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Organic nitrogen mineralization and substrate limitation of bacteria in Lake Michigan

Abstract—Labile organic nitrogen mineralization and the apparent degree of bacterial substrate limitation were examined to consider seasonal relationships between substrate availability and bacterial activity in Lake Michigan. Accumulation rates of ammonium nitrogen in amino acid fortified and unfortified samples of epilimnetic Lake Michigan water, incubated in the dark, provided reasonable estimates of potential and actual rates of organic nitrogen mineralization. The labile organic nitrogen demand (LOND), defined as the difference between these respective rates, provided an index of heterotrophic potential. LOND ranged from ~1–3 ng-atoms N liter h^{-1} (during May–June and November) to 3–9 ng-atoms N liter h^{-1} (during July–October) as compared to actual organic nitrogen mineralization rates of <1 ng-atom N liter h^{-1} in some unfortified samples. The high LOND, relative to actual turnover, observed in late summer is consistent with the hypothesis that growth rates of epilimnetic Lake Michigan bacteria are strongly limited by organic substrate during late stratification.

Recent work on microbial food webs in Lake Michigan suggests that bacterial population sizes may be controlled by grazers, whereas growth rates are more likely limited by organic substrate availability (Gardner et al. 1986; Scavia and Laird 1987). Despite the importance of organic nutrients as substrates for bacteria, the degree to which these compounds limit bacterial growth rates in aquatic environments is still not clear (Wright 1984). Quantification of interactions between dissolved organic compounds and bacterial production is complicated by our incomplete understanding of the composition, availability, and supply rates of the various organic compounds (e.g. Cole et al. 1984). Labile organic compounds are not easy to identify and measure at ambient concentrations, because they constitute a very small part of the total dissolved organic matter (DOM) pool and are often removed from solution by bacteria as fast

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as they are supplied (Iturriaga and Zsolnay 1983; Fuhrman 1987). Some of these compounds can be chemically measured at low levels [e.g. dissolved free amino acids (DFAA); Gardner and Miller 1980; Mopper and Lindroth 1982; Fuhrman and Bell 1985], but their flux cannot be directly related to the *total* turnover of labile organic substrates because the simultaneous fluxes of other unmeasured organic compounds are not known. Total flux of DOM to bacteria can theoretically be estimated from bacterial production estimates, obtained by measuring radiolabeled metabolite incorporation into bacterial components (e.g. Karl 1979; Fuhrman and Azam 1980, 1982; Simon and Tilzer 1987) and growth efficiencies. These data are sometimes difficult to interpret, however, because they involve conversion factors that may vary with location or involve physical manipulations such as filtration, with possible release of DOM (Fuhrman and Bell 1985). Also growth efficiencies are usually not accurately known and may vary within and among investigations.

Although the composition and amounts of all organic compounds assimilated by bacteria are not known, the relative degree of substrate limitation can be approximated by comparing the heterotrophic potential of microbes to mineralize labile organic nitrogen to ambient mineralization rates. We here estimate actual and potential organic nitrogen flux in epilimnetic Lake Michigan water by examining dark ammonium accumulation in the presence and absence of added amino acids (to saturate microbial uptake sites; Gardner et al. 1987). The degree of bacterial substrate limitation, here called labile organic nitrogen demand (LOND), is calculated as the difference between estimates of potential and actual flux of labile organic nitrogen. LOND can reasonably be assumed to relate directly to the degree of substrate limitation because incubation conditions are identical for the untreated and fortified samples except for the addition of DFAA as substrate. Although the LOND involves a suite of organic compounds rather than single compounds and is determined chemically rather than with isotopes, it conceptually resembles the heterotrophic potential or maximum uptake velocity (Wright and Hobbie 1965).

Water samples were collected from the epilimnetic mixed layer at a site offshore from Grand Haven, Michigan, where the total water depth is 100 m. The general approach used to examine nitrogen dynamics in lake water samples has already been described (Gardner et al. 1986, 1987). To summarize, lake water samples were collected and held at in situ temperatures until experiments were begun, usually within 24 h of collection. (Due to a sample-transport delay, the August 1987 experiment was not begun until about 48 h after initial sample collection.) Half of the samples were fortified with 0.79 or 0.94 μM of dissolved free amino acids (DFAA = mixture AA-S-18, Sigma Chemical Co.) to approximately saturate microbial uptake sites (Gardner et al. 1986); the other half was unfortified. Half of each group was held in the dark at in situ temperature (dark treatment), whereas the other half was held in the same incubator under 12 : 12 L/D conditions (light treatment). One-milliliter samples were removed from each treatment at 1–2-d intervals (Gardner et al. 1986), filtered (Gardner and Vanderploeg 1982), and analyzed fluorometrically for ammonium and primary amines after the two forms of nitrogen were separated by cation exchange chromatography and reacted with *o*-phthalaldehyde in the presence of 2-mercaptoethanol (Gardner 1978).

