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The role of DON and the effect of N:P ratios on occurrence of cyanobacterial blooms: Implications from the outgrowth of *Aphanizomenon* in Lake Kinneret

Abstract—Supply (or loading) ratios of biologically available nitrogen and phosphorus, N:P, have often been suggested as the major determinants for the presence or absence of N_2 fixing cyanobacteria in aquatic environments. Increasing evidence that some components of the dissolved organic nitrogen (DON) pool can play an active role in supplying N nutrition either directly or indirectly to phytoplankton implies that this source of N must be considered in any attempt to apply the N:P resource ratio approach to predict or explain phytoplankton population composition. For example, the unprecedented bloom of *Aphanizomenon ovalisporum* that occurred in Lake Kinneret from mid-September through October 1994 derived most of the N required for growth directly or indirectly from DON rather than from N_2 -fixation. This would suggest that factors other than apparent low N:P ratios were important in causing the outgrowth of the cyanobacteria. The present analysis of the *Aphanizomenon* bloom in Lake Kinneret emphasizes (1) the need to include the DON pool as a potential source of available N for planktonic microbiota; (2) at least for some cyanobacteria, the presence of heterocysts does not necessarily imply active nitrogen fixation; and (3) the development of diazotrophic cyanobacterial blooms in nature is generally due to a multiplicity of environmental factors.

In both marine and freshwaters considerable amounts of nitrogen (N) are associated with the pool of dissolved organic nitrogen (DON), which frequently greatly exceeds the concentrations of total dissolved inorganic nitrogen, DIN (Antia et al. 1991). There is now compelling evidence that some components of the DON pool can play an active role in supplying N nutrition directly or indirectly to phytoplankton and bacteria. The capability of some algae to derive N directly from organic N compounds such as amino acids and purines has long been known (see review by Antia et al. 1991). Probably in most cases, indirect supply of N from

the DON pool is more important for phytoplankton. For example, studies by Palenik and Morel (1990) showed the presence of L-amino acid oxidases on the surface of algal cells that serve to liberate NH_4 , which is subsequently transported to the cell interior. Urea (one of the more frequently measured components in the DON pool) is almost ubiquitously used by phytoplankton as a nitrogen source, often preferentially to NO_3 (McCarthy 1972; McCarthy et al. 1982). It has also been shown that some components of indigenous freshwater and marine DON pools such as purines, amino acids, and amino sugars are susceptible to relatively rapid bacterial degradation, giving rise to NH_4 or urea (Berman et al. 1999). Moreover, the hydrolytic action of UV and visible light irradiation is known to degrade DON, yielding nitrogen-rich compounds (including NH_4) that are biologically available (Bushaw et al. 1996). A further indication of the dynamic nature of N cycling in aquatic environments is the fact that not only are some DON components degraded and/or taken up by phytoplankton and bacteria, but that considerable quantities of DON compounds may be directly excreted by algae (Bronk et al. 1994) or released by bacteriophage, viruses, or grazers of various size, shape, and dietary preference (Antia et al. 1991; Turk et al. 1992).

Supply (or loading) ratios of biologically available nitrogen and phosphorus, N:P (Schindler 1977), or, alternatively, the environmental ratios of total nitrogen:total phosphorus, TN:TP (Smith 1983) have often been proposed as the major determinants for the presence or absence of N_2 -fixing cyanobacteria, mainly for lakes but also elsewhere (see recent reviews by Hyenstrand et al. 1998 and Smith and Bennet 1999). A simpler criterion for defining limiting N levels sufficiently low to stimulate the development of N_2 -fixing cyanobacteria was proposed by Horne and Commins (1987)

Table 1. Lake Kinneret: *Aphanizomenon* biomass and mass balances for N and P in epilimnic waters from mid-August to mid-October 1994.*

