

## PHYTOPLANKTON PIGMENTS IN COASTAL LAKE MICHIGAN: DISTRIBUTIONS DURING THE SPRING ISOTHERMAL PERIOD AND RELATION WITH EPISODIC SEDIMENT RESUSPENSION<sup>1</sup>

*David F. Millie*<sup>2</sup>

Florida Marine Research Institute, Fish & Wildlife Conservation Commission & Florida Institute of Oceanography,  
100 Eighth Avenue S. E., Saint Petersburg, Florida 33701, USA

*Gary L. Fahnenstiel*

Lake Michigan Field Station, Great Lakes Environmental Research Laboratory, National Oceanic and  
Atmospheric Administration, 1431 Beach Street, Muskegon, Michigan 49441, USA

*Hunter J. Carrick*

School of Forest Resources–Fisheries & Wildlife, Pennsylvania State University, University Park, Pennsylvania 16802, USA

*Steven E. Lohrenz*

Department of Marine Science, University of Southern Mississippi, Stennis Space Center, Mississippi 39529, USA

and

*Oscar M. E. Schofield*

Institute of Marine and Coastal Sciences, Rutgers University, 71 Dudley Road, New Brunswick, New Jersey 08901, USA

Phytoplankton pigment distributions during the spring isothermal periods of 1998 and 1999 and their association with episodic sediment resuspension were characterized in coastal waters of southern Lake Michigan. Total and phylogenetic group chl *a* concentrations (derived using chemical taxonomy matrix factorization of diagnostic carotenoids) corresponded with assemblage and group biovolumes estimated from microscopic enumeration ( $P \leq 0.001$ ). Diatoms and cryptophytes dominated assemblages and together typically comprised greater than 85% of relative chl *a*. Total chl *a* concentrations and both fucoxanthin:chl *a*<sup>-1</sup> and alloxanthin:chl *a*<sup>-1</sup> ratios were similar across depths ( $P > 0.05$ ), indicating uniform distributions of and photophysiological states for assemblages and diatoms and cryptophytes, respectively, throughout the mixed water column. Total chl *a* concentrations were not always spatially uniform from near-shore to offshore waters, with the greatest variability reflecting the influence of tributary inflows upon coastal assemblages. Sediment resuspension strongly influenced water column particle density and light climate; however, total and group chl *a* concentrations did not correspond with coefficients of  $K_d$  and suspended particulate matter concentrations ( $P > 0.05$ ). The correspondence of both light attenuation and suspended particulate matter concentration with relative diatom chl *a* ( $P \leq 0.001$ ) indicated an apparent association between sediment resuspension and diatoms. This, and the negative association ( $P \leq 0.0001$ ) between relative

diatom and cryptophyte chl *a*, corresponded with the spatial dominance of diatom and cryptophyte chl *a* in near-shore and offshore waters, respectively. The presence of viable chl *a* and fucoxanthin within the surficial sediment layer, established this layer as a potential source of meroplanktonic diatoms for near-shore assemblages.

**Key index words:** CHEMTAX; chlorophyll; cryptophytes; diatoms; HPLC; Laurentian Great Lakes; photopigments

**Abbreviations:** CHEMTAX, CHEMical TAXonomy;  $K_d$ , vertical extinction coefficients; SPM, suspended particulate matter

Phytoplankton abundance and composition reflect the combined effects of the physical and chemical environments and associated biological responses. However, linkages between environmental forcing and phytoplankton within coastal waters remain poorly understood, in part due to the dynamic hydrodological, nutrient, and irradiance conditions that influence phytoplankton growth and distribution (Demers et al. 1989, Claustre et al. 1994). Moreover, sediment, nutrient, and biological inputs from tributaries episodically, and often dramatically, impact coastal assemblages (e.g. Schaub and Gieskes 1991, O'Donohue and Denison 1997, Heiskanen and Tallberg 1999).

The water column in Lake Michigan during the spring isothermal period is characterized by intense vertical mixing. Since 1992, synoptic-scale sediment resuspension has been an annually recurrent coastal feature during this period in the southern portion of

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<sup>2</sup>Author for correspondence: e-mail david.millie@fwc.state.fl.us.

the lake (Fig. 1A). This episodic resuspension of silt- and clay-like particles is initiated by late-winter storms after ice out, may extend greater than 3000 km<sup>2</sup>, and may persist for more than a month (Mortimer 1988, Eadie et al. 1996). Resuspension initiates near-shore (in 10–20 m depth) and offshore transport of suspended particulate matter (SPM) occurs soon after, most likely through episodic wind events (Eadie et al. 1996, McCormick et al. 2003, Miller et al. 2003). During an event in March 1998, greater than  $3 \times 10^{12}$  g of sediment was resuspended from the lake floor (Cotner et al. 2000).

Inherently, sediment resuspension would be thought to influence phytoplankton. Light and phosphorus availabilities appear to control phytoplankton growth and abundance, respectively, within Lake Michigan during the spring isothermal period (Fahnenstiel et al. 1984, Scavia and Fahnenstiel 1987). Increased light attenuation by resuspended particulate matter compresses the photic zone into a smaller fraction of the water column (see Cloern 1987) and may invoke severe light limitation to impacted assemblages. However, resuspension may introduce sediment-derived nutrients (Eadie et al. 1996, Cotner et al. 2000), thereby alleviating phosphorus limitation and compensating for lower light levels (Fahnenstiel et al. 2001). Resuspension also may afford a mechanism by which viable, benthic taxa, and/or

dormant, resting cells from the sediments (meroplankton; Lund 1954) are introduced into plankton and transported throughout coastal waters. If resuspension is significant and prolonged, phytoplankton abundance might significantly increase within impacted waters.

The effects of resuspension in relation to the more persistent meteorologically driven holomixis on Lake Michigan phytoplankton are unknown. We hypothesized that resuspension events would affect the spatial and temporal distributions of phytoplankton pigments throughout coastal waters. As such, we characterized total and phylogenetic group chl *a* concentrations (derived using diagnostic photopigments) throughout the spring isothermal periods of 1998 and 1999. The correspondence between phytoplankton pigments and sediment resuspension also was assessed.

#### MATERIALS AND METHODS

Synoptic survey cruises within southeastern Lake Michigan were conducted onboard the *R.V. Laurentian* during the spring isothermal periods of 1998 and 1999. Sampling stations (Table 1) were established inside and outside of sediment-impacted waters along transects (Fig. 1). At each station, PAR (400 to 700 nm) profiles of the water column were collected using a Sea-Bird (SeaBird Electronics, Inc., Bellevue, WA, USA) CTD package equipped with a Biospherical Instruments down-welling PAR sensor (Biospherical Instruments, Inc., San Diego, CA,