Water-collection and sample-analysis procedures for four 1987 experiments (May, June, August, November) were the same as previously described for the untreated 1986 samples (Gardner et al. 1987) with the following exceptions: 1987 experiments were limited to 7-d incubations (vs. up to 14 d for 1986 samples) with sampling and analysis generally done at daily intervals. Samples were incubated in 2.37-liter tissue-culture bottles instead of (or in addition to) 70-ml bottles. Amino acid nitrogen added to the large bottles was 0.79 μg-atom N liter^{-1} as compared to 0.94 for the small bottles. Duplicate bottles for each treatment were examined in 1987 to provide information on the precision of dark ammonium accumulation measurements.

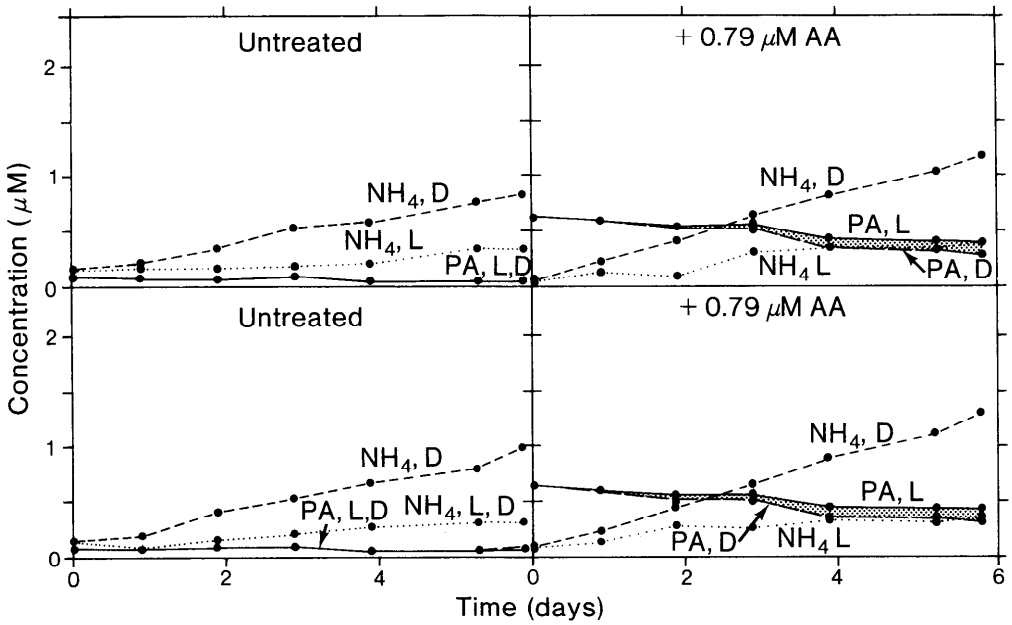

Fig. 1. Changes in ammonium and primary amino nitrogen with time of incubation in 2.37-liter bottles of Lake Michigan water sampled from the mixed surface layer (2–5-m depth) on 22 June 1987. Temperature, 19°C. Each graph represents results from a dark and a light-dark bottle. Samples represented in the left and right columns were untreated and fortified with 0.79 μM of an amino acid mixture (Sigma amino acid standard solution AA-S-18). The slopes of dark ammonium accumulation vs. time were assumed to represent actual (untreated samples) and potential (fortified samples) organic nitrogen mineralization rates (*see text*). Shaded area represents primary amine release by phytoplankton (*see* Gardner et al. 1987). Light : dark (12 : 12 L/D) conditions—L; dark conditions—D; primary amine—PA.

Organic nitrogen mineralization rate (i.e. flux) was assumed to equal the rate of ammonium accumulation in the dark after a 1- or 2-d delay was allowed for phytoplankton to use up available energy reserves needed for ammonium assimilation. Maximal or potential organic nitrogen mineralization rates were estimated from the ammonium accumulation rates in dark bottles fortified with amino acids to approximately saturate microbial uptake sites. Concentrations of added DFAA were selected to nearly saturate uptake sites but still remain within scale for our analytical measurements of the primary amine peak. V_{max} in Lake Michigan is reached at amino acid levels of about 0.8 μM (of an amino acid mixture) in both summer (Gardner et al. 1986) and spring (unpubl. data). Actual turnover rates were estimated as the rates of ammonium accumulation in unfortified dark bottles. LOND was estimated as the difference between the potential and actual rates.

