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A numerical model of nitrogen fixation and its application to Lake Valencia, Venezuela*

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SUMMARY. 1. A numerical model for calculation of daily and annual nitrogen fixation in lakes is presented. The model is based on empirically-derived equations for the rates of nitrogen fixation by heterocysts (nitrogen-fixing cells) in relation to light and on functions for the vertical and temporal distributions of heterocysts and light in a lake.

2. Applications of the model to Lake Valencia, Venezuela, between December 1980 and December 1981 indicated that nitrogen fixation is largely a surface phenomenon in this lake: 80% of diurnal fixation occurred within 1 m of the water surface.

3. Nitrogen fixation is largely restricted to periods of lake stratification, when the phytoplankton have sufficient light for growth, but dissolved inorganic nitrogen is scarce. Nitrogen fixation was maximal late in the stratification period of 1981: 85% of fixation occurred within the last 3 months of the 9-month period.

4. The annual nitrogen fixation in Lake Valencia is 26 kg ha^{-1}, which is comparable to the nitrogen fixation in temperate eutrophic lakes with seasonal blue-green algal blooms. However, nitrogen fixation accounted for only 23% of the total nitrogen supply to Lake Valencia in 1981.

Introduction

Nitrogen fixation, like carbon fixation, is sensitive both to the abundance of fixers and to light intensity (Carr & Whitton, 1982). Several numerical models have been developed to estimate daily and annual carbon fixation from the temporal distribution of insolation, water clarity, and empirically-established relationships between photosynthesis and light intensity (e.g. Fee, 1973; Bannister, 1974). Recently, Flett *et al.* (1980) modified the photosynthesis model of Fee (1973) to permit calculation of nitrogen fixation over time and space. Flett replaced Fee's photosynthesis light–response function with an experimentally-determined light response function for nitrogen fixation per litre of water. In this paper, we describe a nitrogen fixation model in which fixation is normalized to the heterocyst,

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the cell primarily responsible for nitrogen fixation under aerobic conditions (Carr & Whitton, 1982). The model also allows for variation of heterocyst abundance and of the light response of nitrogen fixation per heterocyst over time and depth. We apply our model to Lake Valencia, Venezuela, a highly eutrophic lake that receives nutrients from allochthonous sources at a very low nitrogen:phosphorus ratio. Our objective is to demonstrate the use of the model and to determine whether nitrogen fixation adds enough nitrogen to Lake Valencia to alleviate nitrogen limitation.

The model

Our model relies for its prediction of daily nitrogen fixation on the empirical determination of four functions: (1) the distribution of insolation over the day, (2) the extinction of photosynthetically available light (PAR) as a function of depth, (3) the nitrogen fixation per heterocyst as a function of light intensity at particular depths, and (4) the distribution of heterocyst abundance with depth. The four functions are combined in the interpolation scheme illustrated in Fig. 1. The first step is to divide the upper, euphotic region of the water column into layers and to divide each day into time increments. The divisions in both cases should be small because steep vertical gradients in heterocyst concentration are common and because the relationship between fixation and light intensity is not linear (Lewis & Levine, 1984). Averaging light intensities over time, for example, neglects brief episodes when the light intensity is especially favourable or unfavourable for fixation. Exponential interpolation in the light extinction function is the basis for calculation of the percentage of surface light penetrating to each of the water layers. The product of total surface irradiance during a time interval and the percentage light penetration gives the light reaching each of the depth increments over the time interval.

The light–response function is determined from measurements of nitrogen fixation in samples from a number of depths over a range of light intensities *in situ*. The shapes of the light–response curves are described by an equation (Lewis & Levine, 1984) modified from a photosynthesis model by Platt, Gallegos & Harrison (1980): $N=N_s(1-e^{-a})e^{-b}+D$, where $a=\alpha I N_s^{-1}$, $b=\beta I N_s^{-1}$, N is the amount of nitrogen fixed per heterocyst per unit time, N_s is a parameter representing maximum fixa-

