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Chlorophyll budgets: response to food web manipulation

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Abstract. Budgets for chlorophyll *a* and selected degradation products were constructed during summer stratification in 1984 and 1985 in two lakes. In Paul Lake, the reference ecosystem, pigment sedimentation showed no significant interannual differences. In Tuesday Lake, fish manipulations in May 1985 changed the zooplankton from an assemblage of *Bosmina* and small cyclopoids to one of large cladoceran grazers. Sedimentation of pigments, especially the grazing indicator pheophorbide *a*, increased significantly as the grazer assemblage changed. Mean grazer size was positively related to pheophorbide deposition rate in both lakes. Results of this whole-lake experiment indicate that major changes in lake food webs alter pigment deposition rates.

Introduction

The analysis of long-term variability in ecosystems remains one of the central challenges of ecology (Likens 1983). Both basic and applied studies require information on background variability to determine the significance of disturbances to natural systems. Paleolimnology is one of the few tools available to both terrestrial and freshwater ecologists that can provide data on time scales of decades to millenia. However, in many respects the interpretation of the paleolimnological record is uncertain (Binford et al. 1983). Studies of the linkages between water-column processes and the sedimentary record are necessary to resolve these uncertainties.

Chlorophyll *a* and its degradation products are among the most intensively studied paleolimnological indicators (Brown et al. 1977; Daley et al. 1977). Pigment budget studies show that photodegradation is a major loss process for chlorophyllous pigments, that high pigment sedimentation entails rapid clearance of pigments from the photic zone, and that feces of certain zooplankters are effective vectors of pigments from the mixed layer to the sediments (SooHoo & Kiefer 1982a,b; Welschmeyer & Lorenzen 1985; Carpenter et al. 1986). These studies show that pheopigments are completely destroyed by photodegradation within a few days, so that only those pigments that sink rapidly from the photic zone will be preserved in

sediments.

Pheophorbide *a*, derived from chlorophyll *a* by cleavage of the phytol chain and removal of the Mg atom, has received particular attention as an indicator of grazing. Production of pheophorbide *a* by herbivorous zooplankton has been demonstrated in both laboratory and field experiments (Daley, 1973; Shuman & Lorenzen 1975; Carpenter & Bergquist 1985; Conover et al. 1986). Correlations between zooplankton community structure and pheophorbide *a* deposition are known from the sea (Welschmeyer & Lorenzen 1985), Lake Michigan (Kitchell & Carpenter 1987), and small lakes (Carpenter et al. 1986). However, other processes, such as photodegradation, resuspension, and sediment focusing, act with grazing to determine pigment deposition rates. Small-scale experiments cannot address these large-scale complications. In comparisons of lakes, or long-term studies of a single lake, grazing effects may be confounded with simultaneous changes in other factors that influence pigment deposition. To date, there has been no multi-lake experimental test of the hypothesis that changes in zooplankton community structure alter pheophorbide deposition.

Here we report changes in pigment budgets during a whole-lake experiment that enabled us to examine the relationship between pigment sedimentation and plankton community dynamics. Paul Lake, the reference ecosystem, was not manipulated and exhibited only minor changes in the plankton community during 1984–1985 (Carpenter et al. 1987). Therefore, the interannual variability in pigment budgets could be determined by comparing results from Paul Lake in 1984 and 1985. In Tuesday Lake, a baseline study in 1984 was followed by fish community manipulations in May 1985. Addition of piscivorous bass and removal of planktivorous minnows caused dramatic changes in the zooplankton. The *Tropocyclops-Bosmina*-rotifer assemblage that dominated Tuesday Lake in 1984 gave way to a *Daphnia-Holopedium* assemblage by late July 1985, causing substantial changes in the phytoplankton community and a reduction in primary productivity (Carpenter et al. 1987). This paper reports pigment budgets for Paul and Tuesday lakes during 1984 and 1985. We hypothesized that changes in zooplankton community structure in Tuesday Lake would lead to increased rates of pheophorbide deposition.

