

Mass Flux and "Nutritional Composition" of settling Epilimnetic Particles in Lake Michigan¹

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Gardner, W. S., B. J. Eadie, J. F. Chandler, C. C. Parrish, and J. M. Malczyk. 1989. Mass flux and "nutritional composition" of settling epilimnetic particles in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 46: 1118–1124.

A series of sediment-trap samples, collected at a 30-m depth in southeastern Lake Michigan, was analyzed to evaluate the seasonal flux and nutritional value of settling epilimnetic particles as potential food for benthic organisms. Flux was highest in the spring (due in part to resuspension), lowest in the summer during stratification, and intermediate during autumn months. Organic content of the particles ranged from 10% ash free dry weight (AFDW) in March through May samples to 17–19% in July–August samples. During the summer, microbial degradation of organic materials occurred in the trap bottles without added preservative, as evidenced by less AFDW in nonpreserved trap bottles than in similar chloroform-preserved bottles. The percentage of AFDW occurring as lipid ranged from 3.5% in April–May up to 14% during May through August. Dominant lipid classes were hydrocarbons, polar lipids including phospholipids and chlorophyll *a*, and free fatty acids. The ratio of *n*-alkane C-17 (algal indicator) to *n*-alkane C-29 (terrestrial or resuspension indicator) and the ratio of biogenic silica to AFDW in preserved samples both reached a maximum in May, shortly before lipid content peaked in the benthic amphipod, *Pontoporeia hoyi*. This observation agrees with the hypothesis that *P. hoyi* receives much of its nutrition from the spring algal bloom.

On a analysé une série d'échantillons de sédiments recueillis à 30 m de profondeur dans le sud-est du lac Michigan, afin d'évaluer le taux saisonnier et la valeur nutritive du dépôt des particules de l'épilimnion, qui peuvent servir de nourriture au benthos. Le dépôt était maximal au printemps (en partie à cause de la remise en suspension), minimal durant la stratification estivale et moyen durant l'automne. La part organique des particules a varié entre 10 % du poids sec sans cendres de mars à mai, à 17–19 % en juillet et août. Durant l'été, la dégradation microbienne des matières organiques se faisait dans la bouteille d'échantillonnage sans aucun ajout, comme en témoigne le poids sec plus faible dans ces bouteilles que dans celles contenant du chloroforme. Le pourcentage de lipides dans le poids sec sans cendres a varié de 3,5 % en avril-mai à 14 % de mai à août. Les principaux types étaient de hydrocarbures, des lipides polaires comme des phospholipides et la chlorophylle *a*, ainsi que des acides gras libres. Dans les échantillons chloroformés, le ratio de *n*-alcane C-17 (indicateur algéen)/*n*-alcane C-29 (indicateur terrestre ou de remise en suspension), ainsi que le ratio silice biogène/poids sec sans cendres étaient maximaux en mai, peu de temps avant que la teneur lipidique ne culmine chez *Pontoporeia hoyi*. Cette observation appuie l'hypothèse voulant que cet amphipode benthique reçoive une bonne partie de sa nourriture de la prolifération d'algues printanière.

Received June 29, 1988
Accepted March 9, 1989
(J9795)

Reçu le 29 juin 1988
Accepté le 9 mars 1989

Benthic invertebrates are important prey for fish in Lake Michigan and the other Laurentian Great Lakes, but the pathways of energy from primary production to the benthos have only recently been examined (e.g. Gardner et al. 1989). The dominant macroinvertebrate in the upper Great Lakes, *Pontoporeia hoyi*, is an important prey for many Great Lakes fish (Mozley and Howmiller 1977). This species is a detritivore that feeds on organic matter enriched with bacteria (Marzolf 1965). However, *Pontoporeia* growth appears to be strongly dependent on material settled from the water column following the spring diatom bloom (Cederwall 1977; Weiderholm 1973; Johnson 1970; Johnson 1988). In Lake Michigan, lipids in *P. hoyi* increase in the spring soon after the bloom

(Gardner et al. 1985a; Gauvin et al. 1989; Landrum 1988). Diatom settling is the major factor causing phytoplankton removal from the epilimnion in the spring whereas zooplankton grazing is a more important factor later in the year during stratification (Scavia and Fahnenstiel 1987).

