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DYNAMICS OF LAKE MICHIGAN PHYTOPLANKTON: MECHANISMS CONTROLLING EPILIMNETIC COMMUNITIES

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ABSTRACT: Lake Michigan epilimnetic algal and particulate organic carbon sedimentation rates, determined from moored and floating sediment traps, and algal loss rates due to crustacean zooplankton grazing, determined from manipulation experiments with natural assemblages, were estimated during 1983 and 1984 field seasons. Sedimentation was the most important algal loss in spring when colonial diatoms and calanoid copepods dominated the plankton. Grazing was the most important loss during summer when phytoflagellates and Daphnia *spp. dominated. Comparisons between algal community production and loss due to sedimentation and grazing suggest that natural mortality may be significant, but it does not dominate control. An hypothesis is offered for overall control of phytoplankton dynamics in Lake Michigan.*
ADDITIONAL INDEX WORDS: Algae, eutrophication, zooplankton, aquatic productivity, sedimentation rates.

INTRODUCTION

Rarely will growth rates alone control phytoplankton dynamics. Combined physical, chemical, and biological forces act on both growth and loss processes and both are important (e.g., Kalff and Knoechel 1978, Reynolds *et al.* 1982). Sinking has long been cited as a potentially significant factor controlling population abundance (Hutchinson 1967, Smayda 1970, Sommer 1984, Reynolds and Wiseman 1982), especially for systems dominated by diatoms. Grazers may also impart significant losses (Riley 1946, Crumpton and Wetzel 1982, Thompson *et al.* 1982) and nonpredatory mortality has been claimed as a potential major loss and carbon shunt in freshwater systems (Jassby and Goldman 1974, Forsberg 1985).

While the difference between growth and loss rates controls algal dynamics, the two processes have seldom been measured simultaneously for a given water body. Previous comparisons were often based on laboratory extrapolations for certain processes (e.g., cases in Forsberg 1985) or on results from enclosures (Reynolds *et al.* 1982). For the Great Lakes, most analyses have relied on model interpolation of static observations (e.g., Scavia 1979a,1980a; Scavia and Bennett 1981; Bierman and Dolan 1981). While such interpolations are instructive, lack of process rate estimates seriously impedes model validation and thus limits their utility in that context (Simons and Lamb 1980; Scavia 1979b, 1980b, 1983).

Recent observations of dramatic changes in certain lower trophic-level conditions in lakes (e.g., water clarity, phytoplankton composition) have been linked to changes in upper food-web interactions (Shapiro *et al.* 1975, Edmondson and Litt 1982, Carpenter and Kitchell 1984, Carpenter *et al.* 1985, Scavia *et al.* 1986b). Food-web interactions may affect loss mechanisms such as zooplankton grazing, but they can also affect algal growth by altering nutrient cycles. Lake Michigan fish (Wells 1985, Jude and Tesar 1985) and zooplankton (Evans and Jude 1986, Scavia *et al.* 1986b) have undergone recent major species composition changes; these changes have apparently driven the lake toward a new condition with clearer water (Scavia *et al.* 1986b) and different phytoplankton species composition (Fahnenstiel and Scavia 1987a). While arguments continue regarding phytoplankton control from below and from above the food web (e.g., Kitchell *et al.* 1987, Sca-

via *et al.* 1987), factors regulating algal dynamics must be sorted to connect altered zooplankton community structure with changes in algal composition. The purpose of the present study was to elucidate these mechanisms.

Rates of growth, grazing loss, and sedimentation of phytoplankton were measured in southeastern Lake Michigan during 1983 and 1984. Phytoplankton production, growth, and dynamics for these years are described elsewhere (Fahnenstiel and Scavia 1987a,b,c), as are dynamics and controls of heterotrophic bacterioplankton (Scavia *et al.* 1986a, Gardner *et al.* 1986. Scavia and Laird 1987) and nutrient fluxes (Laird *et al.* 1987). Here we describe variation in two algal loss mechanisms, grazing and sedimentation. These losses are evaluated in the context of observation variability and a series of hypotheses is offered for control of Lake Michigan phytoplankton dynamics.

METHODS

Ambient Conditions

Water for all experiments and measurements was collected from the region of the 100-m depth contour, 26 km west of Grand Haven, Michigan. Temperature was measured with an electronic bathythermograph on board the *R/V Shenehon*; a thermistor mounted in the hull of a drifter buoy (Mini-TOD, Polar Research Laboratory, Inc.); thermistor chains (Saylor and Miller 1983) moored in this region; and from the NOAA data buoy NDBC 45007 located 50 km from our site in 152 m of water. Phytoplankton samples, preserved with acid Lugol's iodine, were filtered or settled onto slides (Fahnenstiel and Scavia 1987a). Conversion of phytoplankton taxon counts to carbon concentration was based on measurements of shapes and sizes and on carbon contents of Strathman (1966).

Zooplankton were collected with vertical hauls of a 0.5-m aperture, 153-μm mesh plankton net. Animals were preserved in sugar-formalin (Haney and Hall 1973) after narcotizing with club soda. Zooplankton dry weight was determined by converting abundance estimates with taxon-specific dry weights from either published values for Lake Michigan (Hawkins and Evans 1979) or from original weight measurements on the 1983 and 1984 samples.

Sedimentation

Sedimentation rates were determined from 10-cm and 20-cm diameter free-floating traps in 1983 and from 20-cm diameter moored and free-floating traps in 1984. The height:diameter ratio for all traps was 5:1 and trap design was that described by Eadie *et al.* (1984). Free-floating traps were suspended in a 100-cm X 100-cm square array (Fig. 1a) below a window-shade drogue (1 m width) which was attached (Fig. 1b) to a satellite-tracked drifter buoy (Mini-TOD, Polar Research Laboratory, Inc.). In 1984, to minimize potential collection bias due to wave-induced oscillations, we fixed the top of the drogue to a lower resistance, spar- type buoy which was tethered to the satellite-tracked buoy. We also fixed a 75-cm diameter wave damper to the bottom of the trap array. With less than even 1-foot waves, the spar buoy became fully submerged, illustrating the neutralization of wave motions.

Floating traps were located at a depth approximately equal to the depth of the mixing layer and moored traps were set in pairs at four depths ranging from 10 to 50 m. Both trap types were left in the lake for periods of 4 to 29 days. Collection bottles (500 mL) were poisoned with glutaraldahyde, formalin, chloroform, acid Lugol's, or basic Lugol's, depending on the intended use of trap material. After trap retrieval, all but the Lugol's-preserved collection bottles were centrifuged and the supernatant syphoned off. The remaining material was dried in a 60°C oven, carefully scraped out, and weighed. The dry material was then analyzed for organic carbon by either wet oxidation after acidification with an Oceanography International Carbon Analyzer or by combustion on a Perkin Elmer CHN Analyzer. Lugol's-preserved collection bottles were subsampled and slides were prepared for phytoplankton enumeration as described in Fahnenstiel and Scavia (1987a). Flux rates were calculated by dividing the weight (total mass or carbon) of material caught in the trap by trap crossectional area and deployment duration. Volume-specific fluxes were calculated by dividing flux by the depth of water above the trap, which was the mixing-layer depth in most cases.

Grazing Losses

Grazing experiments were modeled after those described by Lehman (1980) and Lehman and Sandgren (1985). Water pumped from depth