Methods

Recent limnological descriptions of Paul and Tuesday lakes were provided by Elser et al. (1986a,b) and Carpenter et al. (1986). Since these papers

contain detailed descriptions of most of our procedures, methods will be recounted briefly here.

The pigment mass-balance equation (Carpenter et al. 1986) is

$$N_{\text{chl}} + N_{\text{cdp}} = D_{\text{chl}} + D_{\text{cdp}} - P_{\text{chl}} + X_{\text{cdp}} + S_{\text{chl}} + S_{\text{cdp}} \quad (1)$$

where the chl subscript refers to chlorophyll *a* and the cdp subscript refers to the sum of the chlorophyll degradation products that we measured (chlorophyll *a'*, pheophytin *a*, and pheophorbide *a*). *D* is the change in pigment standing stock in the water column. *P* is production of chlorophyll *a*, *N* is non-planktonic input of pigment, *X* is photodegradation of pigment, and *S* is sedimentation of pigment (all units $\mu\text{mol m}^{-2} \text{week}^{-1}$, Carpenter et al. 1986). No photodegradation term appears for chlorophyll *a* because we assumed that all chlorophyll *a* was in living cells which protected it from photodegradation (Welschmeyer & Lorenzen 1985; Carpenter et al. 1986). All terms on the right side of eq. 1 were measured directly (see below). The left side of eq. 1, which represents total non-planktonic input, was calculated by difference. Confidence intervals for all budget terms were computed by first-order error propagation which incorporated the variances and covariances of the variables that we measured (Carpenter et al. 1986).

Sampling

Pigment budgets were determined from 4 June to 22 August 1984 and from 3 June to 28 August 1985. By performing the studies during summer stratification, we hoped to minimize the effects of mixing and autumnal leaf fall on the pigment budgets. Solar radiation was measured continuously with a Belfort pyrheliometer. Each lake was sampled weekly.

Profiles were taken of temperature and dissolved oxygen with a YSI meter and light penetration with a submersible quantum sensor. Samples for pigment analysis and carbon fixation measurements were taken at depths of 100, 50, 25, 10, and 1% of surface irradiance in 1984, and at those depths plus 5% of surface irradiance in 1985. Additional pigment samples were taken at the depths of the sediment traps. Phytoplankton samples were pooled from the samples in the mixed layer, and zooplankton was collected by vertical hauls of a 75 μm mesh Nitex net.

Sediment trap contents were collected weekly in 1984 and biweekly in 1985. Water depth at the trap stations was 12 m in Paul Lake and 18 m in Tuesday Lake. Deep trap series were sampled in both 1984 and 1985, and additional shallow trap series were sampled in 1985 only. Duplicate deep

traps were suspended in anoxic water receiving less than 0.01% of surface irradiance with temperatures 4.2°–4.8°C at 10 m in both 1984 and 1985. In 1985 only, duplicate shallow traps were suspended at 5 m in Paul Lake and 4 m in Tuesday Lake. In both lakes, this shallow trap series was near the top of the hypolimnion, with water temperatures 5°–10°C, oxygen concentrations 1–3 mg/l, and irradiance 1% to 3% of that at the surface. Each trap had three cylindrical collection chambers 5.08 cm ID × 25 cm long. Each trap in the shallow series had three control chambers to correct for wall growth (White & Wetzel 1973).

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 h on each sampling date. Activity of ¹⁴C was determined by liquid scintillation counting. Initial dissolved inorganic carbon concentrations were determined from total inflection point alkalinity (Gran 1952) and pH (Wetzel & Likens 1979).