In this study, we measured seasonal changes in the sources, input rates, and nutritional value of settling particles by quantifying their mass flux and composition (ash free dry weight, organic nitrogen, biogenic silica, lipid content, and class composition). The particles were collected at a site in southeastern Lake Michigan where the bottom sediments are characterized by high populations of *P. hoyi* ($6900 \cdot \text{m}^{-2}$) and oligochaetes ($3000 \cdot \text{m}^{-2}$) (Nalepa 1987) and where lipid concentrations in *P. hoyi* have been studied (Gardner et al. 1985a; Gauvin et al. 1989; Landrum 1988). The composition of alkanes in the particles was determined to provide insights about the relative role

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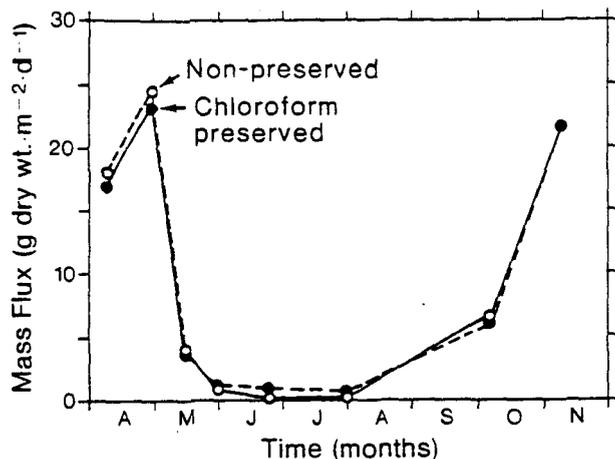


FIG. 1. Temporal mass flux of particles collected in sediment traps suspended at a depth of 30 m at a 45-m water-depth station in south-eastern Lake Michigan. Data points on the X axis are placed at the mid-point of each sampling interval.

of autochthonous production versus terrestrial or resuspension inputs as factors supplying particles at this site.

Methods

Sediment traps (318-cm² collection area) were placed at a depth of 30 m at a 45-m deep station located offshore from Grand Haven, Michigan (near Station H-31; Nalepa 1987) using previously described techniques (Eadie et al. 1984). Particles were collected during the period of April 23 to November 26 at intervals ranging from about 2 wk to 2 mo as indicated in Fig. 1. For each setting, three sediment traps were suspended at the same depth. One collection bottle was untreated ("non-preserved sample"), whereas the contents of the two others were preserved with about 25 ml of chloroform to prevent microbial activity ("preserved samples"). Mass flux and nutritional content were examined for both preserved and nonpreserved particles, to evaluate the stability of different organic fractions during trap collection. After collection, one of the preserved samples was used for hydrocarbon analysis. Samples from the other two treatments were dried for at least 3 d in a 60°C air oven, scraped out of the bottles, weighed, ground with a mortar and pestle, and stored at 4°C until analysis. Trap collections for the different treatments were not replicated, but previous studies with triplicate traps at each of four stations in Lake Michigan showed coefficients of variation in sample weights that ranged between 1 and 10% (mean 5.5%; Eadie et al. 1984).

A measured portion of the dried samples was ashed at 550°C for 1 h to determine ash free dry weight (AFDW) that was assumed to represent total organic matter. "Organic" (Kjeldahl) nitrogen was measured after it was converted to ammonium by digestion in an aqueous mixture of 20% concentrated H₂SO₄, 6.7% K₂SO₄ and 0.8% HgO (at 200°C for 1 h and at 360°C for 25 min). This procedure was modified from Technicon Industrial Method No. 327-74 (September 1974). The digestate was diluted to original volume (20 ml) and 100 µL of the solution was diluted with 10 ml of citric acid buffer (0.5% citric acid adjusted to pH 9.5 with NaOH) and analyzed fluorometrically for ammonium (Gardner 1978). Biogenic silica was extracted and analyzed by auto analyzer using Technicon components (Krausse et al. 1983). Lipids were extracted and

analyzed gravimetrically using micro techniques (Gardner et al. 1985b). A measured portion (10–20 µL) of each gravimetric extract was sealed under nitrogen and stored frozen until analysis by thin-layer chromatography with flame ionization detection (TLC-FID; Parrish 1987a; Parrish et al. 1988). The lipid classes in 2–4 different extracts from each trap sample was separated by Chromarod TLC. The precision (SD) of the TLC-FID determination of each lipid class in four separate extracts was, on average, ± 5% of the sum of the lipid classes. Separate chloroform-treated samples were Soxhlet-extracted overnight in acetone/hexane (1:2) for alkane analysis by gas chromatography. Extract volumes were reduced to less than 1 mL, then eluted with 12 mL pentane from a 0.6 × 10 mm column of activated silica gel and dried under a stream of nitrogen to 1 mL. They were analyzed on an HP 5890 gas chromatograph equipped with a 25 M BP-1 capillary column and flame ionization detector.

Results and Discussion

As noted in previous Lake Michigan studies (Eadie et al. 1984), mass flux was much higher in spring and autumn during holomixis than in late summer when the lake was stratified (Fig. 1). This difference can be attributed to the downward flux of resuspended particles during holomixis and to the production of diatoms produced in response to the mixing of nutrients into the photic zone (Eadie et al. 1984). During the stratified period, particles and nutrients from the hypolimnion are not substantially resuspended into the epilimnion except during periodic upwellings (Mortimer 1971; Bell and Eadie 1983). The nutritional value of organic matter associated with resuspended particles may be low because much of the available nutrients would likely have been removed from them by previous grazers, predators, or bacteria.

