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Anatomy of the recurrent coastal sediment plume in Lake Michigan and its impacts on light climate, nutrients, and plankton

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[1] As part of the Episodic Events Great Lakes Experiment, we sampled total suspended matter (TSM), light climate, nutrients, and plankton along cross-margin transects in southern Lake Michigan during February, March, and April 1998–2000 to capture conditions before, during, and after the occurrence of storm-driven recurrent coastal sediment plumes to define the anatomy of the resuspension events and get insights into their interactions with nutrients and plankton. Variability in timing and strength of winter storms among years led to different timing, intensity, and extent of plumes among years. TSM concentrations in the core of plumes varied between 15 and 30 mg L^{-1}, and photic depth was reduced to ~1 to 2 m, thus potentially seriously limiting phytoplankton growth in plume areas. Total P concentration was highly correlated with TSM and river influence. Chlorophyll concentrations were lower in plume regions than in adjacent areas, in contrast to the relatively constant chlorophyll concentration across the plume predicted by a coupled hydrodynamic and nutrient-phytoplankton-zooplankton model. Contrary to expectation, protozoan microzooplankton (MZ) biomass was not more abundant in the plume than adjacent waters, but was highest in nearshore areas receiving river inflow. Storms affected horizontal distribution of zooplankton. Because of the lower concentrations of phytoplankton in the plume, the plume over the short term had a negative impact on zooplankton during this food-limiting season. Our results combined with those of other EEGLE studies lead us to conclude that storms and storm-driven plumes had a negative effect on the planktonic food web.

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1. Introduction

[2] Satellite imagery sometimes revealed the presence of an extensive plume of resuspended sediments during winter and winter-spring transition in the southern basin of Lake Michigan with a clear offshore projection (e.g., Figures 1a, 1c, and 1d) associated with major storm systems [*Eadie et al.*, 2002]. The offshore projections of this recurrent plume also correspond to the region of high sediment deposition (e.g., projections in Figures 1c and 1d match up well). Preliminary observations made with a few grab samples in and out of the plume of March 1996 showed high total suspended material (TSM), elevated phosphorus and a different phytoplankton and microzooplankton community in the plume area, which suggested the plume could have significant implications to particle transport, nutrient cycling, and plankton community structure [*Eadie et al.*, 2002]. These few observations served as the foundation for hypotheses of plume effects and a major multidisciplinary program, Episodic Events Great Lakes Experiment (EEGLE) [*Eadie et al.*, 2002]. Major goals of EEGLE were to describe and understand cross-isobath transport of biogeochemically important materials associated with resuspended sediments of major storm events and how these inputs affect the ecosystem [e.g., *Schwab et al.*, 2000; *Eadie et al.*, 2002]. We were interested in examining the EEGLE program hypotheses that resuspended sediment would diminish light available for phytoplankton growth, would increase P available to phytoplankton, and would stimulate the microbial food web through injection of P and detrital carbon into the food web [*Eadie et al.*, 2002]. These assumptions formed the foundation of the experimental program as well as a coupled hydrodynamic and nutrient-

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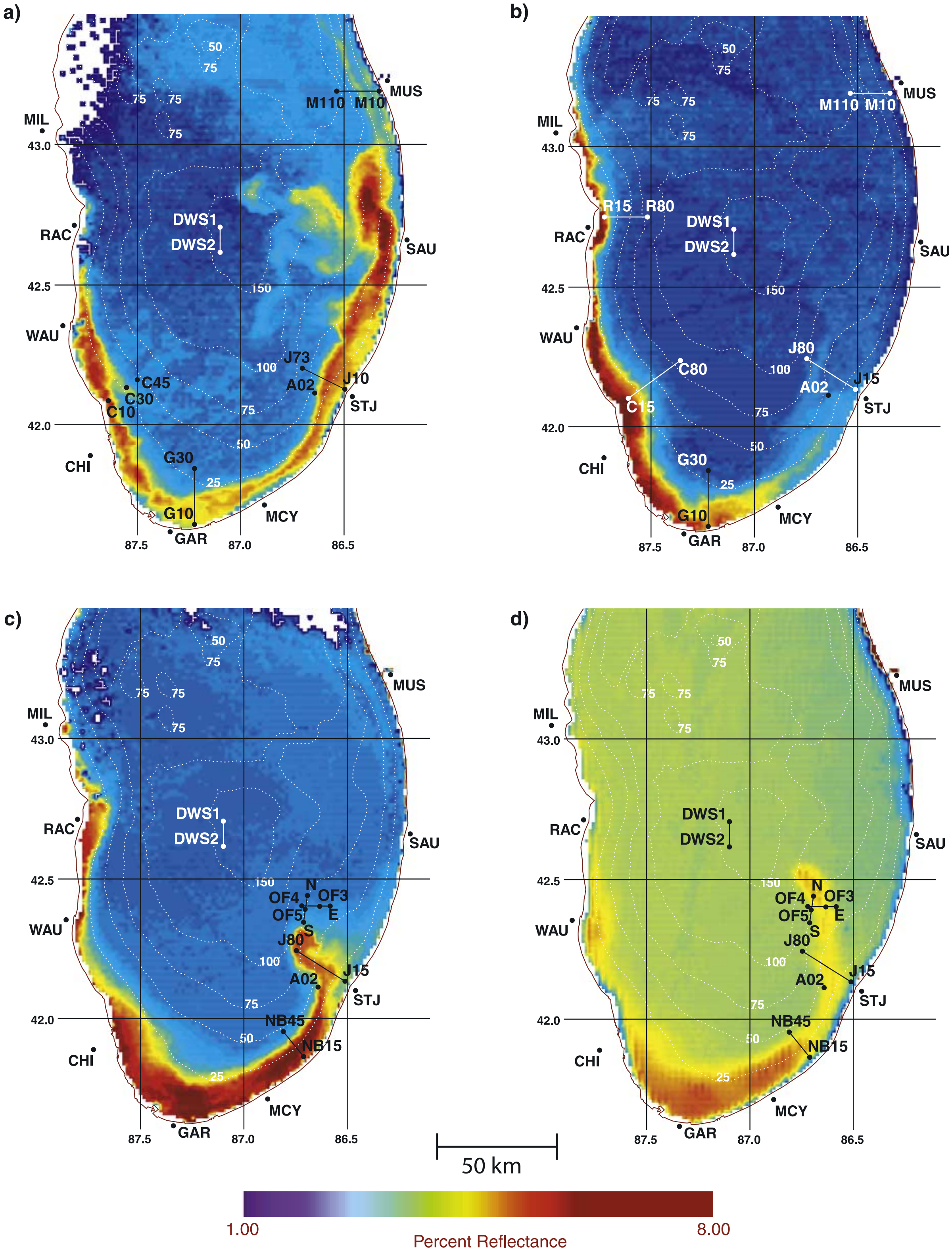


Figure 1. PSS transects and sampling stations superimposed on CoastWatch AVHRR satellite imagery of reflectance (channel 1 minus channel 2) of the recurrent coastal plume during or just before plume cruises: (a) 16 March 1998, (b) 12 March 1999, (c) 9 April 2000, and (d) 12 April 2000. Transects are designated by lines connecting end points, which are sampling stations or the letters N, S, and E referring to the north, south, and east ends of an offshore transect. DWS1 and DWS2 are stations at the ends of the deepwater transect that was sampled on some nonplume cruises. A02 refers to the location of the ADCP used to monitor acoustic backscattering. Other symbols refer to station locations where water samples were collected.

phytoplankton-zooplankton model to predict plume impacts [*Chen et al.*, 2004a, 2004b; *Ji et al.*, 2002].

[3] As part of this hypothesis testing, our research team was to describe from shipboard observations the anatomy of the plume in order to evaluate impact of the plume on plankton and nutrients by measuring their spatial patterns relative to the plume. Few observations had ever been made during winter and winter-spring transition because of difficulty and danger of ship operations and because of lack of interest in this season. Thus we had no empirical foundation for generating detailed hypotheses, and our study was largely exploratory. In particular, we defined finescale spatial structure of suspended sediment, light climate, temperature, nutrients, and plankton on cross-isobath transects (Figure 1) throughout the southern basin from vertically undulating tows of the plankton survey system (PSS: optical plankton counter, CTD, and fluorometer mounted on V-fin) [*Ruberg et al.*, 2001] and from water samples and net tows taken on stations located along the transects in plume and nonplume areas and during plume and nonplume periods. Observations during nonplume periods were designed to serve as controls for plume observations. Some of these observations provided data for a modeling effort that described influences of suspended sediments on the ecosystem [*Ji et al.*, 2002; *Chen et al.*, 2004a, 2004b] and for investigations of plume impacts on bacterial production [*Cotner*, 2000], the microbial food web [*Cotner*, 2000; *Biddanda and Cotner*, 2002] (also P. J. Lavrentyev et al., Microzooplankton response to mesoscale episodic events in Lake Michigan, unpublished manuscript, 2007) (hereinafter referred to as Lavrentyev et al., unpublished manuscript, 2007), and phytoplankton [*Millie et al.*, 2002, 2003]. Consistent with EEGLE hypotheses, earlier reported impacts of the plume have been the injection of dissolved organic carbon (DOC) and particulate organic carbon (POC) that have stimulated heterotrophic production and the microbial food web growth [*Cotner*, 2000; *Biddanda and Cotner*, 2002; Lavrentyev et al., unpublished manuscript, 2007] and resuspended sediments that decreased light intensity and thereby limited phytoplankton growth [*Millie et al.*, 2002, 2003]. Most of these studies were limited to the eastern side of the basin and focused in the St. Joseph region, where offshore transport was expected. Our basin-wide observations are particularly relevant because there is the potential confounding influence of river input, particularly at St. Joseph. Impacts of river influence were never explicitly explored to any great detail in EEGLE. Our results are also relevant because none of the up-to-date finescale observations made with the PSS have been reported or used in ecosystem models. Likewise, basin-wide spatial distribution of P (the limiting nutrient) and the factors that regulate it have not been reported. Furthermore, our observations include the sediment plume of April 2000 (Figure 1), which had not been examined by other studies. This plume was unique in our current knowledge in that it occurred during the spring thermal bar as opposed to plumes occurring during winter conditions. Here we place the effects of the plume in the larger context of the winter and spring thermal fronts.

[4] Other major goals of our team were to evaluate the impact of the plume on copepod feeding [*Bundy et al.*, 2005], which in turn affects reproduction and survival of larval stages, and to determine grazing mortality induced by zooplankton on phytoplankton and microzooplankton. The winter-spring transition is an important time for copepod reproduction, and any impact of the plume on phytoplankton or microzooplankton would impact reproduction of copepods during this period, when food is limiting [*Vanderploeg et al.*, 1992a, 1992b]. Specifically, we were interested in the question: Does the plume and other physical forces affect copepod spatial distribution and the spatial distribution and abundance of its food resources? *Bundy et al.* [2005] did a number of feeding experiments with zooplankton and their phytoplankton and microzooplankton prey on different EEGLE cruises, and they extrapolated results from these experiments to lake-wide implications based on fragmentary information on abundance of zooplankton and prey abundance. Using updated information presented in this paper, we reexamine lake-wide implications.

[5] In this paper, we document the finescale anatomy of the plume and spatial distribution of physical variables, nutrients and plankton associated with the plume, and we deduce from these distributions the impact of the plume on plankton. Further, we compare our detailed observations with predictions from a nutrient-phytoplankton-and zooplankton model to get further insights into the strengths and weakness of EEGLE assumptions and modeling.

2. Methods

2.1. Cruise Schedule

[6] To test EEGLE hypotheses and generally explore consequences of the plume, a schedule of cruises was designed to capture conditions before, during, and after the plume by conducting a "plume" cruise during early March, a "preplume" cruise in late January/early February, and a "postplume" cruise(s) in April for the study years 1998–2000. Within these broad sampling periods, cruise initiation was responsive to weather forecasts and conditions to best capture an event, and yet at the same time, ship operations were limited to periods in which wave height was <2 m. During the pilot year 1998, only preplume and plume cruises were made. Our design included transects, moving counterclockwise in Figure 1, at Racine (showing stations with the letter designation R followed by a number for depth), Chicago (C), Gary (G), New Buffalo (NB), St. Joseph (J), and Muskegon (M) (Figure 1). This design was related to the general cyclonic longshore circulation of the southern basin that would be interrupted by a storm to create a two-gyre offshore flow with offshore transport of plume material in the region near St. Joseph [*Beletsky et al.*, 1999a, 1999b]. Thus a special effort was focused on the St. Joseph transect (Figure 1), and the Muskegon transect served as a control, since it was generally outside of the plume region on the eastern side of the basin. Transects were long enough (typically 20–30 km) to contrast nearshore plume impacted areas with offshore areas not impacted by the plume (Figure 1). Transects were sampled during all time periods whether or not there was a plume, and these nonplume cruises served as explicit controls for plume periods. On some cruises, as time allowed, we surveyed along the deep water station (DWS) transect line between stations DWS1 and DWS2 near the deepest part of

the southern basin to make sure we had a control area completely uninfluenced by the plume (Figure 1). During the event of April 2000, aircraft overflight aided in location of transects through the offshore feature (Figure 1d).

2.2. Sampling on Transects

[7] PSS tows on the transects were closely matched to discrete water bottle sampling for TSM, nutrients, chlorophyll, microzooplankton and vertical net tows for zooplankton. Typically PSS and discrete sampling followed this sequence: discrete sampling at one transect endpoint station, PSS tow from end point to midpoint station, discrete sampling, PSS tow from midpoint to other endpoint station, and discrete sampling. Water samples were collected by Niskin bottles from 2–4 depths at each station to obtain a view of vertical structure. On a few occasions, several stations along a transect were sampled after a PSS tow was first made.

2.3. Visualizing Plume Strength and Timing

[8] To help put the cruises in the temporal and physical context of the plume events and wind forcing, we report time series of backscatter from a 300 kHz acoustic Doppler current profiler (ADCP) and thermistor moored at the 40 m depth located at A02 in Figure 1 and wind speed and direction at the meteorological station at St. Joseph, MI [*Miller et al.*, 2001, 2002] (Figure 2). This location was chosen because the St. Joseph region was the primary region of interest for most plume researchers, since as noted above offshore transport during events was expected in this region. The meteorological observations there may be considered representative of the whole southern basin for major events, because the storm systems driving them are much larger than the size of the southern basin. *Miller et al.* [2001, 2002] showed that backscatter detected storm-generated particles, particularly large particles.