Routine pigment analyses were by fluorometry, with pheopigments determined after acidification (Marker et al. 1980; Strickland & Parsons 1965). Fluorometry yields consistently higher pigment concentrations than high-performance liquid chromatography (Carpenter et al. 1986). Therefore, we converted all fluorometric values to chromatographic equivalents using empirical ratios based on at least 13 samples in each lake each year (Carpenter et al. 1986). Normal-phase high performance liquid chromatography (HPLC) was used to analyze all sediment trap samples, one or two water column samples from each lake each week, and samples from chlorophyll labeling experiments described below (Carpenter et al. 1986).

Carbon-to-chlorophyll ratios (C:Chl, $\mu\text{mol } \mu\text{mol}^{-1}$) were measured monthly in all lakes at the same depths used for carbon fixation incubations, using the chlorophyll labeling method (Redalje & Laws 1981) as modified by Carpenter et al. (1986). To determine C:Chl, the activity of ¹⁴C in the algae (A^* , dpm l^{-1}) was measured and carbon fixation (F , $\mu\text{mol l}^{-1}$) was calculated. The specific activity of algal chlorophyll *a* (R^* , $\text{dpm } \mu\text{mol}^{-1}$ chlorophyll carbon) was determined after purifying the chlorophyll by HPLC. Initial algal carbon (C_i , $\mu\text{mol l}^{-1}$) was then calculated from formulae of Welschmeyer & Lorenzen (1984):

$$C_i = (A^*/R^*) - F \quad (2)$$

Then

$$C:\text{Chl} = C_i/\text{Chl}_i \quad (3)$$

where Chl_i ($\mu\text{mol/l}$) is the chlorophyll concentration at the beginning of the incubation.

Chlorophyll production (P) was computed from primary productivity (PPR, $\mu\text{mol C m}^{-2} \text{ week}^{-1}$) as

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

PPR was integrated over time and depth using the procedure of Carpenter et al. (1986).

Photodegradation was calculated from the rate constants determined by Carpenter et al. (1986) and profiles of pigments and irradiance interpolated for each lake on each day. Photodegradation of pigment j (X_j , $\mu\text{mol m}^{-3} \text{ d}^{-1}$) in a given depth layer on a given day is

$$X_j = C_j[1 - \exp(-k_j I)] \quad (5)$$

where C_j is the concentration of pigment ($\mu\text{mol m}^{-3}$), I is the daily photon flux to the depth layer (Einst m^{-2}), and K_j ($\text{m}^2 \text{ Einst}^{-1}$) is the photodegradation rate constant for pigment j (Welschmeyer & Lorenzen, 1985; Carpenter et al. 1986). Total photodegradation, X , was found by integrating the X_j over depth and time, and then summing the values for each pigment (chlorophyll a' , pheophytin a , and pheophorbide a).

Phytoplankton was preserved with Lugol's iodine, settled, and counted with an inverted microscope. Methods for determining volumes and biovolumes were given by Elser et al. (1986a). Preserved zooplankton was counted and animal sizes were determined with a dissecting microscope. For both phytoplankton and zooplankton, replicate fields were counted until the standard error fell below 10% of the mean.

Grazing rates were estimated using previously published regression models. On each sampling date, phytoplankton and zooplankton were each divided into 11 size classes, producing a matrix of 121 combinations of phytoplankton and zooplankton size. The maximum edible particle size for each zooplankton size class was calculated using the regression of Burns (1968). The ingestion rate of each inedible algal size class for each size class of zooplankton was set to zero. The ingestion rate of each edible algal size class by each zooplankton size class was calculated using eq. 5 of Peters & Downing (1984). Total grazing on each date equalled the sum of the ingestion rates for all combinations of algal size and zooplankton size. Algal biovolume was converted to chlorophyll using the regressions of Elser et al.

