# Love Handles in Aquatic Ecosystems: The Role of Dissolved Organic Carbon Drawdown, Resuspended Sediments, and Terrigenous Inputs in the Carbon Balance of Lake Michigan

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## ABSTRACT

During the unstratified (winter) and stratified (summer) periods of 1999 and 2000, we examined carbon (C) dynamics in the upper water column of southern Lake Michigan. We found that (a) bacterial respiration (BR) and planktonic respiration (PR) were major sinks for C, (b) C flux through bacteria (CFTB) was diminished in winter because of reduced bacterial production (BP) and increased bacterial growth efficiency (BGE) at colder temperatures, and (c) PR exceeded primary production (PP) during the spring–summer transition. Drawdown of dissolved organic C (DOC), resuspended organic matter from the lake floor, and riverine organic matter likely provided organic C to compensate for this temporal deficit. DOC in the water column decreased between winter and summer (29–91 mg C m$^2$ d$^{-1}$) and accounted for 20%–53% of CFTB and 11%–33% of PR. Sediment resuspension events supported elevated winter heterotrophy in the years that they occurred with greatest intensities (1998 and 2000) and may be important to interannual variability in C dynamics. Further, riverine discharge, containing elevated DOC (5×) and dissolved P (10×) relative to lake water, peaked in the winter–spring season in southern Lake Michigan. Collectively, terrigenous inputs (river, stream, and groundwater discharges; storm water runoff; and atmospheric precipitation) may support approximately 10%–20% of annual in-lake heterotrophy as well as autotrophy. Terrestrial subsidies likely play a key role in the C balance of even very large lakes, representing a critical linkage between terrestrial and aquatic ecosystems.

**Key words:** land–lake linkages; carbon balance; respiration; bacterial growth efficiency; dissolved organic carbon; sediment resuspension; terrigenous matter; southern Lake Michigan.

## INTRODUCTION

*A lake is the landscape's most beautiful and expressive feature. It is the earth's eye.*—Henry David Thoreau (1854)

There is a general consensus in the literature that heterotrophic secondary production in aquatic ecosystems is tightly coupled to planktonic primary productivity in time and space (Azam and others 1983; Cole and others 1988; Williams 1998; Carignan and others 2000). However, this consensus has been challenged by studies demonstrating that terrigenous dissolved organic carbon (DOC) also provides substantial carbon (C) for aquatic bacteria

(Wetzel 1992; Tranvik 1992; Cole 1999) and has short residence times in the aquatic environment (Opsahl and Benner 1997; Hedges and others 1997). Furthermore, oligotrophic systems generally are characterized by primary production–planktonic respiration (PP:PR) ratios less than 1 (Smith and Hollibaugh 1993; del Giorgio and others 1999; but see Carignan and others 2000), and most temperate lakes are supersaturated with respect to atmospheric carbon dioxide ($CO_2$) (Cole and others 1994; Dillon and Molot 1997). In oligotrophic systems, gross bacterial production (production + respiration) can approach that of primary production; it is less, but still significant, in eutrophic systems (Biddanda and others 1994, 2001; del Giorgio and others 1997).

Seasonal cycles in respiratory activity have major impacts on the food web structure and the C balance of natural waters (Pomeroy and Wiebe 1993; Sherr and Sherr 1996). However, few studies have attempted to address seasonal changes in the respiratory activity of bacterioplankton. Seasonal studies in Newfoundland waters and on the southeastern US continental shelf documented shifts between net autotrophy during winter–spring and net heterotrophy during summer–fall (Pomeroy and others 1991; Griffith and Pomeroy 1995). Pomeroy and Wiebe (1993, 2001) argued that during periods with cold temperatures, heterotrophic bacterial metabolism is low and systems tend to be autotrophic, whereas during warmer periods, bacterial heterotrophic metabolism is high and systems tend to be heterotrophic.

Even though respiration is a major pathway for C flow in the aquatic environment, measurements of plankton respiration (PR) are scarce relative to primary production (PP) measurements (Williams 1984; Rivkin and Legendre 2001). To our knowledge, there are no published measurements of PR for the Laurentian Great Lakes of North America, with the exception of Lake Superior (Biddanda and others 2001).

Microbial biomass dominates the plankton in Lake Michigan (Fahnenstiel and others 1998), as in oligotrophic marine ecosystems (Cho and Azam 1988). Past studies in Lake Michigan demonstrated organic substrate (C or N) limitation of bacterial production (BP), (Gardner and others 1989) and inorganic phosphorus (P) limitation of PP (Stoermer and others 1978). Earlier studies of BP (but not bacterial respiration [BR]) also suggested that bacterial C demand may not be met by phytoplankton PP alone, implying that allochthonous inputs are required (Scavia and others 1986; Scavia and Laird 1987). It has been suggested that DOC built up during the winter–spring season and nutrients derived from resuspended benthic sediments as well as river runoff may fuel heterotrophic C demand in the southern Lake Michigan basin (Eadie and others 1984; Cotner and others 2000). In the present study, our objective was to assess the contribution of autochthonous and allochthonous subsidies (analogous to the fat reserves of "love handles" in humans) as C sources for organisms living in the euphotic zone of southern Lake Michigan.

## MATERIALS AND METHODS

Lake Michigan is the sixth largest lake in the world in surface area as well as volume (Beeton 1984). During the winter and summer of 1999 and 2000, we quantified plankton biomass and respiration and measured bacterial abundance, growth, and respiration in the surface waters (less than 10 m) of southern Lake Michigan (Figure 1). Water samples were collected from one to five discrete depths in the water column with 10-L Niskin bottles equipped with silicon O-rings and closure bands. Most of the samples were obtained during four cruises of the R/V *Lake Guardian* (March 1999, June 1999, March 2000, and May 2000); additional samples were obtained from two cruises of the R/V *Laurentian* (March 1999 and March 2000). Detailed respiration measurements were made on water samples collected from a depth of 5 m at eight sites during 1999 and six sites during 2000, representing nearshore and offshore locations.

For the enumeration of heterotrophic bacterial abundance (BA), a 5-ml aliquot of each water sample was preserved with 2% final concentration of 0.2 μm-filtered formaldehyde. At the end of each day, 1-ml subsamples were acridine orange–stained, filtered onto 0.2-μm black Poretics filters, mounted on slides, and frozen (−80°C) until observation by epifluorescence microscopy (Hobbie and others 1977). Between 20 and 40 fields of view and a minimum of 300 cells were examined for every sample.