2.4. Chlorophyll, Chemical, and Physical Variables

2.4.1. Chlorophyll, Total Suspended Solids, and Particulate Organic Carbon

[9] Chlorophyll *a* was used as a surrogate for phytoplankton abundance. Phytoplankton species composition was not determined on our cruises but was determined on other cruises and reported elsewhere [*Millie et al.*, 2002, 2003]. Chlorophyll *a* (Chl) was determined by filtering 200 mL of water through Whatman GF/F filters, extracting the filters in N, N-dimethylformamide, and analyzing the extract fluorometrically [*Speziale et al.*, 1984]. Total suspended matter (TSM) was determined gravimetrically by filtering between 100 and 2,000 mL of lake water through preweighed Whatman GF/C 47-mm filters, and weighing the filters after drying at 60°C for at least 48 hours. Water (200 mL) for particulate organic carbon (POC) analysis was filtered onto precombusted GF/F 25-mm filters and analyzed on a CHN analyzer. Measurements of all variables were made in duplicate, and precision between replicates was better than 5%.

2.4.2. Nutrients and Chloride

[10] Nutrients were analyzed on a Technicon AutoAnalyzer II using standard colorometric techniques [*American Public Health Association*, 1990]. Dissolved nutrients were determined on lake water samples that were filtered through a 0.2-μm Nucleopore filter. Ammonia concentration (NH_4) was determined by the Bertholet reaction. Phosphorus concentrations were determined by the molybdate/ascorbic acid method. Total phosphorus (TP) and total dissolved phosphorus (TDP) were determined after digesting 50 mL of unfiltered and filtered sample, respectively, with potassium persulfate in an autoclave for 30 min. [*Menzel and Corwin*, 1965]. Nitrate + nitrite, hereafter known as nitrate (NO_3), was determined using the cadmium reduction method. Chloride concentrations were determined by the mercuric thiocyanide/ferric ammonium sulfate method. All nutrient measurements were made in duplicate, and precision between replicates was better than 5%.

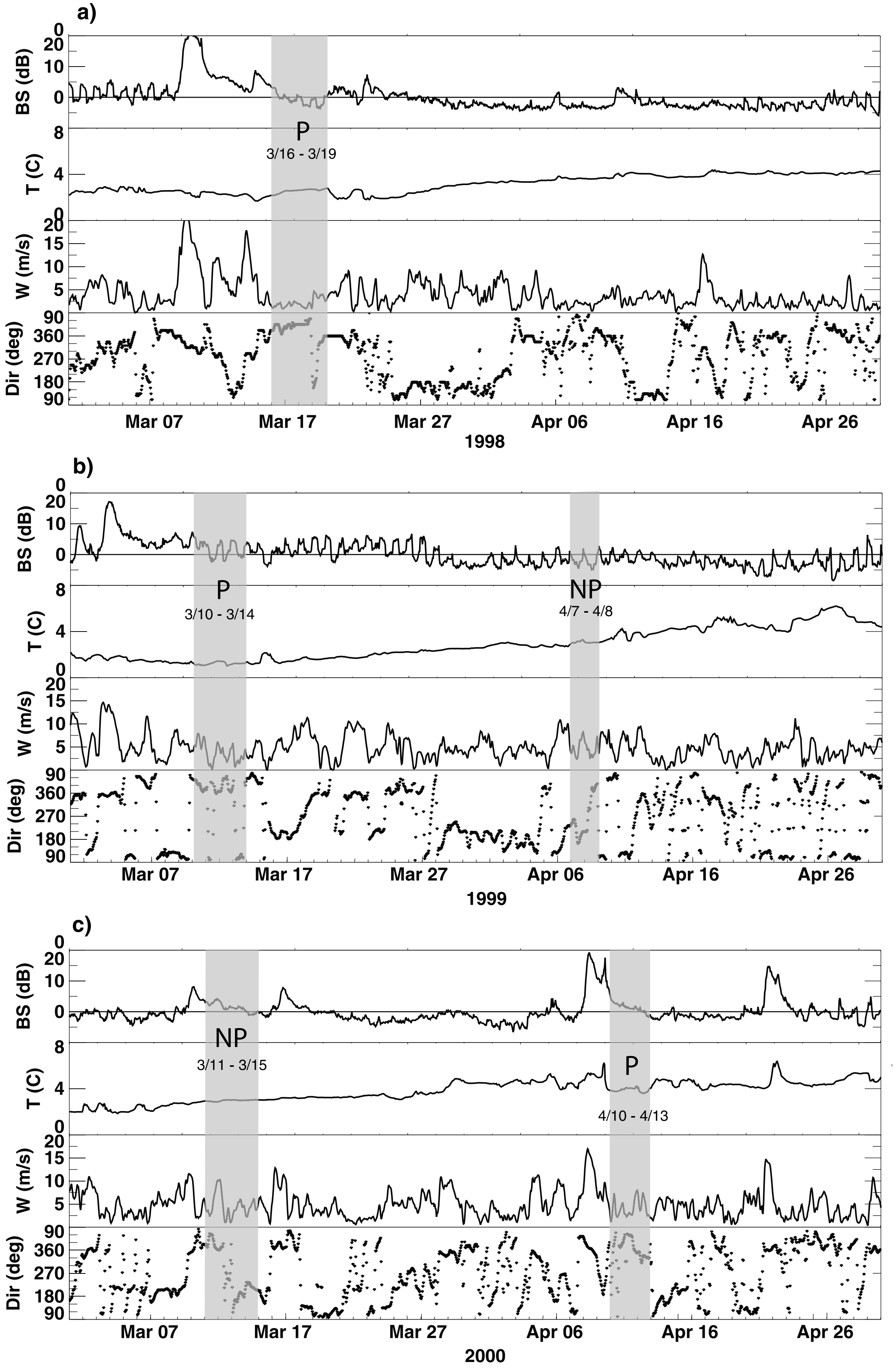
[11] We used chloride concentration as a conservative tracer of river influence, as chloride concentrations are much higher in rivers than the open lake. The magnitude of the proportion of river water contribution to a water sample was estimated by $CLDIFF = Cl_x - Cl_o$, where Cl_x is chloride concentration in the lake water sample, and Cl_o is chloride concentration in offshore water, i.e., the chloride concentration on given cruise for the station farthest offshore. High values of *CLDIFF* indicate strong riverine influence.

2.5. Plankton Survey System (PSS)

[12] The PSS consisted of a mini optical plankton counter (OPC; Model 2T, Focal Technologies, Dartmouth, NS), an Aquatracka III fluorometer (which has 4 decade logarithmic amplifiers, Chelsea Technology Group, Surrey, UK), and OS200 CTD (Ocean Sciences, San Diego, CA) mounted on a V-fin [*Ruberg et al.*, 2001] that was continuously raised or lowered at 0.25 m s^{-1} between 1 and 2 m of the bottom and surface as the boat moved at 2.5 m s^{-1} to create a sinusoidal path along the transects (see Figures 3–6, middle). The PSS mapped out temperature, chlorophyll fluorescence, number and biomass of zooplankton sized particles (>0.25 mm equivalent spherical diameter using the standard software for conversion of size categories to equivalent volume of spheres), and light attenuance (LA). The LA meter on the OPC is analogous to a 10-cm path length transmissometer, with the output of the LA meter being proportional to the voltage applied to red laser diodes to maintain a constant intensity at the receiver of the OPC.

[13] The fluorometer and LA meter were calibrated to convert the profiles of fluorescence and LA to predicted chlorophyll *a* and total suspended material (TSM) (Table 1). PSS results were matched with water samples collected at various depths at the end points or points along transect paths immediately before or after towing the PSS. Linear regressions were developed from extracted chlorophyll *a* and antilog of PSS fluorometer volts for each cruise.

Figure 2. The physical and temporal context of the March and April cruises in (a) 1998, (b) 1999, and (c) 2000 revealed by acoustic backscatter (BS) and temperature (T) on the ADCP at A02 and wind speed (W) and direction measured at the meteorological station at St. Joseph, Michigan. Shaded areas indicate cruise periods. N and NP designate plume and nonplume cruises, respectively.


a)
BS (dB)
0
20
10
0
8
T (C)
4
0
W (m/s)
20
15
10
5
Dir (deg)
90
360
270
180
90
P
3/16 - 3/19
Mar 07
Mar 17
Mar 27
Apr 06
Apr 16
Apr 26
1998
b)
BS (dB)
0
20
10
0
8
T (C)
4
0
W (m/s)
20
15
10
5
Dir (deg)
90
360
270
180
90
P
3/10 - 3/14
NP
4/7 - 4/8
Mar 07
Mar 17
Mar 27
Apr 06
Apr 16
Apr 26
1999
c)
BS (dB)
0
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W (m/s)
20
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3/11 - 3/15
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Mar 07
Mar 17
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Apr 06
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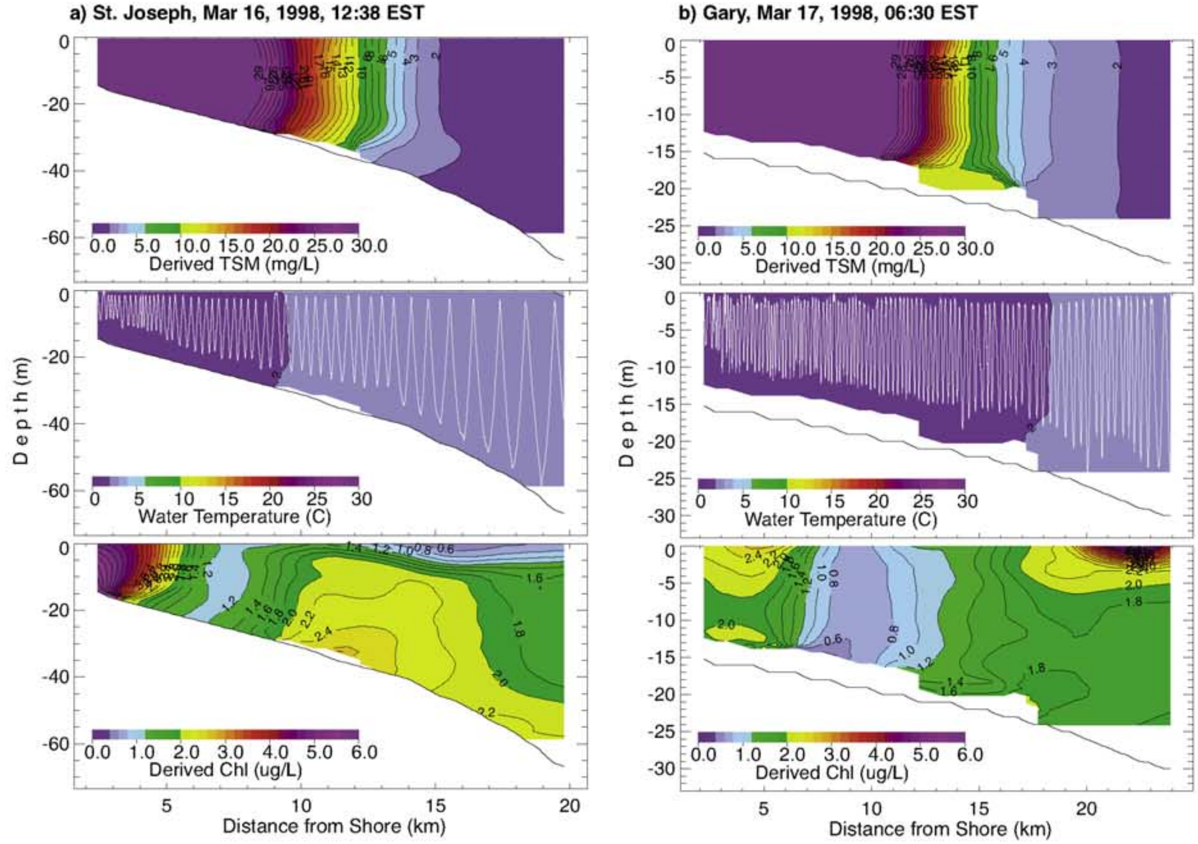
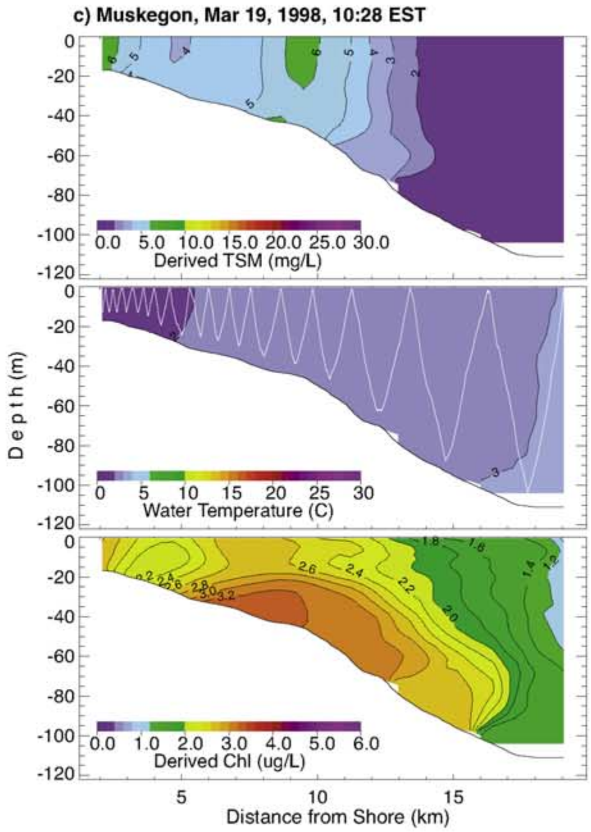
Apr 26
2000