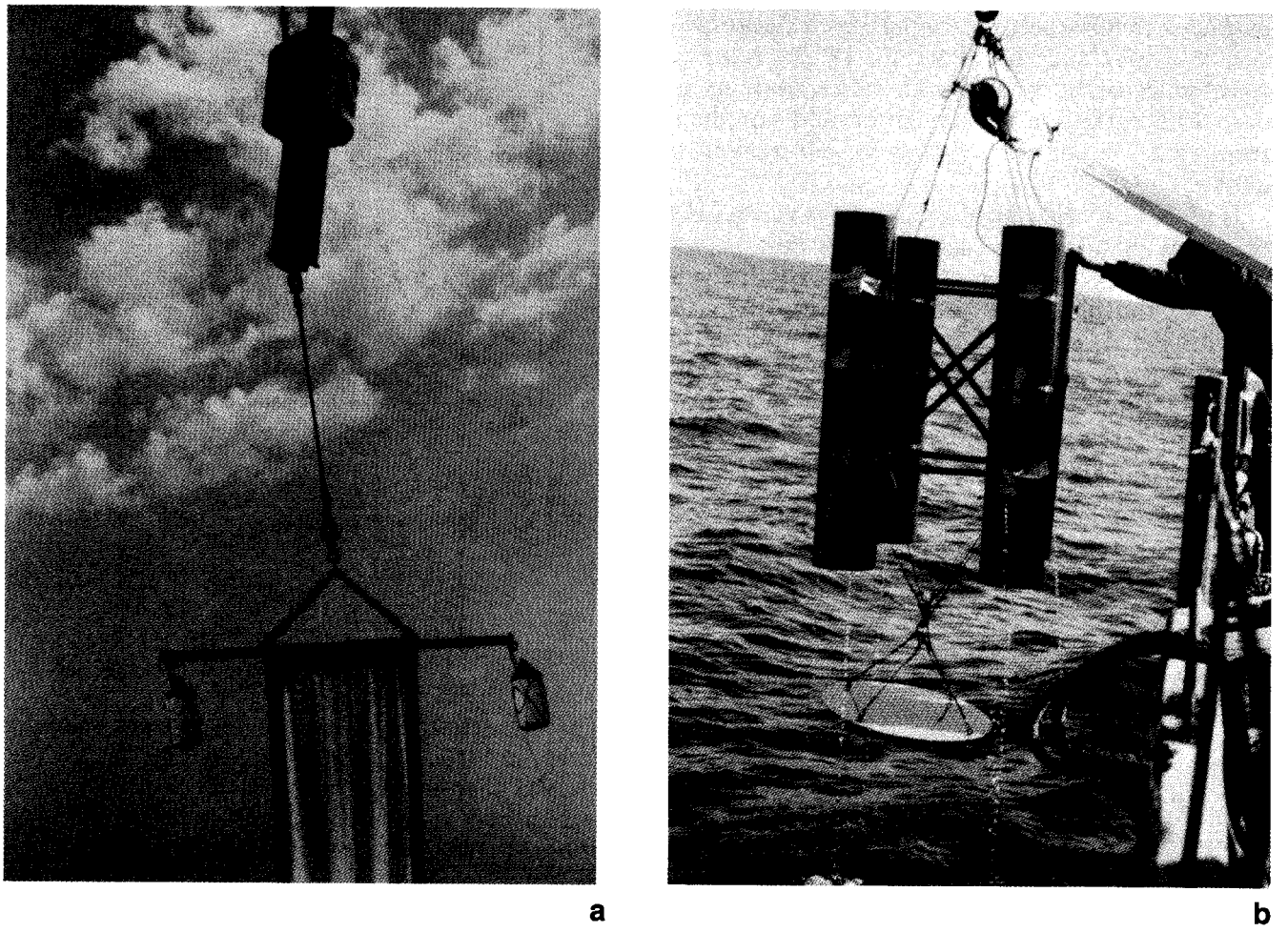

FIG. 1. a) Drogue and drifter buoy and b) floating sediment trap system used in 1983.

through a high-speed, high capacity pump was passed through a 153-μm mesh plankton net to remove animals before dispensing into a 1,000-L tank. Experimental animals were then collected from the water column by vertical haul of a 0.5-m aperture, 153-μm closing net through the depth region of interest approximating natural densities when the animals were added to the tank. After filling, the tank was covered and shaded during transport to shore.

At shore, tank contents were mixed and syphoned into plastic pails for preparation. For "no-zooplankton" treatments (0X), syphoned water was passed through a 153-μm Wisconsin-type plankton net to remove crustaceans. These animals were saved and added to unscreened water for the 2X treatment. Unscreened water was used for the 1X treatment and an appropriate volume of water was passed through a 153-μm net to collect animals for the 4X treatment. Water and animals from the pails were poured gently into replicate 20-L clear, polycarbonate carboys which were capped with neoprene stoppers. To minimize differences in the effect of zooplankton-recycled nutrients at the different zooplankton abundances (Lehman 1980), carboys were spiked with PO_4, the limiting nutrient (Schelske 1979, Fahnenstiel and Scavia 1987b), to a final P concentration of 0.23 μm. Carboys were then placed on rotating racks in water-cooled incubators and exposed to screened natural light and appropriate ambient temperatures. Incubation time was usually 24 hours but never longer than 36 hours. Samples, taken before and after incubation, were processed for chlorophyll *a* and phytoplankton abundance. Chlorophyll *a* samples were collected on glass fiber filters, ground and

extracted in 90% acetone, and assayed fluorometrically (Strickland and Parsons 1972). Animals were collected by pouring the entire contents of each 20-L carboy, after incubation and sampling, through a 153-μm net and they were preserved as above.

If plots of specific algal growth rates versus zooplankton abundance in each carboy from this type of experiment (e.g., Fig. 7a) are linear, then the slope of the plot is an estimate of zooplankton weight-specific clearance rate, and the intercept is an estimate of algal intrinsic growth rate. Slope, intercept, and significance of the linear fit of algal net growth on zooplankton biomass were determined by linear regression. Algal net growth rate, r, was calculated from:

$$r = (1/T)\ln(A/A_0)$$

where A and A_0 are final and initial chlorophyll *a* concentrations and T is the duration of the incubation. Algal carbon loss rates due to zooplankton grazing were calculated by (weight-specific clearance rate) X (epilimnion zooplankton dry weight concentration) X (ambient phytoplankton carbon concentration).

To limit expectations on grazing loss rate comparisons within and among years and between other phytoplankton gain and loss rates, we calculated standard errors of loss estimates by propagating errors from clearance rates, zooplankton abundances, and phytoplankton abundances. Standard errors of clearance rates were determined from the linear regressions. Errors for zooplankton and phytoplankton abundances represent natural variability rather than only estimation errors because they are based on variation in the mean of depth- and/or time-dependent samples for each date. With zooplankton abundance estimates from only single net hauls in 1984, we applied to those data the typical coefficient of variation (CV) from the 1983 estimates (ca. 30%, Lehman, J. T., University of Michigan, and D. Scavia, unpublished data). Coefficients of variation for clearance rate ranged from 13 to 57%; for phytoplankton carbon concentration from 10 to 20%; and for zooplankton abundance from 20 to 40%. Standard errors of phytoplankton loss rates, determined from these error estimates through first-order error propogation, ranged from 30 to 70%.

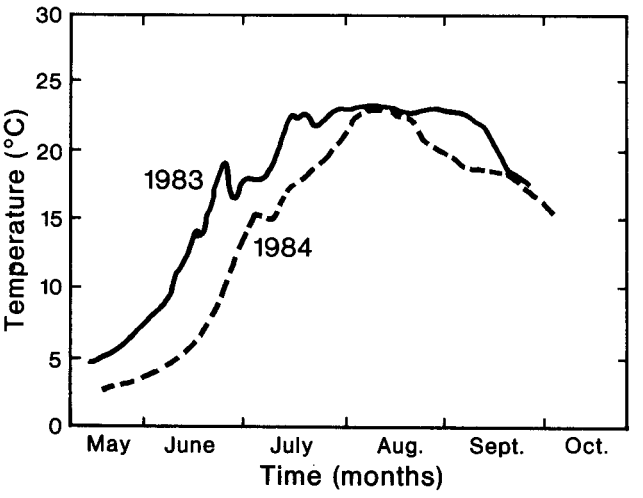

FIG. 2. Surface temperatures for 1983 and 1984.

RESULTS

Ambient Conditions

Thermal stratification temporal patterns were different in 1983 and 1984. The lake was warm earlier in 1983 than in 1984 (Fig. 2). Weak stratification was present in early June 1983 but not until late June in 1984 and establishment of thermocline depth at ca. 10 m was delayed about 3 weeks in 1984 compared to 1983. Maximal temperature (ca. 23°C) was reached in mid-July 1983 and in August 1984.

Epilimnetic algal carbon concentrations were highest in early spring and decreased to minimal values by mid-summer stratification in both years (Fig. 3), a common feature of Lake Michigan phytoplankton (Scavia *et al.* 1986b). Concentrations were somewhat higher and remained high longer in 1984 than in 1983. Epilimnetic phytoplankton abundance and composition during those years are described in detail elsewhere (Fahnenstiel and Scavia 1987a). In general, spring populations were dominated by net diatoms, whereas midsummer populations were dominated by phytoflagellates. The transition from diatoms to phytoflagellates occurred later in 1984 than in 1983, coincident with the delay in thermal stratification.

Epilimnetic zooplankton biomass remained low (ca. 8 μg L^{-1}) until late June 1984 when it increased to approximately 50 μg L^{-1} (Fig. 4). Daytime epilimnetic concentrations remained in that range through July; concentrations from night tows on two dates in July were similar to those from day

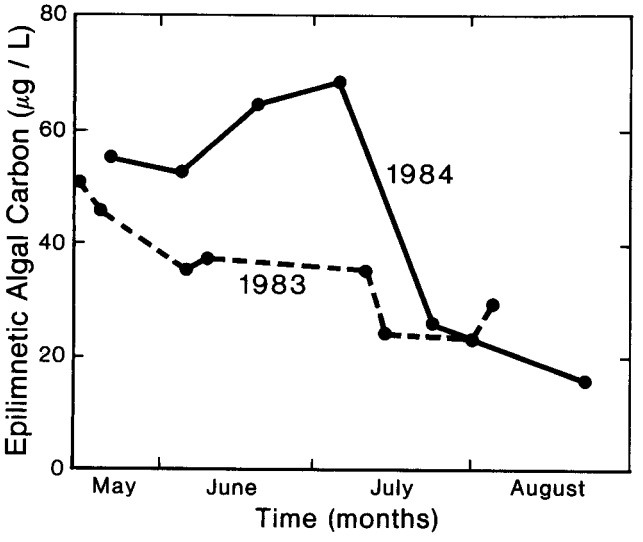

FIG. 3. Epilimnetic average algal carbon concentration for 1983 and 1984. Values are means from 2–3 depths within the epilimnion on each date.

tows on the same two dates. In late-August 1984 epilimnetic concentration decreased to 2 μg L^{-1}.