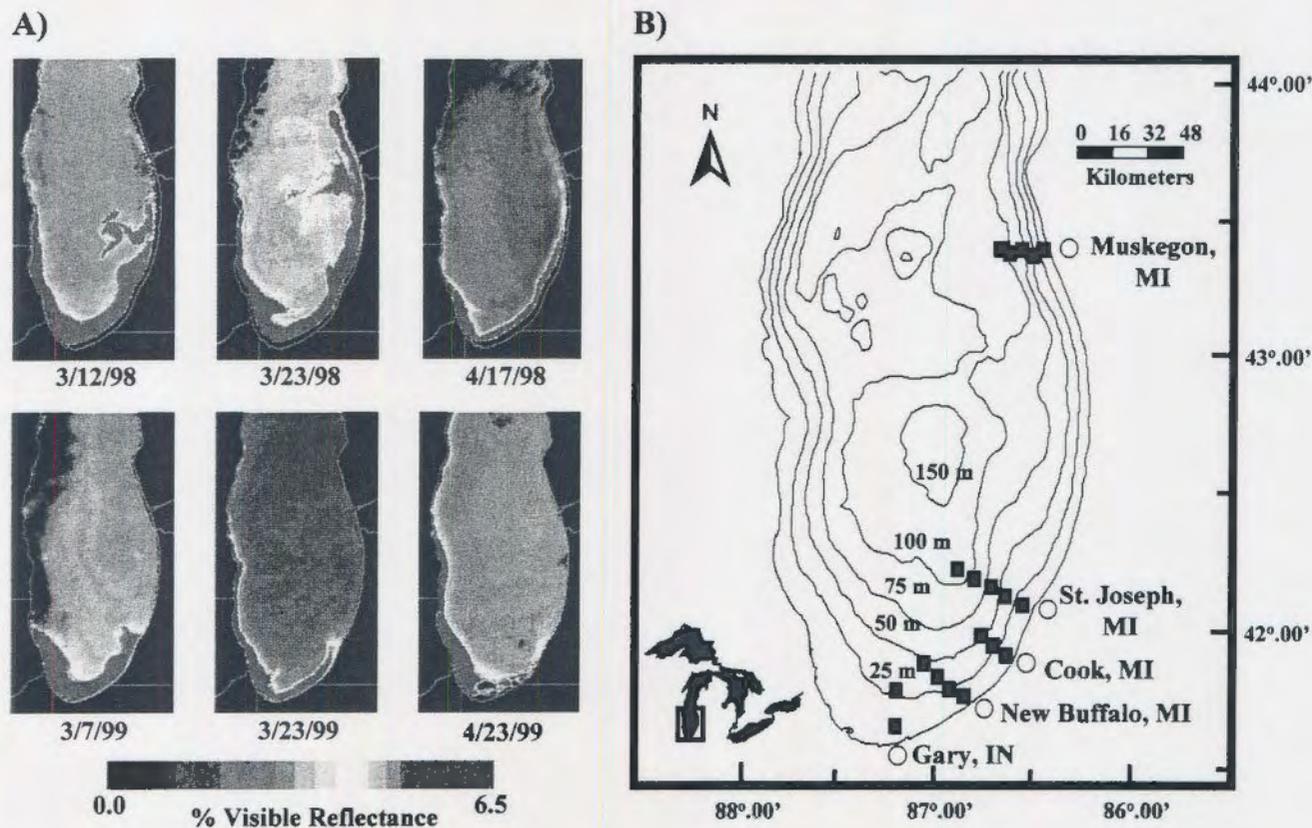


FIG. 1. (A) Distribution of sediment resuspension, as illustrated by channel 1–2 reflectance imagery from the NOAA 14 satellite, during 1998 and 1999. (B) Location of sampling stations along the Cook, Gary, Muskegon, New Buffalo, and Saint Joseph transects. Inset: Study area relative to the Laurentian Great Lakes system.

USA). Coefficients of  $K_d$  were calculated from PAR profiles (after Wetzel 2001). Modified Niskin bottles (all rubber parts were replaced with Teflon-coated or silicone; Fahnenstiel et al. 2003), cast to selected depths, collected water for assessment of phytoplankton and total SPM. SPM concentrations were determined gravimetrically after drawing 0.5- to 3-L aliquots under low vacuum onto pre-rinsed, tared, Whatman (Whatman International Ltd., Maidstone, Kent, UK) GF/F and/or Poretics (Poretics Corporation, Livermore, CA, USA) 0.4- $\mu\text{m}$  polycarbonate filters. Surficial sediments were collected on 23 March 2000 by box cores from 45-m depth along the New Buffalo transect (41° 57.17' N, 86° 48.41' W) for assessment of photopigments.

Phytoplankton pigments were characterized using HPLC. Initially, 1-L aliquots of water were drawn under low vacuum onto GF/F glass-fiber filters that were immediately frozen and stored at  $-80^\circ\text{C}$ . At time of pigment analysis, frozen filters were placed in 100% acetone, sonicated, and extracted in darkness at  $-20^\circ\text{C}$  for 12 to 16 h. Filtered extracts (200  $\mu\text{L}$ ) were injected directly into a Hewlett-Packard model 1100 HPLC equipped with a single monomeric (Hewlett-Packard ODS Hypersil; 100  $\times$  4.6 mm, 5  $\mu\text{m}$  [Hewlett-Packard, Palo Alto, CA, USA]) and two polymeric (Vydac 201TP, 250  $\times$  4.6, 5  $\mu\text{m}$  [The Nest Group, Inc., Southborough, MA, USA]) reverse-phase  $C_{18}$  columns in series, a photodiode array detector, and a Hewlett-Packard model 1046A fluorometer placed in-line. The mobile phases and solvent flow rates followed that described by Pinckney et al. (1996). The column temperature was  $38^\circ\text{C}$ . Pigments were identified and quantified using authentic standards.

Microscopic examination first determined the presence of four phylogenetic groups (diatoms, cryptophytes, chl *b* containing taxa, and cyanobacteria) within phytoplankton assemblages during the study periods (see below). Pigments used as chemotaxonomic markers for these groups included fucoxanthin, chl  $c_1/c_2$ , and diadinoxanthin (diatoms); alloxanthin and  $\beta$ , $\epsilon$ -carotene (cryptophytes); neoxanthin, violaxanthin, lutein, and chl *b* (chlorophytes); zeaxanthin (cyanobacteria); and chl *a* (all algae; see Millie et al. 1993, Jeffrey et al. 1999). Group absolute and relative chl *a* concentrations then were derived from suites of pigments using chemical taxonomy (CHEMTAX) matrix factorization program (Mackey et al. 1996). CHEMTAX calculates the contribution of a given algal group, defined in terms of its pigment complex, to total chl *a* based on carotenoid:chl *a*<sup>-1</sup> ratios (for critical appraisals of CHEMTAX applications, see Wright et al. 1996, Mackey et al. 1998, Descy et al. 2000, Schlüter et al. 2000, Wright and van den Enden 2000). Because carotenoid:chl *a*<sup>-1</sup> ratios within Lake Michigan phytoplankton assemblages might be expected to vary depending on species composition, cell physiological state, PAR, and so on, the pigment data set was divided into subsets by sampling depth (0–5, 6–10, 15–25, 30–50, and 70–100 m) within transects (Cook, Gary, Muskegon, New Buffalo, Saint Joseph), months (March, April), and years (1998, 1999) before independent CHEMTAX calculations (c.f. Mackey et al. 1998, Schlüter et al. 2000, Wright and van den Enden 2000).

To relate pigment data and phytoplankton abundance, the correspondence of diagnostic pigments with CHEMTAX-derived group chl *a* concentrations first was determined by Pearson product moment correlation analyses. The relationship between total and group chl *a* concentrations with cell biovolumes then was verified for the dominant phylogenetic groups (see below). Briefly, phytoplankton at select sites (representing sediment-impacted and adjacent waters) immediately were preserved with Utermöhl solution and the species composition later enumerated using standard microscopic techniques. Phytoplankton biovolumes were determined by first measuring cell dimensions and then back-calculating cell size from volume estimates (after Fahnenstiel and Scavia 1987b). Pigment and composition biovolumes for 19 stations subsequently were selected (from Millie et al. 2003) for correlation analysis.

Plots of mean absolute and relative pigment concentrations (averaged across the water column) were plotted to illustrate spatial distribution of pigment variables along transects during each sampling period. In 1999, sampling density provided opportunities to construct detailed contour plots of chl *a* concentrations along the Muskegon and Saint Joseph transects (refer to Table 1 and Fig. 1). For contour plotting, a kriging algorithm (linear variogram model) provided interpolation between sampling and depth points for contours.

