SHERR, B. F., E. B. SHERR, AND T. BERMAN. 1983. Grazing, growth, and ammonium excretion rates of a heterotrophic microflagellate fed with four species of bacteria. Appl. Environ. Microbiol. **45:** 1196–1201.

STARR, R. C. 1978. The culture collection of algae at the University of Texas at Austin. J. Phycol. **14:** 47–100.

STEIN, J. R. [ED.]. 1973. Handbook of phycological methods. Cambridge.

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Distribution of labile dissolved organic carbon in Lake Michigan

Abstract—Bioassay-measured, labile dissolved organic carbon (LDOC) concentrations were compared in near-bottom and near-surface Lake Michigan water between April and October 1986. In five of seven experiments, the LDOC concentration was higher in near-bottom water. LDOC reached 40.2% of the total DOC pool in the near-bottom water in late May and 13.8% in the near-surface water in early July. Concentration in near-bottom water was highest during early stratification; concentration in surface water varied less but was highest in early July. The data suggest that an allochthonous source of labile organic C may be important.

Identifying primary sources of labile dissolved organic carbon (LDOC) in pelagic systems has taken on new interest in light of recent evidence that a major portion of the C fixed via autotrophic production passes through heterotrophic bacteria (Lovell and Konopka 1985; Scavia et al. 1986; Scavia and Laird 1987; Nagata 1987) and that much of the bacterial production is grazed (Scavia and Laird 1987; Nagata 1987). This transfer of LDOC to primary consumers captures C that might otherwise be lost.

Recently, we reported that in Lake Michigan a disequilibrium between phytoplankton organic C production (supply) and bacterial C use (demand) on seasonal and spatial scales may exist (Scavia and Laird 1987). Although annual bacterial C demand (236 g C m^{-2} yr^{-1}) appeared to be balanced by annual phytoplankton net C production (225 g C m^{-2} yr^{-1}), summer bacterial C demand (1,087 mg C m^{-2} d^{-1}) could not be satisfied by net summer phytoplankton C production (627 mg C m^{-2} d^{-1}), indicating that a large discrepancy exists between DOC demand and supply. This discrepancy was even more dramatic when restricted to the summer epilimnion. We suggested that seasonal and spatial disequilibrium between organic C supply and demand could explain the apparent deficit. The hypothesis suggested that temporal disequilibrium is driven when bacterial production is low (winter or early spring) and LDOC accumulates, exceeding bacterial demand. Also, spatial disequilibrium is driven by accumulation of organic matter in cold, deep regions through sedimentation of phytoplankton, detritus, and other decaying material. These supplies of LDOC would then become available throughout the water column during winter mixing.

Strayer (1988) generalized the issue of secondary production in ecosystems and questioned the need for our disequilibrium hypothesis. He based his analysis on model calculations demonstrating that because organic C is recycled, total consumer C demand may exceed organic C inputs to ecosystems. Extension of that model analysis (Scavia 1988) corroborated that consumer demand can be met by autotrophic production on an annual water-column basis in Lake Michigan; it also suggested, however,

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that the bacterial epilimnetic summer demand would remain greater than concurrent organic C supply even if organic C is recycled. The need to test empirically the LDOC temporal and spatial disequilibrium hypothesis remained. We explored this hypothesis by comparing seasonally, through a simple bioassay, the concentration of "available" DOC in surface and deep water.

Water samples were taken from the epilimnion and lower hypolimnion (10 m above the sediment) in opaque Niskin bottles (5 liter) aboard the RV *Shenehon*. In a similar study, resuspended natural marine sediments increased microbial production and were considered a potentially important source of high-quality biomass for consumers (Wainright 1987). We chose to use material from the near-bottom hypolimnetic layer rather than from the near-sediment region (1 m above the bottom) to minimize the chance of introducing sedimentary material.

Sampling was in July 1985 and between April and October 1986. Transparency profiles and water temperature were determined from vertical casts of an electronic bathythermograph coupled to a 25-cm light-path Sea Tech transmissometer and pressure transducer. Station location was the 100-m depth contour, 26 km west of Grand Haven, Michigan (43°1′11″N, 86°36′48″W).

Bacterial C content and LDOC were determined from dilution-growth experiments set up ashore ~2 h after water collection. We inoculated 20-liter carboys (filled with 0.2-μm filtered water from each depth of interest) with 100 ml of 2–5-μm-filtered (Nuclepore) epilimnetic water and incubated them at epilimnetic temperatures in the dark. Bacterial subsamples were preserved daily to monitor abundance changes. Particulate organic C (POC) measurements and bacterial biovolume were determined initially and then again when the bacterial abundance plateaued. Bacterial cell sizes were determined from projections of photographic slides as described by Scavia and Laird (1987).