Calcite precipitation ("whitings"), which was intense in late August 1984, may have influenced epilimnetic zooplankton abundance. We do not have data to test that hypothesis, nor do we have information on diurnal variations in the zooplankton during the late-August 1984 cruise. However, biomass concentration determined from a daytime 0 to 40-m net tow in August 1984 was 65.8 μg L^{-1}, not unlike that determined for dates earlier in 1984 and in 1983 suggesting that the animals migrated to the 20 to 40-m stratum. Except for the fact that concentrations were high earlier in 1983 (Lehman, J. T., and D. Scavia unpublished data) compared to 1984, the overall dynamics of epilimnetic zooplankton biomass concentrations were similar in both years.

Zooplankton species composition in 1984 was similar to that in 1983 but different from years prior to 1983 (Scavia *et al.* 1986b; Lehman, J. T., and D. Scavia unpublished data). In spring, copepods (primarily juvenile and adult *Diaptomus* spp.) dominated. *Daphnia pulicaria* dominated July-August 1983 zooplankton (Scavia *et al.* 1986b). In midsummer 1984, *Daphnia* were also dominant (e.g., 70% by weight on 23 July) but *D. pulicaria, D. galeata mendotae*, and *D. retrocurva* were all significant contributors.

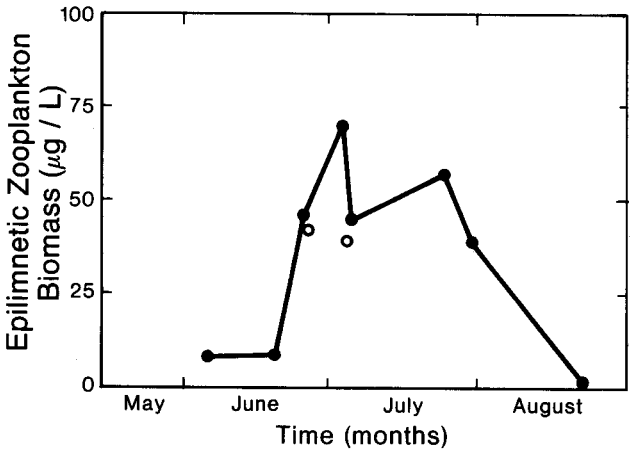

FIG. 4. Epilimnetic zooplankton dry weight biomass from day samples in 1984 (closed symbols). Open symbols represent night collections.

Horizontal Fluxes

The effect of water mass movements on the rate of change of a property of interest at a given station is determined by the product of current speed and horizontal gradient of the property. Drogues were deployed during our studies to follow water masses and to assess the potential impact of currents on our rate studies. The most common features of the epilimnetic drogue tracks were inertial circles (ca. 17-hr period, 2.8 km diameter) and larger-scale direction changes. Direction changes occurred at a frequency of 3–5 days, similar to that observed from longer- term drifter deployments (Pickett *et al.* 1983). Mean net drifter velocity was less than 2.5 km d^{-1}, which is similar to current speeds estimated from vector-averaging current meters deployed during summer 1984 in the same region (J.S. Saylor, NOAA Great Lakes Environmental Research Laboratory, Ann Arbor, personal communication). Basin-scale offshore epilimnetic chlorophyll gradients, calculated from an array of eight southern-basin stations with approximate spacing of 30–50 km visited by the Environmental Protection Agency (Rockwell *et al.* 1980) in summer 1976, averaged 0.0033 μg chl L^{-1} km^{-1} (S.E. = 0.0030). Dividing this gradient by mean chlorophyll concentrations during the same period (1.18 μg chl L^{-1}) and multiplying by the advective transport term (2.5 km d^{-1}) yields a rate of algal change due to horizontal water movements, which corresponds to an effective exponential growth rate of

only 0.007 d^{-1}. Similar calculations for stations with spacings of 8.5–35.0 km, visited in 1985 on north-south and east-west transects from our station, yielded -0.0071 μg chl L^{-1} km^{-1}, 1.14 μg chl L^{-1}, and a net loss rate of only 0.016 d^{-1}. Continuous, 5 to 10-km horizontal *in vivo* fluorescence transects within the region of study in 1984 revealed no significant variation on smaller scales. These calculated rates of algal change due to horizontal water movements are over an order of magnitude smaller than rates of growth, grazing, and sinking measured as part of this study (see Fahnenstiel and Scavia 1987b and below). Thus, combination of low current speeds and small horizontal gradients minimizes the confounding effects of water-mass transport in the summer epilimnion.

Sedimentation

Differences between estimates from our two floating-trap sizes in 1983 (Fig. 5a) were not significant, although the smaller diameter (10 cm) traps appeared to collect more material than larger traps (20 cm). The mean coefficient of variation (CV) among the four traps for each deployment was 28.5%. Fixed and floating traps, deployed in 1984, also showed some variability, but no systematic bias was found for mass flux (Fig. 5b) or carbon loss estimated by algal counts (Fig. 5c). Mean CV among deployments for mass flux was 32.5%; CV for algal carbon loss, based on a combination of replicate algal counts, replicate traps, and fixed versus floating traps, was 26.6% for each deployment. Because differences among trap-types were not significant, flux estimates were based on means of all traps in each deployment. Based on the above results, precision of trap-based estimates is assumed to be 30%.

While our mass flux estimates decreased by about a factor of 10 from unstratified to stratified periods, particulate organic carbon (POC) loss varied less (Table 1) because the organic content of the trap material increased in summer.

Sedimentation of algal carbon, determined from phytoplankton counts of trap collections, showed similar seasonal patterns in 1983 and 1984 (Fig. 6). Very high loss rates (5–12 μg C L^{-1} d^{-1}) in early spring gave way to minimal losses (< 0.5 μg C L^{-1} d^{-1}) during summer stratification. Algal carbon collected in spring traps was 95–99% diatoms. In summer, even though epilimnetic diatoms were scarce (< 5% of algal carbon, Fahnenstiel and