Samples for bacterial counts were preserved at the beginning and end of the experiments with ~1% Formalin. Bacterial abundance was determined by the acridine orange direct-count method (Hobbie et al. 1977).

Experiments were conducted in 1987 to evaluate the potential containment effects of our incubation procedure, examine the precision of the dark ammonium accumulation in duplicate bottles, and provide data on organic nitrogen mineralization rates in Lake Michigan (e.g. Figs. 1 and 2). The large bottles generally produced results similar to the small ones when compared directly (Fig. 2) and the results were similar to previous kinetic nitrogen mineralization data obtained with 70-ml bottles that were incubated for up to 14 d (Gardner et al. 1986, 1987). The average range (±SE) of duplicate measurements of dark ammonium accumulation rate was 26±10% (N = 6) of the mean for the fortified samples and 16±2% (N = 4) for the unfortified samples that had measurable rates. The ranges of values ob-

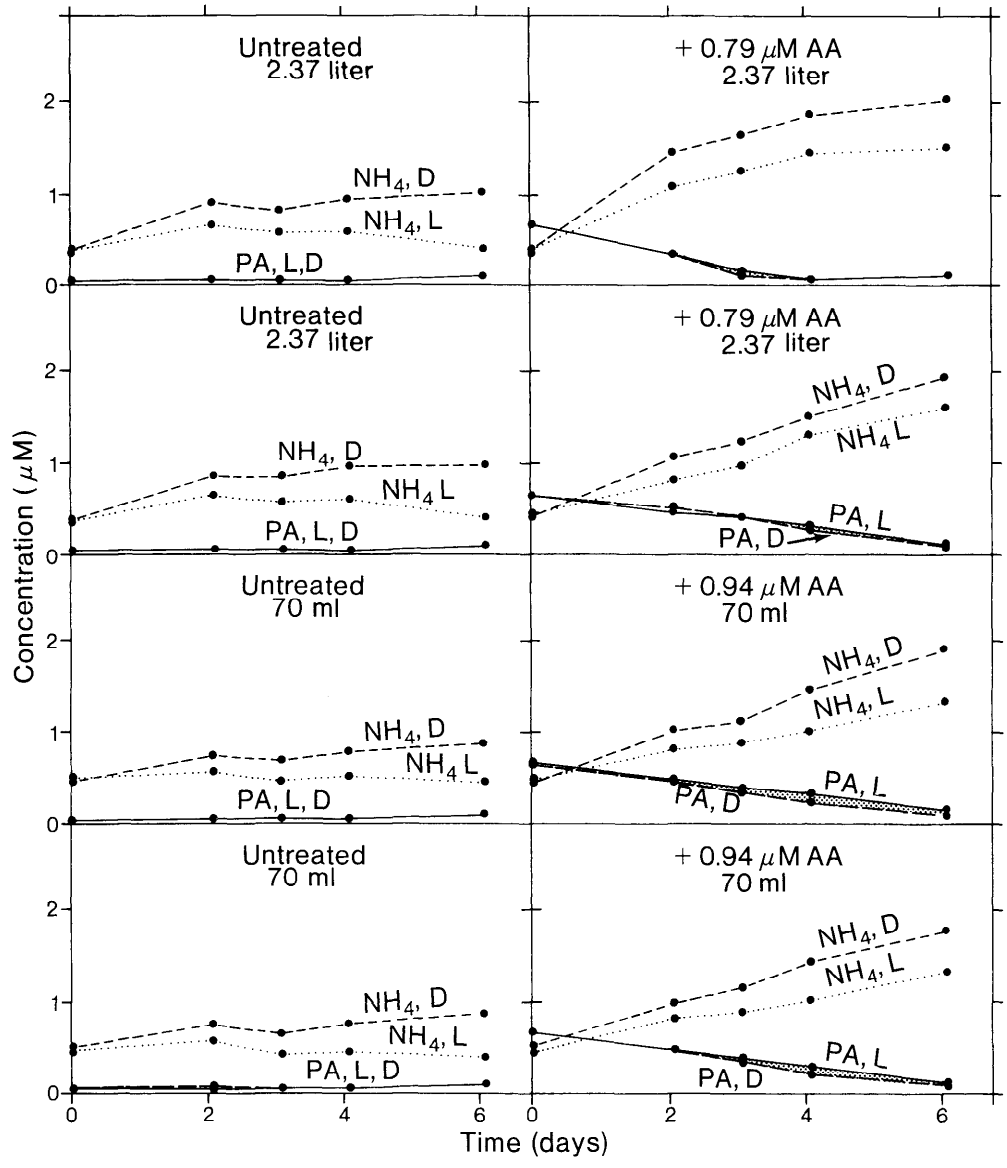

Fig. 2. Changes in ammonium and primary amino nitrogen with time of incubation in 2.37-liter and 70-ml bottles of Lake Michigan water sampled from a depth of 5 m on 20 August 1987. Temperature, 24°C. Other details as in Fig. 1.

tained from fortified samples never overlapped those from untreated portions of the same samples. Bacterial abundances at the end of incubations were generally similar to those at the beginning of the experiments and resembled in situ abundances for epilimnetic samples from the same site (Fig. 3; Scavia et al. 1986; Scavia and Laird 1987).

In agreement with previous results (Gardner et al. 1986, 1987), primary amine concentrations remained at or below chemical background levels (~0.07 μM) in unfortified samples and decreased in a generally linear pattern in treatments with amino acid additions. On the other hand, phytoplankton release of primary amines, determined by a light/dark approach (Gardner et al. 1987), was evident in May, June, and No-

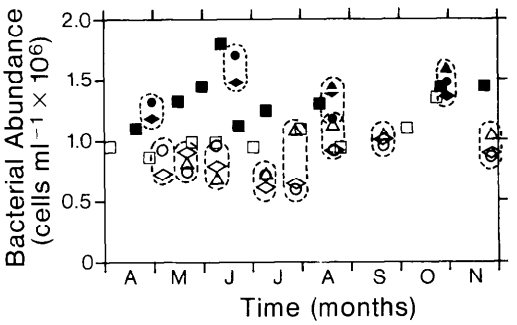

Fig. 3. Initial (triangles) and final abundances of bacteria in samples of untreated (diamonds) and amino acid fortified (circles) lake water taken in 1986 (open symbols) and 1987 (closed symbols) and incubated in the dark to measure ammonium accumulation rates. Data from specific experiments are enclosed by dashed lines. Squares represent field measurements of bacterial abundances from the same Lake Michigan site during 1986 and 1987 (unpublished data provided by D. Scavia and G. Laird).