Figure 2



a) St. Joseph, Mar 16, 1998, 12:38 EST

b) Gary, Mar 17, 1998, 06:30 EST

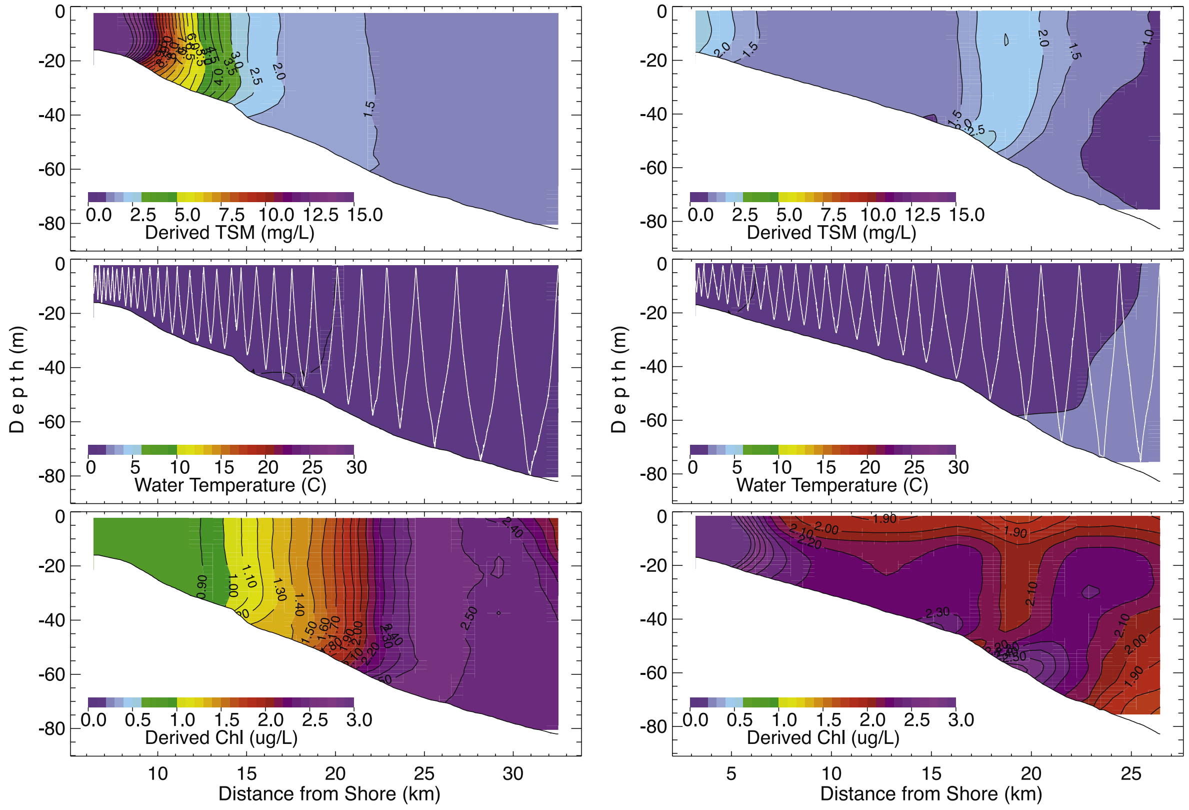


c) Muskegon, Mar 19, 1998, 10:28 EST

Figure 3. Plume event of March 1998: plots of total suspended matter (TSM), water temperature, and derived chlorophyll *a* along transects sampled by the plankton survey system (PSS). The sinusoidal trace on the water temperature panel shows the path of the PSS. Time shown is time at the midpoint of the transect. Refer to Figure 1 for transect locations.

a) Chicago, Mar 11, 1999, 05:29 EST

b) St. Joseph, Mar 12, 1999, 21:22 EST



c) Gary, Mar 13, 1999, 06:32 EST

d) Muskegon, Mar 14, 1999, 09:10 EST

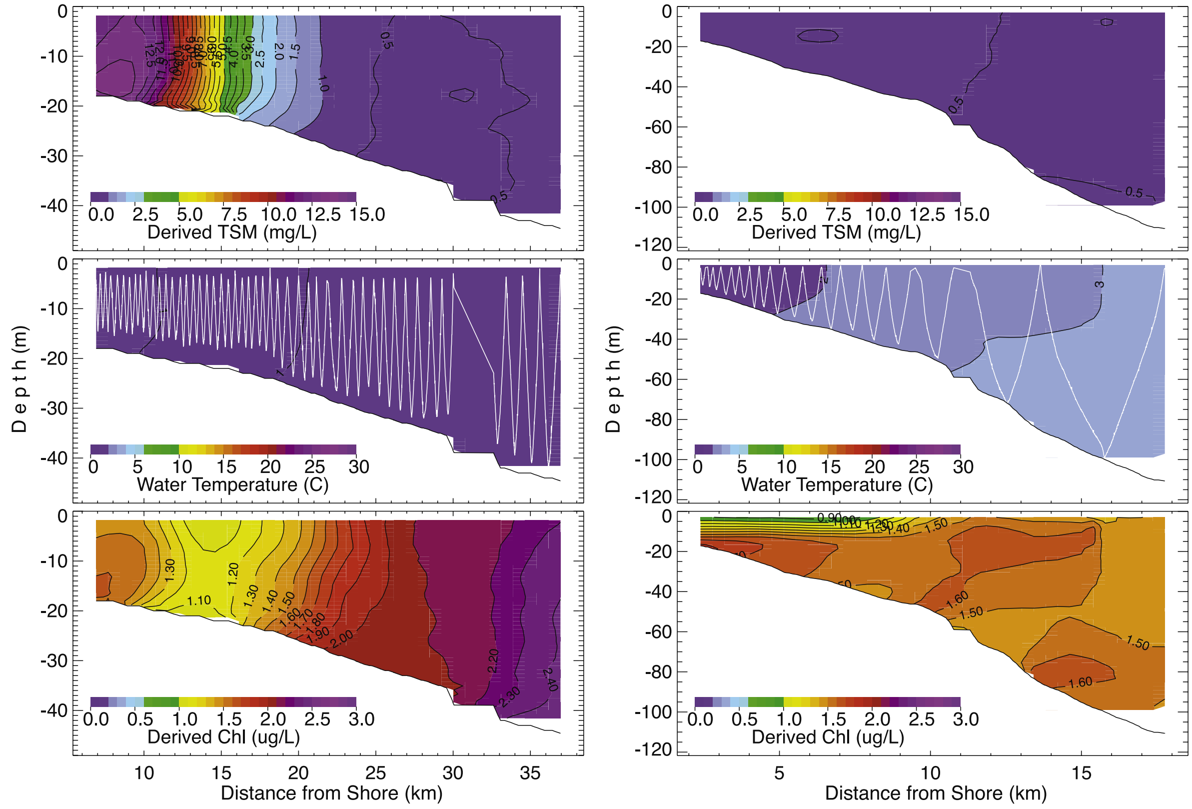


Figure 4. Plume event of March 1999: plots of total suspended matter (TSM), water temperature, and derived chlorophyll *a* along transects sampled by the plankton survey system (PSS). The sinusoidal trace on the water temperature plot shows the path of the PSS. Time shown is time at the midpoint of the transect. Note that scale on chlorophyll is different from that in Figure 3.

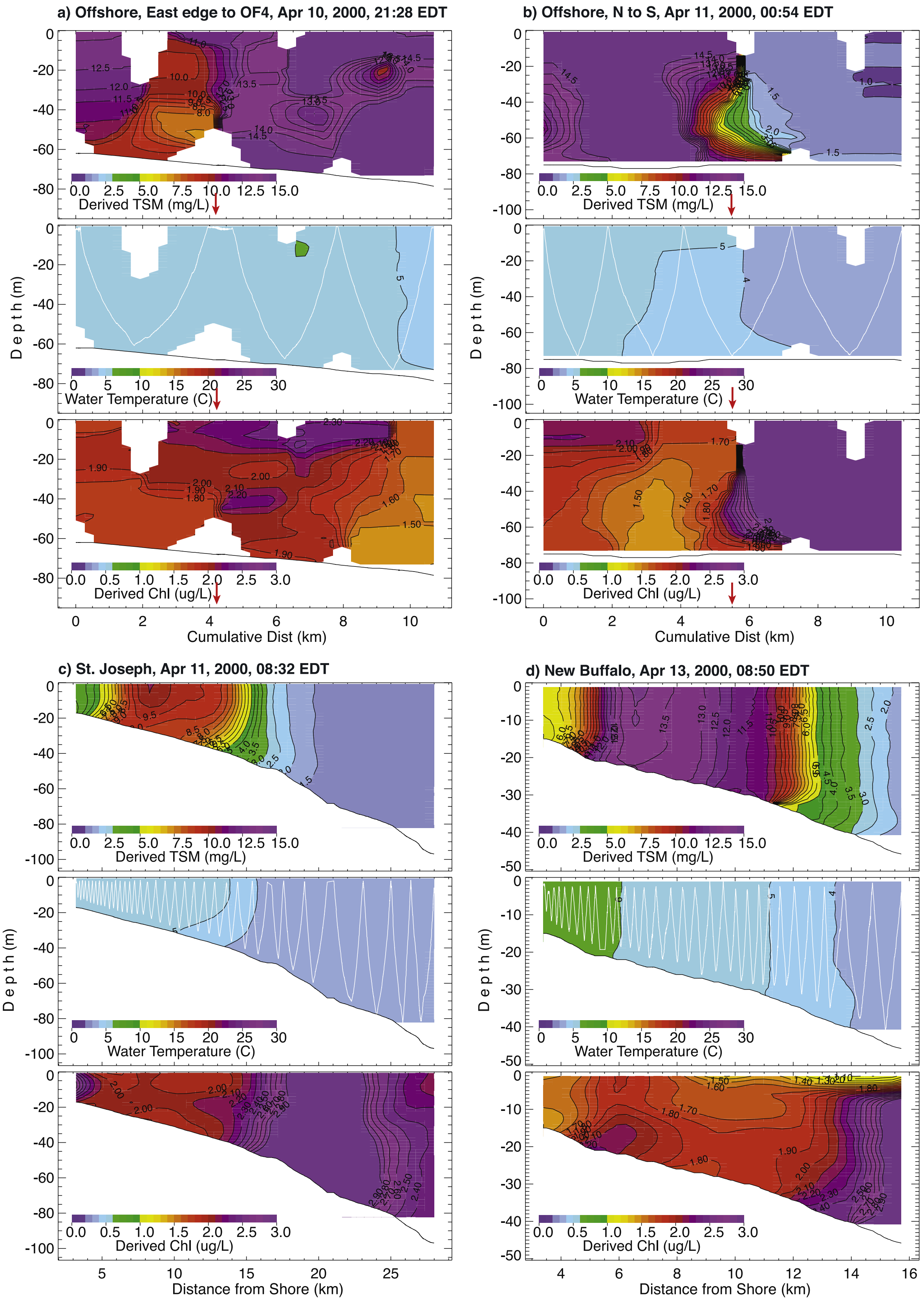


Figure 5. Plume event of April 2000: plots of total suspended matter (TSM), water temperature, and derived chlorophyll *a* along transects sampled by the plankton survey system (PSS). The sinusoidal trace on the water temperature plot shows the path of the PSS. Time shown is time at the midpoint of the transect. The arrows on the cumulative distance axis on the transects in Figures 5a and 5b show the locations, respectively, of OF3 and OF5. Refer to Figure 1 for transect locations.

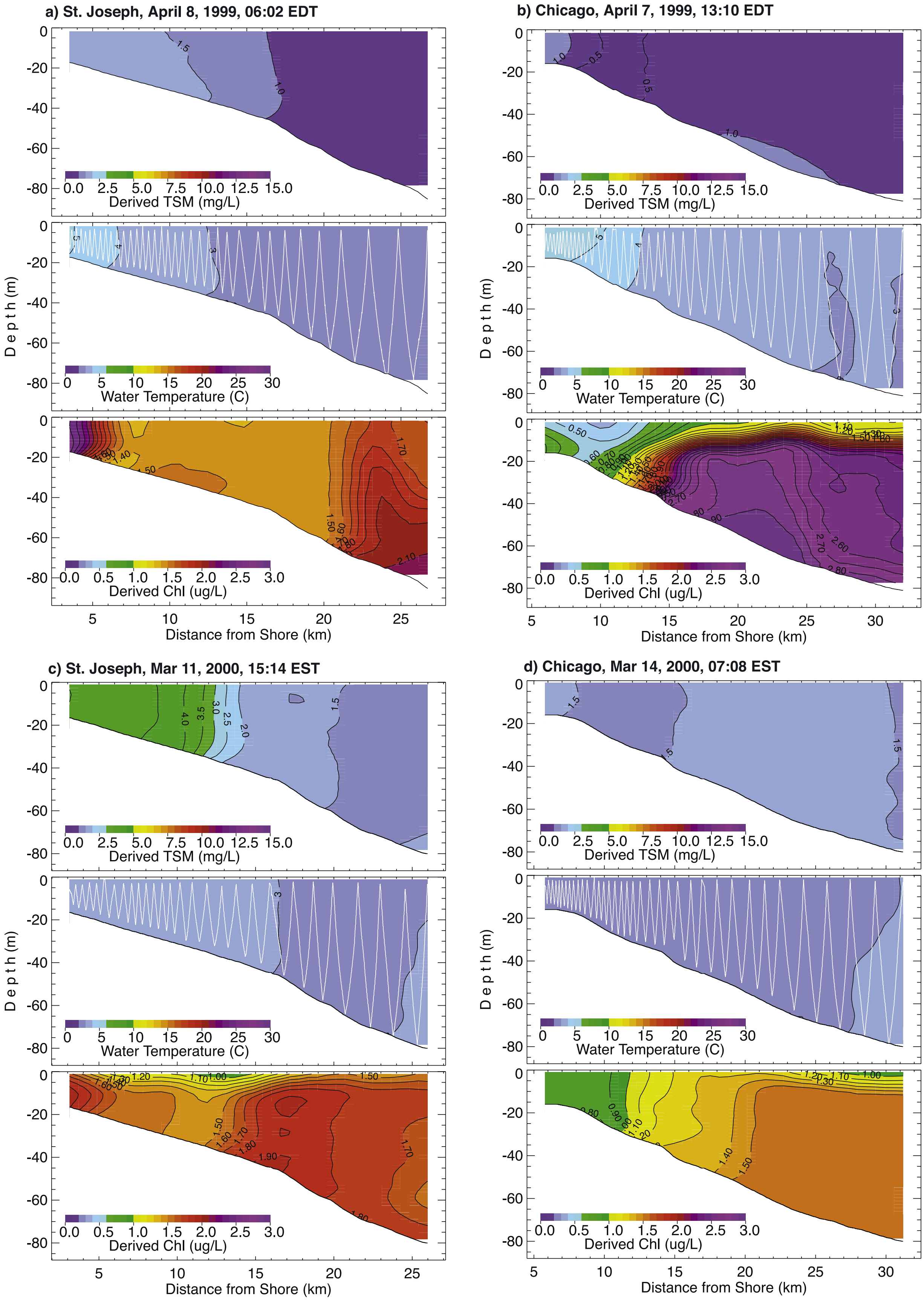


Figure 6. Nonplume PSS transects: cross shelf transects in nonplume periods showing plots of derived total suspended matter (TSM), water temperature, and derived chlorophyll *a* on St. Joseph and Chicago transects in (a, b) early April 1999 and (c, d) early March 2000.