POC and DOC were measured with an Oceanography International carbon analyzer after persulfate digestion (Golterman et al. 1978). POC was collected on precombusted glass-fiber filters (Whatman GF/F); filtrates were used for DOC determination. Refiltered filtrates served as carbon blanks. Bacterial biovolume (μm^3 ml^{-1}), when used in C content calculations, was corrected for cells passing the glass-fiber filters by counting and sizing cells passing the filter.

Bacterial C content (pg C μm^{-3}) was determined from the change in POC concentration divided by the change in bacterial biovolume concentration during incubation. Bacterial C consumption (our estimate of LDOC) was calculated for each experiment as the product of bacterial cell C content (pg C μm^{-3}) and final bacterial biovolume (μm^3 ml^{-1}) divided by an assumed growth efficiency of 20% (Bjørnsen 1986*a*; Tranvik and Hofle 1987).

A preliminary dilution experiment, done in July 1985 on epilimnetic, metalimnetic, midhypolimnetic, and near-bottom water, showed the typical lag, exponential growth, and plateau phases for bacterial growth. We consider the plateau phase as the point when available LDOC is consumed and refer to it as "final biovolume." Almost twice as many bacteria were produced from near-bottom water as from other depths (Fig. 1), suggesting that a greater supply of LDOC is available in that region. We repeated this experiment in 1986, focusing on comparing concentrations of biovolume and LDOC from deep and surface waters between April and October.

Thermal stratification began in late May 1986 and the thermocline deepened to 30 m by mid-October (Fig. 2). Surface-water bacterial cell concentrations in 1986 ($1.02 \pm 0.14 \times 10^6$ cells ml^{-1}, mean ± SD, $N = 9$) were within the range previously reported for the region (Scavia and Laird 1987). Water-column bacterial cell volumes averaged 0.056 ± 0.05 μm^3 (mean ± SD) in the surface, 0.023 ± 0.017 μm^3 in the metalimnion, and 0.029 ± 0.014 μm^3 in the hypolimnion when a thermocline was present. These values are similar to volumes found in 1985 (Scavia and Laird 1987) and 1984 (Scavia et al. 1986) for the same offshore station.

Bacterial C contents averaged 0.37 ± 0.09 pg C μm^{-3} ($N = 7$) (mean ± SE) in epilimnetic water and 0.18 ± 0.07 pg C μm^{-3} ($N = 6$) in the hypolimnetic water; the average values were not significantly different ($\alpha =$

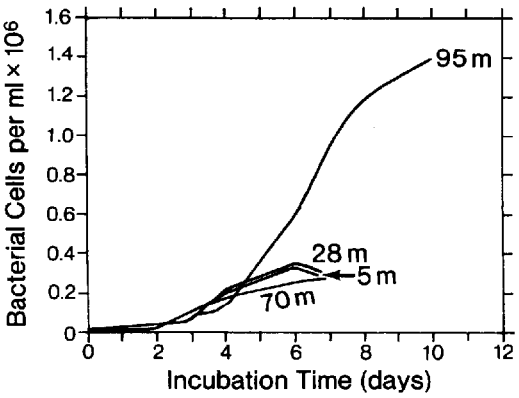

Fig. 1. Bacterial abundances (~6% counting error, assuming Poisson statistics) during dilution-growth experiments for water from 5-, 28-, 70-, and 95-m depths in July 1985.

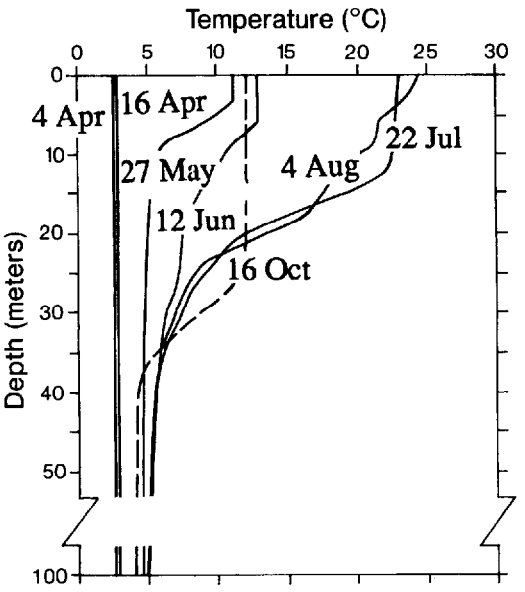

Fig. 2. Seasonal temperature profiles in southern Lake Michigan, 1986.

0.1; two-tailed t-test). The average cell C value, 0.28 ± 0.24 ($N = 13$) pg C μm^{-3}, was greater than our earlier Lake Michigan estimate of 0.154 (Scavia and Laird 1987) and estimates of others (0.039–0.188, mean = 0.106: Nagata 1986; 0.121: Watson et al. 1977), but similar to estimates by Bjørnsen (1986*b*) (0.35 ± 0.03).