Table 1. Mean DFAA-N decreases, ammonium-N increases, and percent conversion of added DFAA-N to ammonium-N in dark experimental bottles over intervals extending from day 1 (or 2) after incubations began until day 6 or 7 when the experiments were completed. Changes in concentration are expressed as μg-atoms N liter^{-1}. Fortified samples received 0.79 (2.37-liter bottles) or 0.94 (70-ml bottles) μg-atom DFAA-N liter^{-1} at the beginning of the experiments. May and June means were obtained from duplicate 2.37-liter bottles; August and November means were obtained by averaging the means from duplicate 2.37-liter and 70-ml bottles, respectively. DFAA-N was calculated by multiplying the primary amine concentration by the factor 1.38 to account for the amino acids that are not measured in the fluorometric peak.

Sampling date, 1987	Amino acid removal	Net ammonium accumulation			% Conversion
		Untreat.	Fort.	Net	
1 May, 4°C	0.16	0.14	0.30	0.16	100
22 Jun, 19°C	0.37	0.72	1.04	0.32	86
20 Aug, 24°C	0.46	0.13	0.79	0.66	143
2 Nov, 12°C	0.47	0.89	1.31	0.42	89

vember (e.g. shaded areas of Fig. 1), but was not pronounced in August (Fig. 2) when phytoplankton activity was apparently low.

Ammonium concentrations generally changed only moderately with time in light treatments but increased in dark treatments without added amino acids (Figs. 1 and 2). Ammonium accumulation in the dark unfortified samples likely resulted from mineralization of amino acids (and other labile organic nitrogen compounds) that were produced from living phytoplankton (as indicated by the shaded areas in Fig. 1) but could also have resulted in part from decomposition of phytoplankton in the dark bottles. The linearity of dark ammonium accumulation patterns generally observed with time of incubation (after the first 1–2 d; e.g. Fig. 1) suggests that ammonium production was relatively constant over time and that the incubation periods of several days may have been suitable for reasonable approximations of nitrogen transformation rates. An apparent decrease in ammonium production rates in the August sample after the second day (Fig. 2) may have been due to a limited supply of available labile organic nitrogen in this sample. As mentioned above, amino acid release was minimal in this sample. Other kinetic data (low rate of ammonium uptake in the light for the amino acid fortified sample; Fig. 2) suggested that the activity of phytoplankton was relatively low in this sample. The heterotrophic potential remained high, however, as evidenced by the high removal rates of added amino acids and correspondingly high accumulation rates of ammonium in the dark (Fig. 2).