Table 1. PSS Sensor Calibrations[a]

Regression	N	$a \pm SE$	$b \pm SE$	R^2
TSM on ln LA				
January–March 1998	75	−183.959 ± 5.688	38.889 ± 1.171	0.937
February–April 1999	134	−203.053 ± 6.068	43.597 ± 1.287	0.901
February–April 2000	104	−142.769 ± 3.247	30.514 ± 0.680	0.951
Chl on Antilog F				
March 1998	11	−0.772 ± 0.298	0.077 ± 0.007	0.925
All except March 1998	262	0.137 ± 0.051	0.030 ± 0.001	0.808
k_{PAR} on TSM				
January 1998 to April 2000	47	0.107 ± 0.016	0.076 ± 0.002	0.974

[a]Coefficients of linear regressions ($Y = a + bX$) relating total suspended matter (TSM, mg·L^{-1}) to light attenuance (LA, unitless) of optical plankton counter; chlorophyll *a* concentration (Chl, μg·L^{-1}) to fluorescence (F, V); and relation between diffuse attenuation coefficient of photosynthetically active radiation (k_{PAR}, m^{-1}) and TSM for cruises during the winter-spring transition (January–April) in 1998–2000. All regressions are significant at $P < 0.001$ level.

Regressions were also done for combined cruises for different time periods (i.e., preplume, plume, and post-plume) among years to derive a set of as few regressions possible to adequately characterize the chlorophyll *a* versus fluorescence response.

[14] Nonphotochemical quenching (NPQ) associated with photoinhibition of photosynthesis during daylight hours of high incident radiation (~09:00–16:00 EST) reduced the fluorescence response per unit chlorophyll in surface waters (<10 m deep) [*Kiefer*, 1973; *Morrison* 2003]. To account for this artifact, surface data exhibiting NPQ (low values relative to those for deeper water at the same site) were removed. The quenching response was not seen within the plume because of high light attenuation by suspended sediments. Individual cruises and combined cruises for different time periods (January–February, March, early April, late April) generally gave similar Chl-fluorescence regressions with a slope of ~0.03. Data from the March 1998 cruise following the most intense storm event we observed yielded a slope of 0.077. Therefore we used one regression for March 1998 (R^2 = 0.92) and another for all other results (R^2 = 0.81; Table 1). The high slope of the March 1998 data may have been a result of poor physiological health of the phytoplankton on this cruise (see section 3). Note that the predicted chlorophyll values from the regression equations can be an underestimate of measured chlorophyll *a* for surface samples for midday runs of the PSS.

[15] We calibrated the LA meter by conducting linear regression analyses of TSM versus ln LA (Table 1). A separate regression was determined for the winter-spring transition for each of the different years, in part, because we replaced the standard laser diodes of the OPC by high-intensity diodes after first year [*Ruberg et al.*, 2001], possibly causing a change in responsiveness of the LA meter. Excellent regressions (R^2 > 0.9) were obtained in all cases.

[16] We do not report results from OPC to map out zooplankton biomass during plume events, but do report representative results during nonplume periods. During the plume event of March 1998, the plume was so turbid that the intensity of the collimated beam at the OPC receiver dropped below the threshold necessary to detect zooplankton. This problem was corrected before the next field season by increasing laser diode intensity by a factor of 9.3; however, the OPC detected much more biomass than net tows, because the OPC detected storm-suspended debris and particle aggregates in addition to zooplankton [*Liebig et al.*, 2006].

2.6. Light Climate Along Transects

[17] The diffuse attenuation coefficient (k_{PAR}) of photosynthetically active radiation (PAR) is proportional to TSM in estuaries [*Cloern*, 1987]. To map out continuous spatial distribution of k_{PAR} using the PSS along transects (Figure 7), we converted OPC LA readings to TSM readings, and converted TSM to k_{PAR} using a regression between k_{PAR} and TSM (R^2 = 0.97; Table 1) from our and other EEGLE cruises; k_{PAR} was determined from vertical profiles of PAR [e.g., *Wetzel*, 2001] measured by a Biospherical Instruments (San Diego, CA) PAR sensor. We did not use the direct approach of developing a regression between k_{PAR} and LA because we were unable to make simultaneous measurements of PAR and LA on some of our cruises.

[18] We used k_{PAR} to estimate photic depth for algal photosynthesis (Z_p), assuming Z_p is the depth of 1% surface irradiance (i.e., $Z_p = 4.61/k_{PAR}$), and used it to map out along the transects the photic depth/mixing depth ratio [*Sverdrup*, 1953; *Cloern*, 1987]: Z_p/Z_m, where Z_m is mixing depth, which in our case of isothermal conditions is water depth. Low values (<0.2) of Z_p/Z_m have been used to indicate areas where downward mixing prevents significant algal growth by mixing algae below the photic zone, while high values (~1) indicate potential areas of bloom formation in coastal or estuarine environments [*Sverdrup*, 1953; *Cloern*, 1987; *Fahnenstiel et al.*, 2000]. Continuous estimates of Z_p/Z_m along transects (Figure 7) were obtained from predicted k_{PAR} and from water depths available for all locations on transects. We also generated continuous estimates of the ratio $\overline{I_m}/I_0$, the mean irradiance in the mixed water column ($\overline{I_m}$) relative to surface irradiance (I_0) from Z_p/Z_m values [e.g., *Fahnenstiel et al.*, 2000]. For low values (<1.3) of Z_p/Z_m, as those seen in our study, $\overline{I_m}/I_0 = 0.217\ (Z_p/Z_m)$ to close approximation; thus traces in Z_p/Z_m and $\overline{I_m}/I_0$ parallel each other (Figure 7).

2.7. Microzooplankton and Zooplankton Abundance

2.7.1. Microzooplankton (Protozoa)

[19] Microzooplankton (MZ) samples were collected from 2 to 4 discrete depths at each station. Since MZ vertical distribution was nearly uniform on all sampling occasions, here we present water column averaged data. Microzooplankton biomass was determined by methods

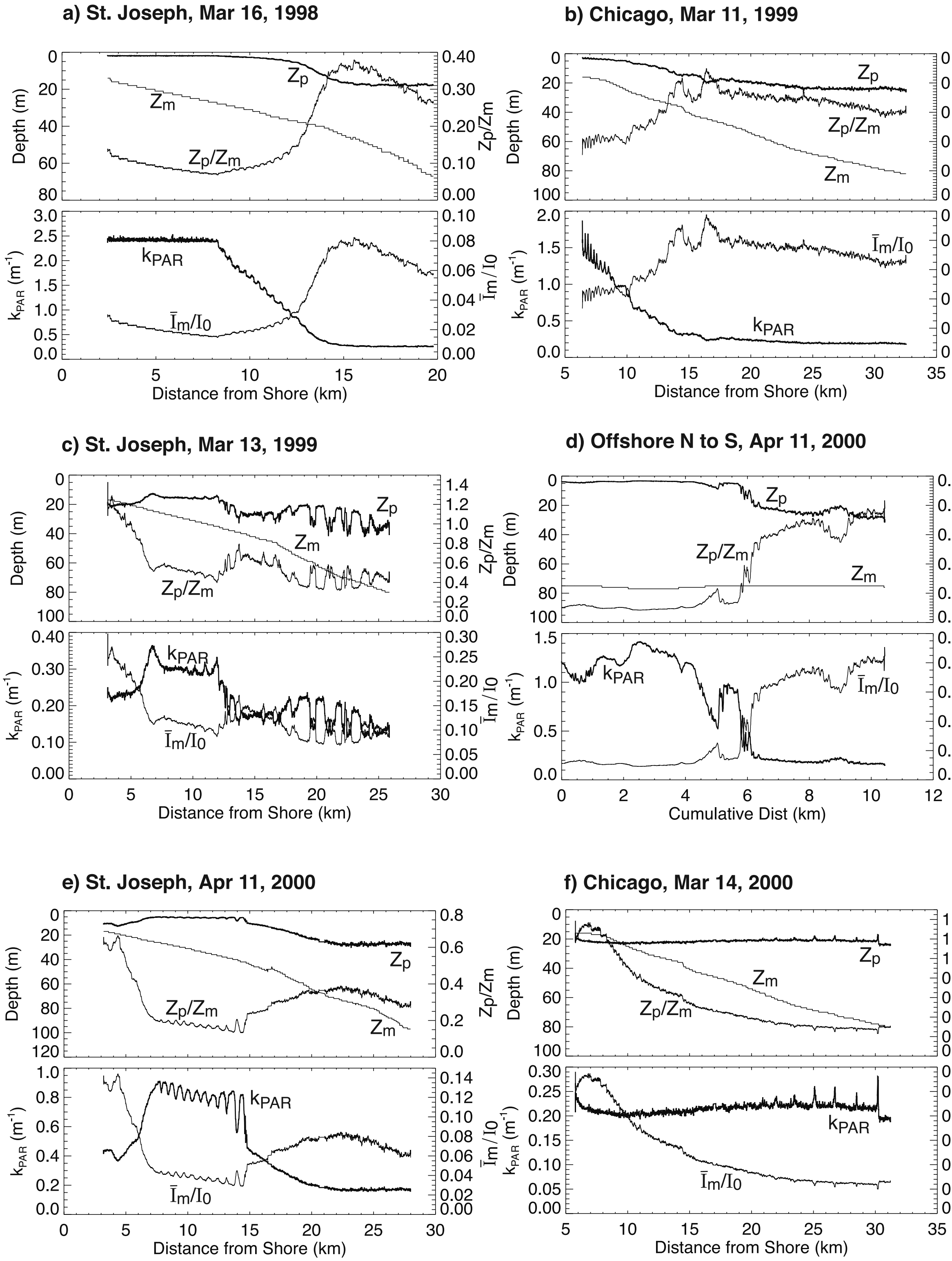

a) St. Joseph, Mar 16, 1998
b) Chicago, Mar 11, 1999
c) St. Joseph, Mar 13, 1999
d) Offshore N to S, Apr 11, 2000
e) St. Joseph, Apr 11, 2000
f) Chicago, Mar 14, 2000

Figure 7. Examples of k_{PAR}, photic depth (Z_p), mixing depth (Z_m), Z_p/Z_m, and $\overline{I_m}/I_0$, the ratio of average water column irradiance ($\overline{I_m}$) to surface irradiance (I_0) along transects for (a–e) plume and (f) nonplume cruises. Refer to Figures 3a, 4a, 4b, 5b, 5c, and 6d for respective transects showing TSM, temperature, and chlorophyll *a*.

described elsewhere [*Gardner et al.*, 2004]. Briefly, cells preserved with Lugol's iodine (final concentration 1%) were counted and their linear dimensions measured in 20–50 mL settling chambers under an Olympus IX-70 inverted differential interference contrast microscope. Heterotrophic dinoflagellate and ciliate cell volumes were converted to carbon following *Menden-Deuer and Lessard* [2000] and *Putt and Stoecker* [1989], respectively.

2.7.2. Zooplankton (Crustacea)

[20] Mesozooplankton, hereafter called zooplankton (Z) were collected at each site with a 50-cm-diameter, 2.5-m-long, 153-μm mesh, conical net equipped with an internal calibrated TSK flow meter (Model 005WA200, KAHL Scientific Instrument Corporation, El Cajon, CA). The net was hauled vertically through the water column at a speed of 0.5 m s^{-1} from 2 m above the bottom to the surface. Zooplankton were narcotized with Alka-Seltzer and preserved in 2–4% sugar formalin solution [*Haney and Hall*, 1973]. In the laboratory, subsamples were taken with a Stemple pipette until 600 individuals were identified. All cladocerans and adult copepods were identified to species, immature copepodites to genus, and nauplii combined into one group using the keys of *Wilson and Yeatman* [1959] and *Brooks* [1959]. Zooplankton counts from subsamples were converted to individuals per cubic meter using information on volume subsampled and tow length given by the flow meter; precision ($SE/\overline{X}$) between replicate tows averaged 7%. Zooplankton biomass was estimated from lengths using published length-weight regressions [*Culver et al.*, 1985; *Malley et al.*, 1989]. A subsample of 10 individual adult male and female copepods and 25 individual nauplii, copepodites, and cladocerans were measured using Image-Pro Plus (Media Cybernetics, Silver Spring, Maryland) video imaging software to determine an average dry weight for each taxon. We applied average taxon specific dry weight from Station J45 determined on each cruise to all stations, as there was little variation among sites. To express results in terms of carbon for comparison with microzooplankton data, we converted dry weight given by the regressions to carbon by multiplying by 0.45 [*Parsons et al.*, 1984].