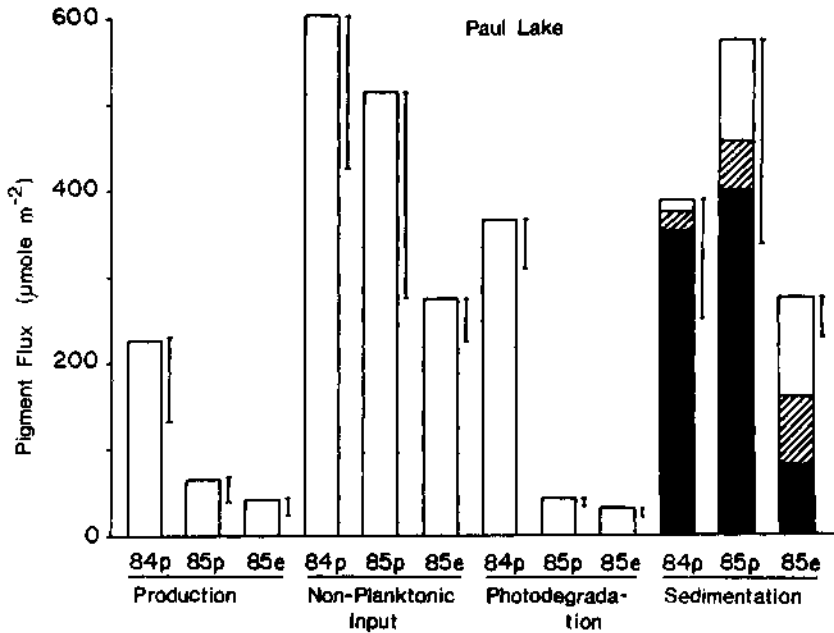


Fig. 1. Pigment budgets for Paul Lake. Four types of pigment fluxes are shown for each of three budgets. The fluxes are chlorophyll *a* production, non-planktonic input of pigments, photodegradation of pigments, and sedimentation of pigments (open bar = chlorophylls *a* and *a'*; hatched bar = pheophytin *a*; and black bar = pheophorbide *a*). Budgets are for the photic zone in 1984 (84P) and 1985 (85P), and for the epilimnion in 1985 (85E). The height of each vertical bar denotes half of a 95% confidence interval for the corresponding mean pigment flux.

(1986a) and the ratios of fluorometric to chromatographic chlorophyll mentioned above.

Relationships among the time series of the variables that we measured were analyzed by first-order autoregression to correct for possible effects of serial correlation (Box et al. 1978).

Results

The data provide three pigment budgets (eq. 1) for each lake. Photic zone pigment budgets for 1984 and 1985 are based on chlorophyll production and pigment photodegradation in the photic zone, and sedimentation to the deep series of sediment traps. For 1985, epilimnetic pigment budgets were calculated, based on chlorophyll production and pigment photodegradation above, and sedimentation to, the shallow series of traps.