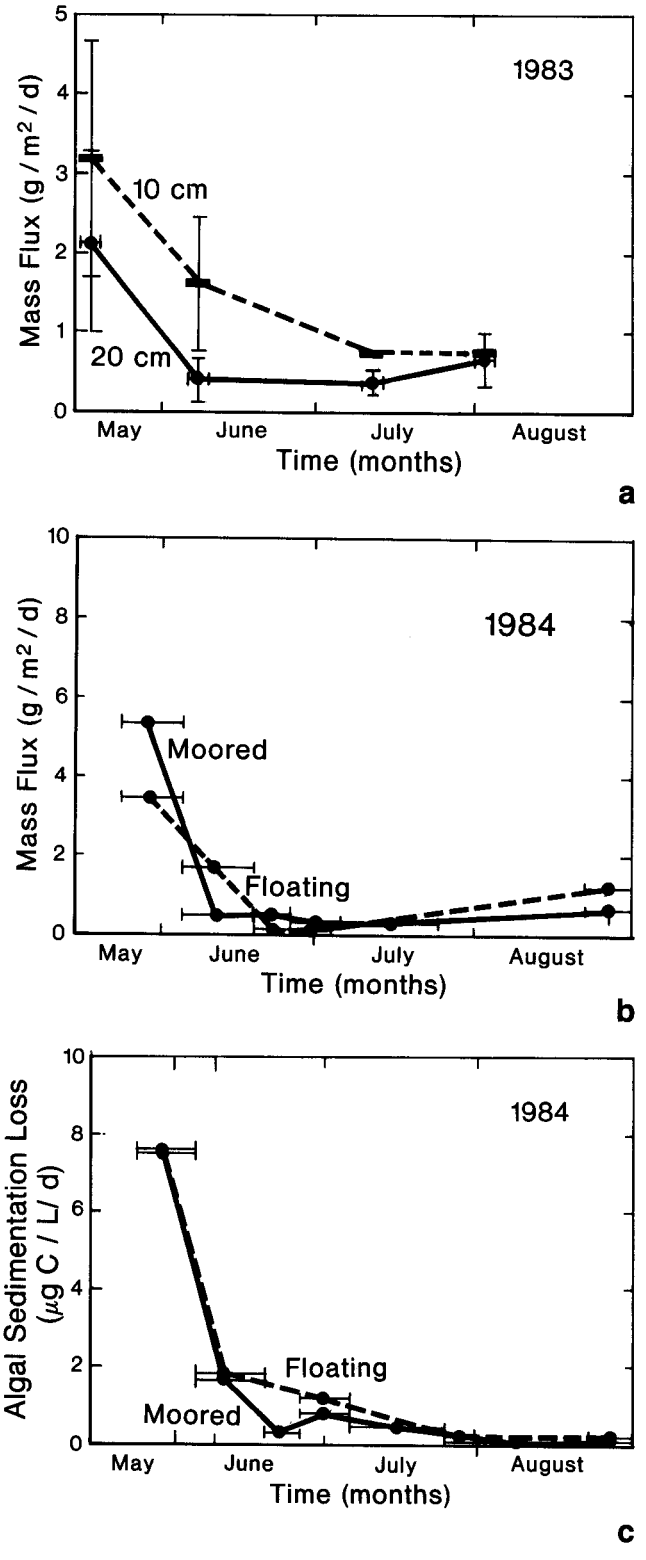

FIG. 5. Sedimentation fluxes from 1983 and 1984 deployments. (a) Comparison of 10-cm and 20-cm floating traps in 1983, (b) comparison of moored and floating traps in 1984 in terms of mass flux, and (c) algal carbon flux.

TABLE 1. Carbon flux ($\mu g\ C\ L^{-1}\ d^{-1}$) from Lake Michigan surface water.

Date	POC	Algae	% Algae
1983			
5/16-5/25	12.1	11.5	95.0
6/6-6/10	11.0	5.3	48.2
7/10-7/14	7.4	0.05	0.67
8/1-8/5	10.4	0.02	0.19
1984			
5/21-6/4	34.5	7.50	21.7
6/4-6/18	14.8	1.70	11.5
6/18-6/25	5.4	0.50	9.3
6/25-7/5	4.5	1.02	22.7
7/5-7/24	13.1	0.45	3.4
7/24-7/30	–	0.22	–
7/24-8/22	–	0.03	–
8/22-8/31	16.7	0.14	0.8

Scavia 1987a), they constituted 23-62% of trapped algal carbon.

The percentage of POC represented by viable algal cells was 95% in May 1983, 48.2% in June 1983, and averaged 16.3% in May-June 1984 collections (Table 1). These values decreased to 0.4% and 2.1% for July-August 1983 and 1984, respectively. Therefore, during summer most POC leaving the epilimnion was detrital.

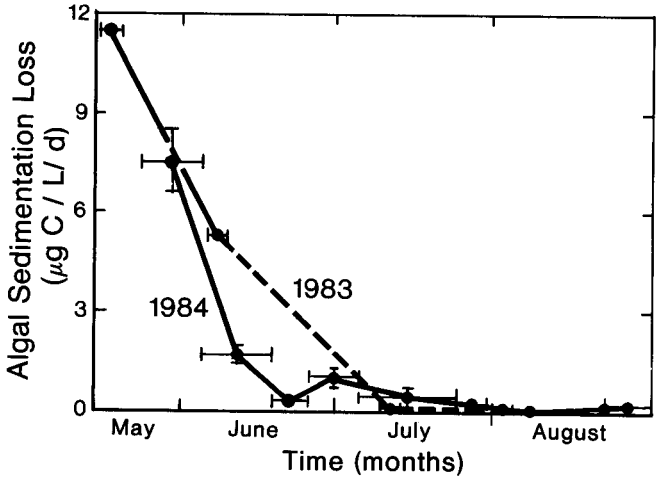

FIG. 6. Sedimentation loss rates form algal counts of trap collections in 1983 and 1984. Horizontal bar lengths represents deployment duration; vertical bars are mean ± one S.E. from multiple deployments in 1984.

Crustacean Grazing Loss

Grazing experiments were designed to estimate algal community losses caused by crustacean zooplankton. Because we manipulated zooplankton biomass by selective screening with 153-μm mesh nets, our experiments do not include grazing effects of the smaller zooplankton (e.g., rotifers). Although grazing losses are not uniform across the algal assemblage (e.g., Reynolds *et al.* 1982, Knisely and Geller 1986), we estimated net grazing impact on the entire algal assemblage by calculating algal growth rates in the experimental bottles from changes in chlorophyll *a* concentrations.

Under the hypotheses of the model underlying the grazing experiments, plots of specific algal growth rate versus zooplankton abundance should be linear if the effect of zooplankton-regenerated nutrients is small or minimized by nutrient additions. A sample plot of results from the 25 June 1984 experiment is shown in Fig. 7a. Slopes of the resulting curves from these experiments provide estimates of zooplankton clearance rates (mL μg dry wt^{-1} d^{-1}) and intercepts provide estimates of net algal growth rates in the absence of zooplankton. Linear regression statistics for results from experiments done with epilimnetic and hypolimnetic day- and night-sampled assemblages in 1984 (Table 2) illustrate the validity of this linearity assumption.

Algal growth rate estimates from these analyses range up to 0.42 d^{-1} and are not unlike those determined by several other techniques (Fahnenstiel and Scavia 1987b). Epilimnetic clearance rates ranged between undetectable levels and 2.03 mL μg^{-1} d^{-1}; most values were in the range of 1 to 2 mL μg^{-1} d^{-1} during the period of thermal stratification in 1984 (Table 2).

Our day/night-epilimnetic/hypolimnetic series experiments (4-5 July and 23 July 1984, Table 2) revealed some differences in clearance rate that depend both on time and location of the sampled zooplankton assemblage. Clearance rate for the day-sampled epilimnetic assemblage was higher than that of night (2.03 vs 1.59 mL μg^{-1} d^{-1}). The rate for the day-sampled hypolimnion assemblage was lower than that of the night assemblage (1.87 vs 2.91 mL μg^{-1} d^{-1}). Clearance rate determined for the day-sampled hypolimnion assemblage on 23 July was lower than that estimated for the day-sampled epilimnetic assemblage on the same date (0.25 vs. 1.76 mL μg^{-1} d^{-1}). None of the rate differences were statistically significant (two-tailed T-tests, a = .05). Because all experiments were run

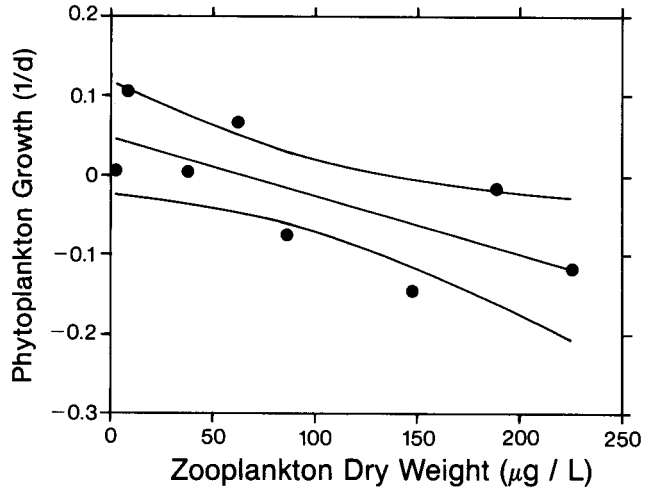

FIG. 7a. Plot of algal growth rate (closed symbols), determined from rates of cholrophyll change in different enclosures versus zooplankton dry weight in those enclosures. Regression results from this 25 June 1984 experiement are shown as least-squares fit and 90% confidence limits.

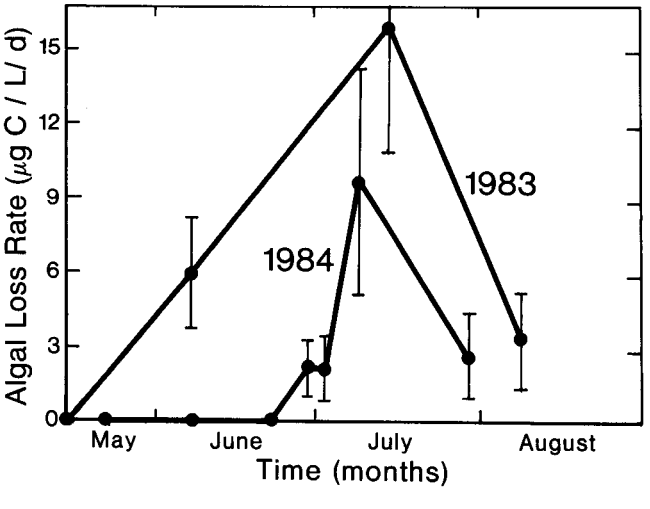

FIG. 7b. Algal loss rates due to zooplankton grazing. Vertical bars represent mean ± one S.E.

for at least one full day/night cycle, the rate differences reflect the composition of collected zooplankton rather than true diurnal clearance rate variation.