3. Results

3.1. Overview of Cruises

[21] During the three years of study we observed a large storm-induced plume in early March 1998, a small plume in early March 1999, and a moderate to large plume in early April 2000 (Figures 1 and 2). The plumes in 1998 and 1999 occurred during the winter thermal front (colder water inshore), and the April 2000 plume occurred during the spring thermal front (warmer water inshore). Thus we had two plumes of different spatial extent at the time of the winter front (<4°C water inshore) in 1998 (Figure 2a) and 1999 (Figure 2b) along with a “control”, or “nonplume”, period in March 2000, when no plume occurred because of low or moderate winds (Figure 2c). Results from the relatively calm nonplume conditions (Figure 2b) of the April 1999 (post-plume) cruise served as a control period for the “surprise” plume of April 2000. Although we have data from all preplume cruises in 1998, 1999, and 2000, much of our attention will be focused on transects made during the relatively narrow time period of March and April, which had both plume and “nonplume” conditions. Therefore we grouped data into plume and nonplume periods to emphasize contrasts that would lead to generalizations of plume impacts.

3.2. The 1998 Plume Cruise

3.2.1. Physical Environment and PSS Tows

[22] The plume of March 1998 was the most intense (high TSM, high reflectivity) and extensive (spatial coverage) plume observed during the study period (Figures 1 and 2). On 9 March, winds and acoustic backscatter were >20 m s^{-1} and >20 dB at A02 and the meteorological station at St. Joseph. A second peak in winds (17 m s^{-1}) and backscatter (~9 dB) occurred 2 days before start of the cruise (Figure 2a). The plume cruise of 16–19 March 1998 followed one week after the peak of the storm as indicated by the peak in backscatter (Figure 2a). Thus the plume was intense and one week old before the cruise started, but sediment resuspension was likely refreshed 2 days before the cruise.

[23] Extremely high TSM concentrations (>30 mg L^{-1}) were seen within the 30 m depth contour of plume-impacted regions of the St. Joseph and Gary transects (Figures 3a and 3b, top). The plume at the time we sampled was composed largely of inorganic sediment (silts and clays) based on the estimated weight contribution of the organic component (estimated as 2 × POC concentration) of TSM, which varied between 4–7% for stations C10, G10, and J10. The plume region was also a region of very high light extinction (k_{PAR} = 2.5 m^{-1}) compared to offshore water (k_{PAR} < 0.4 m^{-1}) (Figure 7a). Photic depth in the plume region was ~1 m, and Z_p/Z_m and <0.1 in the plume, even in shallow water, and $\overline{I_m}/I_0$ was ~0.02. This plume region was also colder (<2°C) than offshore water. Chlorophyll *a* (Chl) concentration was extremely high in shallow water near St. Joseph, but decreased with distance offshore within the plume, and then increased outside of the plume region. The maximum Chl concentration seen here was about twice Chl concentration seen in other years (see below). The high slope of the Chl versus fluorescence regression for this cruise (Table 1) may indicate the phytoplankton were in poor physiological health at the time of sampling. At Gary there was no Chl maximum inshore and, as on the St. Joseph transect, there was a Chl minimum at the inside edge of the plume. On the Muskegon transect there was very little TSM, and Chl was relatively uniform until about 12 km, after which it decreased with distance offshore (Figure 3c).

[24] Although lake surface conditions were too rough to deploy the PSS along the Chicago transect, we collected water samples that gave us point estimates of TSM and Chl along this transect (Figure 1). TSM was moderately high and Chl low inshore: Concentrations of TSM were 11.6, 1.0, and 2.8 mg L^{-1}, and Chl were 0.36, 0.75, and 1.50 μg L^{-1}, respectively, at C10, C30, and C45.

3.2.2. Nutrients, Microzooplankton (MZ), and Zooplankton (Z)

[25] Nutrients, MZ and Z varied with distance offshore, side (west or east) of basin, river input, and plume presence (Figures 8a–8d). High chloride at the shallow site on the St. Joseph transect suggests Chl may have been influenced by the St. Joseph River (Figure 8b), the major tributary of the southern portion of the basin. Extremely high total phosphorus (TP) (38–48 μg L^{-1}) found in the inshore (J10, G10) plume sites (Figures 8b and 8c), where total suspended solids (TSM) were high (Figure 3a). Dissolved phosphorus (DP) was a small fraction of TP and there was not much variation among stations whether in the plume or not. Likewise nutrients may have been somewhat influenced by river influence. MZ concentrations were slightly higher in inshore plume region at St. Joseph, but lower in inshore regions of the Chicago and Gary transects. Z concentrations were higher inshore than offshore on the

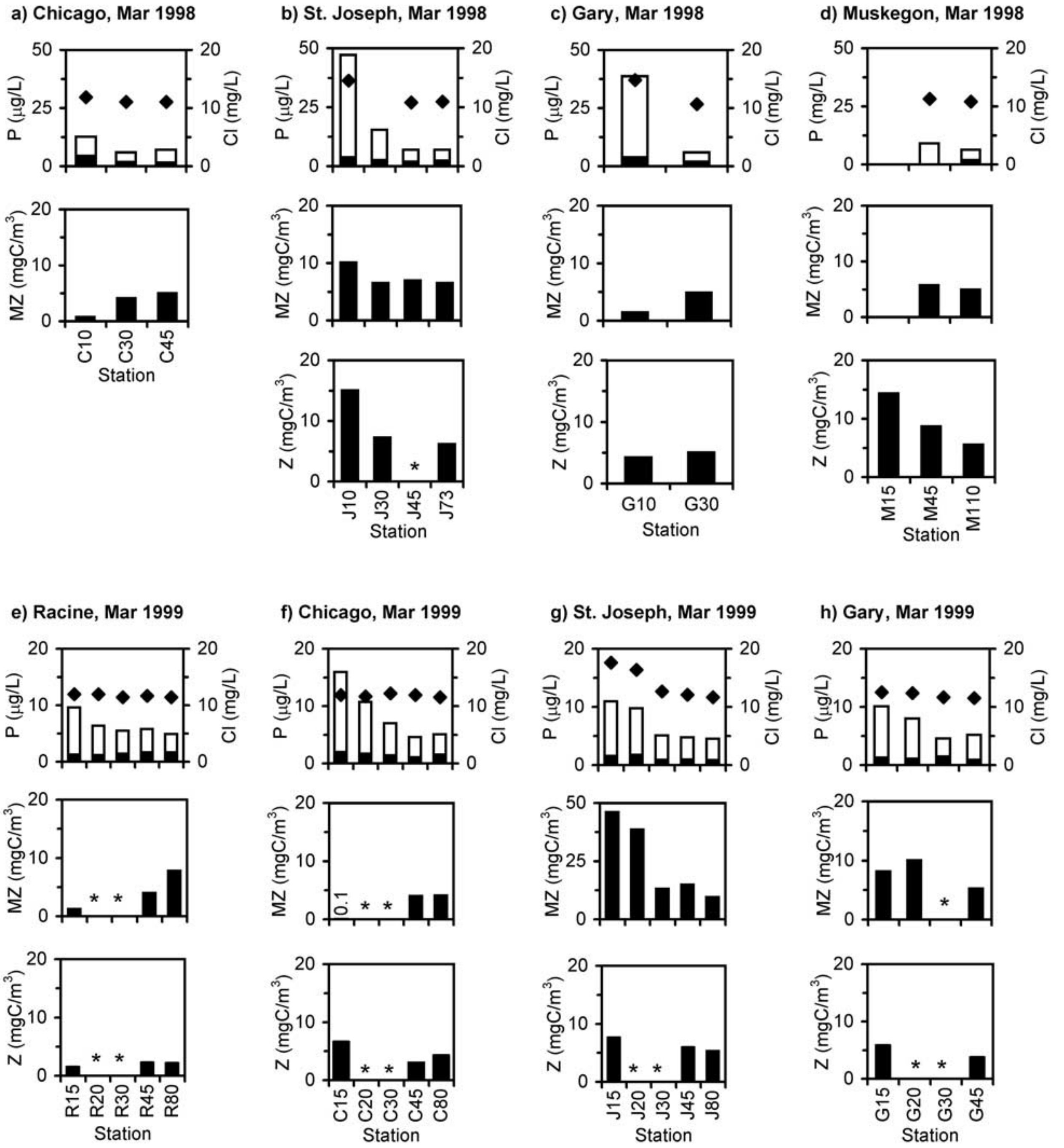


Figure 8. Chloride (Cl; diamonds, top plots), P as total dissolved P (dark part of histogram), and total P (total length of histogram), microzooplankton (MZ), and zooplankton (Z) concentrations on transects during plume cruises. Asterisks on graphs indicate data gaps.

Muskegon transects, whereas the Gary transect had low values inshore (G10) and offshore (G30).

3.3. 1999 Plume Cruise

3.3.1. Physical Environment and PSS Tows

[26] The March 1999 plume was less intense and extensive than that of 1998, and most of the impacted area was restricted to the SW part of the basin (Figure 1b). Southwestward wind of about 7–15 m s^{-1} generally prevailed over southern Lake Michigan on 2–9 March (Figure 2b). The regular 1-day oscillations in backscatter following this peak (Figure 2b) are probably caused by large vertically migrating zooplankton, probably *Mysis* [*Miller et al.*, 2001, 2002]. Elevated TSM was restricted to the <20-m contours (<10 km from shore) of the Chicago and Gary transects (Figures 1 and 4a and 4c). In nearshore waters of Chicago (Figure 7b), maximum k_{PAR} (1.5 m^{-1}) was much less, and minimum photic depth (2 m) and $\overline{I_m}/I_0$ (0.04) were somewhat greater than in the plume of 1998. In marked contrast to the plume of 1998, there was little TSM (<2 mg L^{-1}) along the

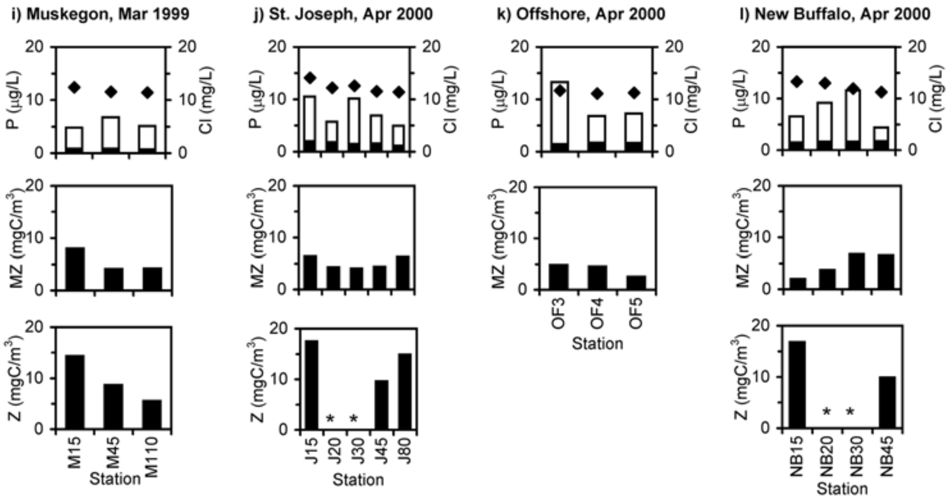


Figure 8. (continued)

St. Joseph transect (Figure 4b), and this was reflected in the relatively low k_{PAR} (~0.25 m^{-1}) and relatively great photic depth (~20 m) along the entire transect, including nearshore waters (Figure 7c). This was a colder year with cold water (2°C) extending farther offshore (St. Joseph = 25 km; Figure 4) than in 1998 (St. Joseph = 10 km; Figure 3). Very low Chl values were seen within the plume on the Chicago transect (Figure 4a). Low Chl values were seen within the plume region at Gary, particularly at the plume transition (Figure 4c). Highest Chl values were seen for the St. Joseph (Figure 4b) transect and the Racine transect (not shown, largely out of plume region: Figure 1), where Chl was uniform in concentration at ~2.4 μg L^{-1}. Chl values were moderate and relatively uniform along the Muskegon transect (Figure 4d). The low values of Chl seen at the surface on some of the midday transects are artifacts related to NPQ decreasing the response of the fluorometer.

3.3.2. Nutrients, Microzooplankton (MZ), and Zooplankton (Z)

[27] Overall nutrient concentrations were lower in the 1999 plume event. Elevated TP was found in the nearshore region on all transects (Figure 8e–8i), with the highest (16 μg L^{-1}) associated with high TSM at Chicago. Extremely high chloride concentrations at nearshore stations (J15, J20) of the St. Joseph transect (Figure 8g) indicated that there was a very strong influence of the St. Joseph River there. Extremely high MZ concentrations (38–45 μg L^{-1}) were found at these river-influenced stations. Slightly elevated values were seen in the nearshore of the Muskegon transect, also outside of plume influence. The Gary transect showed little effect of the plume, as nearshore stations were not much different from the offshore station. Z biomass was relatively constant across all transects.

3.4. 2000 Plume Cruise

3.4.1. Physical Environment and PSS Tows

[28] The April 2000 plume event was of intermediate intensity and extent compared to those of March 1998 and 1999. The plume is also of great interest in that there was strong offshore transport of water [*Rao et al.*, 2002] and suspended sediments, as seen from the satellite images of the plume event at the height of the storm and a few days later during our cruise (Figures 1c and 1d). Maximum winds and backscatter were 17 m s^{-1} and 19 dB (Figure 2c). This plume was the youngest examined in that the cruise was initiated <2 days after the maximum wind forcing and <1 day after the second major peak in backscatter at A02 (Figure 2c).

[29] Unlike the other events, elevated TSM was associated with warm water in April 2000. This feature is evident from the cross-isobath transects at St. Joseph (Figure 5c) and New Buffalo (Figure 5d), as well as in the offshore feature, particularly N to S transect (Figures 1d and 5b). In the latter case it is obvious that warm sediment-laden nearshore water was transported far offshore. Offshore transport is also evident from the location of the TSM maximum at intermediate rather than the shallowest depth contours along St. Joseph and New Buffalo transects (Figures 5c and 5d). In all cases, low Chl was associated with high TSM; note especially the Offshore N to S, St. Joseph, and New Buffalo transects (Figures 5b–5d).

[30] The complex spatial structure of TSM was reflected in light climate. In moving south through the offshore feature into unaffected offshore water, k_{PAR} changed from 1.4 to 0.2 m^{-1}, photic depth from 5 to 30 m, and $\overline{I_m}/I_0$ from 0.01 to 0.08 (Figure 7d).