Composition of Trap Material

Seasonal compositional changes were observed for all of the organic constituents. Relative to total dry weight, organic components (AFDW), Kjeldahl nitrogen, biogenic silica, and total lipid) were higher in the late spring and in summer than during spring and autumn (Fig. 2). Expressed as a ratio to total organic matter (AFDW), organic nitrogen and biogenic silica underwent only moderate changes in composition during the sampling period, but total lipid concentration more than tripled in preserved samples during the interval of 7 May to 9 June compared with values in the early spring (Fig. 3). This selective increase in lipids may be important in energy fluxes as lipids tend to be transferred to consumers more efficiently than other classes of organic materials and are also readily stored by invertebrates (Lee 1975).

Unique treatment-specific patterns were observed for different constituents. The AFDW concentrations in nonpreserved samples were similar to those in the chloroform-preserved ones during spring and autumn but were consistently lower in the summer months (Fig. 2). The composition of particles actually reaching the benthos is probably intermediate between that of the two treatments as some decomposition and grazing of particles would occur during the time that the particles are settling the rest of the way to the bottom. Epilimnetic decomposition processes are likely enhanced by relatively high temperatures in the summer. In addition, the ratio of newly-formed "labile" particles to old-resuspended "refractory" particles would likely

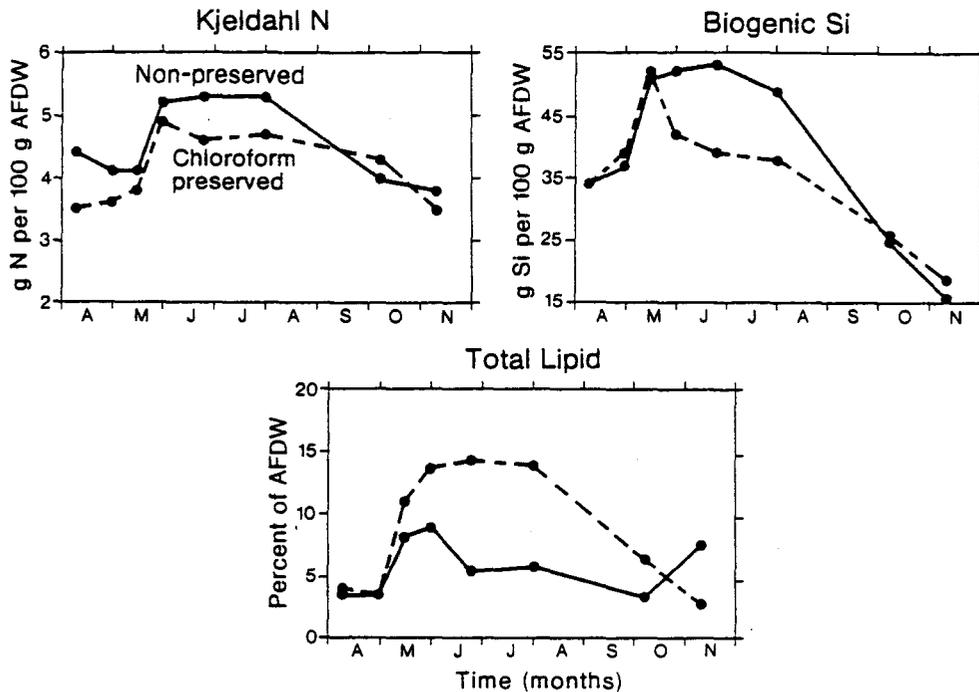


FIG. 2. Content of ash free dry weight (percent of dry weight), organic nitrogen (milligrams N (grams dry wt)⁻¹), biogenic silica (milligrams Si (grams dry wt)⁻¹), and total lipid (percent of dry weight) in sediment-trap materials collected at intervals over the period of March 27 to November 26, 1986. The nonpreserved sample of October–November was contaminated with dead fish.