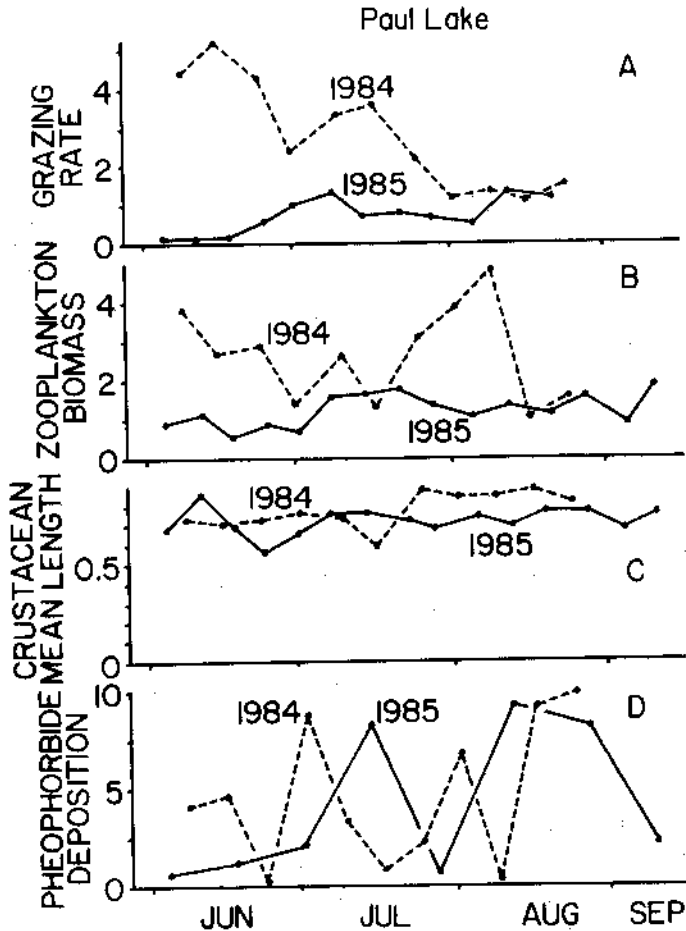


Fig. 2. Variables related to grazing and pheophorbide *a* deposition versus time in 1984 (dashed line) and 1985 (solid line) in Paul Lake. (A) Grazing rate (umole chlorophyll *a* m⁻² week⁻¹). (B) Zooplankton biomass (g dry mass m⁻²). (C) Crustacean mean length (mm). (D) Pheophorbide *a* deposition (umole m⁻² day⁻¹).

In Paul Lake, chlorophyll *a* production was less in 1985 than in 1984 (Fig. 1). Primary production was also less in 1985 than in 1984 (Carpenter et al. 1987). This interannual variability in production is within the range known from many lakes (Carpenter & Kitchell 1987). In 1985, epilimnetic chlorophyll production was not significantly different from chlorophyll production in the photic zone (Fig. 1).

Non-planktonic inputs to the photic zone of Paul Lake were not significantly different in 1984 and 1985 (Fig. 1). However, photodegradation was substantially reduced in 1985 because there was less pigment in the photic

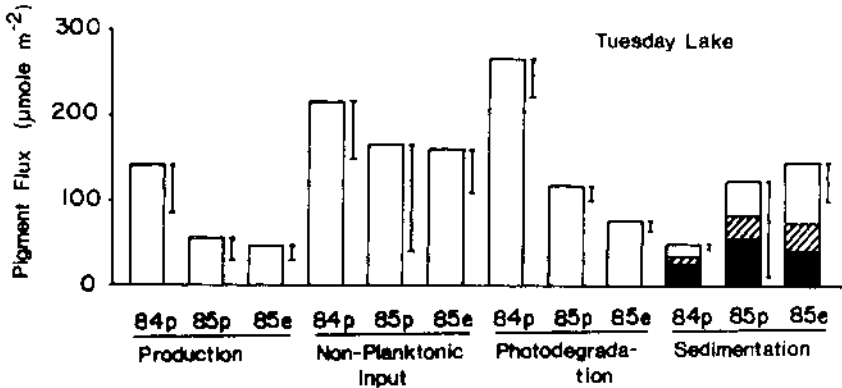


Fig. 3. Pigment budgets for Tuesday Lake. Format as in Fig. 1.

zone. Total pigment sedimentation from the photic zone was not significantly different in the two years. In both years, pheophorbide *a* was the dominant pigment in the sediment traps. In 1985, sedimentation from the epilimnion was significantly less than sedimentation from the photic zone. Pheophorbide was relatively less abundant in the shallow series of sediment traps. Greater sedimentation in the deeper series of traps indicates that sediment focusing occurred in Paul Lake (Hilton 1985).

