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Intense winter heterotrophic production stimulated by benthic resuspension

Abstract—A major episodic sediment resuspension event (25-yr high), which was triggered by atmospheric and water column instability in an El Niño year, temporarily altered the dynamics of autotrophy and heterotrophy in Lake Michigan. Resuspended sediments, rich in organic and inorganic nutrients, especially phosphorus, stimulated heterotrophic production despite low water temperatures (2°C or less). During the resuspension event, southern basin winter heterotrophic bacterial productivity was high (64% of summertime productivity), especially along the margins of the lake. The mean bacterial cell size increased in regions where productivity was highest during the resuspension event. Although resuspended sediments stimulated bacterial secondary productivity, they simultaneously decreased water-column light availability and autotroph biomass. Consequently, heterotrophic bacteria were temporally decoupled from the commonly recognized source of organic matter for bacterial production—photoautotrophy. Variation in the magnitude and frequency of these resuspension events likely influences variation in interannual productivity in this system. Such previously underappreciated, intermittent, and ephemeral benthic–pelagic exchange events may significantly influence plankton dynamics and biogeochemical cycling in coastal marine and freshwater ecosystems.

Physical forcing greatly influences productivity in aquatic ecosystems by moving organisms and materials from region to region. Many of the physical factors impacting biological dynamics are predictable and periodic, such as daily and seasonal variation in stratification patterns and mixing depth, internal waves (Karl 1999), and tides (Imberger et al. 1983). Episodic phenomena are more difficult to characterize, but their importance to ecological dynamics can be equally significant. For example, variation in the frequency and duration of El Niño-Southern Oscillation influences productivity, microbial dynamics, nutrient limitation, and food web composition (Karl 1999) in the ocean. In small lakes, intermittent turbulence influences phytoplankton biomass and species composition by directly resuspending cells from the lake sediments (Carrick et al. 1993).

Most planktonic metabolic activity in oligotrophic aquatic ecosystems is microbial (Biddanda et al. 1994), and in temperate systems, productivity is minimal in winter because of cold temperatures (Pomeroy and Wiebe 1988) and low light levels. At low temperatures (near 0°C), some evidence suggests that primary production is suppressed less than bacterial and grazer processes (Pomeroy and Wiebe 1988). However, several studies have shown that high organic carbon substrate availability can compensate bacterial growth for low temperatures (Pomeroy et al. 1991; Putland 2000).

In this study, we examined the influence of an episodic physical event on productivity and nutrients in one of the Laurentian Great Lakes. A large storm that tracked from north to south across the long axis of Lake Michigan in early March 1998, coupled with little thermal resistance to mixing, generated a massive sediment resuspension event in the southern basin of the lake. More than 3×10^{12} g of sediment was resuspended from the lake floor. Over half (1.65×10^{12} g) of this material was observed at depth contours <60 m, especially along the southeast margin of the lake where concentrations were greater than 10 mg L^{-1} and as high as 35 mg L^{-1} (Fig. 1). In January, before the resuspension event, the coastal shelf particulate matter concentrations in the water column were low (<5 mg L^{-1}) and total suspended material (TSM) was not elevated in this region of the lake. The 1998 resuspension event was the largest in 25 yr.

Lake Michigan resuspension events typically occur in both the spring and fall when the lake is not thermally stratified (Eadie et al. 1996). Three survey cruises were conducted on Lake Michigan in winter (RV *Lake Guardian*; 28 Jan–4 Feb), early spring (RV *Laurentian*; 15–18 Mar) and summer (RV *Laurentian*; 29 Aug–1 Sep) 1998. On each of the cruises, transects were conducted from nearshore to offshore regions, where resuspension effects were not observed. At each site, 2–6 depths were sampled depending on the maximum depth.