An unpaired *t*-test or analysis of variance assessed differences among total and group chl *a* concentrations across each transect for each cruise period. A Tukey test determined the significance between pairs of means within each analysis of variance. To relate phytoplankton abundance to sediment resuspension, the correspondence among  $K_d$ , SPM concentrations, and pigment concentrations for singular 1998 and 1999 data sets and a combined data set were determined by correlation analyses. Absolute and relative group contribution values were transformed (to natural logarithms and square root, arcsine, respectively) before statistical analysis to increase the variance and homogeneity of normalcy within data sets.

## RESULTS

Sediment resuspension occurred along the southeastern shoreline of Lake Michigan in 1998 and 1999. Resuspension extended north of the Muskegon transect and a significant distance offshore in 1998, whereas it only extended as far north as the Saint Joseph transect in 1999 (Fig. 1A). Isothermal and/or near-isothermal profiles (ca. 3.5 to 5° C) indicated a holomictic water column at all stations during the study. Values of  $K_d$  ranged from 0.21 to 2.49 and 0.10 to 0.66  $\text{m}^{-1}$ , whereas SPM concentrations ranged from 0.72 to 35.28 and 0.82 to 6.30  $\text{mg}\cdot\text{L}^{-1}$  among transects during 1998 and 1999, respectively. Values of  $K_d$  displayed a positive as-

TABLE 1. Sampling locations, frequency, and number in Lake Michigan.

Transect	Dates	Total samples	Maximum depth at stations in meters (distance from shore in km)
Cook, IN	18 March 1998	11	10 (0.04), 30 (7.9), 45 (11.4)
Gary, IN	17 March 1998	5	10 (0.5), 30 (23.8)
New Buffalo, MI	26 March 1999	18	10 (1.7), 20 (5.9), 30 (11.5), 45 (16.5)
	15 April 1999	27	10, 20, 30, 45
Muskegon, MI	19–29 March 1998	42	45 (10.1), 110 (18.4)
	4–11 April 1998	14	10 (1.4), 20 (3.9), 30 (5.8), 45, 80 (13.7), 110
	23–25 March 1999	87	10, 15 (2.5), 20, 30, 35 (7.5), 45
	13–22 April 1999	99	50 (10.9), 80, 85 (14.3), 100 (16.6), 110
Saint Joseph, MI	13–23 March 1998	16	10 (1.9), 30 (9.7), 45 (16.4), 73 (23.3), 110 (32.2)
	5 April 1998	9	30
	23–25 March 1999	48	10, 20 (5.0), 30, 45, 80 (26.0), 110
	18 April 1999	46	10, 20, 30, 45, 80, 110

Refer to Figure 1B for location of sampling transects.

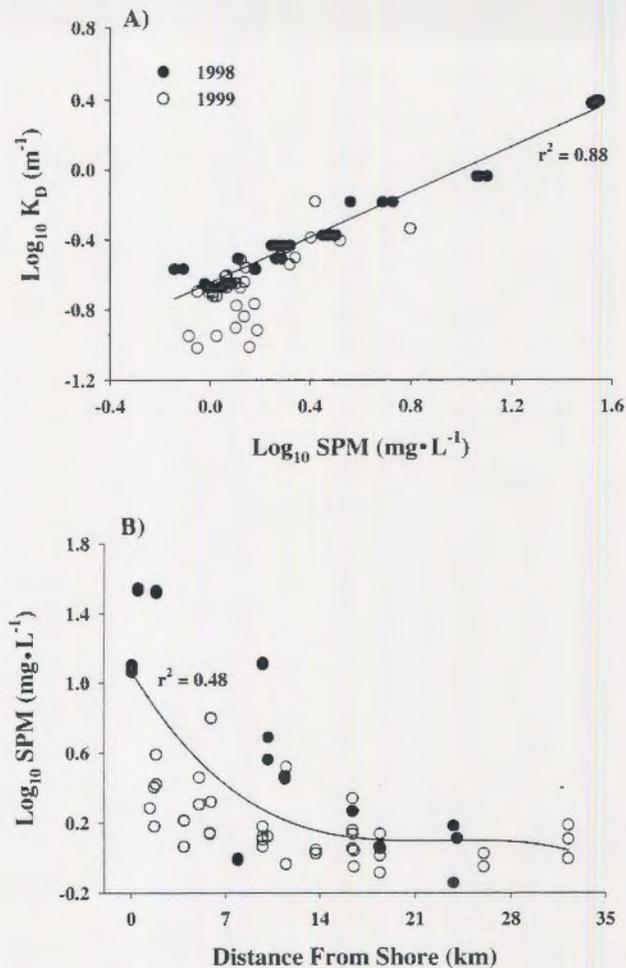


FIG. 2. Relationships between (A) water-column SPM concentrations and  $K_d$  values and (B) SPM concentrations as a function of distance from shore during 1998 and 1999. Trend lines, with associated determination coefficients, represent the "best fit" relationships ( $P \leq 0.001$ ,  $n = 64$ ) as predicted by linear and polynomial least-squares regression.

sociation with SPM concentrations (Fig. 2A); however, a stronger relationship ( $r^2 = 0.98$ ,  $n = 36$ ) existed in 1998 than in 1999 ( $r^2 = 0.50$ ,  $n = 29$ ). Sediment resuspension within subsurface and near-surface waters ( $\leq 15$  m depth) displayed a negative association with the distance of sampling stations from shore and was greatest during 1998 (Fig. 2B).

Microscopic examination revealed that diatoms and cryptophytes comprised the bulk of the phytoplankton assemblages (for a detailed taxonomic listing, see Millie et al. 2003). Briefly, diatom assemblages primarily were composed of the centrics *Aulacoseira islandica* (O. Müll.) Simonsen, *Aulacoseira italica* (Ehrenb.) Simonsen, *Cyclotellus* spp. Round, *Cyclotella ocellata* Pantocsek, and *Stephanodiscus medius* Håk. and the pennates *Diatoma tenuis* (c. Agardh, Lyngb.), *Fragilaria crotonensis* Kitton, *Rhizosolenia longiseta* Zacharias, *Synedra acus* var. *ostenfeldii* Krieger, *Synedra filiformis* Grunow, *Synedra ulna* (Nitzsch) Ehrenb., and *Tabellaria fenestrata* (Lyngb.)

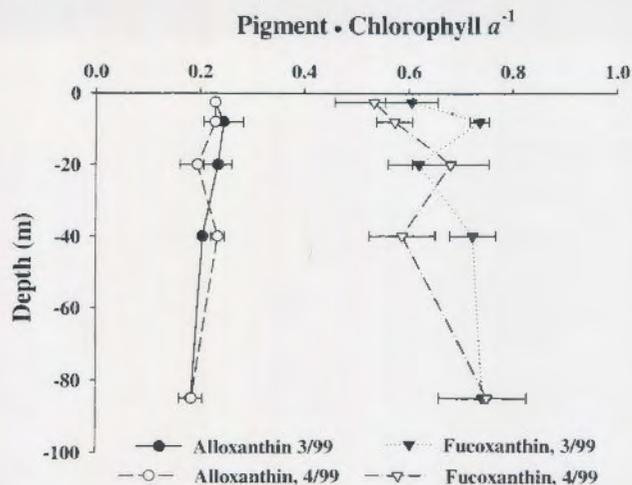


FIG. 3. Final fucoxanthin:chl  $a^{-1}$  and alloxanthin:chl  $a^{-1}$  ratios derived from CHEMTAX matrix factorization for assemblages as a function of sampling depth during March and April 1999. Data represent mean ratios  $\pm$  SE for values of the Muskegon and Saint Joseph transects and are plotted at the midpoint of the depth interval (0–5, 6–10, 15–25, 30–50, and 70–100 m) for which they were calculated.