Seasonal trends in pheophorbide *a* sedimentation rate in Paul Lake were similar in 1984 and 1985 (Fig. 2). Pheophorbide sedimentation rate was not significantly correlated with time in either year (first-order autoregression analyses: 1984, $P = 0.2$; 1985, $P = 0.1$). Both zooplankton biomass and grazing rates were generally lower in 1985 than in 1984, consistent with the interannual differences in algal production and standing crop (Fig. 1; Carpenter et al. 1987). However, the mean size of crustacean grazers was similar in both years (Fig. 2). First-order autoregression analysis showed no significant relationship between pheophorbide deposition and grazing rate ($P = 0.66$) or zooplankton biomass ($P = 0.61$). However, a significant positive relationship existed between pheophorbide deposition and mean crustacean length ($P = 0.04$).

In Tuesday Lake, chlorophyll production in 1984 was less than that in 1985 (Fig. 3). Non-planktonic inputs were not significantly different in the two years. Photodegradation was reduced in 1985, because pigment standing stocks were lower. Sedimentation was higher and more variable in 1985 than in 1984. Pheophorbide was the dominant pigment in the deep series of sediment traps in both years. In 1985, sediment collections by the shallow and deep series of traps were not significantly different, providing no evidence of sediment focusing in Tuesday Lake (Hilton 1985).

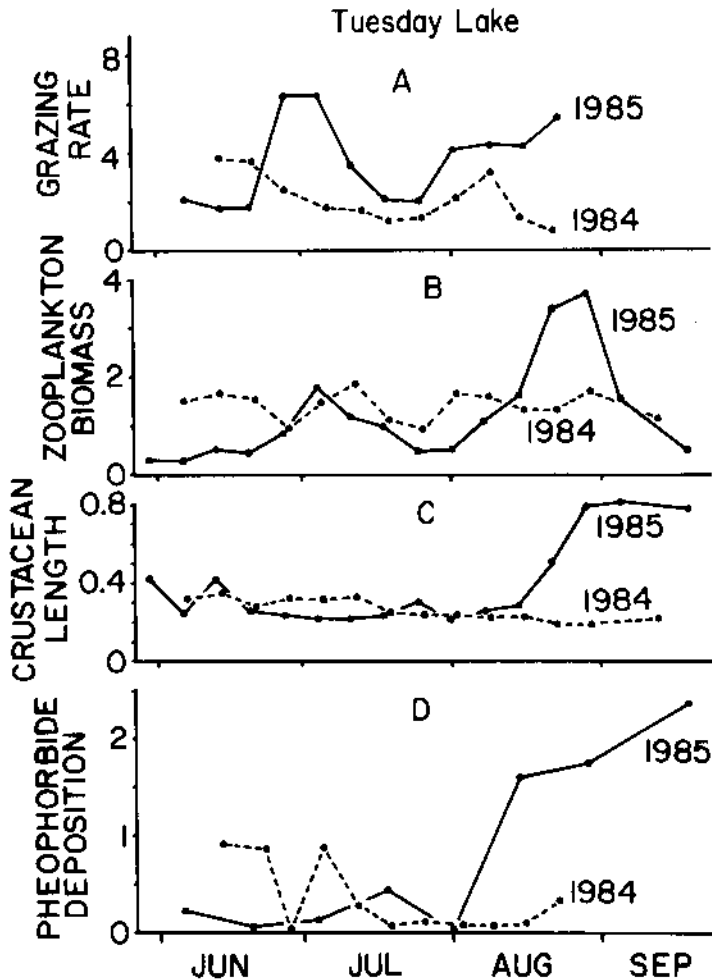


Fig. 4. Variables related to grazing and pheophorbide *a* deposition versus time in 1984 (dashed line) and 1985 (solid line) in Tuesday Lake. Food web manipulations occurred in May 1985. (A) Grazing rate ($\mu\text{mole m}^{-2} \text{ week}^{-1}$). (B) Zooplankton biomass (g dry mass m^{-2}). (C) Crustacean mean length (mm). (D) Pheophorbide *a* deposition ($\mu\text{mole m}^{-2} \text{ day}^{-1}$).