Microbial measurements—Bacterial productivity was measured with tritiated leucine incorporation (20-nM final concentration) and a theoretical conversion factor (3.1 kg C per mol leucine incorporated [Kirchman 1993]). Size-fractionation of productivity was estimated by filtering onto 0.2- or 1.0-μm pore-size filters (Poretics). Bacterial abundance and size were measured with epifluorescence microscopy (Hobbie et al. 1977). A SPOT digital camera was used to photograph 500–1,000 cells at each sampling site. Image analysis was performed with Image Pro Plus software. Cell carbon was estimated from cell volume assuming an ellipsoidal shape and applying a conversion of 0.25×10^{-12} g C μm^{-3} (Psenner 1993).

Nutrient measurements—TSM was determined gravimetrically, soluble reactive phosphate (SRP) and ammonium were measured colorimetrically with an Alpkem autoanalyzer (American Public Health Association 1992), and total dissolved phosphorus was determined similarly after persulfate digestion (American Public Health Association 1992). An estimate of biologically available phosphorus associated with particles was determined after filtration onto a glass-fiber filter and extraction in 0.1-N NaOH (Williams et al. 1980); particulate organic P (POP) was determined colorimetrically after combustion and extraction in 1 N HCl (Solorzano and Sharp 1980); and particulate C and N (POC and PON, respectively) were measured in a Perkin-Elmer Model 2400 CHN analyzer. Chlorophyll was determined fluorometrically after extraction in 90% acetone (Wetzel and Likens 1991). Dissolved organic carbon (DOC) was determined by high-temperature combustion with a Shimadzu 5000 TOC analyzer (Sharp et al. 1993).

Contouring—Estimates of southern basin inventories of nutrients were obtained by contouring the region south of 43.5°N latitude. Contours were constructed from geometric