Bacterial production (BP) was estimated from rates of protein synthesis using [³H]-leucine (Simon and Azam 1989) supplied at saturating levels (20 nM) to 10-ml lake samples in dark incubations at in situ temperatures. Rates of [³H]-leucine incorporation were converted to bacterial C production using the standard conversion factor of 2.3 kg C produced per mole of leucine incorporated (Simon and Azam 1989). Saturation and time-course uptake curves were determined once during every research cruise.
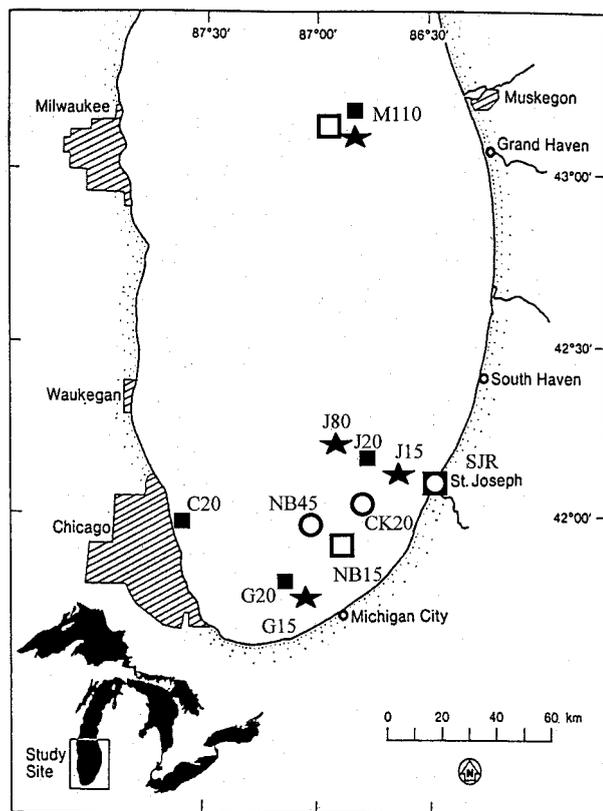
**Figure 1.** Location of sampling sites in southern Lake Michigan during 1999 (March, filled squares; June, filled stars) and 2000 (March, open circles; May, open squares). Each site is described by letters, which refer to the transect (C = Chicago, CK = Cook, G = Gary, J = St. Joseph, M = Muskegon, NB = New Buffalo, SJR = St. Joseph River), and numbers, which refer to the isobath (in meters). Site locations are only approximate; for exact bearings, refer to http://www.glerl.noaa.gov/eegle/cruises.

Total community (or plankton) and bacterial respiration were measured by following changes in dissolved oxygen ($O_2$) in sealed 300-ml biological oxygen demand (BOD) bottles during dark incubations of unfiltered (PR) and less than 1 μm water fractions (BR), respectively, at in situ temperatures (Biddanda and others 1994) (Figure 2). The less than 1-μm water fraction was generated by gently pumping water through a polycarbonate Nuclepore cartridge filter (1-μm pore size). We filtered no more than 20 L of a given sample through a filter cartridge at a time and backflushed the filters with Nanopure water (Barnstead, Dubuque, Iowa) be-

tween samples. Our monitoring of bacterial abundance in unfiltered and less than 1-μm fraction samples revealed that more than 95% of the heterotrophic bacteria present in the water samples consistently passed through the filter and significant numbers of cyanaobacteria were not found in the filtrate.

The possibility of artifacts arising from size-fractionation and long-term incubations were of concern. Therefore, parallel samples were incubated for monitoring changes in BA and BP along with time-course dark incubations measuring the decline in dissolved $O_2$ for the estimation of respiration (Figure 2). A comparison of the results from unfiltered and less than 1-μm water fraction samples suggested that, in general, there was a tendency for both BA and BP to increase over time (also see Biddanda and others 1994; Pomeroy and others 1994). However, the fact that both BA and BP were consistently similar in both treatments (unfiltered and less than 1-μm water fractions) at the beginning of the experiments (time zero), suggested that initial conditions were unchanged by filtration (see also Biddanda and others 1994).

Measurement of respiration as the decrease in dissolved $O_2$ concentrations in a given water mass can be directly related to the oxidation of organic matter in aerobic systems (Hopkinson and others 1989; Williams 1984). In cold and oligotrophic waters such as Lake Michigan, where we expected very low rates of respiration, we routinely ran respiration incubations for up to 4 days to obtain measurable changes in dissolved $O_2$ concentrations (Figure 2). Dissolved $O_2$ measurements were made with a Mettler DL 21 titrator (Hightstown, New Jersey) by automated Winkler titration based on potentiometric end-point detection (Graneli and Graneli 1991). As a rule, we were unable to obtain significant rates of respiration when the rates were close to or below 20 nM $O_2$ h$^{-1}$ because regressions of time versus dissolved $O_2$ concentrations were nonlinear. It is our experience, and that of others (Pomeroy and others 1994), that multipoint and replicate measurements of dissolved $O_2$ concentrations over the shortest possible time yield the most realistic estimates of respiration.

Bacterial growth efficiency (BGE) was estimated as the ratio of net production (growth) to gross production (growth + respiration). Net bacterial C production (BP) was estimated from time-averaged rates of [$^3$H]-leucine incorporation in parallel incubations of less than 1 μm water fractions (see Figure 2). The amount of C respired by bacteria (BR) was estimated from $O_2$ consumption in the less than 1-μm size fraction, assuming a respiratory quotient
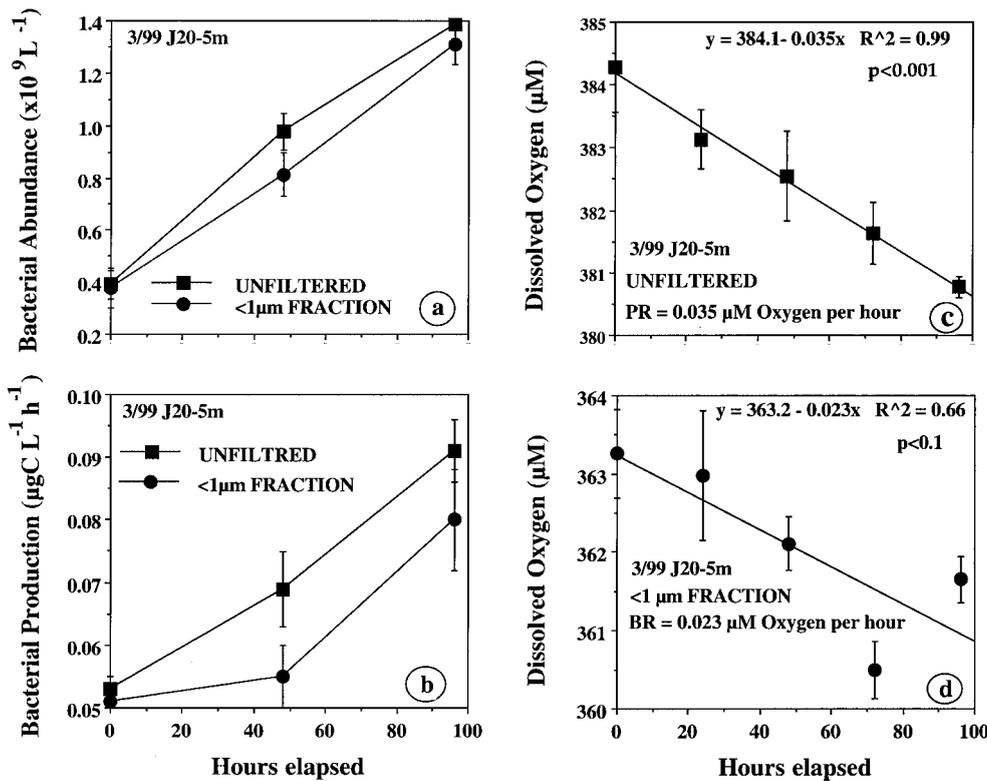
**Figure 2.** Tracking parallel changes in (**a**) bacterial abundance (BA), (**b**) bacterial production (BP) and dissolved oxygen in dark incubations during the measurement of (**c**) plankton respiration (PR) in unfiltered water and (**d**) bacterial respiration (BR) in the less than 1 μm water fraction in Lake Michigan. Example shows results from experiments conducted with water samples collected from a depth of 5 m at Station St. Joseph, located in southeastern Lake Michigan, having a total water column depth of 20 m during March 1999 (3/99 J20-5m).

of 1 and Redfield stoichiometry of respired organic matter (Redfield and others 1963). C flux through the bacteria (CFTB) is equal to BP + BR.