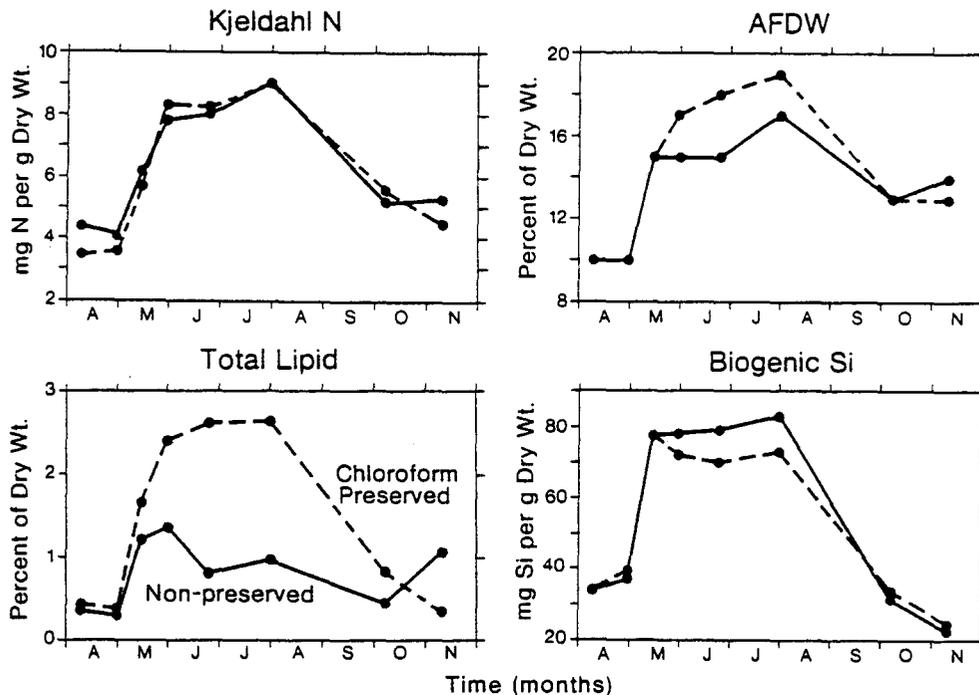


FIG. 3. Content of organic nitrogen, biogenic silica, and total lipid expressed as percent relative to ash free dry weight in sediment-trap materials collected at intervals over the period of March 27 to November 26, 1986. The nonpreserved October–November sample was contaminated with dead fish.

be higher during summer stratification (Eadie et al. 1984). Kjeldahl nitrogen and biogenic silica concentrations were not dramatically different in the two fractions throughout the season, but were higher, relative to AFDW, in the nonpreserved samples than in the preserved ones during summer (Fig. 3). This result may have been due in part to selective degradation of organic compounds containing low levels of nitrogen and bio-

genic silica (e.g. lipids and carbohydrates). Of all the components that we examined, lipids showed the most evidence of degradation. Except for one untreated sample (October–November) that was contaminated with dead fish, lipids were consistently lower in the nonpreserved samples than in the preserved ones, especially during June and July (Figs. 2 and 3). Also, portions of the mineralized nitrogen and silica were prob-

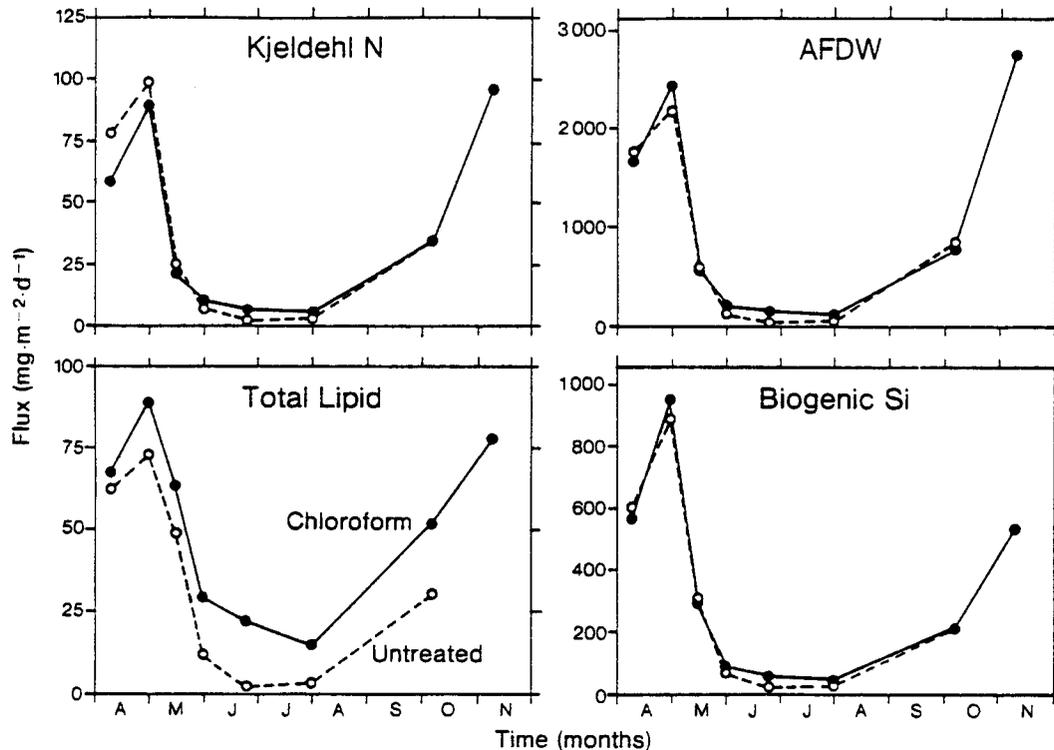


FIG. 4. Temporal flux of AFDW, organic nitrogen, biogenic silica, and total lipids in particles collected in sediment traps suspended at a depth of 30 m at a 45-m water-depth station in southeastern Lake Michigan. Dots represent nonpreserved samples. Circles represent preserved samples.

ably measured along with the organic forms in the collected samples. In contrast, CO_2 from mineralized carbon would likely be lost when the samples were dried.