Maximum C biomass at peak of <i>Aphanizomenon</i> bloom (early to mid-October):		
550–830 $\mu\text{g N L}^{-1}$	(based on 10–15% of measured wet weight biomass)	(a)
1,280 $\mu\text{g N L}^{-1}$	(based on measured C:chlorophyll ratio, 63.9:1)	(b)
Measured C:N:P (by weights):		
106:20:1	(Nishri, pers. comm.)	(c)
Maximum calculated N biomass:		
105–160 $\mu\text{g N L}^{-1}$	(from a and c)	
245 $\mu\text{g N L}^{-1}$	(from b and c)	
Maximum calculated P biomass:		
5.2–7.8 $\mu\text{g P L}^{-1}$	(from a and c)	
12.1 $\mu\text{g P L}^{-1}$	(from b and c)	
Measured changes in ambient N concentrations (mid-August to mid-October 1994):		
DON	–219 $\mu\text{g N L}^{-1}$	
DIN	–52 $\mu\text{g N L}^{-1}$	
PON	+217 $\mu\text{g N L}^{-1}$	
Measured changes in ambient P concentrations (mid-August to mid-October 1994):		
TDP	–12 $\mu\text{g N L}^{-1}$	
Particulate P	+4 $\mu\text{g P L}^{-1}$	

* All concentrations based on 1 to 10 m averages made at a central lake station A. Measurements of wet weight biomass and C:N:P were provided by courtesy of U. Pollinger and A. Nishri, respectively.

who suggested that this occurred when total dissolved inorganic N (DIN) concentrations were <50–100 $\mu\text{g N L}^{-1}$.

The main point of this paper will be to suggest that the available portion of the DON pool must be included in any consideration of potential N supply to aquatic microbiota in order to realistically depict N fluxes and recycling in aquatic ecosystems. Unless the flux of available N coming either directly or indirectly from DON is taken into account, the application of N:P supply ratios to predict or explain the development of diazotrophic cyanobacterial blooms can be misleading.

The 1994 Aphanizomenon bloom in Lake Kinneret—The unprecedented bloom of the diazotrophic cyanobacterium, *Aphanizomenon ovalisporum*, in Lake Kinneret in 1994 can serve as an example to illustrate the importance of recognizing the potential of DON as an N source for phytoplankton. In a previous paper (Berman 1997) it was shown that DON and DIN concentrations in the epilimnion declined during the months September–October 1994 concomitantly with equivalent increases in particulate organic nitrogen (PON), associated with the development of the *Aphanizomenon* bloom (Table 1). (Note, a reasonable mass balance was also obtained for the phosphorus fractions.) Thus it was proposed that most of the N required by the cyanobacteria was supplied, either indirectly or directly, from the DON pool rather than by N_2 fixation. This scenario did not preclude the possibility that a small amount of the N_2 was fixed by the cyanobacteria if some cells were in hot spots (microzones) of low N concentration. We have also shown that *Aphanizomenon* and other cyanobacteria and algae grow well (and more rapidly than by N_2 fixation) on a variety of organic N compounds that served, either indirectly (after bacterial degradation) or directly, as N sources (Berman and Chava 1999).

In a recent paper, Gophen et al. (1999) propose that the

Aphanizomenon bloom developed on the basis of active N_2 fixation resulting from a condition of “combined N deficiency and P sufficiency.” They conclude that the bloom in mid-September and October 1994 was caused mainly by the combination of (1) a prolonged (~11 yr) low TN:TP ratio in the lake epilimnion during summer–fall; and (2) a concomitant increase in available P. These conditions are posited to have caused the outgrowth of an actively N_2 fixing population of *Aphanizomenon*. Ancillary factors such as high water temperatures and low turbulence are also acknowledged but are deemed secondary. Furthermore, it is suggested that changes that occurred subsequently in the long-term characteristics of the phytoplankton assemblage were the result of an estimated 700 tons of new N added to the lake by N_2 fixation during the 1994 cyanobacterial bloom.