Samples for dissolved organic C (DOC) analysis were passed through precombusted (4 h at 450°C) Whatman GF/F glass fiber filters under low vacuum pressure (less than 10 cm of Hg). The filtrate was collected directly in precombusted glass vials (4 h at 550°C), which were sealed with Teflon-lined caps and stored frozen until analysis. DOC concentrations were determined by high temperature (680°C) oxidation with a Shimadzu (Kyoto, Japan) TOC 5000 carbon analyzer (Benner and Strom 1993).

Water samples for chlorophyll were filtered onto GF/F filters, frozen in the dark, extracted in acetone, and analyzed fluorometrically (Parsons and others 1984). Total suspended matter (TSM) was determined gravimetrically (American Public Health Association 1992). Vertical mass flux was estimated from moored sediment traps (Eadie and others 1984). Representative average values for chlorophyll, TSM, and vertical mass flux corresponding to the sampling dates and locations in the present study were obtained from the EEGLE (Episodic Events Great Lakes Experiment) data web page (http://www.glerl.noaa.gov/eegle). Total dissolved P levels were determined on a Technicon

Auto Analyzer II system (Saskatoon, Canada) using standard colorimetric procedures following sample digestion with 5% potassium persulfate (Menzel and Corwin 1965).

PP was measured over 24-h incubations under simulated in situ light and temperature by monitoring the uptake of $^{14}C$-sodium bicarbonate (Fahnenstiel and Scavia 1987; G. L. Fahnenstiel, personal communication). Most of the PP in southern Lake Michigan (65%–95%) occurred in less than 10 m water, with peak activity occurring between 0 and 5 m (Fahnenstiel and Scavia 1987; G. L. Fahnenstiel unpublished). Because PP data for 2000 were not yet available, we assumed that the rates were similar to 1999 values; therefore we used an average PP value for comparison to heterotrophic C demand during 2000. The rates we report agree well with previously published PP data for Lake Michigan (Fee 1973; Fahnenstiel and Scavia 1987).

To examine C dynamics in the euphotic zone, we integrated pools and rates through the 10-m depth. Depth-averaged estimates of biomass and concentrations were made by adding up all available measurements from the upper 10 m of the water column and dividing the result by the number of measurements. Depth-integrated water column estimates of rate processes were calculated by step-wise additions of m³ units to a depth of 10 m (0–10

m). Respiration measurements were made with samples obtained from the 5-m depth. We extrapolated measured respiration at 5 m from 0 to 10 m because this is approximately equal to the depth of the mixed-layer and euphotic zone. Moreover, most of the PP in Lake Michigan also occurs in less than 10 m of water (see above). Correlations between parameters were based on linear regressions, and comparisons between parameters were based on the two-tailed $t$-test for independent samples (McClave and Sincich 2000).

Most of the river discharge into the southern Lake Michigan basin comes from western Michigan (Eadie and others 1984). Daily river discharge data for the four major western Michigan rivers (Muskegon, Grand, St. Joseph, and the Kalamazoo) were obtained from the United States Geological Survey (USGS) web site (http://water.usgs.gov/). These estimates are conservative because for three of the rivers (Muskegon, Grand, and St. Joseph) the flow data were obtained from locations considerably upstream of the lake due to a lack of recording stations (after 1995) in the vicinity of the river mouth. Discharge data for 2000 were not yet available. However, a record of the past 5 years shows that the seasonal trends and the magnitude of river flow are similar from year to year.

## RESULTS

BA in southern Lake Michigan during March and June 1999 ranged from approximately 0.5 to 2.5 × $10^9$ $L^{-1}$. Depth-averaged BA values for March ($1.17 \times 10^9$ $l^{-1}$; $n = 16$) and June 1999 ($0.95 \times 10^9$ $L^{-1}$; $n = 16$) were not significantly different from each other ($P > 0.05$). BA during March and May 2000 were similar to the values for 1999 and ranged from approximately 0.3 to 2.2 × $10^9$ $L^{-1}$. Depth-averaged BA values for March ($1.14 \times 10^9$ $L^{-1}$; $n = 12$) and May 2000 ($1.31 \times 10^9$ $L^{-1}$; $n = 12$) were also not significantly different ($P > 0.05$). There were also no significant differences between the average BA for 1999 ($1.06 \times 10^9$ $L^{-1}$; $n = 32$) and the average BA for 2000 ($1.22 \times 10^9$ $L^{-1}$; $n = 24$).

BP generally reflected the trends in bacterial abundance. BP values ranged from approximately 0.5 to 5.0 µg C $L^{-1}$ $d^{-1}$ over the course of the study. Depth-averaged values for March (2.7 µg C $L^{-1}$ $d^{-1}$; $n = 16$) and June 1999 (3.3 µg C $L^{-1}$ $d^{-1}$; $n = 16$) were not different from one another ($P > 0.05$). Similarly, depth-averaged values for March (1.5 µg C $L^{-1}$ $d^{-1}$; $n = 12$) and May 2000 (2.2 µg C $L^{-1}$ $d^{-1}$; $n = 12$) were not different from one another ($P > 0.05$). However, there were significant differ-

ences ($P < 0.05$) between the average BP for 1999 (3.0 µg C $L^{-1}$ $d^{-1}$) and the average BP for 2000 (1.9 µg C $L^{-1}$ $d^{-1}$). In the present study, overall BP rates were positively correlated with BA ($r^2 = 0.63$; $P < 0.05$).

The distribution of DOC in surface waters also reflected the distribution patterns of BA and BP; it averaged 214 µM ($n = 16$) in March 1999 and 178 µM ($n = 16$) in June 1999. In March 2000, DOC averaged 216 µM ($n = 12$) and 124 µM ($n = 12$) in May 2000. DOC concentrations in the present study were positively correlated with chlorophyll levels ($r^2 = 0.55$; $P < 0.05$). Chlorophyll levels averaged 1.6 µg $L^{-1}$ in March 1999, 1.9 µg $L^{-1}$ in June 1999, 2.8 µg $L^{-1}$ in March 2000, and 1.1 µg $L^{-1}$ in May 2000.

Under the prevailing low-temperature conditions (2–5°C during winter and 7–19°C during spring–summer), low rates of plankton metabolic activity were found (Table 1). On average, in 1999, summer rates of BR and PR were approximately seven-fold and approximately six-fold higher than winter rates, respectively. However, in 2000, only PR (not BR) varied significantly between the seasons. Furthermore, there were no differences in BR or PR interannually in 2000 ($P > 0.05$). We were unable to make respiration rate determinations of the bacterial fraction in some offshore sites (no data) where the rates were below the level of detection by our techniques (Table 1). Both BR ($r^2 = 0.51$; $P < 0.05$) and PR ($r^2 = 0.84$; $P < 0.001$) were positively correlated with water temperature.

The contribution of BR to PR was highly variable between 20% and 90%, and was not significantly different between years. There were no differences in the BR/PR ratio between seasons in 1999. However, there were significant seasonal differences in the BR/PR ratios in 2000: winter BR/PR was higher than summer BR/PR ratios ($P < 0.001$).