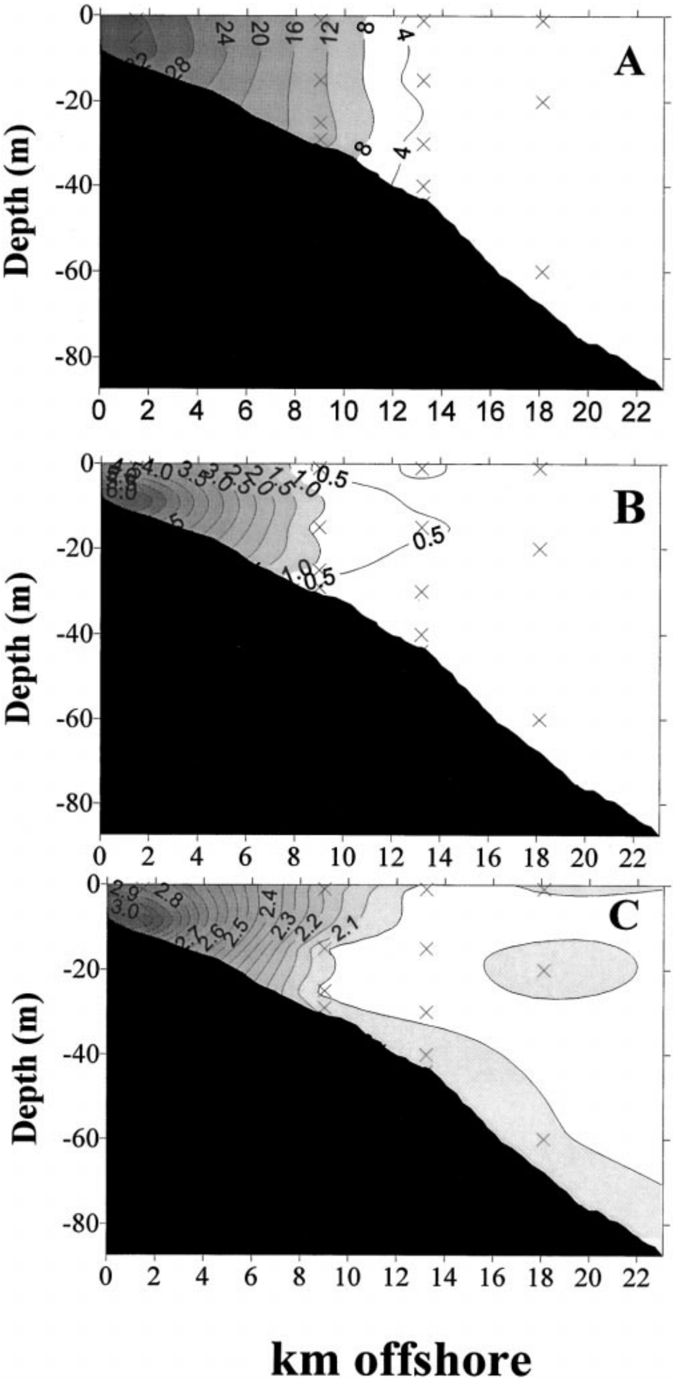

Fig. 1. Contour plots of (A) TSM (mg L^{-1}), (B) SRP (μg P L^{-1}), and (C) DOC (mg C L^{-1}) off of St. Joseph, Michigan, during the March 1998 cruise. Site locations are indicated with an ×.

means of each parameter at sampling sites (2–6 depths per site). Means of parameters (in g or mg m^{-3}) and water depth were contoured with a Kriging protocol (Surfer 6.0; Golden Software) and then multiplied to obtain whole basin estimates. Contours were constructed from 11 sites along transects in the southern basin. Spatial coverage was focused on regions where resuspension historically occurs, but site selection was also influenced by near real-time satellite imagery (percentage of visible reflectance). Although the spatial coverage in the basin was limited to the resuspension region, gradients were steep and variation outside of the resuspension region was low (Fig. 1).

Our measurements in March 1998 showed a band of resuspended sediment around the periphery of the lake that was most intense in the extreme south and southeastern regions of the basin. These particles were most likely resuspended from depths shallower than 10 m (Fig. 1). POC concentrations increased by nearly a factor of 3 in the shallowest regions of the lake and decreased rapidly in an offshore direction (Table 1). SRP and ammonium concentrations increased by a factor of 5 in the shallow regions relative to offshore sites (Table 1; Fig. 1). Offshore concentrations for all three components were similar to those measured on the January cruise and slightly lower than midsummer values (Table 1).

Our data indicate that resuspended particles were nutrient-rich and likely provided particulate and dissolved organic carbon and nutrients to the water column. The quantities of particulate organic carbon and phosphorus increased measurably between the January and March cruises (Table 1). Particulate carbon increased from 195 to 881 μg C L^{-1} in the nearshore region, whereas particulate P increased from 5.5 to 21 μg P L^{-1}. Particulate N was also increased in the nearshore region. In March, POP was also slightly increased at the offshore sites, but much less than at the nearshore sites. The mean C:P (molar) in January was 92, and it decreased to 64 in the nearshore region in March (Table 1). Furthermore, TSM, SRP, and DOC concentrations were highest in the shallowest regions that we sampled (<10 m; Fig. 1).

These elevated nutrient concentrations presumably had a significant impact on heterotrophic bacterial production in the southern basin of the lake. Aquatic bacteria can be limited by both organic carbon and inorganic nutrients, especially P (Cotner et al. 1997), and they have efficient uptake permeases even at low nutrient availability (Cotner and Wetzel 1992) and high biomass requirements (Bratbak 1985). There was a marked increase in bacterial biomass from the January to March cruises (Table 1), suggesting that bacterial biomass was an important sink for dissolved P and other nutrients released by resuspended particles.

Bacterial productivity during the resuspension event was extremely high in the nearshore region of Lake Michigan and coincided with regions where concentrations of suspended material were high (Table 1). In fact, the highest volumetric winter rate was much greater than the highest rate measured in August 1998 (4.0 vs. 1.7 μg C L^{-1} d^{-1}). Although the shelf region (<60-m depth) represents only 13% of the volume of the entire southern basin, bacterial production there was 37% of total basin productivity in March. Furthermore, March bacterial production for the entire southern basin was 64% of rates measured in August. Such high winter productivities were surprising, given the cold temperatures. However, previous laboratory studies have shown similar stimulatory effects of resuspended sediments in coastal waters (Wainright 1987) and high substrate concentrations at cold temperatures (Wiebe et al. 1993).