As previously observed (Gardner et al. 1987), dark ammonium accumulation was greater in bottles fortified with amino acids than in similar bottles without amino acid additions. Increases in ammonium accumulation in fortified samples over those in unfortified samples were generally about equal to decreases in amino acid-N in the same samples after corrections were made for the amino acids that do not respond to the fluorometric technique (Gardner et al. 1987; Table 1). Likewise, ammonium regeneration was related to amino acid degradation in marine waters (Hollibaugh 1978; Hollibaugh et al. 1980). The apparent quantitative conversion of amino acids to ammonium in Lake Michigan supports our assumption that dark ammonium accumulation rates were about equal to heterotrophic mineralization rates of amino acids (and possibly other forms of labile organic nitrogen) and is consistent with the idea that ammonium is excreted by bacteria that are exposed to substrates with high labile nitro-

Table 2. Comparisons of rates of actual and fortified dark ammonium accumulation in experimental bottles and calculated LOND values for epilimnetic Lake Michigan samples collected in 1987. All rates are expressed as ng-atoms N liter^{-1} h^{-1}.

Sampling date	Untreated			Fortified			LOND
	$\bar{x}$	N	SE	$\bar{x}$	N	SE	
1 May	0.92	2		1.73	2		0.81
22 Jun	5.64	2		8.50	2		2.86
20 Aug	0.12	4	0.07	6.76	4	0.92	6.64
2 Nov	6.14	4	0.46	9.29	4	0.69	3.15

gen content such as DFAA (Billen 1984; Goldman et al. 1987; Hollibaugh 1978; Zehr et al. 1985). In addition to direct release by bacteria, bacterial grazers could have contributed to ammonium regeneration (Goldman et al. 1985). Regardless of the exact source of ammonium, the rate of nitrogen mineralization appears to be largely controlled by the rates of the processes supplying labile organic nitrogen.

LOND was approximately equivalent to, or smaller than, actual organic nitrogen mineralization rates for the waters sampled in May, June, and November but was much higher than the actual rates for untreated samples in August (Table 2). This disparity suggests that the heterotrophic potential was much greater in August than at the other sampling times. This result is not totally surprising because the lack of substantial epilimnetic phosphorus inputs causes phytoplankton production rates to be low during late stratification (Fahnenstiel and Scavia 1987; Scavia and Fahnenstiel 1987). As mentioned above, phytoplankton release of DFAA was also low in this sample (Fig. 2). If phytoplankton release is the major source of labile DOM to bacteria, substrate limitation may be expected when phytoplankton production rates are low, especially when temperatures are optimal for bacterial growth, as occurs in late summer.

To estimate maximal and actual organic nitrogen mineralization rates on a seasonal basis, we combined dark ammonium accumulation data for 1986 (untreated samples in tables 2 and 3, Gardner et al. 1987) with those obtained in 1987 (Table 2) and then calculated LOND by difference (Fig. 4). The maximal mineralization rates ranged

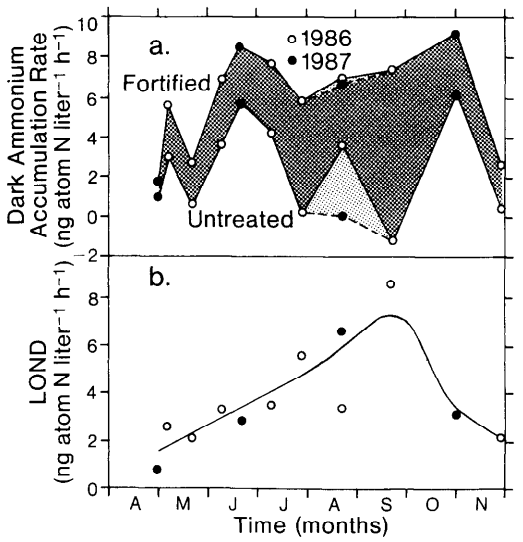

Fig. 4. Seasonal rates of dark ammonium accumulation in unfortified samples (representing actual nitrogen turnover rates) and amino acid fortified samples (representing maximal turnover rates) for waters collected at seasonal intervals in 1986 and 1987. LOND, representing the difference between maximal and actual nitrogen mineralization rates, is shown as the shaded area in the upper graph and separately in the lower graph. The data in the lower graph were visually averaged to give the seasonal curve.