In both years, the water temperature increased by about 10°C from winter to spring, and estimated BGEs varied greatly (2%–49%). There was a negative relationship between BGE and temperature during the study period ($r^2 = 0.36$, $P > 0.05$) (Figure 3). CFTB varied between 0.006 and 0.160 µM C $h^{-1}$; despite a tendency to be higher in 2000 than 1999, it showed no significant interannual variability ($P > 0.05$). CFTB correlated positively with temperature ($P < 0.05$) and negatively with BGE (BGE = −184.8 CFTB + 26.2; $r^2 = 0.79$, $P < 0.001$), suggesting that at higher temperatures BR may increase relative to BP. In 1999, CFTB was approximately six fold higher during the summer than in the winter ($P < 0.05$); however, in 2000, there was no significant seasonal difference in

**Table 1.** Bacterial Production (BP), Bacterial Respiration (BR), Plankton Respiration (PR), Contribution of BR to PR (BR/PR), Bacterial Growth Efficiency [BGE = BP/(BP + BR)], and Carbon Flux through Bacteria (CFTB) in Lake Michigan

| Station | BP ($\mu$MC/h) | BR ($\mu$MO2/h) | PR ($\mu$MO2/h) | BR/PR (%) | BGE (%) | CFTB ($\mu$MC/h) |
|---|---|---|---|---|---|---|
| Winter 1999 (~4°C) | | | | | | |
| J-20 | 0.0048 | 0.0237 | 0.0355 | 66.6 | 16.8 | 0.0285 |
| G-20 | 0.0044 | 0.0107 | 0.0291 | 36.6 | 29.1 | 0.0151 |
| C-20 | 0.0020 | 0.0041 | 0.0174 | 23.6 | 32.7 | 0.0061 |
| M-110 | 0.0024 | no data | 0.0211 | 50.0[a] | 18.6[a] | 0.0129[a] |
| Average | 0.0034 | 0.0128 | 0.0257 | 42.3 | 24.3 | 0.0156 |
| Summer 1999 (~14°C) | | | | | | |
| J-15 | 0.0036 | 0.0361 | 0.1792 | 20.1 | 49.1 | 0.0396 |
| G-15 | 0.0028 | 0.1580 | 0.2080 | 75.9 | 1.7 | 0.1615 |
| J-80 | 0.0028 | no data | 0.2351 | 50.0[a] | 2.3[a] | 0.1203[a] |
| M-110 | 0.0052 | no data | 0.0380 | 50.0[a] | 21.4[a] | 0.0242[a] |
| Average | 0.0036 | 0.0974 | 0.1652 | 48.0 | 18.5 | 0.0864 |
| Winter 2000 (~2°C) | | | | | | |
| SJR | 0.0965 | 0.0670 | 0.1980 | 33.8 | 59.0 | 0.1635 |
| CK20 | 0.0082 | 0.0430 | 0.0480 | 89.5 | 16.0 | 0.0512 |
| NB45 | 0.0040 | 0.0790 | 0.0970 | 81.4 | 4.8 | 0.0830 |
| Average[b] | 0.0061 | 0.0610 | 0.0725 | 85.4 | 10.4 | 0.0671 |
| Summer 2000 (~12°C) | | | | | | |
| SJR | 0.1100 | 0.0380 | 0.0980 | 38.7 | 74.3 | 0.1480 |
| NB45 | 0.0090 | 0.0490 | 0.1210 | 40.4 | 15.5 | 0.0580 |
| M110 | 0.0100 | 0.0400 | 0.1130 | 35.3 | 20.0 | 0.0500 |
| Average[b] | 0.0095 | 0.0445 | 0.1170 | 37.8 | 17.7 | 0.0540 |

*No data, rates too low to be measured*
[a]*BGE and CFTB data calculated assuming BR = 1/2 PR*
[b]*Average values calculated excluding data from the St. Joseph River (SJR) site*
*For station locations, refer to Figure 1.*

CFTB. Depth-integrated CFTB varied interseasonally in 1999 but not in 2000 (Table 2). Wintertime CFTB and PR were both elevated in 2000 (193 and 209 mg C m$^{-2}$ d$^{-1}$, respectively) relative to 1999 (45 and 74 mg C m$^{-2}$ d$^{-1}$, respectively).

In 2000, the BP, BR, and PR measurements that we made in the St. Joseph River (one of the four major rivers draining into southeastern Lake Michigan) showed no significant interseason differences (Figure 1 and Table 1). In general, the rates of BP, BR, and PR were all elevated in the river relative to the lake. CFTB was about threefold higher in river water than in the lake. The BR:PR ratio averaged about 36%, which was lower than the overall average of 61% for the lake. River BGE averaged about 66%, which was considerably higher than the overall average of 18% for the lake (Table 1).

Comparison of CFTB to PP indicated that bacteria consumed a variable but substantial proportion of PP: 12% in winter 1999, 76% in summer 1999, 55% in winter 2000, and 44% in summer 2000 (Table 2). These results suggested that in
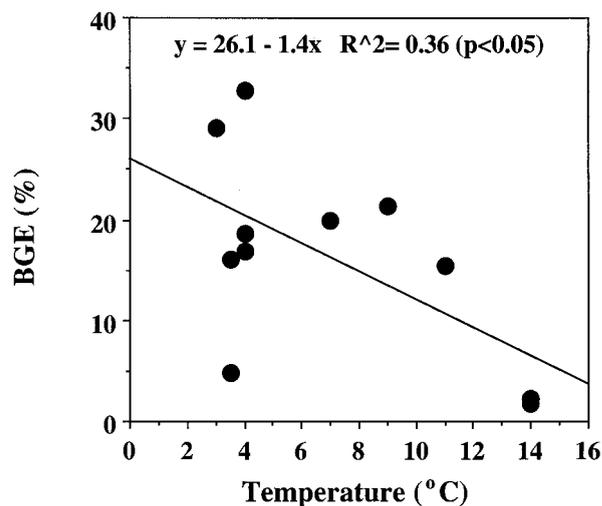


**Figure 3.** Relationship between bacterial growth efficiency (BGE) and water temperature during 1999 and 2000 in Lake Michigan.

winter 1999, much of the PP (around 88%) was available to support planktivorous grazers, for ex-

**Table 2.**  Depth Integrated (to 10 m) Values of Carbon Flux through Bacteria (CFTB), Plankton Respiration (PR), Primary Production (PP), PP Consumed by Bacteria (CFTB/PP), and PP Respired by Total Plankton (PR/PP) in Southern Lake Michigan during 1999 and 2000

| Season | Mean CFTB (mg C m$^{-2}$ d$^{-1}$) | Mean PR (mg C m$^{-2}$ d$^{-1}$) | Mean PP[a] (mg C m$^{-2}$ d$^{-1}$) | CFTB/PP (%) | PR/PP (%) |
|---|---|---|---|---|---|
| Low winter sediment resuspension activity | | | | | |
| Winter 1999 | 44.9 | 74.0 | 360 | 12.5 | 20.5 |
| Summer 1999 | 248.8 | 475.7 | 325 | 76.5 | 146.3 |
| High winter sediment resuspension activity | | | | | |
| Winter 2000 | 193.2 | 208.8 | 350 | 55.2 | 59.6 |
| Summer 2000 | 155.5 | 336.9 | 350 | 44.4 | 96.2 |

[a]*Average regional primary production (PP, n = 6 for winter 1999 and n = 12 for summer 1999. PP for both seasons in 2000 is assumed to be the average of the two seasons in 1999. PP estimates are from* $^{14}$*C-sodium bicarbonate uptake measurements in 24-h incubations under simulated* in situ *conditions (G. Fahnenstiel personal communication)).*

**Table 3.**  Seasonal Draw-Down of Dissolved Organic Carbon (DOC) in Comparison to Carbon Demand of Bacteria (CFTB) and Plankton Respiration of Carbon (PR) during 1998, 1999, and 2000 in Southern Lake Michigan

| Year and Source | Winter–Summer δDOC (mg C m$^{-2}$ d$^{-1}$) | Time-averaged CFTB (mg C m$^{-2}$ d$^{-1}$) | δDOC/CFTB (%) | Average PR (mg C m$^{-2}$ d$^{-1}$) | δDOC/PR (%) |
|---|---|---|---|---|---|
| 1998 Cotner and others (2000) | 73 | 120[a] | 61 | no data | no data |
| 1999 Present study | 29 | 146 | 20 | 275 | 11 |
| 2000 Present study | 91 | 174 | 53 | 273 | 33 |

[a]*Data calculated assuming a bacterial growth efficiency of 20% (Cotner and others 2000)*

port as particulate organic C, or to accumulate in the water column as DOC. On the other hand, during the summer, much less of the PP (around 24%) was available to support similar processes. During 2000, roughly half of PP was available to support other heterotrophic processes in both winter and summer.