Nutrient Flux

The nutritional value of incoming particles as food to benthic and hypolimnetic organisms depends on both the quantity and composition of the particles. The flux of individual constituents was calculated for each sampling period (Fig. 4). Seasonal changes in mass flux (Fig. 1) appear to be quantitatively more important than changes in relative composition (e.g. AFDW, Kjeldahl nitrogen, biogenic silica, or total lipid; Figs. 2 and 3) in determining the rate of delivery of nutrients to the bottom of the lake. This interpretation is complicated somewhat by the fact that resuspended material, dominant in the spring and fall, has lower nutritional content than new material because it contains relatively refractory materials. However, nutritionally-rich large diatoms, that sink quite rapidly, are also most abundant in the spring (Scavia and Fahnenstiel 1987).

Lipid Class Composition and Flux

The lipids in the sediment-trap material were separated into as many as nine different classes by Chromarod TLC. Total aliphatic hydrocarbons (HC), free fatty acids (FFA), sterols (ST), acetone-mobile polar lipids (AMPL), and phospholipids (PL) were present in all extracts (Fig. 5). Small concentrations of diglycerides, hydrolysis products from triglycerides (TG) and PL, were detected in only two nonpreserved samples collected late in the season (data not shown). A small sterol ester/wax ester (SE/WE) peak occurred in the April–May trap sample that was collected soon after the spring diatom bloom. The copepods, *Limnocalanus macrurus* and *Senecella calanoides*, are

likely contributors of WE to this peak (Chandler et al. 1989). Although the trend was not dramatic, ST and AMPL appeared to be proportionally highest in early spring when the diatoms were likely dividing most rapidly. In agreement with this tentative finding, concentrations of ST and AMPL were linearly correlated with growth rate in a marine diatom (Parrish and Wangersky 1987). Sterols are an important component of membranes, while AMPL in diatoms consist of pigments and glycolipids (important lipids in chloroplasts; Parrish et al. 1988). A large peak for total aliphatic hydrocarbons (HC) always occurred in chromatograms of preserved sediment-trap materials. On average, HC accounted for 28% of the TLC-FID-measured total lipids in the eight traps. A high content of HC seems to be characteristic of sediment-trap material from the Great Lakes (Parrish 1987a; C. C. Parrish, unpubl. data). The nature and source of the majority of these aliphatic hydrocarbons are unknown, but they appear to be quite labile. On average, HC constituted only about 10% of the total lipids in nonpreserved sediment-trap samples.

The highest proportion of TG, $8.3 \pm 0.2\%$, was measured in the preserved sediment-trap lipids collected during mid-May. This peak in TG relative to other lipid classes may reflect a significant input of diatom storage material to the sediment trap. It is coincident with a large peak in the $n\text{-C}_{17}$ to $n\text{-C}_{29}$ alkane ratio (Figs. 6 and 7) and with a peak in the ratio of biogenic silica to AFDW (Fig. 3) in the preserved samples. The fact that TG was never the major lipid class in sample extracts suggests that the settling diatoms were likely not under severe nutrient stress, as TG are often the major lipid component in nutrient-limited diatoms (Parrish 1987b; Parrish and Wangersky 1987; S. Kilham, University of Michigan, unpubl. data). Even when HC concentrations were subtracted from the sum of lipid-class concentrations, TG accounted for less than 15% of the