Specific loss rates (d^{-1}) due to zooplankton grazing were calculated by multiplying weight-specific clearance rates by epilimnetic zooplankton biomass. These values ranged between 0.03 and 0.14 d^{-1} for 1984, with the highest value occurring on 5 July.

TABLE 2. Results from 1984 grazing experiments.

Date	Slope (mL μg^{-1} d^{-1})	Alpha[1]	Comment[2]
21 May	NS[3]	–	E,D
5 Jun	NS[3]	–	E,D
16 Jun	NS[3]	–	E,D
25 Jun	0.73	0.049	E,D
28 Jun	0.72	0.097	E,D
4 Jul	1.59	0.095	E,N
5 Jul	2.03	0.032	E,D
4 Jul	2.91	0.017	H,N
5 Jul	1.87	0.12	H,D
23 Jul	1.76	0.16	E,D
23 Jul	0.25	0.03	H,D

[1]Significance of regression.
[2]Experimental condition: E = epilimnetic assemblage, H = hypolimnetic assemblage, N = night assemblage, D = day assemblage.
[3]NS = Slope assumed equal to zero. Regressions were not performed because algal growth rates did not vary among zooplankton treatments.

Because algal net growth rates did not vary among zooplankton treatments during late spring isothermy (Table 2), algal carbon loss due to grazing is assumed to be insignificant at those times. We used clearance rates, zooplankton epilimnetic biomass, and phytoplankton carbon concentrations for corresponding dates in the May through July 1984 estimates. To determine 1983 loss rates, June to August 1983 zooplankton biomass estimates and June and August 1983 clearance rate estimates (Lehman, J.T., and D. Scavia unpublished data) were combined with algal carbon concentrations from those respective cruises (Fig. 3). Loss fluxes (Fig. 7b) in the spring (early-June 1983, late-June 1984, respectively) were 5.9 and 1.9 μg C L^{-1} d^{-1}; highest rates occurred in July of both years (15.8 and 9.6 μg C L^{-1} d^{-1}). Fluxes in late-July 1984 and August 1983 were lower (2.3 and 3.4 μg C L^{-1} d^{-1}) due to both lower zooplankton abundance and lower algal carbon concentrations.

DISCUSSION

Sedimentation and Grazing Rates

Accuracy of our sedimentation estimates is difficult to assess; however, our trap design and deployments were, in most cases, similar to those recommended by Bloesch and Burns (1980) and should not be seriously biased. Our mass flux estimates averaged 3.4 ± 0.71 g m^{-2} d^{-1} for the unstratified periods and 0.39 ± 0.09 g m^{-2} d^{-1} for the stratified periods (Figs. 5a,b). These estimates are

similar to those found earlier in Lake Michigan. Chambers and Eadie (1981) estimated a near-surface flux of 0.70 ± 0.4 g m^{-2} d^{-1} during the period of stratification in 1977. Eadie *et al.* (1984) estimated fluxes of 6.20 ± 0.64 and 0.65 ± 0.26 g m^{-2} d^{-1} for unstratified and stratified periods in 1978 from traps deployed at 35 m and similar values for 10-m traps during 1980. All of these estimates of summer fluxes are similar to sediment accumulation rates determined from analysis of Lake Michigan sediment cores (Davis *et al.* 1971, Robbins and Edgington 1975, Edgington and Robbins 1976) and, in that sense, reflect net fluxes; higher spring fluxes include resuspension (Eadie *et al.* 1984). Our estimates of POC flux (0.04 - 0.34 g C m^{-2} d^{-1}) are also similar to those determined previously (0.06 - 0.26 g C m^{-2} d^{-1}, Eadie *et al.* 1984).

Our estimates of 1984 epilimnetic zooplankton clearance rates (0.72 - 2.03 mL μg^{-1} d^{-1}) are similar to, but lower than, those determined for 1983 (Scavia *et al.* 1986b; Lehman, J. T., and D. Scavia unpublished data). The difference may be attributable to differences in zooplankton composition. The August 1983 zooplankton was heavily dominated by the relatively large-bodied cladoceran, *Daphnia pulicaria* (over 90% by weight, Scavia *et al.* 1986b); whereas the summer 1984 assemblage was composed of never more than 70% *Daphnia*, with the remaining assemblage being adult and immature copepods. Because *Daphnia* abundance in the 1984 experimental chambers was also low relative to water column composition (45% vs. 70%), the clearance rates may be underestimates. Thus, the difference in grazing pressure exerted by ambient zooplankton assemblages was probably not as large as that suggested by the experimentally determined clearance rates in those years.

Our clearance rates are similar to, but higher than, those determined in other environments and from laboratory experiments. Cladoceran clearance rates are a function of body size (Chow-Fraser and Knoechel 1985). For our summer cladoceran populations (typically 1-2 mm individuals), rates of 6.3-34.5 mL $animal^{-1}$ d^{-1} are expected. These represent weight-specific rates of 0.7-1.6 mL μg^{-1} d^{-1} for the typical 9-22 μg animals, compared to our 1.59 - 2.03 mL μg^{-1} d^{-1} estimates. Laboratory clearance rates for Lake Michigan adult *Diaptomus* spp. range between 0.1 and 0.5 mL μg^{-1} d^{-1} (Vanderploeg and Scavia 1979, Vanderploeg 1981, Bowers 1980), compared to our June estimates of 0.72 and 0.73 mL μg^{-1} d^{-1}. It seems likely that immature copepods in our natural-assemblage experiments would increase the overall weight specific rates over the laboratory adult rates. The Lake Huron assemblage is similar to Lake Michigan's; calanoid copepods dominate in spring and cladocerans dominate in summer. Community-based studies on Lake Huron assemblages labelled with ^{14}C (McNaught *et al.* 1980) suggest that over 70% of the grazing pressure imposed by crustaceans is through naupliar and copepodid stage calanoids; community clearance rates in these studies range from 0.1 to 0.8 mL μg^{-1} d^{-1}.

Our estimates of carbon flux due to zooplankton grazing (2.1 - 15.8 μg C L^{-1} d^{-1}) are also similar to those determined for Lake Huron (McNaught *et al.* 1980). Carbon flux from algae to the Lake Huron crustaceans ranged from 0.1 to 38.0 μg C L^{-1} d^{-1}, with a mean of 8.4 μg C L^{-1} d^{-1} (SE = 4.4, N = 12) for experiments performed between July 1974 and June 1975.

Community Production Versus Loss Rates

We have estimated algal losses attributable to sinking and to grazing by crustacean zooplankton by direct measurement with extant assemblages. Community algal production was also estimated during the same study and those estimates are described in detail elsewhere (Fahnenstiel and Scavia 1987b). Here we use net production determined from 24-h, *in situ*, ^{14}C-incubations at 2-4 depths within the mixing layer. For comparisons between production and loss, only data from thermal stratification periods are used because deep vertical mixing prior to that time hinders interpretation of production and sedimentation estimates. Thus comparisons are for June, July, and August 1983 and July 1984 only. Epilimnetic zooplankton collections for grazing experiments during the $CaCO_3$ whitings in late August 1984 yielded too few animals for significant results.

Algal carbon concentrations changed only slightly during these periods of consideration, (Fig. 3). Except for one time interval (5-23 July 1984) when the rate of change was -2.0 μg C L^{-1} d^{-1}, rates were slow (mean = -0.2 μg C L^{-1} d^{-1}, S.E. = 0.05). Because the effects of horizontal water movement during summer were minimal offshore (see above), production and loss rates should be in reasonable balance.

Growth and loss fluxes for the periods of comparison are listed in Table 3. The two production estimates reported for each time period in July and

TABLE 3. Comparison of production and loss rates ($\mu g\ C\ L^{-1}\ d^{-1}$) during stratification.

Date	Production	Grazing + Sinking	POC Flux
1983			
June	19.0	11.2	11.1
July	3.8	15.9	7.4
	9.7		
August	5.5	3.4	10.4
	13.4		
1984			
Early-July	13.6	10.3	5.0
Late-July	22.0	2.8	13.1
August	16.2	–	16.7
Mean	12.9	8.7	10.6
S.E.	2.2	2.5	1.7

August 1983 are results of 24-hr incubations done 3 days apart. Differences between estimates in each pair reflect natural variability and, to some extent, the difficulty of balancing rates from single-day estimates, which typically vary ± 20% (Fahnenstiel and Scavia 1987b).