Note that no direct measurements of nitrogenase activity were made during the *Aphanizomenon* bloom in 1994. Gophen et al. (1999) based their calculation of extensive N_2 fixation (~700 tons total during 2 months) by the *Aphanizomenon* bloom on the assumed nitrogenase activity of heterocysts multiplied by heterocyst numbers. The literature values for heterocyst N_2 fixation activity from a bloom (comprised of three species of *Anabaena* and *Anabenopsis*) in Lake Valencia (Levine and Lewis 1984) were combined together with *Aphanizomenon* heterocyst abundance data in Lake Kinneret (Pollinger et al. 1998). However, the latter refer only to the maximum number of heterocysts per filament at the optimal depth (maximum photosynthetic activity), not the average number of heterocysts during the bloom. Such estimates are unlikely to characterize either the average heterocyst abundance or N_2 fixation rates throughout the *Aphanizomenon* growth period. Thus the claimed amount of ~700 tons new N from N_2 fixation is probably greatly overestimated. Moreover, we and others (Syderback pers. comm.) have observed heterocysts even when *Aphanizomenon* was growing in the presence of high concentrations of combined

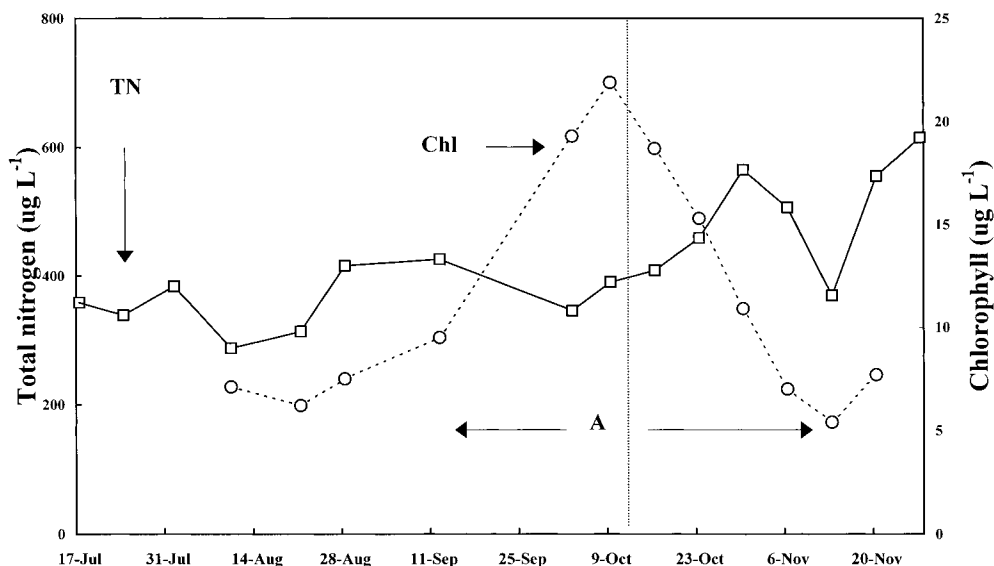


Fig. 1. Concentrations of total nitrogen ($\mu\text{g L}^{-1}$) and chlorophyll ($\mu\text{g L}^{-1}$) in the epilimnion (averaged for 1 to 10 m depths) at a central lake station in Lake Kinneret during July to November 1994. Note that filaments of *Aphanizomenon* were observed only during the period indicated by (A).

N (NO_3 , or, less frequently, NH_4); this has also been shown to occur in some strains of *Anabaena* (Meeks et al. 1983). It is therefore not necessarily true that every cyanobacterial heterocyst observed in the microscope is actively fixing N_2 (Lee and Rhee 1997).