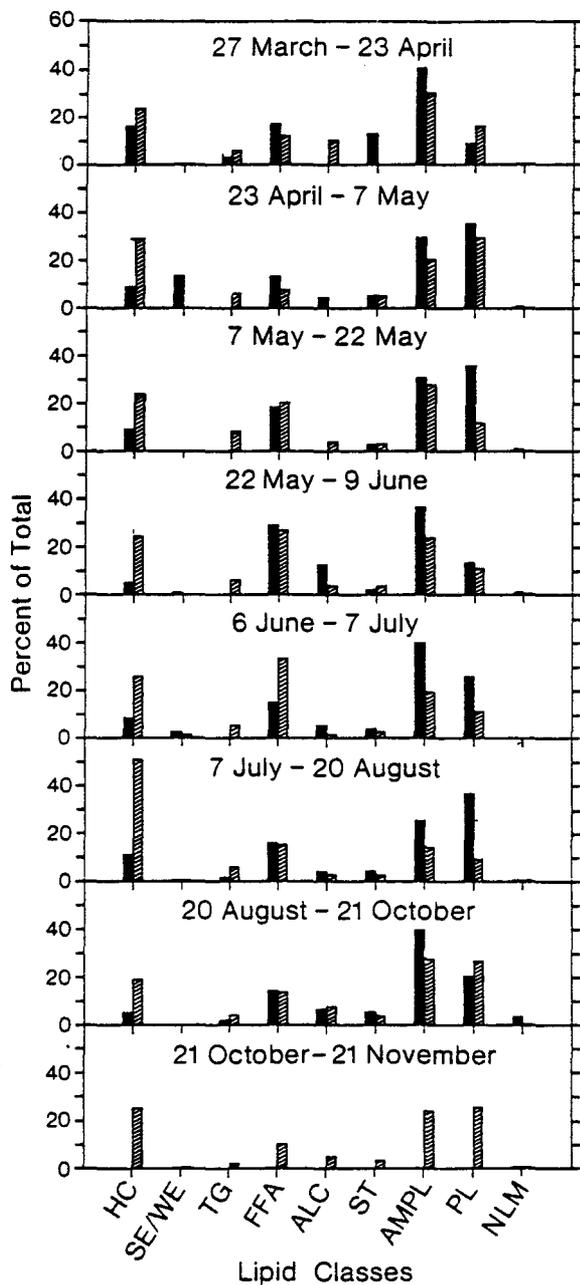


FIG. 5. Relative composition (percent of all classes) of lipid classes in preserved (hatched bars) and nonpreserved (dark bars) seasonal sediment-trap collections. HC = hydrocarbons; SE/WE = sterol esters/wax esters; TG = triglycerides; FFA = free fatty acids; ALC = free aliphatic alcohols; ST = sterols; AMPL = "acetone-mobile polar lipids," including chlorophyll; PL = polar lipids; NML = "nonlipid material."

remaining oxygen-containing lipids in any of the trap samples. Likewise, TG accounted for less than 15% of the lipids in diatoms growing in nutrient replete media (Parrish and Wangersky 1987). Like HC, TG were relatively lower in the nonpreserved sediment-trap material than in the preserved samples. The absence of large increases in FFA with the removal of TG and other lipids in the nonpreserved sediment-trap lipids suggests that the TG in the nonpreserved samples were consumed rather than simply hydrolyzed.

Free fatty acids accounted for about 18% of the lipids, on average, both in the eight treated and in the seven nonpreserved samples. The largest FFA percentages occurred during the sum-

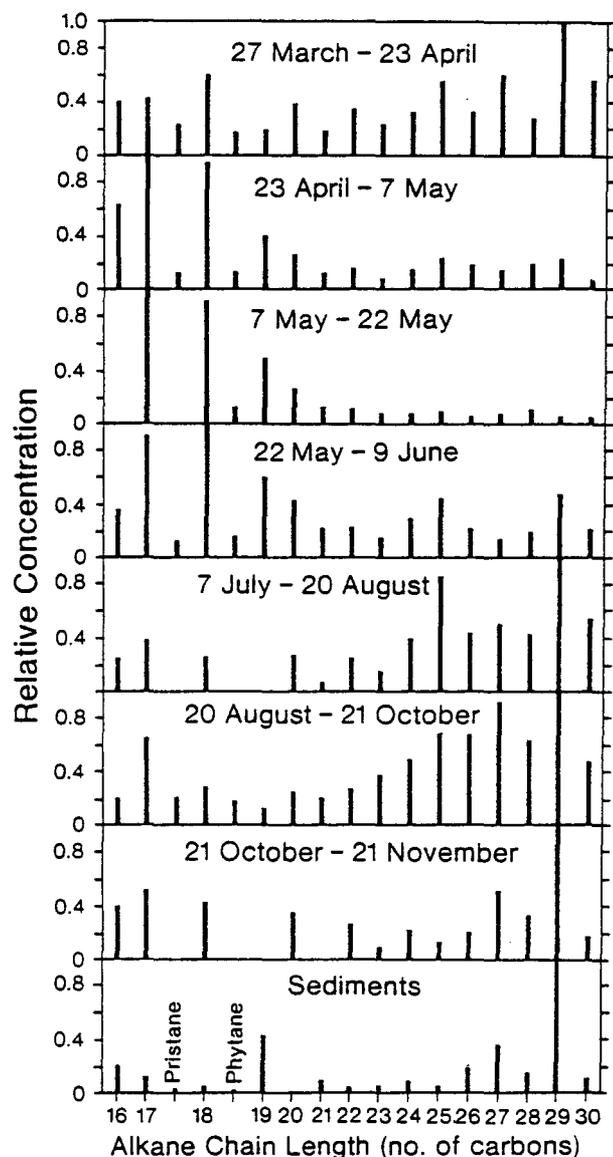


FIG. 6. Normal alkane composition of preserved trap materials (and local surface sediment) for the periods indicated. Short chain lengths are indicators of plankton. Long chain lengths indicate material of terrestrial origin.

mer. Hydrolysis of acyl lipids would be greatest during this period due to the relatively high temperatures.