The bioassay-derived LDOC estimates (Table 1) can be compared with the average water-column total DOC (TDOC) concentrations measured in 1987 (surface, 2.22 ± 0.35 mg C liter^{-1}, $N = 5$; deep, 2.07 ± 0.43 mg C liter^{-1}, $N = 4$; mean ± SE). The LDOC pool constituted 1.8–13.8% of epilimnion TDOC and 3.3–40.2% of deep-layer TDOC (Table 1). Average summer epilimnetic LDOC concentration is equivalent to 9–24 d of summer phytoplankton production (Scavia and Fahnenstiel 1987) and 153–360 d of summer phytoplankton excretion (Laird et al. 1986), yet it would only support 3–6 d of bacterial production (Scavia and Laird 1987). Clearly, the LDOC pool is not static, and a source other than concurrent phytoplankton production is required to support bacterial production.

In 1986 final bacterial biovolume (Fig. 3) and LDOC (Table 1) produced from deep hypolimnetic water was greater than from surface water in five of seven experiments. The difference between the two regions was greatest during early stratification (late May). LDOC increased first in spring from 459 to 831 μg C liter^{-1} in the deep hypolimnetic water and from 174 to 234 in surface water; both decreased by October to 75 and 39 μg C liter^{-1} respectively (Table 1). Applying the average bacterial cell C content, determined from 1986 data, to bacterial sizes and concentrations determined in the July 1985 experiment yielded similar results: C consumption of 120, 132, 192, and 213 μg C liter^{-1} from 5-, 28-, 70-, and 95-m water.

Table 1. Final biovolume (10^5 μm^3 ml^{-1}), calculated LDOC (μg C liter^{-1}), and LDOC as percent of water-column total DOC (TDOC) from bacterial dilution experiments in 1986.

	Depth (m)	Final biovol.	LDOC	TDOC
30 Apr	5	1.22	174	7.8
	90	3.22	459	22.2
27 May	5	1.63	234	10.5
	90	5.84	831	40.2
12 June	5	1.90	270	12.3
	90	1.37	195	9.3
2 Jul	5	2.12	303	13.8
	90	2.84	405	19.5
5 Aug	5	1.34	192	8.7
	90	2.00	285	13.8
21 Aug	5	0.89	129	6.0
	90	0.50	72	3.3
3 Oct	5	0.28	39	1.8
	90	0.53	75	3.6

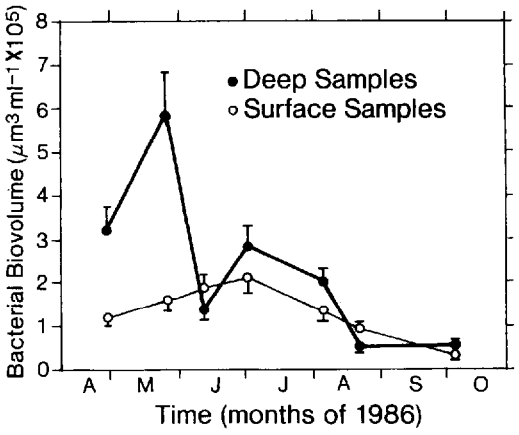

Fig. 3. Bacterial biovolume produced after incubation of water from surface and deep hypolimnetic regions of Lake Michigan. Error bars represent ±1 SE (n = 20–79).

Our overall results of decreasing LDOC concentration during summer—indicating that demand is greater than supply at that time—are consistent with another recent study from the same region in Lake Michigan which demonstrated that bacteria are more substrate limited in summer than in spring (Gardner et al. 1989). Higher LDOC concentrations in the deep region from our study (Table 1, Fig. 3) may be due to a buildup of recently sedimented or resuspended materials that decay over winter. These high concentrations early in the year and decreasing concentrations throughout summer are consistent with our disequilibrium hypothesis.

Although this internal recycling of LDOC may contribute to water-column production, particularly in the warmer epilimnion after stratification, it cannot produce the large, deeper water "pulse" of LDOC observed in late spring. This pulsed input may be related to the allochthonous sources controlled by the offshore movement of a seasonal thermal front, typically referred to in the Great Lakes as the spring "thermal bar." This thermal front is produced and maintained by differential vertical mixing inshore and offshore of the 4°C isotherm during spring. The region inshore of the isotherm, being shallower, warms faster and stratifies vertically sooner than offshore. Water offshore remains colder and well mixed vertically. Surface water at the 4°C isotherm sinks, creating a convergence zone (Bennett 1971; Scavia and Bennett 1980). As the seasonal heating progresses, the 4°C isotherm moves concentrically offshore. The water column in any particular region stratifies vertically as this front passes. By late June the front reaches midlake and the entire lake is stratified vertically.