from about 1.6 to 9 ng-atoms N liter^{-1} h^{-1}. Although these rates tended to be lower in spring than in summer, they sometimes varied considerably between adjacent sampling periods (Fig. 4). The actual mineralization rates ranged from -1.2 to 6.1 ng-atoms N liter^{-1} h^{-1} and also showed sporadic differences among experiments. Interestingly, LOND, representing heterotrophic potential, appeared to have the most predictable seasonal pattern. In all cases the potential mineralization of organic nitrogen was higher than the actual mineralization, but the magnitude of this difference was far greater in August through September than in spring or late autumn. LOND values gradually increased from as low as 1 ng-atom N liter^{-1} h^{-1} in early spring to 3–9 ng-atoms N liter^{-1} h^{-1} in late summer and then decreased to ~2 in November (Fig. 4b). During the peak period, LOND was much higher than actual mineralization rates for labile organic nitrogen. For example, three out of eight experiments conducted during June through September had actual nitro-

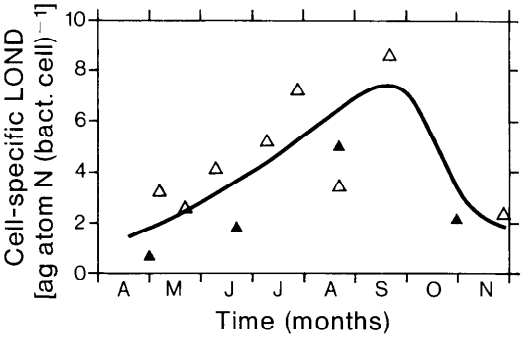

Fig. 5. Bacterial cell-specific LOND for waters sampled at seasonal intervals in 1986 and 1987. One attogram-atom (ag-atom) = 10^{-18} g-atom. The data were visually averaged to give the seasonal curve.

gen mineralization rates of <1 ng-atom N liter^{-1} h^{-1} but LONDs of 3–9 ng-atoms N liter^{-1} h^{-1} (Fig. 4).

High LOND values in late summer relative to those observed in early spring or late autumn could potentially have been caused by an increased bacterial population size as well as by an increase in the cell-specific heterotrophic potential during this period. Although mean epilimnetic bacterial abundances varied from 0.6 to 1.7 × 10^6 cells ml^{-1} on different sampling dates and appeared to be higher in 1987 than in 1986 (Fig. 3; Scavia and Laird unpubl. data), seasonal changes in abundances did not appear to be the major factor causing LOND to peak in late summer. Plots of cell-specific LOND obtained by dividing LOND by bacterial abundances (Fig. 5) yielded a curve similar in shape to that observed for volume-specific LOND (Fig. 4). Thus the seasonal peak in LOND was likely due more to an increase in cell-specific heterotrophic potential than to a seasonal increase in bacterial population size.

The above comparisons agree with the conclusion, supported by bacterial growth rate measurements (Scavia and Laird 1987), that growth rates of epilimnetic bacteria in Lake Michigan are limited by substrate supply during late stratification. Although bacterial abundances in Lake Michigan water were not affected by the addition of amino acid substrate, nitrogen mineralization rates were increased dramatically by amino acid additions. Substrate limitation appeared to be less severe during other parts of the year when phytoplankton production rates (Fahnenstiel and Scavia 1987) and inputs of labile organic compounds were likely greater and when temperature conditions were not as suitable for bacterial growth (e.g. early spring; Scavia et al. 1986; Scavia and Laird 1987). Although the ammonium accumulation rate in the dark does not represent the flux of all organic substrates, it appears to effectively trace DFAA flux in Lake Michigan. This approach would likely be ineffective, however, in ecosystems where nitrogen limitation causes heterotrophs to assimilate ammonium as a nitrogen source (Wheeler and Kirchman 1986; Goldman et al. 1987). Since DFAA are apparently used primarily as carbon rather than nitrogen sources in Lake Michigan (Gardner et al. 1987), the relationship of actual to potential DFAA-N turnover rates may indicate the degree to which bacteria are limited by organic carbon supply. LOND thus seems to be a useful indicator of heterotrophic potential in Lake Michigan; this index may also be applicable to other aquatic environments where nitrogen is not a limiting nutrient for microbial populations.

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