Kützing. Cryptophyte assemblages primarily were composed of *Cryptomonas erosa* Ehrenb., *Rhodomonas minuta* Skuja, and *Rhodomonas lens* Pascher et Ruttner. A few chl  $b$ -containing taxa (chlorophytes and prasinophytes) and cyanobacteria were observed; however, their abundances always were minimal.

Water-column pigments included chls ( $a$ , chlorophyllide  $a$ ,  $b$ ,  $c_1/c_2$ ,  $c_3$ ) and carotenoids (fucoxanthin, *cis*-fucoxanthin, neoxanthin, violaxanthin, diadinoxanthin, diatoxanthin, alloxanthin, lutein, zeaxanthin, crocoxanthin,  $\beta$ , $\epsilon$ -carotene,  $\beta$ , $\beta$ -carotene). Final ratios for fucoxanthin:chl  $a^{-1}$  and alloxanthin:chl  $a^{-1}$  derived from CHEMTAX were consistent ( $P > 0.05$ ) among and between depths and sampling periods, respectively (e.g. Fig. 3). Fucoxanthin and alloxanthin concentrations corresponded (both  $r = 0.96$ ,  $P \leq 0.001$ ,  $n = 269$ ) with CHEMTAX-derived absolute diatom and cryptophyte chl  $a$  concentrations, respectively. Although absolute diatom and cryptophyte chl  $a$  concentrations corresponded with respective group cell numbers and biovolume estimates (Table 2), total chl  $a$  concentrations corresponded only with total biovolume. Both diatom and cryptophyte chl corre-

TABLE 2. Pearson product moment correlation values ( $n = 19$ ) for total and CHEMTAX-derived group chl  $a$  concentrations (mg·L<sup>-1</sup>) with total and group cell numbers and biovolumes.

Chl $a$	Total/group cell number	Total/group cell biovolume
Total	0.23	0.72 <sup>a</sup>
Diatom	0.79 <sup>b</sup>	0.73 <sup>a</sup>
Cryptophyte	0.73 <sup>a</sup>	0.71 <sup>a</sup>

<sup>a</sup> Significance at the 0.001 probability level.

<sup>b</sup> Significance at the 0.0001 probability level.

TABLE 3. Pearson product moment correlation of total and CHEMTAX-derived group chl *a* concentrations ( $\mu\text{g}\cdot\text{L}^{-1}$ ) with  $K_d$  values or SPM concentrations for the combined data set from 1998 and 1999.

Variables	SPM	Cryptophyte chl <i>a</i>	Diatom chl <i>a</i>	Total chl <i>a</i>	Relative cryptophyte chl <i>a</i>	Relative diatom chl <i>a</i>
$K_d$		-0.42 <sup>b</sup>	0.17	-0.04	-0.51 <sup>d</sup>	0.45 <sup>c</sup>
Cryptophyte chl <i>a</i>	-0.55 <sup>d</sup>		0.26 <sup>a</sup>	0.72 <sup>d</sup>	0.75 <sup>d</sup>	-0.63 <sup>d</sup>
Diatom chl <i>a</i>	0.20	0.28 <sup>a</sup>		0.83 <sup>d</sup>	-0.41 <sup>b</sup>	0.56 <sup>d</sup>
Total chl <i>a</i>	-0.09	0.70 <sup>d</sup>	0.84 <sup>d</sup>		0.11	0.02
Relative cryptophyte chl <i>a</i>	-0.61 <sup>d</sup>	0.72 <sup>d</sup>	-0.42 <sup>b</sup>	0.04		-0.92 <sup>d</sup>
Relative diatom chl <i>a</i>	0.58 <sup>d</sup>	-0.60 <sup>d</sup>	0.55 <sup>d</sup>	0.02	-0.85 <sup>d</sup>	

Correspondence for chl *a* with  $K_d$  ( $n = 58$ ) and SPM ( $n = 52$ ) are in the upper and lower triangle, respectively. Similar results were obtained when the 1998 and 1999 data sets were analyzed independently.

<sup>a</sup> Indicates significance at the 0.05 probability level.

<sup>b</sup> Indicates significance at the 0.01 probability level.

<sup>c</sup> Indicates significance at the 0.001 probability level.

<sup>d</sup> Indicates significance at the 0.0001 probability level.

sponded with total chl *a* ( $P \leq 0.001$ , Table 3) and together typically comprised greater than 85% of the relative chl *a*.

Maximum chl *a* concentrations varied ca. 2.5-fold ( $1.8\text{--}4.75 \mu\text{g}\cdot\text{L}^{-1}$ ) among transects (Figs. 4 and 5). Concentrations were relatively consistent throughout depths during all sampling periods (e.g. Fig. 5). Concentrations along transects displayed one of two trends: either concentrations were greatest ( $P \leq 0.001$ ) at near-shore stations and decreased with increasing distance offshore (e.g. Figs. 4, A and B, and 5, C and D) or concentrations remained relatively consistent ( $P >$

0.05) across transects (e.g. Fig. 5, A and B). The greatest chl *a* concentrations (up to  $10.3 \mu\text{g}\cdot\text{L}^{-1}$ ) occurred at the most near-shore station of the Saint Joseph transect (see Figs. 4C and 5, C and D) and appeared to coincide with tributary inflows of the Saint Joseph River at this site. Concentrations along the New Buffalo transect were highly variable, with the greatest concentrations occurring at the most near- and offshore station in March and April 1999, respectively. Chl *a* concentrations did not correspond with coefficients of  $K_d$  and SPM concentrations ( $P > 0.05$ ; Table 3).

Maximum absolute and relative diatom chl *a* concentrations varied ca. 12-fold ( $0.66\text{--}8.18 \mu\text{g}\cdot\text{L}^{-1}$ ) and 2.8-fold ( $0.36\text{--}0.99$ ), respectively, within coastal waters

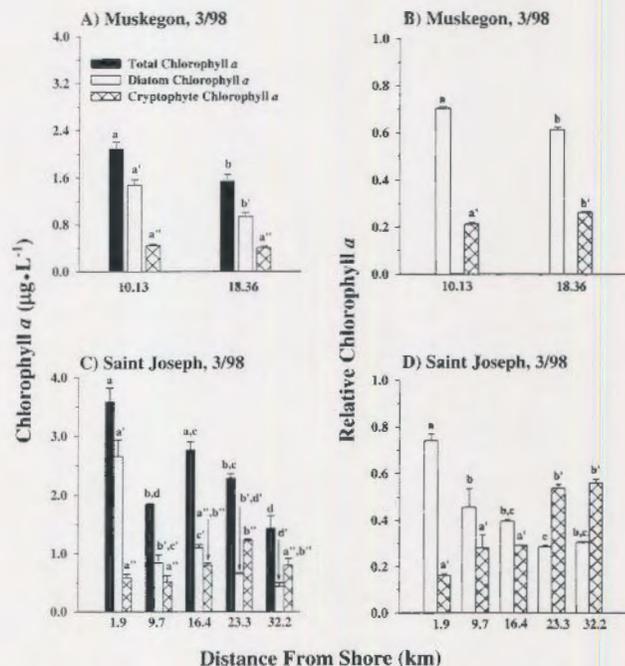


FIG. 4. Total and absolute diatom and cryptophyte chl *a* along the (A) Muskegon and (C) Saint Joseph transect in March 1998. Relative diatom and cryptophyte chl *a* along the (B) Muskegon and (D) Saint Joseph transects. Variables (designated by primes) with the same letter for a transect are not different ( $P > 0.05$ ). Data are means  $\pm$  SE averaged across the water column ( $n = 2\text{--}9$ ).