In winter 1999, only around 20% of PP was respired by the plankton (Table 2). However, during the summer of 1999, PR exceeded PP (146%), indicating that the plankton required additional organic C sources of local PP at this time. Similarly, during the winter of 2000, about 60% of available PP was respired by the plankton, which left approximately 40% for other food web processes, export, or storage. However, during the summer of 2000, the plankton respired almost all of the PP (96%), leaving little for support of other food web processes.

DOC accumulated in lake water during the winter–spring period and was drawn down during the summer (Table 3). The magnitude of DOC draw-down in the present study (covering the years 1999 and 2000) was comparable to previous estimates made in 1998 (Cotner and others 2000). During these 3 years, the winter–summer DOC drawdown in Lake Michigan represented approximately 10%–20% of phytoplankton PP and amounted to approximately 20%–61% of CFTB and around 11%–33% of PR.

Wind-driven sediment resuspension events in southern Lake Michigan occur annually during the winter–spring transition period when the water column is unstratified, but at extremely variable spatial and temporal magnitudes (Eadie and others 1984; Mortimer 1988; Brooks and Edgington 1994; Cotner and others 2000). Evidence of variability in sediment resuspension activity was clearly reflected in total suspended matter (TSM) and mass flux data in sediment traps for the last 3 years (http://www.glerl.noaa.gov/eegle). Basinwide TSM values for the winter–spring (unstratified) period were elevated during 1998 (around 7 mg L$^{-1}$) and 2000 (around 4 mg L$^{-1}$) but reduced during 1999 (around 2 mg L$^{-1}$). Similarly, basinwide mass flux values for the winter–spring (unstratified) period were elevated in both 1998 (approximately 200 mg

**Table 4.** Composition and Quantities of Water Discharged by Four Major Western Michigan Rivers into Southeastern Lake Michigan: Comparison to In-lake Concentrations

| River or Parameter | DOC Average ($\mu$M C) | Total Dissolved P Average ($\mu$M P) | Annual Runoff 9/98 to 8/99 ($10^6$ m$^3$ d$^{-1}$) | Peak Runoff 12/98 to 4/99 ($10^6$ m$^3$ d$^{-1}$) | Multiyear Runoff 9/96 to 8/99 ($10^6$ m$^3$ d$^{-1}$) |
|---|---|---|---|---|---|
| Muskegon River | 860 | 0.68 | 2.0 | 2.6 | 2.3 |
| Grand River | 1870 | 0.87 | 9.0 | 12.0 | 10.2 |
| St. Joseph River | 430 | 0.55 | 7.5 | 10.0 | 9.6 |
| Kalamazoo River | 680 | 0.58 | 2.0 | 2.5 | 2.3 |
| Rivers Total | — | — | 20.5 | 27.0 | 24.0 |
| Rivers Average | 960 | 0.68 | 5.1 | 6.8 | 6.0 |
| Lake Michigan Average | 180 | 0.06 | — | — | — |

DOC, dissolved organic carbon; P, phosphorus
Total dissolved P data from T. Johengen (personal communication)

C m$^2$ d$^{-1}$) and 2000 (approximately 180 mg C m$^2$ d$^{-1}$) but reduced in 1999 (approximately 140 mg C m$^2$ d$^{-1}$). Together with evidence from real-time satellite images, the data demonstrated that 1998 and 2000 were years characterized by stronger winter resuspension activity than 1999 (also see Cotner and others 2000).

One of the potential sources of allochthonous organic C was riverine DOC input. On average, the four major rivers that empty into southern Lake Michigan contained fivefold higher DOC levels and 10-fold higher total dissolved P (TDP) than the lake (Table 4). Dissolved C:P ratios (DOC/TDP) averaged about 1400 for the rivers and about 3000 in the lake. This compositional difference may be reflected in the high BGE (around 66%) recorded for the St. Joseph River during both seasons in 2000 (Table 1). The prevalence of such high river BGE suggests that riverine DOC was of high nutritional quality for bacterial growth.

River discharge peaks during the months of December through April; this seasonality in river flow was seen repeatedly between 1996 and 1999. The annual average for 1998–99 was similar to the multiyear average for years 1996–99, suggesting that there was little interannual variability in river discharge. The annual total discharge from these four major rivers (around $25 \times 10^6$ m$^3$ d$^{-1}$) provided approximately 10 km$^3$ y$^{-1}$, which is about 1% of the volume of the southeastern Lake Michigan basin (1100 km$^3$) (Cotner and others 2000).

## DISCUSSION

For a long time, aquatic ecologists considered lakes and oceans in general to be net autotrophic systems fueled primarily by planktonic PP (Azam and others 1983; Cole and others 1988). However, several recent studies in oligotrophic limnetic and marine waters have shown that PP:PR is less than 1 (Smith and Hollibaugh 1993; del Giorgio and others 1997; Cole 1999; but see Carignan and others 2000). The observations that most temperate lakes are supersaturated in $CO_2$ (Cole and others 1994) and that terrigenous organic matter is rapidly utilized by aquatic bacteria (Tranvik 1992; Amon and Benner 1996) and has a relatively short residence time in the aquatic habitat (Opsahl and Benner 1997; Hedges and others 1997) all support the view that aquatic heterotrophy is subsidized by terrestrial production. Therefore, the role of aquatic bacteria in linking terrestrial PP to aquatic secondary production (*sensu* Cole 1999) is an essential aspect of how lakes function. Results from the present study demonstrate that this linkage function is extremely important to ecosystem metabolism, even in very large bodies such as the Great Lakes.

### Variability in Bacterial Growth Efficiency

BGEs have great relevance to C dynamics because most aquatic metabolism is microbial (Azam 1998) and relatively little of the consumed organic C is assimilated (del Giorgio and others 1997; Biddanda and others 2001). In the present study, BGEs varied between 2% and 49%, which is in the range of values commonly reported for natural waters (del Giorgio and Cole 1998; Biddanda and others 2001). The observed variability in BGEs may reflect variability in available substrate quality for bacterial nutrition, and/or variability in water temperature, or the interactive effects of substrate and temperature (del Giorgio and Cole 1998; Pomeroy and

Wiebe 2001; Rivkin and Legendre 2001). Some of the variability could also be a reflection of errors inherent in the two methods (BP and BR) used for its estimation. However, we have tried to minimize artifactual variability by consistently using the same protocols and by tracking BA, BP, and BR in parallel incubations in our studies (also see Biddanda and others 1994; Pomeroy and others 1994) (Figure 2).