Spatial patterns of bacterial cell size provided further sup-

Table 1. Concentrations of nutrients, bacterial biomass, and production in southern Lake Michigan in 1998.

Parameter	Jan 98	Mar 98 Nearshore	Mar 98 Offshore	Aug 98 Nearshore	Aug 98 Offshore
TSM (mg L^{-1})	1.38 (0.10)	33.9 (0.3)	2.1 (0.2)	—	—
POC (μg L^{-1})	195 (4.7)	881 (75)	246 (23)	373 (25)	268 (12)
PON (μg L^{-1})	18.4 (0.7)	59.0 (14.0)	18.7 (1.9)	32.9 (3.4)	23.5 (1.1)
POP (μg L^{-1})	5.5 (0.2)	21.0 (3.5)	8.9 (0.2)	4.1 (0.3)	3.6 (0.1)
POC : POP (molar)	91.6	64.4	71.2	237	194
POC : PON (molar)	12.4	10.5	17.9	13.2	13.3
TDP (μg L^{-1})	2.89 (0.10)	3.42 (0.44)	1.70 (0.06)	2.46 (0.14)	2.45 (0.08)
SRP (μg L^{-1})	0.27 (0.04)	1.5 (0.1)	0.31 (0.02)	0.52 (0.12)	0.41 (0.04)
AVP (μg L^{-1})	1.83 (0.13)	14.3 (1.06)	2.1 (0.2)	—	—
NH_4 (μg L^{-1})	4.1 (0.3)	28.2 (0.8)	3.9 (0.3)	7.0 (1.7)	11.5 (1.5)
DOC (mg L^{-1})	2.01 (0.09)	2.63 (0.15)	2.09 (0.01)	1.77 (0.07)	1.90 (0.06)
Bacterial C (μg C L^{-1})	28.7 (0.9)	49.6 (2.9)	46.4 (2.1)	30.2 (1.2)	23.9 (1.2)
BSP (μg L^{-1} d^{-1})	—	2.62 (0.57)	0.60 (0.09)	1.38 (0.57)	1.27 (0.14)

TSM, total suspended material; POC, particulate organic carbon; PON, particulate organic nitrogen; POP, particulate organic phosphorus; TDP, total dissolved phosphorus; SRP, soluble reactive phosphorus; AVP, available phosphorus; DOC, dissolved organic carbon; BSP, bacterial secondary production. Nearshore, $<$15-m depths; n = 6–9; Offshore, $>$15-m depths; n = 30–36.

port that resuspension stimulated production (Fig. 2). Most bacterial productivity (69% in the most intense resuspension regions) was in the $>$1-μm size fraction. Typically, more than 95% of aquatic bacteria are smaller than this, but the mode of the size distribution increases at high community growth rates (Ammerman et al. 1984). The average cell diameter in the resuspension plume was 0.7 μm, and many of these cells likely did not pass the 1-μm filter, either because of their size or because they were attached to sediment particles. Free bacteria in the resuspension plume were larger than free bacteria from the pre-plume cruise, and bacteria attached to particles were larger than free bacteria (Fig. 2). Specific growth rate patterns during the resuspension event indicated a strong gradient from nearshore to offshore regions, with nearshore growth rates as high as 0.12 per day and offshore rates $<$0.01 per day, suggesting that resuspended sediments stimulated growth rates independent of changes in biomass across the coastal shelf.

Our calculations suggest that benthic bacteria resuspended along with sediments could not have accounted for the increased biomass in the nearshore regions. On the basis of the mass of material in the plume, approximately 1–2 mm of sediment were resuspended (B. Eadie pers. comm.). We assumed 10^9 bacterial cells per cubic centimeter of sediment, and we estimated the surface area of the lake where increased TSM occurred ($<$60 m; 4.99×10^9 m^2) and the volume of water above this area (2.29×10^{11} m^3). These calculations suggest that $<$2% of the bacterial biomass present in the water column during the resuspension event was directly resuspended from sediments.