3.4.2. Nutrients, Microzooplankton (MZ), and Zooplankton (Z)

[31] Like the other modest plume event (March 1999), nutrient concentrations, particularly TP, did not reach as high levels, and TP was strongly associated with TSM. Maximum TP was 13 μg L^{-1}at OF3 on the offshore transect in April 2000 (Figure 8k). The clear association of TP with TSM can be appreciated from the dome shaped pattern with station depth on the New Buffalo transect (Figure 8l) that matches up nicely with derived TSM plot in Figure 5d. Low or modest (2–7 μg C L^{-1}) MZ biomasses were seen at all stations (Figure 8j–8l), whether inside or outside of the plume (Figure 1d, Figure 5). Z biomass was relatively constant across the two (St. Joseph and Muskegon) transects sampled (Figure 8j and 8l).

3.5. "Nonplume" Cruises

3.5.1. Physical Environment and PSS Tows

[32] We show results of Chicago and St. Joseph transects as example nonplume cruise transects (Figure 6), since these

sites typically fell within the plume impacted area during plume cruises, were sampled on most cruises, and demonstrate differences between the eastern and western sides of the southern basin. The St. Joseph and Chicago transects for both April 1999 and March 2000 nonplume cruises show low TSM (Figure 6) as expected for these calm periods (Figures 2b and 2c), and temperature profiles (Figure 6) along the transects were generally similar to those taken in corresponding periods for plume cruises (Figures 3–5). On both cruises, Chl was relatively uniform with distance offshore of St. Joseph, although high nearshore values were seen in April 1999 (Figure 6a). On both cruises, low Chl was seen in the nearshore area at Chicago (Figures 6b and 6d). Except in nearshore regions, Chl varied between 1.5–2.5 μg L^{-1} in April 1999 and 1.4–1.7 μg L^{-1} in March 2000. In the far offshore region along the DWS transect (Figure 1), Chl concentrations (not shown) were uniform with depth with values of 1.6 and 0.9 μg L^{-1} in April 1999 and March 2000, respectively. These values were considerably lower than those observed on the offshore portions of the cross-isobath transects. In the absence of elevated TSM, k_{PAR} was uniformly low ($\sim$0.23 m^{-1}), low and photic depth uniformly high ($\sim$20 m) along cross isobath transects, as shown for example, in the Chicago transect of March 2000 (Figure 7f), and both Z_p/Z_m and $\overline{I_m}/I_0$ decreased monotonically with distance offshore.

3.5.2. Nutrients, Microzooplankton (MZ), and Zooplankton (Z)

[33] On nonplume cruises, low TP values ranging between 4 and 8 μg L^{-1} were seen (Figure 9), and the highest value was seen nearshore at New Buffalo, where river influence is suggested by high chloride values (Figure 9e). DP values were also low, but because TP values were so low, DP represented a larger fraction of TP than on plume cruises. On nonplume cruises, we observed the same contrasting pattern of high or moderate inshore MZ biomasses on the eastern side of the basin, and low inshore MZ biomasses on the western side of the basin as was seen on plume cruises. Biomass at nearshore stations on the Chicago transect were always very low compared to the offshore stations (Figures 9a and 9g), while nearshore transects at St. Joseph, Muskegon, and New Buffalo were similar to or higher than offshore stations (Figures 9b, 9c, 9d, 9e, and 9h). Z biomasses were relatively constant across transects.

3.6. Patterns and Relationships Across Cruises and Years

3.6.1. Nutrients

[34] As obvious above from individual cruises, high values of total phosphorus (TP, Figure 8) were associated with high TSM areas (Figures 3–5) of the plume, and generally low values of TP were found during nonplume periods (Figure 9). Exploration of the association of TP with TSM and with the riverine influence variable *CLDIFF* for all data during January–April using linear regression showed a strong association between TP and TSM and a secondary influence of *CLDIFF* on TP (Table 2). The TP versus TSM and TP versus *CLDIFF* regressions had respective R^2 values of 0.87 and 0.30. The combined regression of TP on TSM and CLDIFF explained 90% of the variation.

[35] Concentrations of total dissolved phosphorus (TDP) were much lower and less variable than TP. In all cases, TDP was <5 μg L^{-1}, and somewhat higher values were seen within plume areas of plume cruises (Figures 8a–8c), although the percent contribution of TDP to TP in plume areas was much lower (e.g., Figures 8b and 8c). Although we obtained significant regressions of TDP versus TSM, of TDP versus *CLDIFF*, and of TDP on both variables (Table 2), these regressions explained little of the variation in TDP ($R^2 <$ 0.21). The same intercept ($\sim$1.6 μg L^{-1}) on all regressions and low slopes on TSM and *CLDIFF* imply a generally low and constant background level.

3.6.2. Microzooplankton (Protozoa) Biomass

[36] Highest microzooplankton (MZ) biomass was not associated with the plume, and a complicated spatial pattern that varied between eastern and western sides of the southern basin was observed: highest MZ biomass was found at nearshore stations of the eastern side, and lowest on the western side. Chl concentration and MZ biomass exhibited dissimilar patterns on the eastern side of the basin, but they exhibited similar trends on the western side, where they were typically low at the inshore stations of the transects, particularly at Chicago. The similarity of pattern on the western side of the basin can be appreciated from plot and regression analyses of relative Chl concentration and MZ as a function of station depth on the Chicago transect (Figure 10): in all cases the highest value of Chl or MZ (by definition, relative value = 1) found on a transect was at the most offshore site sampled, and both Chl and MZ sharply increased with increasing depth contour or distance offshore.

[37] When the maximum Chl concentration (6 μg L^{-1}) observed in the study was found in the nearshore region of the St. Joseph transect (Figure 3a) during the plume event of March 1998, a modest MZ concentration (10 μg C L^{-1}) was found at J10 (Figure 8b). At the time of the extreme maximum MZ (38–45 μg C L^{-1}) seen at J15 and 20 (Figure 8g) during the weak plume event (March 1999), Chl concentrations were moderately high ($\sim$2–3 μg L^{-1}) across this transect (Figure 4b).

[38] Regression analysis, underscoring results obvious from individual transects, showed MZ biomass for all March transects (J, NB, M) on the eastern side of the basin was not associated with TSM, a marker of plume, but was associated ($P < 0.05$, $n = 25$) with the river influence variable, *CLDIFF*, and Chl. Regressions of MZ versus TSM, MZ versus *CLDIFF*, and MZ versus Chl gave R^2 values of 0.000, 0.727, and 0.202, respectively. Multiple linear regression of MZ on *CLDIFF* and Chl gave a significant regression with an R^2 of 0.85.

3.6.3. Zooplankton (Crustacea)

[39] Zooplankton (Z) biomass (estimated from net tows) tended to be higher at nearshore stations on transects on the eastern side of the basin during plume cruises. This pattern was particularly strong at St. Joseph and Muskegon during the plume event of March 1998 (Figures 8b and 8d), and at New Buffalo (Figure 8l) during the plume event of April 2000.

[40] During nonplume cruises, the tendency for higher inshore biomasses on the eastern side of the basin was less developed. Somewhat lower or nearly equal values were seen at nearshore stations along St. Joseph (Figures 9b and 9d) and Muskegon (Figure 9h) transects, but higher inshore values were seen at New Buffalo (Figure 9e). OPC results (Figure 11) showed that vertical distribution of zooplankton-sized particles was relatively uniform, showing a very slight

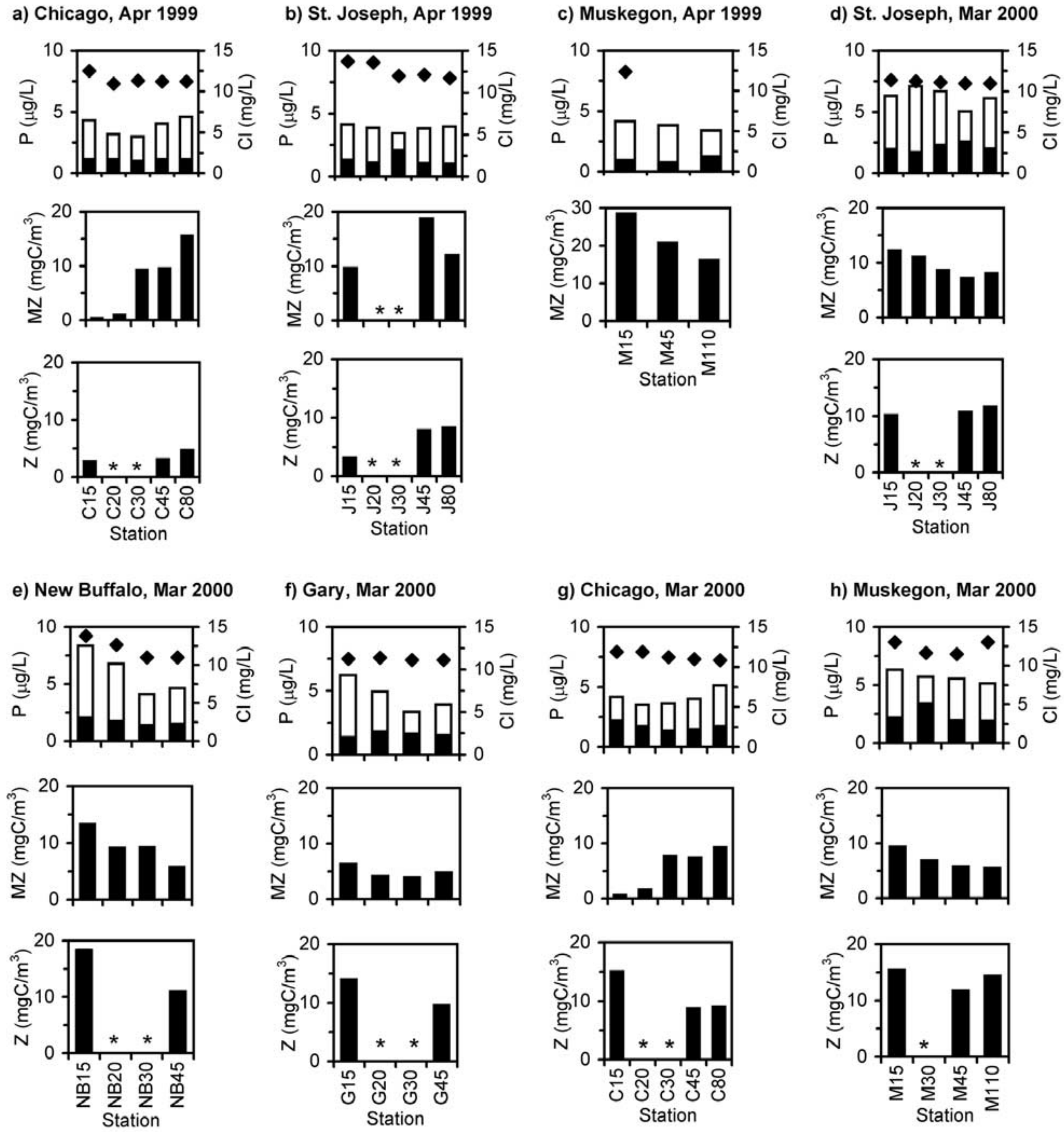

a) Chicago, Apr 1999
b) St. Joseph, Apr 1999
c) Muskegon, Apr 1999
d) St. Joseph, Mar 2000
e) New Buffalo, Mar 2000
f) Gary, Mar 2000
g) Chicago, Mar 2000
h) Muskegon, Mar 2000

Figure 9. Control cruise transects: Chloride (Cl; diamonds, top plots), P as total dissolved P (dark part of histogram) and total P (total length of histogram), microzooplankton (MZ), and zooplankton (Z) concentrations on transects during April 1999 and March 2000, when a plume was not present. Asterisks on graphs indicate data gaps.

tendency for more biomass at greater depths in the water column at a given depth contour. This was the case for both early morning and midday transects.

[41] The other trend in Z biomass was the generally lower concentration seen at all stations in 1999 compared to 1998 and 2000. This difference was seen on both plume (Figure 8) and nonplume cruises (Figure 9). Mean [±*SE*(*N*)] concentration across all stations for January–March in 1998, 1999, and 2000 was 8.21 ± 0.92(13), 5.74 ± 1.05(27), and 12.19 ± 0.53(26), and for January–April in 1999 and 2000 was 5.72 ± 0.81(36) and 12.21 ± 0.52(33) μg C L^{-1}, respectively. Differences among years were all significant ($P < 0.05$).

[42] In addition to the difference in Z biomass, there was a major shift in zooplankton community dominance structure (Figure 12). Normally, as in 1998 and 2000, the zooplankton community was dominated by adult diaptomids, mainly *Leptodiaptomus* spp., but in 1999 it was dominated by adult and late copepodite stages of the cyclopoid copepod *Diacyclops thomasi*, which is usually a

Table 2. Linear Regressions Expressing Relationships for Total Phosphorus and for Total Dissolved Phosphorus on Total Suspended Matter or CLDIFF or Both TSM and CLDIFF for All January–April Cruises 1998–2000[a]

Dependent Variable	*N*	Intercept	Independent Variables		R^2
			TSM	CLDIFF	
TP	170	3.770 ± 0.203	0.951 ± 0.028		0.873
TP	141	4.960 ± 0.543		3.071 ± 0.391	0.302
TP	140	3.397 ± 0.215	0.947 ± 0.033	0.763 ± 0.170	0.899
TDP	162	1.586 ± 0.070	0.051 ± 0.009		0.152
TDP	137	1.645 ± 0.083		0.172 ± 0.059	0.052
TDP	136	1.543 ± 0.079	0.063 ± 0.012	0.019 ± 0.062	0.206

[a] Units: total phosphorus (TP), $\mu g \cdot L^{-1}$; total dissolved phosphorus (TDP), $\mu g \cdot L^{-1}$; total suspended matter (TSM), $mg \cdot L^{-1}$; and CLDIFF, $mg \cdot L^{-1}$. All regressions were significant at the $P < 0.005$ level.

secondary dominant [*Agy*, 2001]. In 1999, *Leptodiaptomus* concentration greatly decreased, while cyclopoid concentrations greatly increased relative to 1998.