It has been argued that bacteria grow less efficiently in the summer than in the winter because maintenance costs are likely to be highest at elevated temperatures (Sherr and Sherr 1996; Cimbleris and Kalff 1998). At low temperatures, such as those prevailing in Lake Michigan during the winter (2–4°C), bacterial metabolism is suppressed relative to phytoplankton growth (Pomeroy and Deibel 1986) (Table 1). Such winter minima in BP and BR have been recorded over a wide range of latitudes (Griffith and Pomeroy 1995; Pomeroy and Wiebe 1993). Our results for 1999, where winter respiration was severalfold lower than summer rates, were consistent with these observations. Low winter water temperatures and low BR may allow substantial accumulation of PP as DOC or particulate organic carbon (POC) in the water column or allow POC to fall to the lake floor without concurrent heterotrophic consumption.

At low temperatures, bacteria require increased substrate concentrations to grow and respire at rates comparable to those under high temperatures (Pomeroy and Wiebe 2001). Enhanced substrate levels can compensate for the temperature suppression of bacterial metabolism at very low temperatures (for example, winter minima). In the present study, winter respiration was elevated in 2000 relative to 1999. Although water column DOC levels were comparable during both years, benthic resuspension occurring during the winter may have contributed to the observed high levels of respiration during 2000 and a threefold higher drawdown of DOC in 2000 compared to 1999. Consistent with this argument, we observed very high rates of heterotrophic bacterial metabolism in the nearshore region of lake Michigan during a large resuspension event in 1998 (Cotner and others 2000).

## Temperature Response of Bacteria and Implications for Climate Warming

We observed a negative relationship between BGE and water temperature in Lake Michigan (Figure 3), as some investigators have hypothesized (Sherr and Sherr 1996) and others have shown empirically (Rivkin and Legendre 2001). Further, CFTB was maximized at elevated temperatures. Results also suggest that the bulk of the CFTB at elevated tem-

peratures was likely to be channeled toward respiration rather than growth.

Recently, Rivkin and Legendre (2001) demonstrated a negative relationship between BGE and temperature in a survey of marine ecosystems. In their study, temperature alone explained approximately 54% of the variability in BGE,—a finding similar to our results. Rivkin and Legendre's (2001) results indicated an approximate 2.5% decrease in BGE per °C increase, whereas our results from Lake Michigan showed an approximate 1.4% BGE decrease per °C. Variability and interactive effects between DOC quantity and quality and temperature (Pomeroy and Wiebe 2001) may account for the remainder of the variability in BGE in Lake Michigan and other aquatic systems.

Wiebe and Pomeroy (1991) argue that even a slight warming of the water in high-latitude systems is likely to produce large-scale changes in food web structure as well as function—first, as a result of differences in the relative sensitivities of bacteria and algae to temperature and, second due to the early onset of water column stratification. Warming trends, such as the increased duration of summer stratification over recent years in the Laurentian Great Lakes region (McCormick and Fahnenstiel 1999), may elevate respiratory losses of C via bacteria due to reduced BGE at high temperatures. Consequently, this is likely to result in decreased net storage of organic C in the water column or sediments. However, this scenario does not take into account the effects of temperature on PP. Furthermore, increased seston C:P ratios at higher temperatures (J. B. Cotner unpublished) may offset increased respiratory losses. Clearly, the sensitivity of complex aquatic food webs to changing temperatures and other climate variables needs to be studied in terms of ecosystem-level functional responses.

## Bulk Inventory, Seasonality, and Interannual Variability

BA, chlorophyll, and DOC levels found in the present study were similar to those reported for Lake Michigan in earlier studies (Moll and Brahce 1986; Scavia and others 1986; Scavia and Laird 1987; Cotner and others 2000) and were in the range of values reported for a wide variety of limnetic and marine systems (Cole and others 1988; Simon and others 1992; Biddanda and others 2001). The values for Lake Michigan were somewhat higher than those of the oligotrophic Lake Superior, but they were lower than those found in eutrophic waters (Biddanda and others 2001). During 1999–2000, both phytoplankton biomass and

BA remained relatively invariant between seasons and years, whereas DOC varied seasonally—but not between years. The results from the DOC inventory for both years (1999 and 2000) in Lake Michigan suggested that there was a substantial accumulation of DOC in the wintertime, which is apparently drawn down in the summer. The winter–summer drawdown of DOC was as much as 36–92 $\mu$M C and may be an important part of the C balance in the lake.

Our [3H]-leucine–based measurements of BP rates (approximately 0.5–5.0 $\mu$g C $L^{-1}$ $d^{-1}$) were about an order of magnitude lower than those reported for Lake Michigan in the 1980s using [3H]-thymidine (2–90 $\mu$g C $L^{-1}$ $d^{-1}$) (Scavia and others 1986; Scavia and Laird 1987). Because the [3H]-leucine method (Simon and Azam 1989) and the [3H]-thymidine method routinely yield comparable estimates of BP rates in nature (Biddanda and others 1994 and citations therein), we could not ascribe any particular methodological reason for this discrepancy. However, our BP measurements were similar to more recent estimates in Lake Michigan (Cotner and others 2000) and were in the range of values reported for a wide variety of oligotrophic limnetic and marine systems that have comparable levels of chlorophyll (Cole and others 1988; del Giorgio and others 1997; Biddanda and others 2001).

In size-fractionation experiments, the contribution of BR to PR was always substantial (20%–90%)—indicative of a major role for bacterioplankton in pelagic C flux in southern Lake Michigan. The contribution of BR to PR routinely exceeds 50% in both freshwater and marine environments (del Giorgio and others 1997; Biddanda and others 2001). Results from the present study are consistent with the view that heterotrophic bacterioplankton are responsible for a large fraction of the $O_2$ consumption and C oxidation in the water column (Sherr and Sherr 1996; del Giorgio and others 1997; Biddanda and others 2001).

The rates of BR (0.01–0.15 $\mu$M $O_2$ $h^{-1}$) and PR (0.02–0.24 $\mu$M $O_2$ $h^{-1}$) that were measured in the present study were typical of those found in oligotrophic waters and were well within the range of values reported for natural waters (del Giorgio and others 1997; Biddanda and others 2001). There was no significant interannual variability in BR and PR during the 2 years of study. However, both BR and PR increased severalfold from winter to summer in 1999—but not in 2000. Enhanced benthic resuspension activity may have stimulated elevated BR and PR during the 2000 winter. Sediment resuspension events occur intermittently during the winter

months when the water column is unstratified and are dependent on climatological factors (Eadie and others 1984), which may generate profound interannual variability within lake basins.

## Fate of PP and In-lake C Balance

Imbalances between the C requirements of the plankton and C availability are often reported in the literature. PP:PR ratios in several oligotrophic Canadian lakes were always below one, suggesting that planktonic metabolism in these lakes was subsidized by allochthonous inputs ( del Giorgio and others 1999; Cole 1999). In some other Canadian lakes, however, P:R ratios were equal to and exceeded one (Carignan and others 2000). The question of the fate of PP and within-system C balance is key to understanding the overall role of aquatic ecosystems within the biosphere.

Few studies have examined seasonal changes in planktonic metabolic rates (Pomeroy and Wiebe 1993; Griffith and Pomeroy 1995). Although it is clear that small lakes and other water bodies are influenced by terrestrial C (Wetzel 1984, 1992), it is still unclear whether large oligotrophic lakes are net autotrophic (Carignan and others 2000) or net heterotrophic (del Giorgio and others 1999) on an annual basis, and the answer may depend to a large extent on the particularities of a specific basin. In the present study, PP was sufficient to support the C demand of the heterotrophic bacteria and all the plankton during the winter (PP > PR) but not during the summer (PP $\leq\leq$ PR). If we consider the total flux of C through the plankton (sum of PR and plankton secondary production, the latter of which was not measured in this study), this quantity would be expected to easily exceed the amount of available PP, especially during the summer.