Satellite data from the Coastal Zone Color Scanner (Mortimer 1988) suggest that high concentrations of dissolved organic matter (DOM) received from the inflow of the four major rivers along the eastern shore of Lake Michigan may be trapped between the shore and this thermal front. If, as the front moves offshore in its seasonal transition, it carries with it warm water containing relatively rich organic matter, the result could be a wave of high bacterial production moving offshore along the front.

This DOM-rich material, however, may not be confined to the surface water. In summer 1980 and 1981, nutrient enrichment from the Grand River plume was found offshore in the metalimnion as the thermal front moved offshore (Moll and Brahce 1986). In 1988 and 1989 relatively high TDOC concentrations were found in the region just below the thermocline (G. A. Laird unpubl. data) during early stratification. Thus, a stronger coupling to allochthonous inputs may occur, at least at that time.

Annual buildup of LDOC in the deep regions, which becomes available to the surface waters during winter mixing, may not contribute as significantly as we suggested earlier in our disequilibrium hypothesis (Scavia and Laird 1987). At least in spring, allochthonous sources focused by the spring thermal front movement may contribute significantly to the LDOC pool and may help account for some of the previously noted imbalance between bacterial and phytoplankton production.

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References

BENNETT, J. R. 1971. Thermally driven currents during the spring and fall transition periods, p. 535–544. *In* Proc. 14th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

BJØRNSEN, P. K. 1986*a*. Bacterioplankton growth yield in continuous seawater cultures. Mar. Ecol. Prog. Ser. **30:** 191–196.

———. 1986*b*. Automatic determination of bacterioplankton biomass by image analysis. Appl. Environ. Microbiol. **51:** 1199–1204.

GARDNER, W. S., J. F. CHANDLER, AND G. A. LAIRD. 1989. Organic-nitrogen turnover and substrate limitation of bacteria in Lake Michigan. Limnol. Oceanogr. **34:** 478–485.

GOLTERMAN, H. L., R. S. CLYMO, AND M. A. M. OHNSTAD. 1978. Methods for physical and chemical analysis of freshwaters. IBP Handbook 8. Blackwell.

LAIRD, G. A., D. SCAVIA, AND G. L. FAHNENSTIEL. 1986. Algal organic carbon excretion in Lake Michigan. J. Great Lakes Res. **12:** 136–141.

LOVELL, C. R., AND A. KONOPKA. 1985. Primary and bacterial production in two dimictic Indiana lakes. Appl. Environ. Microbiol. **49:** 485–491.

MOLL, R., AND M. BRAHCE. 1986. Seasonal and spatial distribution of bacteria, chlorophyll, and nutrients in nearshore Lake Michigan. J. Great Lakes Res. **12:** 52–62.

MORTIMER, C. H. 1988. Discoveries and testable hypotheses arising from Coastal Zone Color Scanner imagery of southern Lake Michigan. Limnol. Oceanogr. **33:** 203–226.

NAGATA, T. 1986. Carbon and nitrogen content of natural planktonic bacteria. Appl. Environ. Microbiol. **52:** 28–32.

———. 1987. Production rate of planktonic bacteria in north basin of Lake Biwa, Japan. Appl. Environ. Microbiol. **53:** 2872–2882.

SCAVIA, D. 1988. On the role of bacteria in secondary production. Limnol. Oceanogr. **33:** 1220–1224.

———, AND J. R. BENNETT. 1980. Spring transition period in Lake Ontario—a numerical study of the causes of the large biological and chemical gradients. Can. J. Fish. Aquat. Sci. **37:** 823–833.

———, AND G. L. FAHNENSTIEL. 1987. Dynamics of Lake Michigan phytoplankton: Mechanisms controlling epilimnetic communities. J. Great Lakes Res. **13**(2): 103–120.

———, AND G. A. LAIRD. 1987. Bacterioplankton in Lake Michigan: Dynamics, controls, and significance to carbon flux. Limnol. Oceanogr. **32:** 1017–1033.

———, ———, AND G. L. FAHNENSTIEL. 1986. Production of planktonic bacteria in Lake Michigan. Limnol. Oceanogr. **31:** 612–626.

STRAYER, D. 1988. On the limits to secondary production. Limnol. Oceanogr. **33:** 1217–1219.

TRANVIK, L. J., AND M. G. HOFLE. 1987. Bacterial growth in mixed cultures on dissolved organic carbon from humic and clear waters. Appl. Environ. Microbiol. **53:** 482–488.

WAINRIGHT, S. W. 1987. Stimulation of heterotrophic microplankton production by resuspended marine sediments. Science **238:** 1710–1712.

WATSON, S. W., T. J. NOVITSKY, H. L. QUINBY, AND F. W. VALOIS. 1977. Determination of bacterial number and biomass in the marine environment. Appl. Environ. Microbiol. **33:** 940–954.

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