Production and loss fluxes from June and July 1983 and early July 1984 are in reasonable balance; however, production can exceed loss considerably (e.g., late July 1984, Table 3). Part of this discrepancy may be caused by growth and loss estimates not being measured entirely for the same communities. Size-fractionation experiments suggest that, at least during summer 1984, about 20% of primary production was in the picoplankton (<1 μm) range (Fahnenstiel and Scavia 1987b; G.A. Laird, GLERL/NOAA, unpublished data). While that size fraction would be included in the ^{14}C-based production estimates, some of it would likely be immune to crustacean grazing. We did not investigate grazing by micro-zooplankton. The small algal size fraction would also not be included in our sedimentation loss estimates because the picoplankton were not included in the microscopic algal counts of trap collections. In fact, algal growth rates, based on changes in cell abundance, were slightly less than ^{14}C-based rates during summer (Fahnenstiel and Scavia 1987b). Thus, we could lower our estimate for "effective" production (i.e., production available to sedimentation and grazing as we have measured them). As mentioned above, crustacean grazing losses during summer 1984 may be underestimated because our experimental manipulations resulted in underrepresentation of the voracious *Daphnia* species. Corrections to this underestimation would then result in higher clearance rates for July 1984. While there are bases for decreasing effective production estimates and for increasing grazing loss estimates for summer 1984, the actual magnitude of the adjustments is unknown.

If errors due to environmental fluctuations and experimental artifacts are random, better comparisons of production and loss rates come from averages (Table 3). Summer mean epilimnetic production is 12.9 $\mu g\ C\ L^{-1}\ d^{-1}$ (S.E. = 2.2, N = 8). Mean summer loss rate (grazing plus sinking) is 8.7 $\mu g\ C\ L^{-1}\ d^{-1}$ (S.E. = 2.5, N = 5), for a "residual" loss of 4.2 $\mu g\ C\ L^{-1}\ d^{-1}$ (S.E. = 3.3). This suggests that, on average, 32.6% of net production may be lost to processes other than sedimentation and crustacean grazing; however, if 20% of the production is in the picoplankton range, then the imbalance is easily explained. Even if we consider 4.2 $\mu g\ C\ L^{-1}\ d^{-1}$ as an upper bound on the imbalance, it is small compared to those calculated previously (e.g., Jassby and Goldman 1974, Reynolds *et al.* 1985, Forsberg 1985). The residual loss, if real, could be due to algal mortality or to catabolic processes. Because our net production estimates are based on 24-hr incubations and because the growth rates based on these estimates are consistent with, or only slightly greater than, net growth determined by other techniques (Fahnenstiel and Scavia 1987b), catabolic losses are likely incorporated in our net production estimates and should not cause major production-loss calculation imbalances. Thus, our data point toward nonpredatory mortality as a small contributor to algal dynamics. While this loss mechanism may not be a major factor in controlling algal dynamics, it may provide a significant immediate source of organic carbon for heterotrophic bacteria. Sources and fates of such organic materials in Lake Michigan are discussed in detail elsewhere (Scavia *et al.* 1986a, Scavia and Laird 1987).

The potential danger associated with this type of difference calculation is in production and loss estimation errors; errors from both ignorance of short-term environmental variability and from limitations in experimental designs. While single-day production estimates are likely subject to only 20% error (Fahnenstiel and Scavia 1987b), measurements made with the same procedures only 3 days apart on two occasions in 1983 were 2.4- and 2.6-fold different (Table 3). Coefficients of variation for grazing losses ranged from 30 to 70%, based on error bounds for clearance rate regression esti-

mates, diurnal and vertical variation in zooplankton abundance, and vertical variation in algal carbon concentrations. Little is known about other sources of variability in the Lake Michigan zooplankton, including meso-scale patchiness, day-to-day variability, and diurnal feeding rhythms. Sedimentation losses are less subject to large errors caused by day-to-day variability because they are estimated from a natural integrative process in our 4- to 29-day deployments. The average coefficient of variation among replicate traps, between fixed and floating traps, and between two different sized traps was 30%; however, the chance of overestimation or underestimation of actual vertical flux cannot be ignored for methodological reasons (Walsby and Reynolds 1980, Gardner 1985). Because of these estimation errors, especially those due to natural short-term variability, our comparison imbalances (Table 3) are not surprising. Only major imbalances can be considered significant in light of short-term environmental variability and error estimates on process measurements.

Detritus Dynamics

Information on particulate organic carbon (POC) dynamics in Lake Michigan suggests that our calculated imbalance between production and loss rates may be real. Epilimnetic POC concentrations typically decrease from ca. 400 μg C L^{-1} in June to 200 μg C L^{-1} in September (H.A. Vanderploeg, B.J. Eadie, and D. Scavia, Great Lakes Environmental Research Laboratory, Ann Arbor, MI, unpublished 1977–1984 data), which represents a loss flux of 2.2 μg C L^{-1} d^{-1} over the 90-day period. Comparison of this flux to our sedimentation losses from the summers of 1983 and 1984, 10.6 (S.E. = 1.7) μg C L^{-1} d^{-1}, suggests that POC must be newly generated in the epilimnion after stratification at a rate of about 8.4 μg C L^{-1} d^{-1}. Thus, 80% of POC collected in summer traps is newly generated in the epilimnion. Because a very small portion of POC collected in our summer traps is recognizable algae, this POC production likely represents detritus production. There are two potential sources of detrital C in Lake Michigan's offshore epilimnion during summer; nonpredatory algal mortality and zooplankton egestion. If we assume that nonpredatory mortality is not important, then all of this 8.4 μg C L^{-1} d^{-1} must come from zooplankton egestion. However, comparing the required egestion rate to zooplankton ingestion (8.7 μg C L^{-1} d^{-1}) yields an unreasonably low assimilation efficiency (3.4%) for the grazers.

Above, we estimated the difference between average production and measured losses to be 4.2 μg C L^{-1} d^{-1}. If this loss is due to nonpredatory mortality, it would add to the detrital pool. Subtracting this rate from the required 8.4 μg C L^{-1} d^{-1} leaves 4.2 μg C L^{-1} d^{-1} to be supplied by zooplankton egestion. Comparing this egestion flux to the ingestion rate suggests that 48% of the ingested algal C is egested (52% assimilation efficiency), which is not an unreasonable estimate. Analyses of carbon flow through a tundra pond ecosystem (Hobbie 1984), eutrophic Frains Lake, Michigan (Saunders 1972), and Lake Ontario (Robertson and Scavia 1979, 1984) suggest respectively, 19%, 17%, and 29% carbon assimilation efficiencies during summer. A 2-year monthly carbon budget for Lake Kinneret zooplankton indicates efficiencies between 23% and 41% (Gophen 1981). As our ingestion rates include only algal food and not total seston, our somewhat higher value (52%) could indicate higher assimilation efficiency with algal foods than with total seston. Or, based on this balance calculation, our calculated higher efficiencies may indicate that not all of the imbalance between algal production and loss is due to natural mortality. Lower natural mortality estimates would result in higher calculated egestion rates, thus lowering calculated assimilation efficiencies. From the perspectives of POC dynamics and balancing algal production, it appears that zooplankton grazing plays a dominant role in algal dynamics. While natural mortality may also be significant, it plays a lesser role. This analysis points again (Robertson and Scavia 1979, 1984; Scavia 1979a, 1980a) to the central role detritus and detritus-zooplankton interactions may play even in the open-water zones of the Great Lakes. This potentially critical role of detritus (particulate and dissolved) in the Great Lakes is consistent with recent analyses in other aquatic environments (e.g., Roman and Tenore 1984, Goldman 1984, Wetzel 1984). Transformation of substantial quantities of autotrophically-fixed carbon to detritus and perhaps to dissolved organic carbon by crustacean zooplankton may also be an important carbon shunt to the microbial food web in Lake Michigan (Scavia *et al.* 1986a, Scavia and Laird 1987).

We could conclude from the above analyses that summer net production, as determined by 24-h, *in situ* ^{14}C incubation in Lake Michigan, may not be balanced completely by sedimentation and grazing

losses, and that physiological death (nonpredatory mortality) may be an important factor in algal dynamics. While this loss mechanism has been invoked before, seldom has its significance been demonstrated when estimated experimentally (e.g., Crumpton and Wetzel 1982, Reynolds *et al.* 1982, Reynolds 1984). Its impact may be felt most dramatically as enhanced sinking losses for diatoms (Kalff and Knoechel 1978, Sommer 1984). Our data do not verify directly the significance of nonpredatory mortality in summer phytoflagellate populations, and we suggest, like Reynolds (1984), that future investigations assess its importance directly, rather than "by difference."