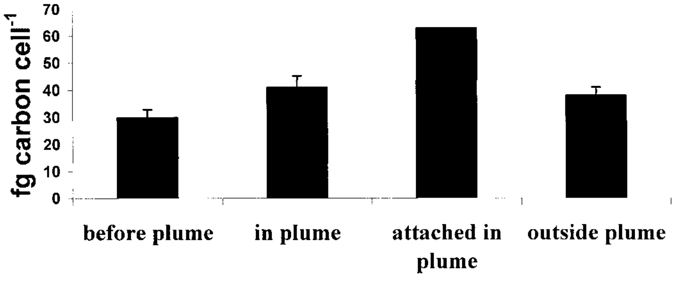

Fig. 2. Effect of the resuspension plume on bacterial cell mass. Data represent femtograms of carbon per cell from the January 1998 cruise (before plume), from all cells within the March 1998 plume (in plume), from particles attached to amorphous particles in the plume (attached in plume), and from cells outside of the region of high particle resuspension (outside plume). Cell carbon was estimated from cell volume assuming an ellipsoidal shape and applying a conversion of 0.25×10^{-12} g C μm^{-3} (Psenner 1993).

Because resuspended material decreases light availability while stimulating bacterial secondary productivity, photoautotrophy and heterotrophy were spatially and temporally decoupled during the resuspension event. In August, bacterial productivity profiles showed a pattern similar to that of chlorophyll, with highest values near the surface or near the deep chlorophyll maximum (Fig. 3). However, during the resuspension event, bacterial productivity increased near the bottom of the lake on all nearshore profiles and to a lesser extent on deepwater profiles (Fig. 3). Particle densities also increased with depth, providing an increased supply of nutrients deeper in the water column. In contrast, March chlorophyll showed a uniform or decreasing pattern with depth.

Seasonal uncoupling of autotrophic and heterotrophic bacterial production suggests an organic matter source for bacterial production other than phytoplankton excretion. Resuspended material provided carbon to the water column, but the ultimate source of this carbon is from both aquatic (autothonous) and terrigenous (allochthonous) sources. Most runoff (60%) into the southern basin occurs on the eastern side of the lake during the winter–spring period when the lake is not thermally stratified and resuspension events are most likely. From March to August, we observed a drawdown of DOC from 2.19 mg L^{-1} C to 1.88 mg L^{-1} in the southern basin. This decrease could account for 61% of bacterial carbon demand during this period, assuming a 20% bacterial growth efficiency (Pomeroy et al. 1991). Phytoplankton excretion of organic carbon could account for 20–

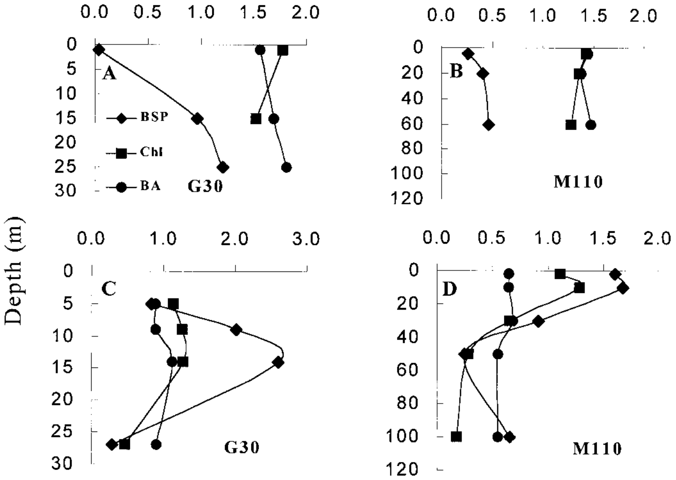

Fig. 3. Depth profiles of bacterial productivity (diamonds; BSP μg C L^{-1} d^{-1}), bacterial abundance (circles; BA number × 10^6 ml^{-1}) and chlorophyll (squares; μg L^{-1}) in (a and b) March and (c and d) August 1998 at two sites in the southern basin of Lake Michigan. Note the differences in the depths between the (a and c) nearshore site and the (b and d) offshore site. Bacterial productivity was measured using tritiated leucine and a theoretical conversion factor (Kirchman 1993).