The HC content of the preserved sediment trap material increased each month until it peaked at $13.3 \text{ mg} \cdot \text{g}^{-1}$ at the end of the summer (July/August trap; Fig. 5). This value is similar to solvent-extractable HC values of $7.4\text{--}11.9 \text{ mg} \cdot \text{g}^{-1}$ in preserved 35-m deep sediment-trap samples collected during the summer of 1978 from four locations in southeastern Lake Michigan (Meyers et al. 1984). However, our HC fluxes of $>5.8 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ were much higher than the "total aliphatic hydrocarbon" flux of $0.074 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ previously measured at 35 m (Meyers et al. 1980). This difference may be due to considerable spatial or temporal variation in hydrocarbon fluxes or to differences in hydrocarbon measurement techniques.

Fatty acids are the major component, by mass, of the TG, FFA, and PL peaks. Sums of these "acyl lipid components" are therefore comparable with the "fatty acid" content previously estimated by analyzing fatty acid methyl esters prepared

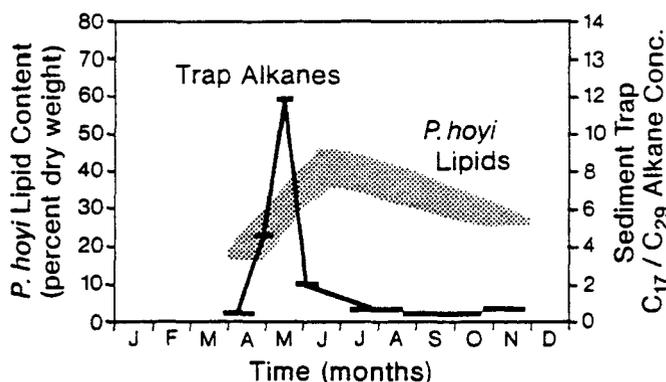


FIG. 7. Seasonal total lipid content of *P. hoyi* averaged over 2 yr of collection (data taken from Gardner et al. 1985; Landrum 1988; Gauvin 1989). Also shown is the ratio of the planktonic *n*-alkane C_{17} to the terrestrial *n*-alkane C_{29} . The April–June peak is a clear signal of autochthonous carbon input. The sediment value for this ratio is 0.2.

from solvent extracts (Meyers et al. 1980, 1984). The acyl lipid content of our preserved sediment-trap material increased each month until mid-summer when it peaked at $13 \text{ mg}\cdot\text{g}^{-1}$. This value is within the range of $0.9\text{--}49 \text{ mg}\cdot\text{g}^{-1}$ given for fatty acid content of sediment-trap material collected between 30 and 40 m during the summer of 1978 (Meyers et al. 1984). The acyl lipid flux measured in June–July was $11 \text{ mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ as compared with $4.6 \text{ mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ in July–August. These two values bracket summer (1978) values for total fatty-acid flux measured in 35-m ($4.9 \text{ mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) and 73-m ($7.9 \text{ mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) sediment traps (Meyers et al. 1980).

Our ALC value of $0.42 \text{ mg}\cdot\text{g}^{-1}$ in June–July is comparable with $0.22 \text{ mg}\cdot\text{g}^{-1}$ previously observed at 40-m depth in southern Lake Michigan, but is much lower than the values of 5 to $60 \text{ mg}\cdot\text{g}^{-1}$ reported for traps deployed between 31 and 35 m (Meyers et al. 1984). The concentration of ST, the cyclic aliphatic alcohols, in our June–July trap was $0.71 \text{ mg}\cdot\text{g}^{-1}$ as compared with the range of 0.1 to $2.1 \text{ mg}\cdot\text{g}^{-1}$ for traps deployed between 30 and 40 m (Meyers et al. 1984).

Evidence for Direct Pelagic–Benthic Energy Coupling

Measuring the alkane composition of particles by gas chromatography provides information about possible sources of the material. For example, *n*-alkanes with chain length C_{23} to C_{33} are strong indicators of a terrestrial source, while chain lengths of C_{12} to C_{20} characterize aquatic plankton (Simoneit 1978; Muller 1987; Thurman 1985). Among these hydrocarbons, C_{17} is particularly useful as a plankton indicator. The three trap collections covering the period 23 April through 9 June had a predominance of autochthonous derived alkanes (Fig. 6). This “phytoplankton signal” agrees with the peak in biogenic silica flux observed in the preserved sample (Fig. 3) and supports other evidence that material collected in traps during this period were predominantly algae (diatoms; Scavia and Fahnenstiel 1987). In contrast, early in the spring and again in late summer–fall, the alkane distribution in the trapped material had a substantial terrestrial component. Terrestrial hydrocarbons are relatively refractory in the lake (Meyers et al. 1984), as indicated by the alkane distribution in the surface sediment from this station (Fig. 6). Thus, these trapped hydrocarbons can be accounted for by both resuspension of surface sediments and fresh terrestrial input from the relatively large (average $44\text{--}m^{-3}\cdot s^{-1}$ flow) nearby Grand River.