Seasonal Algal Losses

With regard to seasonal dynamics, algal carbon sedimentation loss from surface waters was greatest in May of both years. High flux estimates in May 1983 and May/early June 1984 may overestimate net downward flux because these are times of a relatively unstable water column with possible unmeasured upward fluxes due to vertical mixing (Eadie *et al.* 1984). However, our first measurement times in both years occurred during the transition between isothermal conditions and the onset of weak permanent stratification, a period characterized by transient diel stratifications and reduced resuspension. Because the diatom-dominated spring assemblage sinks dramatically from the epilimnion, during even weak stratification, algal carbon fluxes were already reduced by the second measurement sequence each year. Algal sedimentation rates virtually vanish during periods of strong stratification, to ca. 0.035 and 0.2 μg C L^{-1} d^{-1} (0.3% and 2.5% of the spring maximal values). Yet epilimnetic algal carbon concentrations are only reduced to 56% and 33% of their spring maxima in 1983 and 1984, respectively. Thus, the reduced fluxes are not due simply to a clearing of epilimnetic algal carbon, but rather to a dramatic reduction in settling velocities. For example, sinking rates, calculated from algal carbon flux divided by epilimnetic algal carbon concentration, decreased from 2.4 to 0.015 m d^{-1} in 1983 and from 1.1 to 0.080 m d^{-1} in 1984. These rates are typical for diatoms and flagellates (e.g., Smayda 1970, Sommer 1984), and the decrease from spring to summer is consistent with Lake Michigan algal species succession (Fahnenstiel and Scavia 1987a).

Because algal carbon concentrations change only slowly (ca. -0.2 μg C L^{-1} d^{-1}) and because phytoplankton continue to grow at rates averaging 0.33 d^{-1} during summer (Fahnenstiel and Scavia 1987b), loss mechanisms other than sinking must also be important. Grazing is one; nonpredatory mortality may also be significant although not shown directly by our data. The transition from sinking to grazing control of phytoplankton loss is similar in both years and may be related to changes in plankton species composition. Spring populations are dominated by large colonial diatoms and calanoid copepods. The size-range of food preference for these animals is typically 10–20 μm (Vanderploeg 1981), and thus it is not surprising that there appears to be little grazing effect on the algal community as a whole during this time. Summer plankton are dominated by phytoflagellates (3–30 μm) and *Daphnia* spp. The extant phytoplankton are in the size range preferred by these cladocerans and grazing is most intense.

Typical summer grazing loss rate is about 9 μg C L^{-1} d^{-1}, a value not unlike loss rates due to spring sinking (5–12 μg C L^{-1} d^{-1}). The combination of spring diatom sinking and summer grazing on flagellates resulted in a fairly uniform total phytoplankton loss rate from spring through summer 1983 (Fig. 8a). A similar scenario can be outlined for 1984; however, different zooplankton seasonal dynamics resulted in an important change. Zooplankton abundance in 1984 increased later than in 1983 and consequently there was less grazing pressure in spring 1984. This delayed grazing pressure apparently resulted in a temporal refugium (Fig. 8b) wherein the flagellates were able to replace the sinking diatoms and increase in abundance enough to produce an overall increase in phytoplankton carbon concentration (Fig. 3) rather than a simple compositional shift away from diatoms (Fahnenstiel and Scavia 1987a). As grazing pressure increased in summer of both years, total phytoplankton concentration (dominated at that time by flagellates) decreased.

Calcite precipitates (whitings) may have had significant impact on phytoplankton-zooplankton interactions in August 1984. The whitings are basin-wide (Strong and Eadie 1978), regular (Vanderploeg *et al.* 1987) Lake Michigan phenomena in late summer with epilimnetic concentrations of particulate inorganic carbon peaking in early September (B.J. Eadie, GLERL/NOAA, personal communication). Whitings ("milky water") were evident visually during our late August 1984 cruise, but not during our early August 1983 cruise (Secchi disc depth was over 15 m). Minimal whitings in

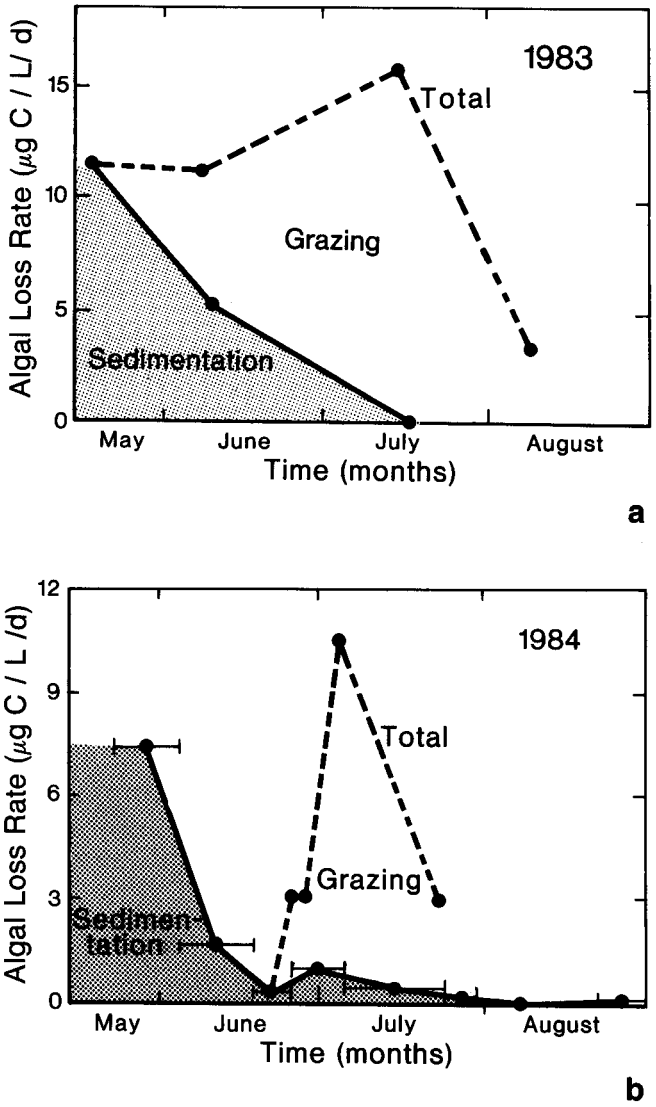

FIG. 8. Partitioning of total loss rate (grazing plus sinking) during the field seasons of 1983 (a) and 1984 (b).

1983 were also evident in particulate inorganic carbon measurements in September of that year (Vanderploeg *et al.* 1987). Because the calcite size spectrum generally overlaps that of organic particles (algae and detritus) and comprises a significant fraction of the total mass in September, the presence of these inorganic particles in 1984 may have influenced zooplankton ingestion and digestion rates (Vanderploeg *et al.* 1987) or their migration.

It is clear that in Lake Michigan, where both phytoplankton and zooplankton species composition can change dramatically from spring to summer, phytoplankton losses must be apportioned both in time and by mechanism. That loss mechanisms are taxon-or group-specific is not surprising. Reynolds *et al.* (1982), for example, found dramatic differences in mechanisms controlling different algal populations in the "Lund Tubes" of Blelham Tarn. Our data will provide similar analysis of population dynamics in a subsequent report; however, in the present context, it is clear that successional dynamics of algal populations both affect, and are affected by, the nature of the imposed losses.

An Hypothesis Concerning the Control of Lake Michigan Phytoplankton Dynamics

Based on our observations of sedimentation and zooplankton grazing, on measurements of phytoplankton production and dynamics (Fahnenstiel and Scavia 1987a, b, c), on results from analyses of other Great Lakes ecosystems (e.g., Scavia 1979a, Robertson and Scavia 1984, Bierman and Dolan 1981), and on other information cited below, we offer the following hypothesis explaining seasonal control of current Lake Michigan phytoplankton dynamics (Fig. 9):

1) Early spring diatom production in Lake Michigan is mixed throughout the water column and, like in Lake Ontario (Scavia 1979a), is controlled initially by temperature and light. As a result, diatom abundance increases slowly throughout the water column (Brooks and Torke 1977) until the lake begins to stratify thermally or until nutrient concentrations (P and Si) are reduced sufficiently from their winter maxima to limit growth (Parker *et al.* 1977) . Grazing does not appear to play an important role at this time of year and thus the major influence on spring phytoplankton dynamics is "bottom-up." That is, the extent of the spring bloom should be predictable, based on winter concentration of available nutrients and on meteorological events influencing the timing of the onset of thermal stratification.