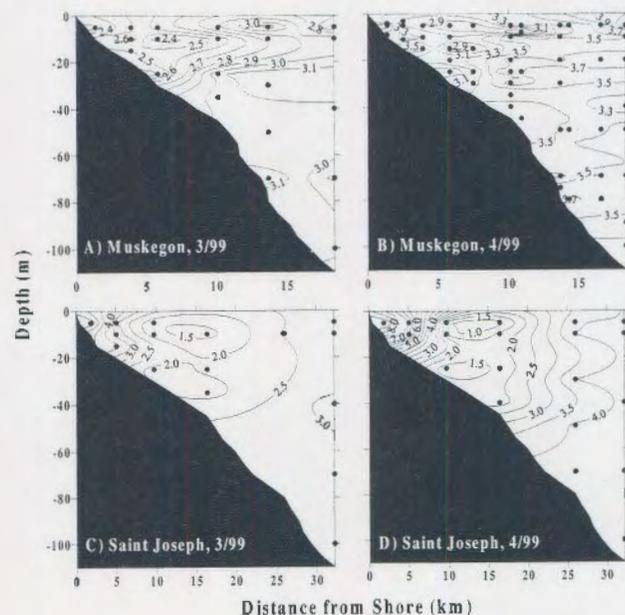


FIG. 5. Spatial distribution of total chl *a* ( $\mu\text{g}\cdot\text{L}^{-1}$ ) along the Muskegon [(A) March, (B) April] and Saint Joseph [(C) March, (D) April] transects during 1999. Filled circles represent sampling density. For contour plotting, a kriging algorithm (linear variogram model) provided interpolation between data means (Muskegon: March,  $n = 87$ ; April,  $n = 99$ . Saint Joseph: March,  $n = 49$ ; April,  $n = 46$ ).

with greatest concentrations occurring at the most near-shore station of the Saint Joseph transect. Typically, diatom chl *a* was the most abundant chl *a* near-shore ( $P \leq 0.001$ ) and decreased with increased distance offshore (Figs. 4, A and B, and 6, A and C). During April 1998, however, this trend was reversed along the Muskegon transect, with both relative and absolute diatom chl *a* ca. 2-fold greater ( $P \leq 0.001$ ) at the offshore than the near-shore station. Although absolute diatom chl *a* was similar ( $P > 0.05$ ) among stations along the Gary transect, relative concentrations did decrease ( $P \leq 0.01$ ) with increased distance offshore. Unlike trends observed elsewhere, relative diatom chl *a* increased ( $P \leq 0.05$ ) with increasing distance offshore along the Cook transect in 1998. Both  $K_d$  and SPM concentrations were positively associated with relative diatom chl *a* ( $P \leq 0.001$  and  $P \leq 0.001$ , respectively; Table 3).

Maximum absolute and relative cryptophyte chl *a* concentrations varied ca. 2.7-fold (0.96–2.6  $\mu\text{g}\cdot\text{L}^{-1}$ ) and 2.9-fold (0.26–0.76), respectively, within coastal waters. In contrast to the trend displayed by diatom chl *a*, absolute and relative cryptophyte chl *a* typically increased ( $P \leq 0.05$ ) with increasing distance offshore with the greatest relative abundance occurring at the most offshore stations and at depth (Figs. 4, A and C, and 6, B and D). Although absolute cryptophyte chl *a* was similar along the Muskegon transect during March 1998, the relative chl *a* was greatest ( $P \leq 0.05$ ) at the most offshore station. Both  $K_d$  and SPM concentrations were negatively associated with

absolute and relative cryptophyte chl *a* ( $P \leq 0.001$ ; Table 3).

Viable photopigments within harvested surficial sediments included both chls and carotenoids (Fig. 7). Pigments indicative of diatoms (chls  $c_{1/2}$ , fucoxanthin, diadinoxanthin; see above) dominated the pigment complex. Only minimal amounts of chl *a* degradation products and pigments representative of cryptophytes, chlorophytes, and cyanobacteria were present.

#### DISCUSSION

Sediment resuspension episodically impacted the particle density and light field of the near-shore water column during the spring isothermal period in Lake Michigan (also see Cotner et al. 2000). A large variability in light attenuation occurred, particularly in 1998 when the extent and intensity of sediment resuspension was greatest (refer to Figs. 1A and 2). The association of SPM with  $K_d$  and the lack of association of total chl *a* with both SPM and  $K_d$  indicated that attenuation primarily was a function of suspended sediment and not of phytoplankton biomass (see Cloern 1987).

Concentrations of chl *a* generally ranged from 1.5 to 4  $\mu\text{g}\cdot\text{L}^{-1}$ , values within the range typically reported for Lake Michigan coastal waters during early spring (cf. Brooks and Torke 1977, Fahnenstiel and Scavia 1987a). The consistent chl *a* concentrations and fucoxanthin:chl *a*<sup>-1</sup> and alloxanthin:chl *a*<sup>-1</sup> ratios across depths indicated uniform distributions of and photo-physiological states for phytoplankton assemblages, respectively, during holomixis (cf. Roy et al. 1996). No consistent correspondence between phytoplankton

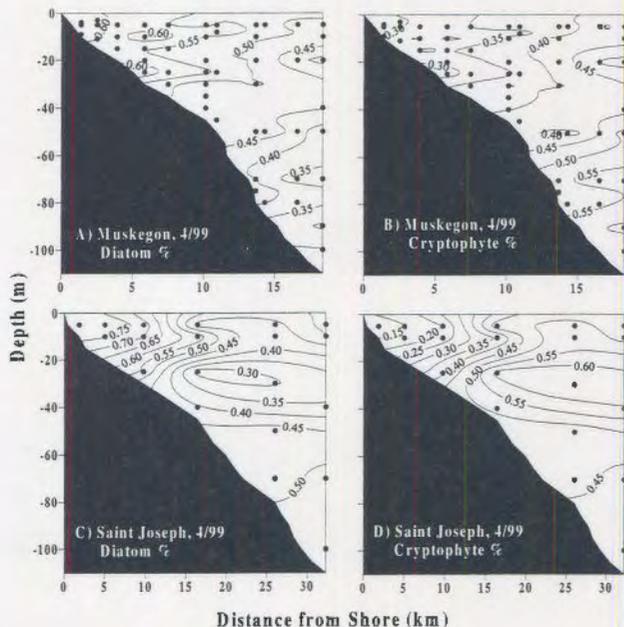


FIG. 6. Spatial distribution of relative chl *a* along the Muskegon [(A) diatom, (B) cryptophyte;  $n = 99$ ] and Saint Joseph [(C) diatom, (D) cryptophyte;  $n = 46$ ] transects during April 1999. Filled circles represent sampling density. For contour plotting, a kriging algorithm (linear variogram model) provided interpolation between data means.

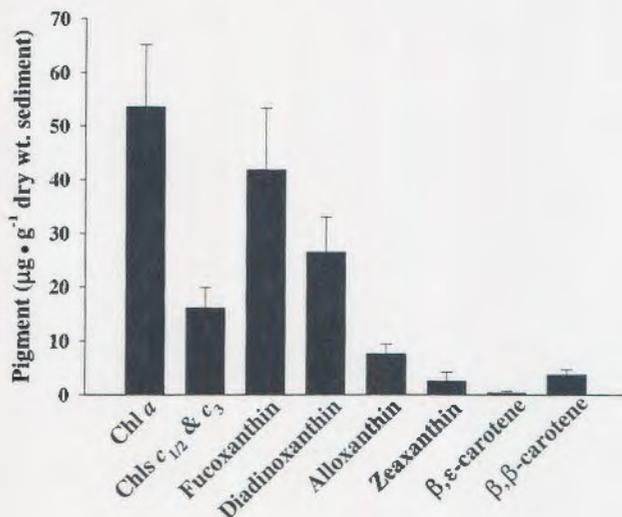


FIG. 7. Photopigments indicative of all algae (chl *a*), diatoms (chls  $c_{1/2}$ , fucoxanthin, diadinoxanthin), cryptophytes (alloxanthin,  $\beta,\epsilon$ -carotene), and cyanobacteria (zeaxanthin) within surficial sediments. Sediments were collected on 23 March 2000 by box cores from 45-m depth along the New Buffalo transect. Data are means  $\pm$  SE ( $n = 2$ ).

abundance (as total, diatom, and/or cryptophyte chl *a*) and both  $K_d$  and SPM concentrations was observed. However, the correspondence of both  $K_d$  and SPM concentrations with relative diatom chl *a* did indicate an apparent association between sediment resuspension and diatoms. This, and the negative association between relative diatom and cryptophyte chl *a*, corresponded with the spatial dominance of diatoms and cryptophytes in near-shore and offshore waters, respectively (also see Fahnenstiel and Scavia 1987b, Carrick and Fahnenstiel 1989, Barbiero et al. 2000, Carrick et al. 2001, Millie et al. 2003).