The timing of lipid increases in *P. hoyi* appears to follow that of the spring diatom bloom as suggested previously (Gardner et al. 1985a, 1989). Lipids in *P. hoyi* increased dramatically at this site during the interval of April to June and then gradually decreased during the rest of the season (Gardner et al. 1985a; Gauvin et al. 1989; Landrum 1988). The lipid increase in *P. hoyi* occurred directly after the peak in the *n*-alkanes C_{17} (planktonic): C_{29} (terrestrial) ratio (Fig. 7). As summer approached, the rate of delivery of “labile” materials decreased substantially and the *P. hoyi* appeared to gradually use up the stored lipids that were assimilated in the spring. As mentioned above, the large size and high density of spring diatoms such as *Melosira* likely cause them to sink to the benthos more readily than smaller phytoplankton (e.g. flagellates and green and bluegreen algae) that occur later in the season and are more heavily grazed by pelagic zooplankton than *Melosira* (Scavia and Fahnenstiel 1987; Fahnenstiel and Scavia 1987).

The alkane ratios (Fig. 7) and biogenic silica to AFDW ratios (Fig. 3) in the preserved samples provided a much stronger signal of nutritional inputs, that appeared to be related to lipid increases in *P. hoyi*, than did the other “chemical indicators” (Figs. 2–4). In contrast to the C_{17} : C_{29} ratios and the biogenic silica:AFDW ratios in the preserved samples, that showed a sharp peak in May, concentrations of AFDW, Kjeldahl nitrogen, and total lipid, remained relatively high and consistent relative to dry weight (or AFDW) during the period of May through August (Figs. 2 and 3).

The high concentrations of lipids in preserved samples during the summer caused the total lipid flux to vary less seasonally than the fluxes of the other components (Fig. 4). Despite the continuing high lipid levels of the preserved trap particles (Figs. 2 and 3) and the relatively high flux of total lipids throughout the season (Fig. 4), the lipid concentrations in *P. hoyi* still decreased from June through August (e.g. Fig. 7). Similarly, *P. hoyi* growth rates are highest in the spring and decrease as the season progresses (e.g. in South Bay, Lake Huron, Johnson 1988). Thus, although the previously suggested relationship between the spring diatom bloom and lipid increases in *P. hoyi* (Gardner et al. 1985a, 1988) is implied by the alkane ratios and biogenic silica concentrations and fluxes, the relationship between total lipids in incoming food and *P. hoyi* lipid assimilation is not as clear. It is possible that *P. hoyi* may not assimilate its storage lipids completely from food lipids as occurs for *Daphnia* (Goulden and Place 1987). Preliminary *P. hoyi* feeding studies (M. Quigley, Great Lakes Environmental Research Laboratory, unpubl. data) indicate that lipid accumulation or loss in *P. hoyi* may not be exclusively related to the lipid content of the food.

To consider whether dietary lipids in the incoming trap materials were quantitatively sufficient to account for the lipid increases in *P. hoyi*, we compared the total lipid flux in settling particles during spring to lipid increases in *P. hoyi*. Based on the data from Fig. 4, the integrated total lipid flux during the period 27 March to 9 June was $4.6 \text{ g lipid}\cdot\text{m}^{-2}$. This flux compared with total lipid increases in *P. hoyi* of $2.1 \text{ g lipid}\cdot\text{m}^{-2}$ (based on a *P. hoyi* biomass of $5.3 \text{ g AFDW}\cdot\text{m}^{-2}$ at the 45-m station (Nalepa et al. 1985), a Ponar grab correction factor of 1.5 (Nalepa et al. 1989), a DW:AFDW conversion factor of 1.1 (Gardner et al. 1985a), and a *P. hoyi*-lipid increase of 24% of DW (Fig. 7)). If our assumptions are reasonably valid, this comparison suggests that incoming lipid supply would be adequate to account for the lipid increases in *P. hoyi* only if a substantial portion of the total lipids in the settling materials

were ingested and efficiently assimilated by *P. hoyi*. However, near-quantitative assimilation of the lipids passing through a 30-m depth by *P. hoyi* seems unlikely because a sizable portion of the lipids may be degraded before reaching the bottom and because portions of the remaining lipids are likely nutritionally unavailable to *P. hoyi* (e.g. refractory hydrocarbons; Meyers et al. 1984) or not readily used for energy storage (e.g. hydrocarbons and pigments) in the animal. An alternative explanation is that *P. hoyi* may synthesize a portion of its lipids from other materials such as carbohydrates. We did not analyze sediment-trap particles for carbohydrates, but proteins (= Kjeldahl nitrogen \times 6.26) and lipids accounted for only 25 to 44% of the total AFDW (based on preserved-sample data of Fig. 3). If "available", carbohydrate constitutes a large portion of the undefined AFDW, particularly in spring diatoms, it may partially account for the *P. hoyi* lipid increases that occur after the spring bloom.

Acknowledgements

We thank J. Bell for assembling and setting the sediment traps, M. Quigley for helpful discussions on *P. hoyi* nutrition, W. Burns, J. Grimes, and D. Morse for helping collect trap samples, and G. Fahnenstiel, P. Landrum, T. Nalepa, and M. Quigley for reviewing the manuscript.

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