Using data from routine monitoring, Gophen et al. (1999) also found that TN in the lake appeared to increase by ~ 750 tons from June through October 1994 and attributed this to the N_2 fixation by *Aphanizomenon*. However, measurements at a central lake monitoring Station A during the months of July through November 1994 do not indicate any significant increase of epilimnic TN concentrations until after the peak

of the *Aphanizomenon* bloom (Fig. 1). The main outgrowth of N_2 fixing cyanobacteria took place only after the sampling date of 12 September until 16 October, (from ~ 800 to $2,500$ filaments ml^{-1} or <10 to ~ 20 μg chlorophyll L^{-1}); during this time no large increases in TN concentrations were observed (Fig. 1). In fact, TN levels were already high by 28 August and only rose significantly from 16 October, after the *Aphanizomenon* bloom had begun to decline. Thus, nitrogen fixation prior to mid-September could not have been the source for the claimed increase of TN. Possibly the apparent rise in TN recorded from 12 to 28 August at Sta. A was due to TN inputs brought to the central region of the lake by seiche-associated water mass movements from the littoral areas (Imberger pers. comm.). Storms beginning on 21–22 October led to a deepening of the seasonal thermocline and mixing of hypolimnic water with high NH_4 concentrations (averaging 500 – 600 $\mu\text{g N L}^{-1}$), thus causing the rise in epilimnic TN measured in late October and November (Fig. 1).

If the potential of DON to act as a source of N is recognized, then a different perception of the Lake Kinneret *Aphanizomenon* episode emerges. Probably the true levels of available N in the lake epilimnion were usually considerably higher in summer–fall than indicated by measuring only the ambient concentrations of NO_3 and NH_4 . Even a conservative, assumed 10% input of available N indirectly or directly from the DON pool (average concentration, 1980–1999, 254 $\mu\text{g N L}^{-1}$) would raise the levels of summer–fall DIN in the epilimnion by $\sim 50\%$ (Fig. 2); average (1980 to 1999) supply ratios of N:P (at:at), calculated as DIN (or as DIN + 10% DON): total dissolved P would increase from 57 to 94.

Ambient epilimnic DIN concentrations from July through October in Lake Kinneret were consistently low for at least 18 yr prior to 1994 (with the exception of 1992 after the extreme N inputs from a century flood of the previous winter) and subsequently (Fig. 2). Nevertheless, only in 1994

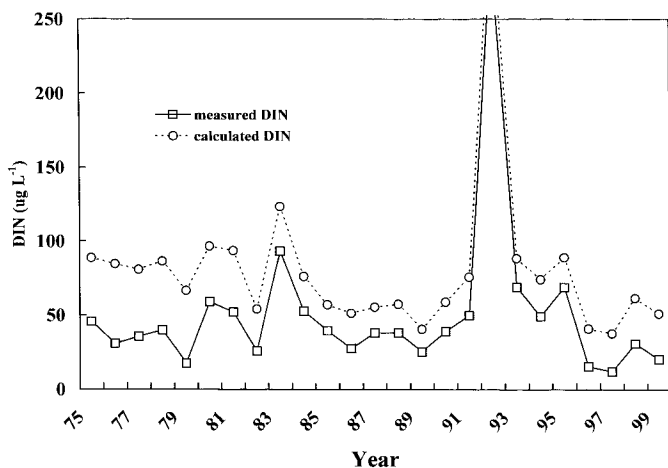


Fig. 2. Lake Kinneret: Average concentrations of epilimnic dissolved inorganic nitrogen ($\mu\text{g L}^{-1}$) measured during July through October at a central lake station (1 to 10 m depth average). The calculated DIN was estimated on the basis of the measured DIN with an assumed addition of 10% N from the measured dissolved organic nitrogen, DON.

and, to a much lesser extent, in 1995 was there any mass development of diazotrophic cyanobacteria despite the frequent occurrence of physical conditions (high epilimnic water temperatures and low turbulence) suitable for the development of these organisms (Berman and Shteinman 1998). Possible explanations for the absence of N_2 fixing cyanobacteria in this lake include generally low levels of available P or available Fe in summer–fall (Pollingher et al. 1988; Wurtsbaugh and Horne 1983), high concentrations of SO_4 ($>6.3 \mu\text{g N L}^{-1}$), and high ratios (>105) of SO_4 to molybdenum (Howarth et al. 1988; K. D. Hambright pers. comm.).