Coastal waters serve as an interface between offshore and terrestrial systems and as a result receive nutrient and particulate loading from both. Total chl *a* concentrations often were greatest near-shore and decreased with increased distance offshore. The greatest and most variable total and diatom chl *a* concentrations occurred at the most near-shore stations of the Saint Joseph transect. Because these stations lie immediately offshore the confluence of the Saint Joseph River and the lake, this variability in phytoplankton abundance most likely reflects the sizable influence of tributary inflows upon the coastal assemblages. Great Lakes tributaries, including the Saint Joseph River, previously have been reported to contribute significant phosphorus loading while also introducing riverine phytoplankton into littoral waters (Schelske et al. 1984, Chang and Rossmann 1988, Klarer and Millie 1989). Schelske et al. (1984) reported that riverine and Lake Michigan phytoplankton were distinct populations and that the phosphorus and light conditions within coastal waters impacted by inflows could allow riverine populations to thrive while simultaneously providing for selective growth of dominant lake taxa. Alternatively, turbulence associated with river flows could have suspended near shore benthic forms into the water column.

Diatoms and cryptophytes dominated phytoplankton assemblages during the study, together often comprising greater than 85% of the total chl *a*. During the late winter, cryptophytes and small centric diatoms typically dominate the lake's phytoplankton. As the spring isothermal period develops, this assemblage is gradually replaced by one comprised mostly of larger centric diatoms with lesser amounts of cryptophytes (Scavia and Fahnenstiel 1987). However, decreased light intensity typically occurs within hydrodynamically active waters. The increased turbidity resulting from near-shore sediment resuspension probably would invoke a severe light limitation to certain phytoplankton and ultimately reduce growth rates. As a result, abundance may remain constant or actually be reduced (see Demers et al. 1989). Brooks and Torke (1977) noted that although the spring diatom increases within the lake commence in late winter, the later initiation of the spring bloom by selected taxa actually coincided with the rapid rise of solar input during early spring. It may be that diatoms (with fucoxanthin as the primary light-harvesting carotenoid) have greater light-harvesting efficiency than cryptophytes within turbid

near-shore waters, thereby providing, in part, a competitive advantage to this phylogenetic group (see Ondrusek et al. 1991). In contrast, cryptophyte relative abundance appeared to increase at depth offshore (refer to Fig. 6) where the presence of accessory phycobilin pigments may provide this group with an advantage in light harvesting. Using microphotometry to assess the absorption efficiency of Lake Michigan phytoplankton, Fahnenstiel et al. (2000) reported the centric diatoms, *Aulacoseira islandica* and *Cyclostephanos* sp., to have greater light-harvesting ability than the cryptophyte *Cryptomonas erosa*. However, without detailed information on species-specific carbon fixation (i.e. the conversion of light into carbon compounds and, ultimately, cell growth), it is impossible to assess the actual efficiency of light utilization and its role in competitive dominance (Fahnenstiel et al. 2000).

Nevertheless, explanations for spatial variability in abundance within a system as dynamic as Lake Michigan are not simple. Light and nutrient availabilities likely control the instantaneous rates of phytoplankton growth and the potential for biomass accumulation, respectively, within the lake during the spring isothermal period (Fahnenstiel et al. 1984, 2001, Scavia and Fahnenstiel 1987). Soluble nitrogen concentrations typically are very high in Lake Michigan ( $100\text{--}200\ \mu\text{g}\cdot\text{L}^{-1}$   $\text{N-NO}_3^-$ ,  $3\text{--}10\ \mu\text{g}\cdot\text{L}^{-1}$   $\text{N-NH}_4^+$ ) and nitrogen never is limiting. Rather, phosphorus is the element most likely limiting phytoplankton photosynthesis and growth (Schelske et al. 1974). Sediment resuspension and intense water-column mixing would favor high nutrient availability through upwelling processes, thereby alleviating any phosphorus limitation within impacted waters. During the March 1998 event, Cotner et al. (2000) attributed stimulation of heterotrophic bacterial biomass and production along the margin of the lake to the resuspension of sediments rich in both particulate organic and inorganic phosphorus. Soluble reactive phosphorus was ca. 5-fold greater within sediment-impacted near-shore waters than in offshore waters ( $1.5$  and  $0.27\ \mu\text{g}\cdot\text{L}^{-1}$   $\text{P-PO}_4^{3-}$ , respectively). They postulated a potential similar effect on phytoplankton despite the extremely low water temperatures. Such an enhancement of phytoplankton abundance along episodic fronts is common and often diatom-dominated (whereas waters adjacent to the front are not), due in part to the "opportunistic nature" of diatoms for nutrients (Claustre et al. 1994). Moreover, Holland (1969) observed that light penetration had no correspondence to alterations in the abundance of Lake Michigan diatoms and attributed most alterations to nutrient dynamics. However, phytoplankton growth rates during this period typically are quite low (ca.  $0.1\ \text{d}^{-1}$ ; Fahnenstiel et al. 2001), and all measures of phosphorus deficiency (including alkaline phosphatase activity, phosphorus-33 turnover, presence of poly-phosphate bodies) indicated no limitation by phytoplankton before, during, and immediately after resuspension events (G. Fahnenstiel, unpublished data).

The abundance of diatoms within littoral and shallow-water systems also has been attributed, in part, to

viable, benthic, and/or resting cells and cysts resuspended within the water column (meroplankton). Meroplankton may influence the taxonomic composition and total abundance of surface assemblages in shallow systems (e.g. Schelske et al. 1995, Carrick et al. 1993, Tester et al. 1995, Roy et al. 1996), and significant resuspension of meroplanktonic diatoms after wind events has been reported from the western basin of Lake Erie (Hartig 1987). A similar occurrence would be expected within southeastern Lake Michigan, a region heavily impacted by sediment resuspension and characterized by intense turbulence during holomixis. Lake Michigan diatoms have large sinking rates (Scavia and Fahnenstiel 1987) and settle rapidly through the water column, particularly upon the onset of thermal stratification (Gardner et al. 1990). Nalepa and Quigley (1987) previously reported the occurrence of viable benthic chl *a* within surficial sediments of near-shore Lake Michigan, with the greatest amounts (up to 212  $\mu\text{g}\cdot\text{g}^{-1}$  sediment) observed during late spring. In this study, the presence of viable chl *a* and fucoxanthin (ca. 53 and 42  $\mu\text{g}\cdot\text{g}^{-1}$  sediment, respectively) within surficial sediments established the sediments as a potential source of meroplanktonic diatoms (also see Klein and Riaux-Gobin 1991, Millie et al. 2003). Cotner et al. (2000) estimated that of the  $>3 \times 10^{12}$  g of sediment resuspended during the March 1998 event, ca.  $1.65 \times 10^{12}$  g occurred in the volume of water ( $2.29 \times 10^{11}$  m<sup>3</sup>) inside the 60-m depth contour. From this, and using the aforementioned sediment pigment concentrations, we estimated that ca.  $0.9\text{--}3.5 \times 10^8$  g of viable chl *a* could be resuspended from the lake's floor in near-shore waters ( $\leq 60$  m deep). This would result in a potential increase of  $0.4\text{--}1.5 \mu\text{g}\cdot\text{L}^{-1}$  chl *a* to the overlying water column during a major prolonged event.