2) When the lake begins to stratify thermally, diatom sinking from the epilimnion is too great to be compensated for by *in situ* growth, which is likely reduced due to Si-limitation, so the diatoms decrease in abundance. Sinking rates increase as growth rates become more nutrient-limited (Tilman and Kilham 1976, Fahnenstiel and Scavia 1987a), and thus the magnitude of sedimentation loss is determined by the timing of nutrient limitation. This transition to Si-limitation of diatom

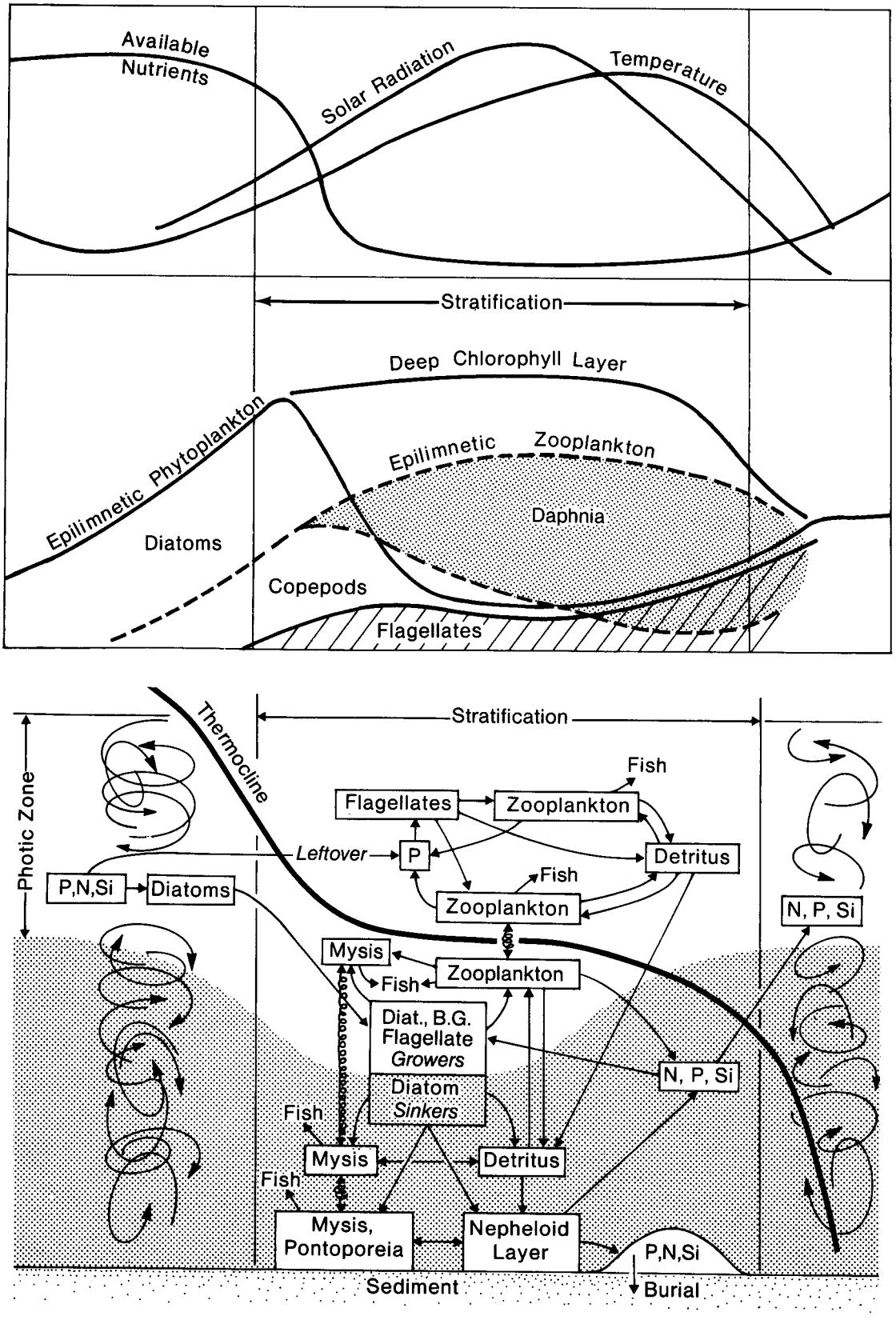

FIG. 9. Schematic representation of the hypothesis for mechanisms controlling phytoplankton dynamics in Lake Michigan.

growth is related to the timing of thermal stratification compared to water-column nutrient depletion (Schelske and Stoermer 1971, Schelske 1985). The latter will be more important in years when stratification is delayed and, in general in the future, if winter available nutrients continue to decline (Scavia *et al.* 1986b). Thus, nutrient-controlled sedimentation is responsible for the major seasonal taxonomic shift among phytoplankton.

3) During the transition from full-mixing to thermal stratification, a large portion of particulate organic carbon (POC) leaving the surface water is leaving as viable diatoms. This "new" material provides nutritionally important food for hypolimnetic-and benthic-dwelling animals (Gardner *et al.* 1985). POC flux from the summer epilimnion is composed primarily of detritus, at least some of which is egested recently by the grazers and is perhaps lysed from algal cells. This flux (110 mg C m^{-2} d^{-1}) is comparable to net epilimnetic algal production (ca. 130 mg C m^{-2} d^{-1}). Production below the thermocline is approximately equal to that above it during summer (Fahnenstiel and Scavia 1987b), thus a total of 240 mg C m^{-2} d^{-1} (110 + 130) is available for sediment accumulation. However, less than 10% of that flux actually accumulates in the sediment (ca. 23 mg C m^{-2} d^{-1}, Eadie *et al.* 1984). Therefore most of each year's summer carbon production is recycled to the water column. This material may add significantly to the chemical make-up of the nepheloid layer (Chambers and Eadie 1981), continue to fuel benthic and hypolimnetic secondary production (perhaps at a lower energy density than in spring, Gardner *et al.* 1985), and be the source of regenerated phosphorus for phytoplankton (Eadie *et al.* 1984) and labile organic carbon for planktonic bacteria (Scavia *et al.* 1986a, Scavia and Laird 1987) after fall overturn and winter mixing.

4) During the period of summer stratification, euphotic-zone phytoplankton communities form a two-layer system (Dugdale 1967, Fahnenstiel and Scavia 1987a). The lower-layer subthermocline populations are growing at rates occasionally higher than those for epilimnetic populations (Fahnenstiel and Scavia 1987b). Growth rates for the subthermocline populations are controlled by a nutrient-light interaction (Fahnenstiel *et al.* 1984) with approximately 50% of water column production occurring below the epilimnion. Phytoplankton carbon concentrations did not change significantly within the DCL from late-spring isothermy through the period of thermal stratification; measured growth and loss rates appear to balance (Fahnenstiel and Scavia 1987c).

The upper, epilimnetic phytoplankton layer is phosphorus limited (Fahnenstiel and Scavia 1987b, Schelske 1979) and is controlled by recycling of phosphorus left in the epilimnion at the end of the spring diatom bloom. Subthermocline phytoplankton populations (Fahnenstiel and Scavia 1987b,c) serve as nutrient sinks preventing flux of available P to the epilimnion from deep water and, as in Lake Ontario (Scavia 1979a), allochthonus loads are not likely to be significant on the time scale of seasonal dynamics. Thus, epilimnetic nutrient supplies are controlled by recycling, which is mediated by zooplankton, as in Lake Huron (Korstad 1983), Saginaw Bay (Bierman and Dolan 1981), and Lake Ontario (Scavia 1979a). In Lake Michigan, the summer zooplankton is dominated by large *Daphnia* spp. which are likely feeding on both phytoflagellates and detritus. Grazing loss rates and phytoplankton growth rates are comparable; sedimentation of live cells is of little significance to summer phytoplankton dynamics. Nonpredatory mortality may be significant but is not the dominant loss mechanism.

5) The current summer dominance by large cladocerans is a new condition for Lake Michigan. Over the past decade, until 1983, the zooplankton was dominated by calanoid copepods throughout the year (Evans *et al.* 1980, Scavia *et al.* 1986b). The emergence of *Daphnia* as an important component of the Lake Michigan zooplankton is influenced strongly by decreased abundance of alewife (*Alosa pseudoharangus*), the dominant planktivore (Wells 1970, Scavia *et al.* 1986b). Because the composition, abundance, and growth rates of phytoplankton in the summer epilimnion are controlled by a combination of zooplankton nutrient supply and grazing, and because the nature of these zooplankton-based controls is influenced by food-web interactions and planktivorus fish (Scavia *et al.* 1986b, 1987; Kitchell *et al.* 1987), the major influence on summer phytoplankton dynamics is "top-down."

6) Subthermocline algal populations have been an important part of Lake Michigan's ecosystem for many years; however, recent changes (Fahnenstiel and Scavia 1987a) in epilimnetic food-web structure have resulted in deeper and broader deep chlorophyll layers (DCL). Thus, while food-web alterations have resulted in decreased summer epilimnetic phytoplankton concentrations and pro-

duction, they appear to have increased those properties below the thermocline. This shift of production to deeper in the water column may have important implications in carbon cycling and ecosystem energetics; it places relatively more emphasis on production of larger cells (net diatoms) deeper in the water column, where direct energy transfer from primary producers to the large invertebrate prey of larval and adult fish can occur. This DCL represents a previously untapped food supply and changing zooplankton composition may have an impact on this resource.

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