40% of bacterial carbon demand during this period, assuming that 10–20% of primary production is excreted (Baines and Pace 1991).

These observations suggest that loading of dissolved organic carbon and other nutrients, such as phosphorus, from resuspension or spring runoff, may be an important stimulus to bacterial production, as well as to algal production, during the spring transition to stratification. A buildup and drawdown of DOC has been observed in other systems, such as Conception Bay (Pomeroy et al. 1991), where a spring bloom generated increased organic matter inventories in the water column and bacteria and particle feeders consumed that material. Unlike this system, DOC accumulation in Lake Michigan is not directly driven by biological production, but is rather a physically-forced episodic event. Nonetheless, our observations in Lake Michigan (Table 1; Fig. 2) suggest that some of the accumulated DOC likely originates from previous autochthonous production in the nearshore region, subsequently made available through turbulent mixing. C : N values in the nearshore region were relatively low (10.5) and less than offshore values during the resuspension event (Table 1), suggesting that autochthonous sources were an important component of this material (Meyers 1994).

Although this resuspension event is recurrent (spring and fall) in Lake Michigan, there is significant variability in its intensity, caused primarily by climate variability. The 1998 event reported here had a mean maximum turbidity approximately double that of the mean 40-yr average, whereas the 1999 event was slightly below the 40-yr mean. The importance of this variability to ecosystem function is unclear, but our calculations suggest that it could have important interannual impacts on productivity. The increased P in bacterial biomass from January to March was more than double the annual P load into this P-limited system. Furthermore, bacterial biomass decreased from March to August (Table 1). Although this biomass could have simply sunk out of the water column without being incorporated into the food web, neutrally buoyant bacteria should remain suspended. We observed no evidence of microbial sinking in sediment traps collected after another resuspension episode in 1999. Assuming a 80 : 1 C : P molar ratio for bacteria (Bratbak 1985), the decrease in bacterial biomass from March to August could represent approximately 5 × 10^7 moles of P that were transferred to the food web. External loading to the southern basin of Lake Michigan is 1.44 × 10^8 moles of P yr^{-1} (Eadie et al. 1984). Therefore, the potential flux of P from sediments to the food web via bacteria alone during the resuspension event was equivalent to 34% of the external load in this P-limited ecosystem. We do not know the significance of this mechanism and the efficiency of bacterial P transfer into the food web at this time.

Climate and food web interactions are extremely relevant to interannual ecosystem dynamics in large, physically dominated systems like the Laurentian Great Lakes. Cold winters with high levels of ice cover minimize winter turbulence in shallow regions and decrease total water column P available for spring production (Eadie et al. 1984). An extremely cold winter in 1977 generated 90% ice cover in the southern basin of Lake Michigan, and the ensuing spring had high Secchi depths and low total P levels (Scavia et al. 1986). Recent mild winters in the Great Lakes region should have the opposite effect (low Secchi depth, high total P levels), and our data from 1998 support this hypothesis. Variation in food web structure and dynamics, as well as decreased nutrient loading, can complicate this simple relationship. A more comprehensive approach should be taken to address this issue.

Resuspended sediments are an intermittent source of dissolved and particulate material to coastal waters. We provide the first empirical field evidence that resuspended sediments stimulate heterotrophic production on an ecosystem scale, even at extremely cold temperatures. Sediment resuspension is observed in all of the Great Lakes, as well as in small lakes and coastal ecosystems. Resuspension of this ''ghost of production past'' enables recovery of previously sedimented carbon, phosphorus, nitrogen, and other nutrients from nearshore sediments before long-term burial in deeper regions of lakes and marine systems. Episodic resuspension can temporarily decouple autotrophic and heterotrophic production in temperate coastal environments when the water column is destratified.

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