The occurrence of resuspension typically coincides with the initiation period of the spring diatom bloom. This annual bloom can contribute up to half of the lake's total annual primary production and serves as a major carbon source to higher trophic levels (Fahnenstiel and Scavia 1987a, Gardner et al. 1990, Brooks and Edgington 1994). Mortimer (1988) suggested that the resuspended material may be associated with the annual bloom. Moreover, many taxa typically observed within the spring bloom are capable of forming resting stages and have been observed as part of the meroplanktonic assemblages within other systems (Sicko-Goad et al. 1986, 1989). Major resuspension could provide a significant pulse of benthic diatoms into the water column, and these taxa, if stimulated by appropriate singular and/or multiple physical/chemical cues, then could undergo selective growth (e.g. Imai et al. 1996). Resuspension, coupled with optimal nutrient/light conditions and near-shore-offshore transport mechanisms, then might provide for development of the spring diatom bloom within nutrient-rich near-shore waters before its propagation offshore (as noted by Stoermer 1968).

However, the approximate juxtaposition of resuspension with the onset of the spring bloom presents a complexity in delineating causative impacts on phy-

toplankton assemblages. In examining the relative phytoplankton composition between sediment-impacted and adjacent waters, Millie et al. (2003) denoted a spatial dissimilarity among assemblages that mirrored SPM concentrations. The large net diatoms and cryptophytes typically comprising phytoplankton of the spring bloom and of optically clear offshore waters were not associated with sediment-impacted waters. Rather, small centric diatoms exhibiting meroplanktonic life histories and large pennate diatoms considered benthic in origin were prevalent. This corresponds with the positive association of SPM with relative diatom chl *a* and, taken together, indicates that sediment resuspension is associated with the presence of meroplankton. However, total and absolute diatom chl *a* and cryptophyte chl *a* displayed a lack of and negative association with SPM concentrations, respectively. As such, although resuspension influenced the composition of near-shore phytoplankton assemblages, it appeared to have little if any impact on total phytoplankton abundance within Lake Michigan coastal waters.

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- Barbiero, R. P., Carrick, H. J., Volerman, J. B. & Tuchman, M. L. 2000. Factors affecting temporal and spatial distribution of diatoms in Lake Michigan. *Verh. Internat. Verein. Limnol.* 27:1788–94.
- Brooks, A. S. & Edgington, D. N. 1994. Biogeochemical control of phosphorus cycling and primary production in Lake Michigan. *Limnol. Oceanogr.* 39:961–7.
- Brooks, A. S. & Torke, B. G. 1977. Vertical and seasonal distribution of chl *a* in Lake Michigan. *J. Fish. Res. Bd. Can.* 34:2280–7.
- Carrick, H. J. & Fahnenstiel, G. L. 1989. Biomass, size structure, and composition of phototrophic and heterotrophic nanoflagellate communities in Lakes Huron and Michigan. *Can. J. Fish. Aquat. Sci.* 46:1922–8.
- Carrick, H. J., Aldridge, F. J. & Schelske, C. L. 1993. Wind influences phytoplankton biomass and composition in a shallow, productive lake. *Limnol. Oceanogr.* 38:1179–92.
- Carrick, H. J., Barberio, R. & Tuchman, M. 2001. Variation in Lake Michigan plankton: temporal, spatial, and historical trends. *J. Great Lakes Res.* 27:467–85.
- Chang, W. Y. B. & Rossmann, R. 1988. Changes in the abundance of blue-green algae related to nutrient loadings in the near-shore of Lake Michigan. *Hydrobiologia* 157:271–8.