I suggest that the success of *Aphanizomenon* in Lake Kinneret in the fall of 1994 was not due to its N_2 fixing capabilities but because of a combination of environmental circumstances (changes in the trace metal and/or chelation characteristics of River Jordan inflows because of development in the catchment area, enhanced levels of bioavailable P, unusually high epilimnic temperatures and low turbulence, see Berman et al. 1998; Pollingher et al. 1998; Hadas et al. 1999). Most of the N required by the developing bloom came from DON that was derived from the breakdown of the extremely high spring 1994 dinoflagellate bloom (Berman et al. 1998). As documented by these authors, the changes that occurred in the annual patterns of phytoplankton development in Lake Kinneret began in early 1994, prior to the appearance of *Aphanizomenon*, and were not induced by any large increase of newly fixed N_2 from the cyanobacterial bloom. Probably *Aphanizomenon*, which had never before been observed in this lake, was introduced fortuitously shortly prior to the fall of 1994 rather than gradually building up to a critical biomass over many previous years. Note that the observed increase of cyanobacterial abundance from 25 to 2,500 filaments ml^{-1} only requires 7 to 19 d at moderate growth rates (1–3 d doubling $^{-1}$).

Conclusions—The above analysis of the 1994 *Aphanizomenon* bloom in Lake Kinneret has general implications concerning the role of DON and effect of N:P ratios on the occurrence of cyanobacterial and other algal blooms. Many hypotheses have been proposed to explain the success of cyanobacteria in frequently dominating phytoplankton populations in aquatic environments (recently reviewed by Hyenstrand et al. 1998). The idea that diazotrophic cyanobacteria will out-compete other algal groups by virtue of their ability to fix N_2 when the supply of combined N (but not other nutrients, such as P) limits the growth of other phytoplankton seems intuitively reasonable. Experimental studies (Rhee and Gotham 1980) confirmed that this was indeed the case with competing algal cultures in chemostats and indicated the critical supply ratios of N:P that might apply to determine successful competition. Variants of the resource ratio approach (Smith 1983) are all based on this idea. However, as pointed out by Reynolds (1997) “competition for available nutrients (by phytoplankton . . .) is in fact differential sensitivity to inadequacy (of some required nutrient).” A competitive situation between two algal species can only arise when a required nutrient decreases to a limiting level for one of the algae. This is true when a second nutrient is also considered. “When one of the nutrients falls to limiting concentrations, it may well discriminate between

(the two algal species) but it is the availability of that nutrient not the ratio between it and the other which is crucial . . . ratios are the consequences of uptake not its drivers. Ratios of nonlimiting resources are meaningless.” Curiously, in many cases where the N:P ratio approach has been applied, no account is made of the absolute concentration levels of N or P fractions being measured.

Although the N:P resource ratio approach has often proved successful in explaining the occurrence or nonoccurrence of diazotrophic cyanobacteria, this has not always been the case (see Smith and Bennett 1999). Reconsidering the effect of low N:P supply ratios on stimulating blooms of actively N_2 fixing cyanobacterial blooms, it becomes evident that such preferential conditions will occur in nature only if the concentrations of available N sources become truly limiting for all components of the phytoplankton. Even if prolonged limitation of combined, available N may be a necessary condition for the development of diazotrophic cyanobacteria, it is unlikely to be a sufficient condition for this to occur. (Note that blooms of N_2 fixing cyanobacteria have also been reported in the presence of high combined N concentrations; e.g., Jacobsen and Simonsen 1993.) Other environmental factors, such as adequate supplies of available P and Fe, elevated pH, relatively high temperatures, low turbulence, and water column light intensity, undoubtedly play a role, probably in a site-specific manner (Hyenstrand et al. 1998). The 1994 *Aphanizomenon* bloom in Lake Kinneret serves to emphasize that the appearance or nonappearance of diazotrophic cyanobacterial blooms in natural waters is usually due to a multiplicity of factors. Furthermore, this example, which is unlikely to be unique, points out that the involvement of DON as a potential direct or indirect source of biologically available N supply to phytoplankton in general, and to cyanobacteria in particular, should not be ignored when attempting to explain the causative factors of algal blooms.

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