3.6.4. Relative Concentrations of Microzooplankton and Zooplankton

[43] Although there was considerable variability among sites and years, the overall pattern that emerged was that biomass of MZ is about the same as that as Z (Figures 8 and 9). The most noteworthy deviation is the extremely high MZ biomass compared to Z biomass inshore at St. Joseph in March 1999 (Figure 8g). Very high MZ relative to Z biomass was also seen on offshore stations of Chicago and St. Joseph during the nonplume cruise of April 1999 (Figures 9a and 9b).

4. Discussion

4.1. Plume Variation Among Years

[44] Different storm strengths and timing among the 3 years studied resulted in plumes of varying extent, timing (March or April), and TSM concentrations. Particularly interesting was the unexpected April plume. By April 2000, all investigators except us had finished all EEGLE studies. Nonplume cruises which occurred during quiescent periods in March and April served as explicit contrasts for plume cruises. This gave us an opportunity to relate light, nutrients, and plankton to TSM and other plume or storm related variables.

4.2. Light Climate and Chlorophyll

[45] The analogy of a turbid estuary has some utility for understanding the light climate and Chl concentrations along transects in Lake Michigan. Storm-driven suspension of bottom sediments resulted in a decline in the light climate analogous to that seen in estuaries. The high correlation between k_{PAR} and TSM, developed from data from 3 years of cruises, implied that the TSM had similar optical properties from year to year. Given the strong influence of particle size on light scattering, the major mechanism of light attenuation, it is likely the plume material in the water column at the time of the plume cruise was the same size during different years. The slope (0.076) of the k_{PAR} versus TSM regression for Lake Michigan is very similar to that of San Francisco Bay (0.06) and other estuaries reported by *Cloern* [1987]. Thus the plume has some analogy to conditions in estuaries; however, the intercept (0.11 m^{-1}), or background k_{PAR}, in Lake Michigan is much lower than estuaries, as for example, San Francisco Bay (0.77 m^{-1}).

[46] During the winter-spring transition in the coastal ocean and Great Lakes, light can be a major limiting force on phytoplankton growth and biomass because in deep areas, phytoplankton are mixed below the photic depth under isothermal conditions [*Sverdrup*, 1953; *Vanderploeg et al.*, 1992a; *Fahnenstiel et al.*, 2000]. *Sverdrup* [1953] was the first to encapsulate this idea in terms of the critical depth, or Z_p/Z_m ratio; when this ratio is less than 1, there can be no bloom initiation. *Cloern* [1987] utilized this concept for turbid estuaries by correlating areas of low primary productivity and Chl in estuaries with turbidity-induced changes in the Z_p/Z_m ratio: values less than 0.2 led to low primary production and Chl concentrations. In the Great Lakes, light, temperature, and nutrients can be limiting during spring isothermal conditions [*Fahnenstiel et al.*, 2000; *Lohrenz et al.*, 2004]. The threshold for light saturation of growth and photosynthesis of offshore phytoplankton occurred at relatively low light intensities equivalent to $Z_p/Z_m \approx 0.2$ [*Fahnenstiel et al.*, 2000]. However, the threshold for saturation of photosynthesis for a March bloom under clear ice cover of Grand Traverse Bay, a deep (190 m) oligotrophic bay on Lake Michigan [*Vanderploeg et al.*, 1992a], occurred at light intensities 2.5 times greater than those in this study. Thus it is possible that in plume-free conditions, nearshore populations could be adapted to higher light intensities than suggested by the offshore populations, and the threshold could be equivalent to $Z_p/Z_m \approx 0.5$.

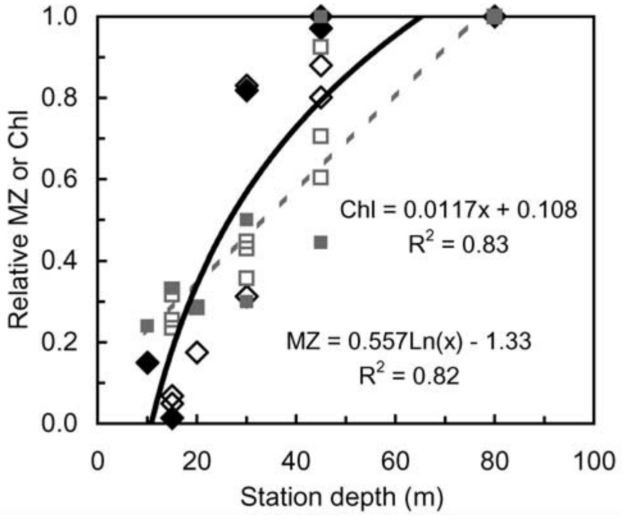


Figure 10. Relative (normalized to each cruise maximum) Chl concentration (squares) and MZ biomass (diamonds) for all dates (February–March 1998–2000) as a function of contour depth along the Chicago transect during both plume (solid symbols) and nonplume (open symbols) cruises. Both plume and nonplume data were used for the regressions, and the single point shown on the 80-m contour represents four repeat observations of Chl and three of MZ.

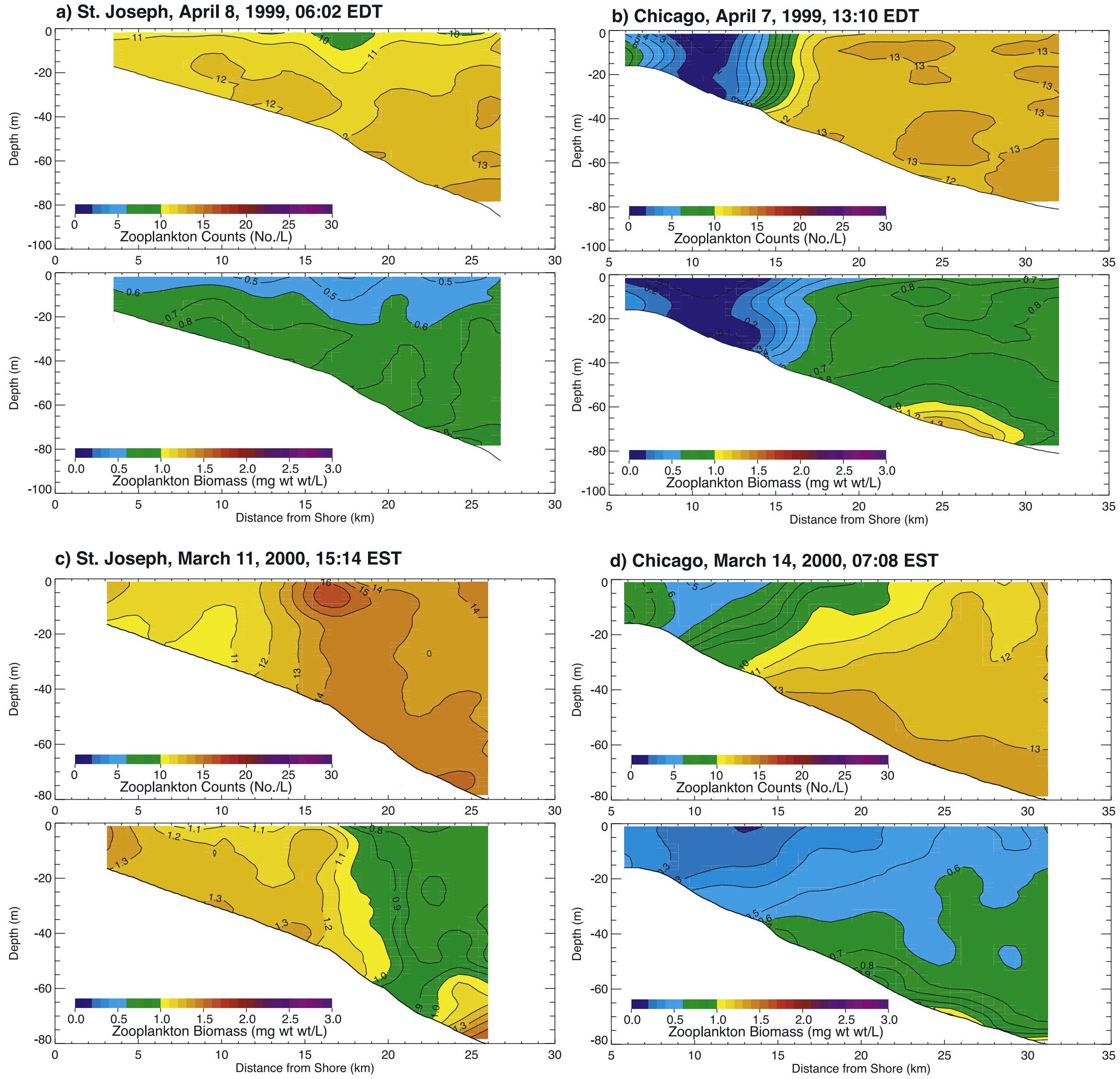


Figure 11. Nonplume PSS transects: cross shelf transects in nonplume periods showing plots of OPC results for zooplankton density (number L^{-1}) and biomass (wet weight L^{-1}) on St. Joseph and Chicago transects in (a, b) early April 1999 and (c, d) early March 2000. These results are companion results for other PSS variables shown in Figure 6.

[47] In the absence of a plume, the cross-isobath values of Z_p would be expected to be relatively constant, and Z_p/Z_m would decrease with increasing depth as shown for the Chicago nonplume transect of March 2000 (Figure 7f). In the scenario of nearshore populations adapted to higher light levels, higher nearshore phytoplankton growth and Chl concentration could be expected. The Muskegon transect of March 1998 (Figure 3c) bears some similarity to the expected pattern of Chl gradually decreasing with increasing water depth. During the nonplume cruises very high inshore Chl was seen at St. Joseph in April 1999 (Figure 6a), while a relatively constant cross-isobath Chl concentrations were seen in March 2000 (Figure 6c). The Chicago transects showed a pattern opposite that expected because of very low inshore Chl values (Figures 6b and 6d). However, in the far offshore at the DWS transect, Chl concentration, as expected, was very low (0.9 μg L^{-1}) throughout the water column.

[48] The light climate in the plume was extremely unfavorable to phytoplankton growth and to the development of high Chl concentrations. As has been observed in turbid estuaries, very high k_{PAR} and low Z_p values were seen in the plume. In contrast to the nonplume pattern of a monotonically decreasing Z_p/Z_m ratio with increasing depth, Z_p/Z_m was low in plume areas and increased in deeper or shallower waters outside of the plume (Figures 7a–7e). Z_p/Z_m values of ~0.1 were often seen (Figures 7a–7e), which is lower than the Z_p/Z_m value of 0.2 in estuaries corresponding to areas of low phytoplankton growth and Chl concentration [*Cloern*, 1987]. More pertinent to the Great Lakes, a value

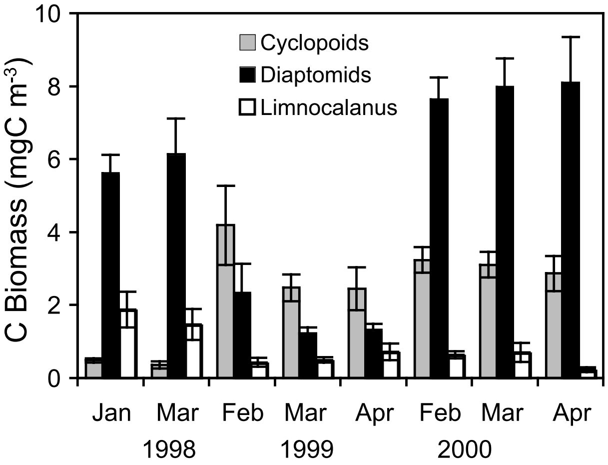


Figure 12. Carbon biomass abundance (mean ± SE) of total cyclopoids, diaptomids, and *Limnocalanus* for different cruises during the winter-spring transition periods of 1998–2000. The January 1998 results refer to a cruise that occurred during late January and early February.

of 0.1 falls well below 0.2, the approximate Z_p/Z_m ratio for light saturation of spring phytoplankton in offshore regions [*Fahnenstiel et al.*, 2000] and far below intensities experienced by blooms occurring under the stable water conditions under clear ice [*Vanderploeg et al.*, 1992a].

[49] Consistent with high TSM, k_{PAR} and low Z_p/Z_m ratio, there was low Chl in plume areas. Extreme examples are the St. Joseph and Gary transects during the March 1998 plume (Figures 3a and 3b), Chicago and Gary transects during the March 1999 plume (Figures 4a and 4c), and St. Joseph, New Buffalo, and offshore N to S transects during in April 2000 plume (Figures 5b, 5c, and 5d). However, it was unlikely that the plume-generated effect of light intensity on Chl would have manifested itself over a period of several days because light-saturated phytoplankton growth is relatively low at this time of year ($\sim$0.1 d^{-1}) [*Fahnenstiel et al.*, 2000] and would be much lower under the extreme light limitation within all parts of the plume. If growth rate limitation over the timescale of several days is not appropriate to explain our shipboard observations a week or longer after generation of the 1998 and 1999 plumes, it is even less appropriate for the April 2000 plume, which we observed within 2 days of the storm and 1 day after observing the peak in backscattering.

[50] As might be expected, the coupled hydrodynamic and N-P-Z model of *Chen et al.* [2004a] predicted fairly constant, only slightly decreasing Chl values with increasing depth along our cross isobath transects during both 1998 and 1999 plumes. We plot their model output in Figure 13 to explicitly compare it with grab sample and PSS Chl results. Light and nutrients are the primary drivers of phytoplankton dynamics in this model. *Chen et al.* [2004a] noted the lack of fit of the model prediction and the few (2–4) stations where grab Chl samples taken along each of the cross-isobath transects. This lack of fit is even more obvious from the continuous record of PSS Chl on the transects. H. A. Vanderploeg et al. (Forgotten forces in Episodic Events Great Lakes Experiment: Can we understand impacts of the recurrent coastal plume in Lake Michigan without considering turbulence, particle coagulation, and zebra mussels, manuscript in preparation, 2007) (hereinafter referred to as Vanderploeg et al., manuscript in preparation, 2007) argue the lack of fit results from neglecting two major forces: (1) turbulent energy of the storm injured phytoplankton and promoted collision and coagulation and settling out of phytoplankton aggregates in plume areas; and (2) filtering of abundant zebra mussels in the nearshore region of the Chicago transect greatly reduced phytoplankton there.