- Claustre, H., Kerherve, Marty, J. C., Prieur, L., Videau, C. & Hecq, J.-H. 1994. Phytoplankton dynamics associated with a geostrophic front: ecological and biogeochemical implications. *J. Mar. Res.* 52:711-42.
- Cloern, J. E. 1987. Turbidity as a control on phytoplankton biomass and productivity in estuaries. *Cont. Shelf Res.* 7:1367-81.
- Cotner, J. B., Johengen, T. H. & Biddanda, B. 2000. Intense winter heterotrophic production stimulated by benthic resuspension. *Limnol. Oceanogr.* 45:1672-6.
- Demers, S., Therriault, J.-C., Bourget, E. & Desilets, H. 1989. Small-scale gradients of phytoplankton productivity in the littoral fringe. *Mar. Biol.* 100:393-99.
- Descy, J.-P., Higgins, H. W., Mackey, D. J., Hurley, J. P. & Frost, T. M. 2000. Pigment ratios and phytoplankton assessment in northern Wisconsin lakes. *J. Phycol.* 36:274-86.
- Eadie, B., Schwab, D., Assel, R., Hawley, N., Lansing, B., Miller, R., Morehead, N. & Robbins, J. 1996. Development of recurrent coastal plume in Lake Michigan observed for the first time. *EOS, Trans. Am. Geophys. Un.* 77:337-8.
- Fahnenstiel, G. L., Scavia, D. & Schelske, C. L. 1984. Nutrient-light interactions in the Lake Michigan subsurface chlorophyll layer. *Verh. Internat. Verein. Limnol.* 22:440-4.
- Fahnenstiel, G. & Scavia, D. 1987a. Dynamics of Lake Michigan phytoplankton: primary production and growth. *Can. J. Fish. Aquat. Sci.* 44:499-508.
- Fahnenstiel, G. & Scavia, D. 1987b. Dynamics of Lake Michigan phytoplankton: recent changes in surface and deep communities. *Can. J. Fish. Aquat. Sci.* 44:509-14.
- Fahnenstiel, G., Lohrenz, S., Kelly, K., Millie, D. & Schofield, O. 2000. Light absorption characteristics of individual phytoplankton cells from a natural community: examples from Lake Michigan during the winter/spring period. *Verh. Internat. Verein. Limnol.* 27:1836-40.
- Fahnenstiel, G. L., Stone, R. A., McCormick, M. J., Schelske, C. L. & Lohrenz, S. E. 2001. Spring isothermal mixing in the Great Lakes: evidence of nutrient limitation and nutrient-light interactions in a suboptimal light environment. *Can. J. Fish. Aquat. Sci.* 57:1901-10.
- Fahnenstiel, G. L., Beckmann, C., Lohrenz, S., Millie, D., Schofield, O. & McCormick, M. J. M. 2003. Standard Niskin and Van Dorn bottles inhibit phytoplankton photosynthesis in Lake Michigan. *Verh. Internat. Verein. Limnol.* 28: In press.
- Gardner, W. S., Quigley, M. A., Fahnenstiel, G. L., Scavia, D. & Frenz, W. A. 1990. *Pontoporeia hoyi*—a direct trophic link between spring diatoms and fish in Lake Michigan. In Tilzer, M. M. & Serruya, C. [Eds.]. *Large Lakes Ecological Structure and Function*. Springer-Verlag, New York, pp. 632-44.
- Hartig, J. H. 1987. Factors contributing to the development of *Fragilaria crotonensis* Kitton pulses in Pigeon Bay waters of western Lake Erie. *J. Great Lakes Res.* 13:65-77.
- Heiskanen, A.-S. & Tallberg, P. 1999. Sedimentation and particulate nutrient dynamics along a coastal gradient from a fjord-like bay to the open sea. *Hydrobiologia* 393:127-40.
- Holland, R. E. 1969. Seasonal fluctuations of Lake Michigan diatoms. *Limnol. Oceanogr.* 14:423-36.
- Imai, I., Itakura, S., Yamaguchi, M. & Honjo, T. 1996. Selective germination of *Heterosigma akashiwo* (Raphidophyceae) cysts in bottom sediments under low light conditions: a possible mechanism of red tide initiation. *Intergov. Com. of UNESCO*, pp. 197-200.
- Jeffrey, S. W., Wright, S. W. & Zapata, M. 1999. Recent advances in HPLC pigment analysis of phytoplankton. *Mar. Freshwat. Res.* 50:879-96.
- Klarer, D. M. & Millie, D. F. 1989. Amelioration of storm-water quality by a freshwater estuary. *Arch. Hydrobiol.* 116:375-89.
- Klein, B. & Riaux-Gobin, C. 1991. Algal pigment diversity in coastal sediments from Kerguelen (sub-Antarctic Islands) reflecting local dominance of green algae, euglenoids and diatoms. *Polar Biol.* 11:439-48.
- Lund, J. W. G. 1954. The seasonal cycle of the plankton diatom, *Melosira italica* (Her.) subsp. *subarctica* O. Mull. *J. Ecol.* 42: 151-79.
- Mackey, M., Mackey, D., Higgins, H. & Wright, S. 1996. CHEMTAX—a program for estimating class abundances from chemical markers: application to HPLC measurements of phytoplankton. *Mar. Ecol. Prog. Ser.* 144:265-83.
- Mackey, M. D., Higgins, H. W., Mackey, D. J. & Holdsworth, D. 1998. Algal class abundances in the western equatorial Pacific: estimation from HPLC measurements of chloroplast pigments using CHEMTAX. *Deep Sea Res.* 45:1441-68.
- McCormick, M. J., Miller, G. S., Murthy, R., Rao, Y. R. & Saylor, J. H. 2003. Tracking coastal flow with surface drifters during the Episodic Events Great Lakes Experiment. *Verh. Internat. Verein. Limnol.* 28: In press.
- Miller, G. S., McCormick, M. J., Saylor, J. H., Murthy, R. & Rao, Y. R. 2003. Temporal and spatial variability of the resuspension coastal plume in southern Lake Michigan inferred from ADCP backscatter. *Verh. Internat. Verein. Limnol.* 28: In press.
- Millie, D. F., Paerl, H. W. & Hurley, J. P. 1993. Microalgal pigment assessments using high-performance liquid chromatography: a synopsis of organismal & ecological applications. *Can. J. Fish. Aquat. Sci.* 50:2513-27.
- Millie, D. F., Fahnenstiel, G. L., Carrick, H. J., Lohrenz, S. E. & Schofield, O. M. E. 2003. Spatial variation in Lake Michigan phytoplankton composition during sediment resuspension events. *Verh. Internat. Verein. Limnol.* 28: In press.
- Mortimer, C. H. 1988. Discoveries and testable hypotheses arising from the Coastal Zone Color Scanner imagery of southern Lake Michigan. *Limnol. Oceanogr.* 33:203-26.
- Nalepa, T. F. & Quigley, M. A. 1987. Distribution of photosynthetic pigments in nearshore sediments of Lake Michigan. *J. Great Lakes Res.* 13:37-42.
- O'Donohue, M. J. & Dennison, W. C. 1997. Phytoplankton productivity response to nutrient concentration, light availability and temperature along an Australian estuarine gradient. *Estuaries* 20:521-33.
- Ondrusek, M. E., Bidigare, R. R., Sweet, S. T., Defreitas, D. A. & Brooks, J. M. 1991. Distribution of phytoplankton pigments in the north Pacific Ocean in relation to physical and optical variability. *Deep Sea Res.* 38:243-66.
- Pinckney, J. L., Millie, D. F., Howe, K. E., Paerl, H. P. & Hurley, J. P. 1996. Flow scintillation counting of <sup>14</sup>C-labeled microalgal photopigments. *J. Plank. Res.* 18:1867-80.
- Roy, S., Chanut, J.-P., Gosselin, M. & Sime-Ngando, T. 1996. Characterization of phytoplankton communities in the lower St. Lawrence Estuary using HPLC-detected pigments and cell microscopy. *Mar. Ecol. Prog. Ser.* 142:55-73.
- Schaub, B. E. M. & Gieskes, W. W. C. 1991. Eutrophication of the North Sea: the relation between Rhine River discharge and the chlorophyll-a concentration in Dutch coastal waters. In Elliot, M. & Ducrot, J.-P. [Eds.] *Estuaries and Coasts: Spatial and Temporal Intercomparisons*. Olsen and Olsen, Fredensborg, Denmark, pp. 85-90.
- Scavia, D. & Fahnenstiel, G. L. 1987. Dynamics of Lake Michigan phytoplankton: mechanisms controlling epilimnetic communities. *J. Great Lakes Res.* 13:103-20.
- Schelske, C. L., Rothman, E. D., Stoermer, E. F. & Santiago, M. A. 1974. Responses of phosphorus limited Lake Michigan phytoplankton to factorial enrichments with nitrogen and phosphorus. *Limnol. Oceanogr.* 19:409-19.
- Schelske, C. L., Davis, C. O. & Feldt, L. E. 1984. Growth responses of river and lake phytoplankton populations in Lake Michigan water. *Verh. Internat. Verein. Limnol.* 22:445-51.
- Schelske, C. L., Carrick, H. J. & Aldridge, F. J. 1995. Can wind-induced resuspension of meroplankton affect phytoplankton dynamics? *J. North Am. Benthol. Soc.* 14:616-30.
- Schlüter, L., Mølenberg, F., Havskum, H. & Larsen, S. 2000. The use of phytoplankton pigments for identifying and quantifying phytoplankton groups in coastal areas: testing the influence of light and nutrients on pigment Chl *a* ratios. *Mar. Ecol. Prog. Ser.* 192:49-63.
- Sicko-Goad, L., Stoermer, E. F. & Fahnenstiel, G. L. 1986. Rejuvenation of *Melosira granulata* (Bacillariophyceae) resting cells from the anoxic sediments of Douglas Lake, Michigan. I. Light microscopy and <sup>14</sup>C uptake. *J. Phycol.* 22: 22-28.
- Sicko-Goad, L., Stoermer, E. F. & Kocielek, J. P. 1989. Diatom resting cell rejuvenation and formation: time course, species records and distribution. *J. Plank. Res.* 11:375-89.

- Stoermer, E. F. 1968. Nearshore phytoplankton populations in the Grand Haven, Michigan vicinity during thermal bar conditions. Internat. Assoc. Great Lakes Res., Proc. 11th Conf. Great Lakes Res., Milwaukee, WI, USA.
- Tester, P. A., Geesey, M. R., Guo, C., Paerl, H. W. & Millie, D. F. 1995. Evaluating phytoplankton dynamics in the Newport River Estuary (North Carolina, USA.) by HPLC-derived pigment profiles. *Mar. Ecol. Prog. Ser.* 124:237-45.
- Wetzel, R. G. 2001. *Limnology: Lake and River Ecosystems*, 3rd ed. Academic Press, San Diego, California, 850 pp.
- Wright, S. W., Thomas, D. P., Marchant, H. J., Higgins, H. W., Mackey, M. D. & Mackey, D. J. 1996. Analysis of phytoplankton of the Australian sector of the Southern Ocean: comparisons of microscopy and size frequency data with interpretations of pigment HPLC data using "CHEMTAX" matrix factorization program. *Mar. Ecol. Prog. Ser.* 144:285-98.
- Wright, S. W. & van den Enden, R. L. 2000. Phytoplankton community structure and stocks in the East Antarctic marginal ice zone (BROKE survey, January-March 1996) determined by CHEMTAX analysis of HPLC pigments. *Deep Sea Res.* 47:2362-400.