanktonic pigments. Deposition of pigments originating exclusively in the plankton (such as the unique carotenoids and xanthophylls of blue-green algae, chrysophytes, and dinoflagellates) is not confounded by allochthonous inputs, but is complicated by resuspension and focusing.

The importance of pheophorbide sedimentation indicates that grazing is the key intermediate process between primary production and sedimentation of chlorophyll degradation products. To remove effects of variability in grazing intensity, we calculated sedimentation rates of pigments per unit herbivore mass and examined correlations with selected plankton variables on a weekly basis (Table 4). Primary production was negatively correlated with ratios of pheo-

phorbide sedimentation and total sedimentation to herbivore biomass. There were no significant correlations between chlorophyll standing crop and ratios of sedimentation to herbivore biomass. Chlorophyll standing stock was also uncorrelated with the raw sedimentation rates.

Body mass of crustacean zooplankton had several significant correlations with sedimentation of pigments per unit herbivore biomass (Table 4). These correlations indicate that large zooplankters are more effective vectors of pigments to sediments than are small zooplankters. We suggest that pigments in the larger, faster sinking feces of larger grazers escape photodegradation more effectively than pigments in smaller, slowly sinking fecal particles.

We conclude that grazing was a major vector of pigments from the epilimnia to the sediments of these lakes. Paul and Peter Lakes, which had greater biomasses of larger grazers than Tuesday Lake, had more pheophorbide, relative to other pigments, in the sediment trap material. Higher percentages of total pigment inputs reached the sediments of Paul (47%) and Peter (51%) Lakes than reached the sediments of Tuesday Lake (14%). These patterns suggest that pigments which have passed through grazers are more likely to be preserved in sediments than pigments of algae that are not grazed.

*Implications for paleolimnology*—The pigment budget calculations show that many factors complicate reconstructions of primary production from pigment deposition rates: systematic differences in C:Chl ratios, resuspension and sediment focusing, photodegradation (most potent for pigments in small, slowly sinking particles), and selective grazing. The common assumption

that pigment deposition rates increase as primary production increases (*see* Wetzel 1983) is contradicted by our data. Paul Lake, lowest in primary production, had the greatest pigment sedimentation, while Tuesday Lake, most productive of the three, had the least pigment sedimentation. Weekly PPR and total pigment sedimentation were negatively correlated ( $r = -0.556$ ,  $P < 0.001$ ). When conditions permitted algae to persist and accumulate in the epilimnion, losses to sediments were small and production was high. Conversely, when pigment sedimentation was high, production was low. This negative relationship between production and sedimentation should not be extrapolated, because our data span a limited range of productivities and correlations on a weekly scale may differ markedly from correlations on an annual scale. However, our data do not support the conventional assumption that production and sedimentation are directly related.

Sedimentary chlorophyll degradation products are a biased sample of the chlorophyll produced in overlying waters. In these lakes, as in the sea (Welschmeyer and Lorenzen 1985), grazers select and partially degrade much of the pigment that reaches the sediments. In lakes, further bias results from the dilution of chlorophyll production with resuspended pigments and the interaction of photodegradation rate and sinking rate. Rapidly sinking particles (such as dead colonial algae or large feces) and particles of any size produced under low light intensity in deep layers escape photodegradation and are effective vectors for transport of pigments to sediment. Slowly sinking particles (such as small dead algae or small feces) that persist in the mixed layer for more than a few days lose most of their chlorophyll degradation products to photodegradation before reaching the sediments. The bias in sediment pigments is similar to the bias in algal taxa preserved in sediments, in which diatoms, desmids, large dinoflagellates such as *Ceratium*, and gelatinous colonies such as *Microcystis* are overrepresented, while small unicells such as *Chlorella*, *Rhodomonas*, *Cryptomonas*, and *Mallomonas* are underrepresented (Livingstone and Reynolds 1981; Reynolds et al. 1982). Therefore, the sedimentary record may be more reflective

of processes that shape algal community structure than of those which govern productivity. Abundant nanoplankton and small grazers, which are conducive to high production (Carpenter and Kitchell 1984), are not conducive to deposition of chlorophyll derivatives in sediments. On the other hand, pigment deposition is high in lakes which harbor large grazers and large, grazing-resistant phytoplankters. Inferences about past productivity should not be based on Chl *a* degradation products alone, but also on information about primary producer and grazer community structure from other chlorophylls, carotenoids, xanthophylls, and microfossils.

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