Additional sources of C may include drawdown of DOC accumulated during winter–spring (Pomeroy and others 1991; Copin-Montegut and Avril 1993; Carlson and others 1994; Williams 1995; Cotner and others 2000), resuspended benthic sediments (Eadie and others 1984; Brooks and Edgington 1994; Cotner and others 2000), and inputs of terrigenous production into the lake (Eadie and others 1984; Mortimer 1988; Opsahl and Benner 1997; Hedges and others 1997). If these allochthonous sources are an important part of Lake Michigan C dynamics, it suggests that even large water bodies, such as Lake Michigan are functioning under a terrigenous production subsidy, as has been hypothesized by Wetzel (1984, 1992). Based on our results, we hypothesize that in temperate aquatic ecosystems the metabolic activities of autotrophs and heterotrophs are typically unbal-

anced during the winter–spring when the water column is unstratified (PP > PR) and closely balanced during the summer–fall when the water column is stratified (PP = PR or PP < PR), (Pomeroy and Wiebe 1993; Griffith and Pomeroy 1995; Sherr and Sherr 1996).

## Role of DOC Drawdown

Several studies have reported evidence of significant levels of DOC buildup in various limnetic and marine systems over the winter–spring period that is then followed by drawdown through the summer–fall season (Scavia and Laird 1987; Pomeroy and others 1991; Copin-Montegut and Avril 1993; Carlson and others 1994; Williams 1995; Cotner and others 2000). Results from the present study also demonstrate substantial drawdown of DOC between winter and summer that could fuel 20%–53% of CFTB and 11%–33% of PR (Table 3). Previous Lake Michigan work showed DOC drawdowns that were comparable to those of the present study: 29 and 91 mg C m$^2$ d$^{-1}$ during 1999 and 2000, respectively (Scavia and Laird 1987, 35 mg C m$^2$ d$^{-1}$ during 1980; Cotner and others 2000, 73 mg C m$^2$ d$^{-1}$ during 1998). These observations reinforce the idea that the winter–summer DOC drawdown occurs seasonally and that the magnitude of the drawdown may vary interannually.

Several processes may be responsible for the accumulation of DOC in Lake Michigan during the winter–spring months. The selective suppression of heterotrophic bacteria over autotrophic phytoplankton at the low temperatures prevailing in the winter (2–4°C) may be one such cause (Pomeroy and Deibel 1986). Excess PP could result in accumulated DOC in the water column, or it could be exported as POC to the sediments. Records for the last several years show that PP in Lake Michigan during the winter was routinely comparable to, and occasionally even higher than, that during the summer (Fee 1973; Fahnenstiel and Scavia 1987).

Other reasons for the accumulation and retention of high levels of DOC in the winter months may involve nutrient limitation and grazing control of heterotrophic bacteria (Cotner and others 1997; Thingstad and others 1997), as well as interaction between low temperatures and substrate concentrations that may regulate bacterial metabolism (Pomeroy and Wiebe 2001). DOC is also produced by various other processes, including direct release from phytoplankton, inefficient grazing, and the excretion, defecation, and death of organisms (Karl 1999). Additionally, river discharge into the lake peaks during the winter–spring period, resulting in extensive accumulations of river-derived dissolved

organic matter in the coastal lake that can be discerned by satellite imagery (Mortimer 1988). River water is characterized by five-fold higher DOC and 10-fold higher TDP concentrations, suggesting that fluvial DOC and TDP that accumulates within the lake may eventually fuel bacterial metabolism and PP during the winter–spring season. Prevailing high winter BGE together with low CFTB (Table 1) may also contribute to DOC accumulation.

## Role of Sediment Resuspension

Extensive sediment trap studies carried out in the southern Lake Michigan basin showed that winter sediment resuspension events are an important mechanism coupling sediment diagenesis to water column processes (Eadie and others 1984). In experimental coastal marine mesocosms, Wainright (1987) demonstrated that resuspended sediments stimulate BP in the overlying water column. More recent work in Lake Michigan (Cotner and others 2000) demonstrated the intense stimulation of winter heterotrophy by sediment resuspension. Of particular interest was their observation that, during resuspension events, heterotrophic processes seemed to dominate water column metabolism. Heterotrophic BP increased, possibly in response to inorganic/organic substrates released from resuspended sediments or decreased competition with autotrophs, whereas autotrophic PP decreased because light transparency was reduced by resuspended sediments (Cotner and Wetzel 1992; Cotner and others 2000).

Results from the present study are consistent with these earlier findings and suggest a key role for sediment resuspension in this lake basin. Winter resuspension events resulted in elevated winter heterotrophy (BR and PR) to levels that were similar to summer rates in the nearshore region. The net effect of winter sediment resuspension in any given year was to dampen seasonal differences. Based on the differences in heterotrophy between more (2000) and less (1999) intense sediment resuspension years (Table 2), we estimate that approximately 40% of CFTB and roughly 30% of PR during the winter, and approximately 10% of CFTB and roughly 7% of PR on an annual basis could be supported by resuspended sediments. Thus, intermittent resuspension of sediments during the unstratified period played a key role in sustaining heterotrophic C demand within the water column, in recycling sedimentary C, and in modulating interannual variability in this lake basin. However, it should be noted that such resuspension-stimulated heterotrophy is mostly restricted to the coastal lake zone (less than 60 m) (Cotner and others 2000).

There may be multiple sources for the origin of organic matter in resuspended sediments. A primary source is likely phytoplankton PP in the overlying water column. A secondary source may be terrigenous organic matter imported via riverine discharge as well as atmospheric deposition. If phytoplanktonic PP exceeds heterotrophic bacterial metabolism (CFTB) during winter, excess PP could be deposited to the sediments; whereas in summer, when PP does not exceed CFTB, less particulate organic matter (POM) is deposited to sediments (Pomeroy and Deibel 1986; Pomeroy and Wiebe 1993). Our previous work during winter resuspension in 1998 (Cotner and others 2000) suggested that intense winter heterotrophy in the water column was likely stimulated by the release of both C and P from resuspended sediments (Eadie and others 1984; Brooks and Edgington 1994). In fact, earlier estimates of mass fluxes of sedimenting C in the water column peaked during winter resuspension and amounted to approximately 5% of annual PP in Lake Michigan (Fee 1973; Eadie and others 1984; Fahnenstiel and Scavia 1987).

There may have been important interactions between DOC drawdown and sediment resuspension in Lake Michigan. A comparison of seasonal DOC values between the years with intense winter sediment resuspension (1998 and 2000) and the year with reduced winter sediment resuspension (1999) revealed that there was more DOC drawdown and more winter heterotrophy in the high-resuspension years (Tables 2 and 3). DOC drawdown in 2000 was about three times higher than it was in 1999. Rates of winter heterotrophy were three to four times higher in 2000 than in 1999. Episodic sediment resuspension events may also be a source of DOC and nutrients to the water column (Eadie and others 1984; Brooks and Edgington 1994; Cotner and others 2000).