The high variability of pigment sedimentation in Tuesday Lake in 1985 accompanied a marked seasonal trend in sedimentation rates (Fig. 4). First-order autoregression analysis showed that pheophorbide deposition decreased with time during 1984 ($P = 0.05$) but increased with time during 1985 ($P = 0.01$). Pheophorbide deposition rates rose in August 1985, coincident with increases in zooplankton biomass and size of crustacean zooplankters. First-order autoregression analyses showed that relationships of pheophorbide deposition to grazing rate ($P = 0.11$) and zooplankton bio-

mass ($P = 0.62$) were not significant. In contrast, pheophorbide deposition and mean crustacean length had a strong positive relationship ($P = 0.0006$).

Discussion

No interannual differences in pheophorbide deposition were evident in the reference ecosystem, Paul Lake (Fig. 2D). In contrast, substantial interannual differences were evident in pheophorbide deposition in Tuesday Lake (Fig. 4D). Changes in pigment deposition in Tuesday Lake were closely correlated with changes in zooplankton community structure. In both lakes, pheophorbide deposition rate was significantly correlated with mean crustacean length. In Tuesday Lake, dominance by large cladocerans after the food web manipulation was associated with increased rates of pheophorbide deposition.

These patterns corroborate the conclusions of several other studies. Welshmeyer & Lorenzen (1985) found much greater pheophorbide sedimentation in marine systems with large copepod grazers than in those with smaller grazers. Carpenter et al. (1986) noted significant positive correlations between pheophorbide deposition rate and mean mass per herbivore. Both papers attributed this effect to rapid sinking and low photodegradation of pigments in the larger feces of larger grazers.

Differences between our results and observations in Lake Michigan illustrate the important interaction of water transparency and grazer size in determining pheophorbide deposition rate. Because the transparency of Tuesday Lake is largely controlled by humic substances (Elser 1987), it did not change as chlorophyll concentrations changed after the manipulation (Carpenter et al. 1987). Since underwater irradiance did not change, the percentage of the pheophorbide lost to photodegradation each day did not change. Therefore, changes in pheophorbide deposition resulted from biological, and not physical, changes in the overlying water. In Lake Michigan, however, transparency and zooplankton community structure changed in concert, with very different consequences for pheophorbide deposition (Kitchell & Carpenter 1987). Following the irruption of alewife in Lake Michigan ca. 1960, daphnid grazers were replaced by metalimnetic diatoms and water transparency declined. Even though zooplankton mean size declined, pheophorbide deposition increased for two reasons:

- pigment sinking rate increased because fecal particle size increased; and
- less of the pheophorbide that was produced was photodegraded, because most grazing took place in the dim light of the metalimnion and overall water transparency was less.

This difference between Tuesday Lake and Lake Michigan shows that paleolimnological interpretations of pheophorbide stratigraphy must consider effects of water transparency and ecological differences among herbivores. Parallel analyses of fossil pigments and zooplankton remains will be instructive.

While our results support the use of pheophorbide *a* as a paleolimnological grazing indicator, caveats and needs for further research are also evident. First, the fine-grained temporal changes in pheophorbide deposition that we detected with sediment traps may be difficult to detect in the more coarse-grained data available from sediment cores. It is encouraging that pheophorbide changes were detected in the core from Lake Michigan, where food web changes were extensive and lasted many years (Kitchell & Carpenter 1987). Further core studies of manipulated lakes are needed to establish the sensitivity of pheophorbide as a paleolimnological indicator. Second, non-planktonic inputs are a dominant component of pigment budgets, even during summer stratification in these relatively stable lakes. Error analysis shows that non-planktonic inputs are significantly different from zero and therefore cannot be attributed to accumulated measurement errors. Non-planktonic inputs may arise from allochthonous inputs, littoral inputs, sediment resuspension, and the magnifying effects of sediment focusing on all inputs (Carpenter et al. 1986). More detailed study of these processes is needed to determine their effects on the sedimentary pigment record.

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