4.3. Nutrients

[51] The plume is a TP-rich area due to the association of P with suspended solids, as indicated by both the TP versus TSM regression and the TP regression on TSM and *CLDIFF* (Table 2). River input can also contribute P to the water column and to the plume in areas where plume and river intersect, such as the area near the St. Joseph R. TDP was not greatly elevated in the plume and there was not a strong association (Table 2: slope = 0.06, R^2 = 0.21) between TDP and TSM. *Lohrenz et al.* [2004] presented evidence that, although P availability influences photosynthetic parameters during the spring in Lake Michigan, admixtures of bottom sediment and lake water to simulate a plume event did little to stimulate phytoplankton growth, whereas admixtures of river water to lake water greatly stimulated growth of lake phytoplankton. Thus they concluded that river input rather than the plume is a major stimulus of nearshore phytoplankton production. They also argued that the importance of the plume to flux of P from sediment to the food web through bacteria (34% of the external load) that *Cotner* [2000] attributed to the plume event of 1998 was an overestimate that was biased by river influence.

4.4. MZ and Z Distributions

[52] Other coastal processes can confound interpretation of impacts of the recurrent coastal plume. Early EEGLE publications have emphasized the importance of the plume to the microbial food web [*Cotner*, 2000; *Biddanda and Cotner*, 2002]. Our observations and those of Lavrentyev (Lavrentyev et al., unpublished manuscript, 2007) of the correlation between MZ and *CLDIFF* (or chloride) strongly emphasize the importance of river input. Lavrentyev et al. (unpublished manuscript, 2007) showed MZ composition displayed a pronounced shift toward the predominance of opportunistic choreotrich and tintinnid ciliates associated with elevated bacterial production within the turbidity zone and river-influenced waters. These ciliates replaced heterotrophic dinoflagellates and mixotrophic oligotrichs, which typically formed MZ biomass in early spring. Ignoring the high MZ concentrations associated with river influence and low MZ concentrations associated with inshore stations on the Chicago transect (particularly at C10, C15, C20), total MZ concentration was relatively flat along transects during plume and nonplume periods. Vanderploeg et al. (manuscript in preparation, 2007) attributed the low ZM and Chl values there to zebra mussel grazing.

[53] The Z concentrations determined from full water column tows imply that zooplankton are relatively uniformly

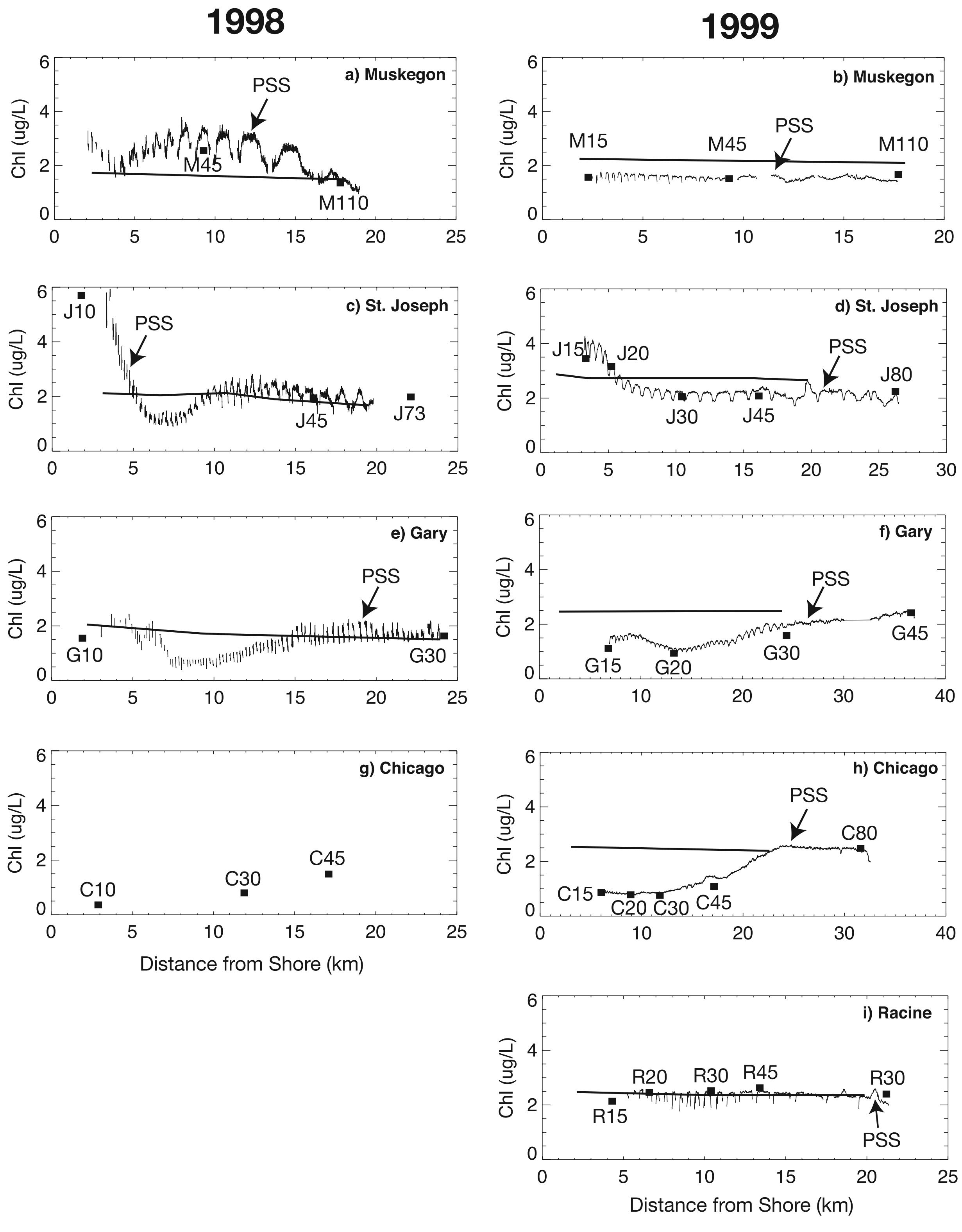


Figure 13. Plots of PSS-predicted chlorophyll and depth-averaged chlorophyll grab samples for distance along the transects compared to model output (solid nearly straight line) from the N-P-Z model of *Chen et al.* [2004a] for plume events in 1998 and 1999. The PSS plots are raw PSS results versus distance plots with surface results (typically <10 m) removed for midday runs that showed the quenching artifact.

Table 3. Estimated Average Fractions of the Water Column Cleared of Phytoplankton (FR_P) and Microzooplankton (FR_{MZ}) by Diaptomids and by the Total Zooplankton Community During the Winter-Spring Transition in 1998, 1999, and 2000

	Diaptomids[a]			Total Zooplankton[b]		
Year	C Conc., μg L^{-1}	FR_P, d^{-1}	FR_{MZ}, d^{-1}	C Conc., μg L^{-1}	FR_P, d^{-1}	FR_{MZ}, d^{-1}
1998	5.94	0.0063	0.0194	6.59	0.0063	0.0212
1999	1.65	0.0011	0.0054	5.48	0.0011	0.0180
2000	7.86	0.0083	0.0259	11.67	0.0083	0.0383

[a] Average clearance rates of 7 and 22 mL d^{-1} for individual *Leptodiaptomus sicilis* (individual mass = 6.6 μg C) [*Bundy et al.*, 2005] normalized per unit C mass were used for calculating rates for diaptomids and nauplii.

[b] Total zooplankton does not include *Limnocalanus*, a large predacious copepod which does not feed appreciably on phytoplankton or microzooplankton [*Liebig and Vanderploeg*, 1995]. Clearance rates of cyclopoids, small predacious copepods, for microzooplankton was assumed to be same as diaptomids [e.g., *Adrian and Schneider-Olt*, 1999], and clearance rates for phytoplankton were assumed to be zero.

distributed horizontally during nonplume periods. Our OPC results suggest that during these same periods, zooplankton are relatively evenly distributed vertically in the water column during day and night. After storm events, higher depth-averaged concentrations were seen in nearshore areas on the eastern side of the basin. Possibly this is caused by an interaction between vertical distribution of zooplankton in the water column relative to upwelling and downwelling during the storms. Higher concentrations were seen on the upwelling (eastern) than downwelling (southern and western sides) after the storms. This would be consistent with zooplankton being found at greater depths in the water column during the storms to escape surface turbulence, as has been observed on Georges Bank, where moderate winds apparently caused nauplii and copepodites of many copepod species to migrate down in the water column to avoid surface turbulence of 10^{-6} W kg^{-1} [*Incze et al.*, 2001].

[54] That MZ biomasses were about the same as Z biomasses has important implications to the relative roles of MZ and Z in regulating phytoplankton production and food availability to Z. Depending on species of MZ, bacteria, picophytoplankton or nano-sized phytoplankton can be ingested [*Simek et al.*, 1995; *Sime-Ngando et al.*, 1999; Lavrentyev et al., unpublished manuscript, 2007]. The high turnover and ingestion rates of MZ relative to Z imply an important role of MZ as grazers and intermediaries between bacteria and Z.

4.5. Copepod Grazing and Implications of the Plume to Copepods

[55] The winter-spring transition is an important time for copepod reproduction in the Great Lakes [*Vanderploeg et al.*, 1992a]. Overwintering adult calanoids utilize stored lipid reserves for reproduction but also strongly depend on phytoplankton and microzooplankton, which are found in limiting concentrations at this time [*Vanderploeg et al.*, 1984, 1992b; *Bundy et al.*, 2005]. In a companion study to our work here, in which natural assemblages of phytoplankton and microzooplankton were offered as food, *Leptodiaptomus sicilis* obtained between 22% and 74% of its carbon ingested from microzooplankton [*Bundy et al.*, 2005]. Biomass of microzooplankton relative to phytoplankton in these experiments was on the order of ~10–20%, and the high ingestion rate of MZ represented a preference of MZ over phytoplankton. The abundance data here on zooplankton allow us to reevaluate the significance of their grazing in affecting phytoplankton and microzooplankton during the winter-spring transition. *Bundy et al.* [2005] assumed there were the equivalent of 3 adult diaptomids L^{-1} (individual mass = 6.6 μg C) or a C concentration of 19.8 μg L^{-1}. On average we saw much lower values (5–12 μg L^{-1}: Figure 12 and Table 3), and we calculated that less than 1% d^{-1} and 4% d^{-1}of the phytoplankton and microzooplankton, respectively, were cleared from the water column 1998–2000 (Table 3).

[56] *Bundy et al.* [2005] concluded from their experiments on EEGLE cruises that, because on average *Leptodiaptomus* ingested only 7% C d^{-1} out of 10% C d^{-1} needed for production, food is limiting and egg production was driven by utilization of stored lipids as suggested by *Vanderploeg et al.* [1992a, 1992b]. These experiments were done on cruises where the MZ concentration ranged from 2 to 9 μg L^{-1}. This upper value does not bracket a few very high values seen in the nearshore, particularly the value of 40 μg L^{-1} at St Joseph in March 1999. Because Z feed on both phytoplankton, which decreased in the plume, and MZ, which were largely independent of the plume, the plume can be considered, at least in the short term, to have a negative affect on zooplankton feeding and reproduction. This is especially true of calanoids (diaptomids), which are omnivores, but may not apply as strongly to cyclopoids, which prey only on motile prey such as MZ and large motile flagellated algae [e.g., *Vanderploeg*, 1994]. However, the large ciliates preferred by both calanoids and cyclopoids also decreased in plume areas.

[57] In contrast to the plume, the area of riverine influence is a region likely to greatly benefit zooplankton there. Both high Chl and MZ were associated with riverine influence on the eastern side of the basin. The high Chl seen in nearshore waters on the St. Joseph transect during the plume event of 1998 provided a rich food source for *Leptodiaptomus*, which were found in high concentration there. The high MZ concentration found in this same location during March 1999 benefited both calanoids and cyclopoids found there. The influence of river inflow received little attention in EEGLE. It is clearly deserving of more research.

5. Conclusions

[58] Earlier EEGLE studies have emphasized the roles of the recurrent sediment plume for injecting nutrients (P, C) into the water column that fueled heterotrophic production and the microbial food web [*Cotner*, 2000; *Biddanda and Cotner*, 2002; *Chen et al.*, 2004b; Lavrentyev et al., unpublished manuscript, 2007] and for diminishing light availability for phytoplankton growth [*Millie et al.*, 2002].

We expanded upon these observations by examining fine-scale distribution of nutrients, plankton, and light climate and how these variables were related to sediment plumes over a large region of the southern basin. For example, the suspended sediment in the plume, by increasing k_{PAR}, altered the expected monotonic decrease in Z_p/Z_m ratio with increasing depth along cross-isobath transects, and it is likely a low Z_p/Z_m ratio was responsible for very low Chl concentrations seen in far offshore waters. Also, TP was strongly associated with TSM throughout the southern basin.

[59] Over the short term, it is likely that the low concentration of phytoplankton associated with the plume decreased feeding rate of zooplankton, because there was not compensatory increase in MZ, and plume-associated MZ were not the large species preferred by copepods. Overall our observations in conjunction with those of *Lohrenz et al.* [2004] who saw no stimulation of phytoplankton growth with admixtures of bottom sediment argue for a lesser benefit of the plume to the food web than originally thought, and even point to negative consequences. Further work is necessary to define plume impacts. In particular, more work is required to carefully evaluate the availability of the nutrients in suspended sediments or determine if storms by increasing sediment resuspension have any effect on increasing nutrient availability to the food web. Vanderploeg et al. (manuscript in preparation, 2007) using circumstantial evidence argue that the poor match between Chl and model output relates to neglecting particle coagulation associated with turbulence and resuspended sediment and with zebra mussel grazing associated with reefs in the Chicago area. Research is required to verify these arguments, particularly the possible impacts of particle aggregation. In view of the stimulatory effect of rivers on the microbial food web, more attention should be paid to evaluating impacts of riverine inputs.

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