## Role of Terrigenous Inputs

Small water bodies are known to be dominated by terrigenous materials (Wetzel 1984, 1992; Molot and Dillon 1996). Large water bodies such as the Great Lakes and the oceans receive much less terrestrial material proportional to their volume (Kirchman 1997; Carignan and others 2000). Many other investigators, however, have argued that even oligotrophic large lakes and oceanic systems are strongly impacted by terrigenous organic matter and nutrients (Wetzel 1984; Cole 1999) and have suggested that aquatic ecosystems in general are likely to be significantly subsidized by terrigenous inputs. Previous work in oligotrophic Lake Michigan has also shown that there is a need for allochthonous subsidies to sustain heterotrophic C demand (Scavia and others 1986; Scavia and Laird 1987; Cotner and others 2000).

The idea of terrestrial materials influencing aquatic systems (Gergel and others 1999) is somewhat analogous to the "outwelling" concept, where estuaries subsidize coastal ecosystems by discharging excess nutrients and organic matter (Odum 1971). Previous estimates of riverine inputs from four major rivers to Lake Michigan alone amounted to approximately 20 mg C $m^2 d^{-1}$ (Eadie and others 1984), which is equal to about 5% of lake PP (approximately 380 mg C $m^2 d^{-1}$) (Fee 1973; Fahnenstiel and Scavia 1987). Atmospheric deposition of C to the southern Lake Michigan basin was estimated to be approximately 14 mg C $m^2 d^{-1}$ (Strand 1978), which is about three-fourths the riverine contribution and is equal to about 3.5% of the PP in Lake Michigan. Additional inputs from direct runoff from smaller rivers, streams, direct precipitation, and groundwater discharge may contribute at least another 5 mg C $m^2 d^{-1}$. Thus, alltogether, allochthonous inputs of C could contribute an amount equal to approximately 10% of the annual PP in Lake Michigan and equals/exceeds the net flux of C into lake sediments (around 22 mg C $m^2 d^{-1}$) (Eadie and others 1984), supporting the argument that this lake is "net heterotrophic."

Further support for this supposition comes from estimates of riverine C inputs. River discharge for the four major rivers alone amounted to about 1% of the volume of the southeastern Lake Michigan basin. Because river water, on average, was characterized by fivefold higher DOC and 10-fold higher TDP levels than Lake Michigan water, we can conservatively expect that riverine DOC could support 5% of bacterial C demand and that riverine TDP could support 10% of PP in southern Lake Michigan. Other terrestrial inputs (smaller rivers, streams, groundwater discharge, and atmospheric precipitation) may equal the input from the four major rivers alone (Eadie and others 1984). Thus, all terrigenous inputs together may support as much as 10% of CFTB and 20% of PP in Lake Michigan (Figure 4).

The watershed of southern Lake Michigan is mostly agricultural and urban. Our detailed measurements of BP, BR, and PR in river water during the winter and summer of 2000 lend support to the idea that riverine dissolved organic matter (DOM) was utilized at very high BGEs by the bacterioplankton (average BGE in river, around 66%) (Table 1). These results also suggest that riverine DOM may be of higher nutritive quality than lake DOM to bacteria (average BGE in lake, around 18%)

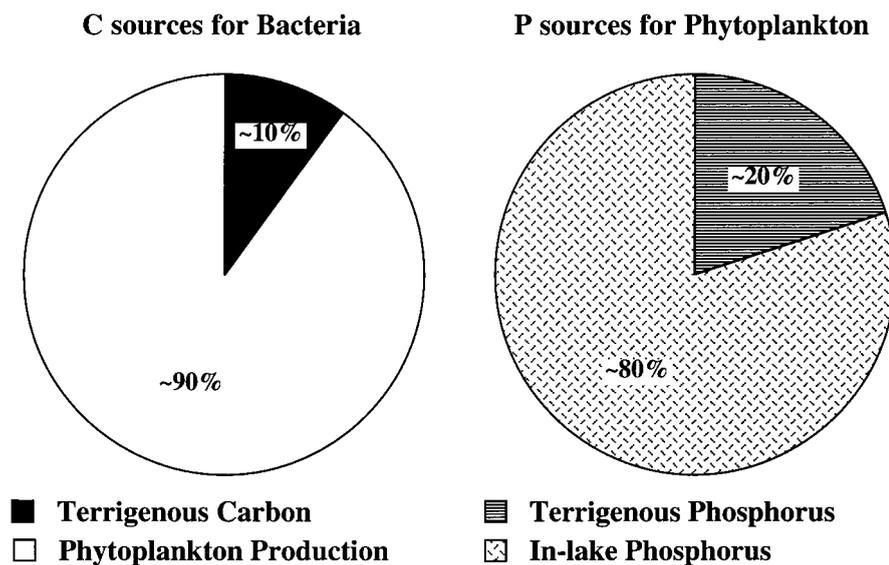**C sources for Bacteria**     **P sources for Phytoplankton**

Figure 4. Conceptual diagram of the proportions of annual bacterial metabolism and phytoplankton production that are supported by in-lake primary production and terrigenous inputs in the euphotic zone of southern Lake Michigan.

■ **Terrigenous Carbon**          ▤ **Terrigenous Phosphorus**
□ **Phytoplankton Production**     ▨ **In-lake Phosphorus**

(Table 1) and may fuel enhanced bacterial metabolism upon mixing with lake water. High BGEs result in minimal respiration of the DOC pool, allowing substantial riverine DOC and POC to be transported into the lake following discharge.

Recently, the magnitude of the influence of the Mississippi and the Orinaco rivers in adjacent coastal marine environments has been described in detail using SeaWiFS satellite imagery (Salisbury and others 2001). Our study indicates that the coastal limnetic environments of large lakes are also greatly influenced by fluvial inputs. As in the past (Mortimer 1988), satellite imagery may be usefully employed in the future to characterize the influence of river-borne constituents in the dynamics of large lakes receiving substantial riverine inflow.

## CONCLUSIONS

Respiration by the plankton constitutes a major pathway for pelagic C flux in southern Lake Michigan. BGEs are variable in nature and are inversely related to water temperature and CFTB. Planktonic C demand in the surface waters of Lake Michigan is seasonally unbalanced with respect to available PP. We found that (a) excess winter–spring PP resulted in increased DOC concentrations that may support approximately 20%–53% of CFTB and approximately 11%–33% of PR, (b) resuspended sediments containing "ghosts of production past" (Cotner and others 2000) may fuel about 10% of CFTB and about 7% of PR, and (c) terrigenous inputs may be equivalent to about 10% of CFTB and PR in Lake Michigan on an annual basis. Additionally, terrigenous inputs of P may support approximately 20%

of Lake Michigan PP. Therefore, even large oligotrophic lakes benefit substantially from terrestrial subsidies.

Microorganisms—both heterotrophs and autotrophs—link terrigenous organic matter and nutrients to aquatic productivity. Appreciation of such land–water linkages should enable us to gain a better understanding of the anthropogenic impacts that originate on land but also extend to lakes and oceans. However, the critically important subject of the "study of linkages amongst ecosystems" remains in its infancy (Gorham 1996). Nearly one and a half centuries ago, Henry David Thoreau (1854) correctly captured the essence of a lake with his observation that "a lake is the earth's eye." It should come as no surprise, then, that we see so many signs of the surrounding landscape reflected within the lakes.

ered by T. Johengen, B. Eadie, and A. Winkelman of NOAA-GLERL were obtained from the EEGLE web page (http://www.glerl.noaa.gov/eegle). River discharge data for four western Michigan rivers was obtained from the United States Geological Survey (USGS) web page (http://water.usgs.gov/cgi-bin/ daily_flow?mi). We are thankful to Judith Olson and Megan Ogdahl for technical help. Manuscript preparation benefited from discussions with the LiMNology Group of the University of Minnesota.

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