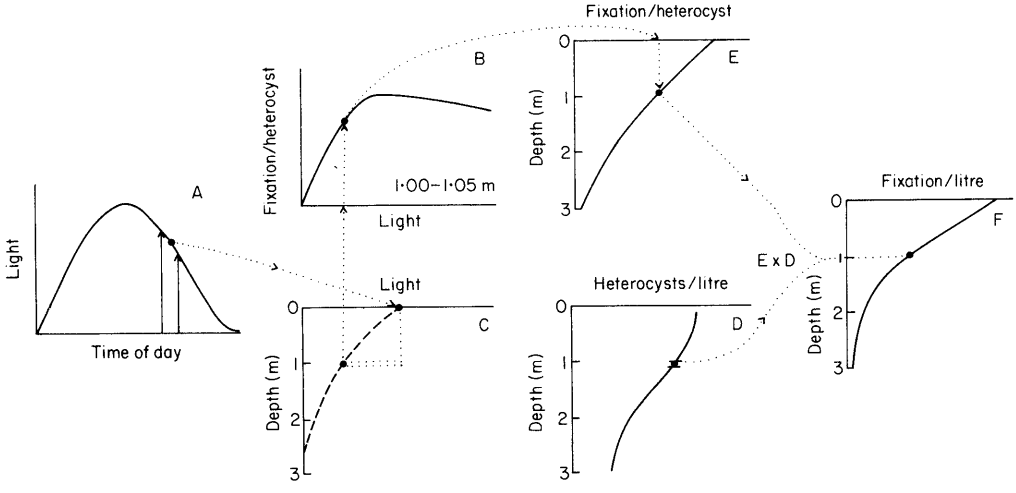

FIG. 1. A graphical representation of the method used to model the depth profile of nitrogen fixation (F) from four empirical functions: insolation *v.* time (A), light extinction *v.* depth (C), fixation per heterocyst *v.* light intensity (B), and heterocyst abundance *v.* depth (D). The light received at a given depth increment (C) is calculated from light extinction and insolation, the fixation rate per heterocyst at a given depth (E) is calculated from the light received and the light response function, and the fixation rate per litre at a given depth (F) is calculated from the fixation rate per heterocyst and heterocyst abundance.

tion in the absence of inhibition by high light intensities, D is the fixation rate per heterocyst in the dark, I is light intensity (PAR), α is the slope of the rising limb of the light–response curve, and β is a parameter for inhibition. Because we have found that the parameters vary with the depth of sample origin (Lewis & Levine, 1984), the light–response curves are blended across sampling depths in a linearly proportional manner. The heterocyst concentrations at a particular depth are obtained by interpolation from the nearest direct estimates. The product of heterocyst concentration and fixation per heterocyst at a depth yields the fixation per unit volume at that depth. Numerical integration over both time and depth yields the daily nitrogen fixation per unit area. The total mass of nitrogen fixed in the euphotic zone is calculated by multiplying the volume of water within each depth interval by the depth-specific fixation rates and summing over the water column. To calculate fixation on those days when water samples are not taken, the model interpolates exponentially between heterocyst counts and linearly between the fixation rates per heterocyst predicted by the light–response equations. Annual fixation is estimated as the sum of the daily fixation rates.

A simplified version of the model can be applied to the aphotic zone of a lake if significant fixation is measured in this region. Model components dealing with light are omitted from the simplified version. In addition, variability in heterocyst abundance may be ignored and fixation can be expressed on a water-volume basis. The latter step is mandatory if part of the aphotic zone is anaerobic, because many nonheterocystous blue-green algae and bacteria can fix nitrogen at low oxygen tensions (Carr & Whitton, 1982).

To calculate nocturnal fixation, the model must be supplied with measurements of nitrogen fixation made at night. Light–response functions determined empirically at midday include estimates of dark fixation in surface waters, but these estimates are for heterocysts that are exposed to light when collected, an hour or so before incubation. As dark fixation proceeds, reductant formed during photic periods is exhausted, causing fixation rate to diminish (Fay, 1976). Because we do not have regular measurements of nitrogen fixation in Lake Valencia at night, we assume that the nocturnal fixation rate in the euphotic zone is equal to the daytime heterocyst-specific fixation rate at the bottom of the euphotic zone, which is dark.

The model assumes that heterocyst concentrations and the parameters of the light–response curves change smoothly over depth and between sampling dates, that the fixation rate at the bottom of the euphotic zone is similar to the sustained nocturnal rate throughout the layer, that the vertical distribution of heterocysts does not change between dawn and dusk, and that the lake is horizontally homogeneous for all pertinent model parameters. Previous studies have shown that, for Lake Valencia, the last two assumptions are incorrect. Diel vertical migrations of heterocystous blue-green algae are common during calm weather (Levine & Lewis, 1984) and the lake is horizontally patchy with regard to both heterocyst abundance and fixation rate per heterocyst (Levine & Lewis, 1985). The consequences of discrepancies between our model assumptions and reality will be discussed later in this paper.

Lake description

Lake Valencia is a large (351 km^2) warm monomictic lake in north-central Venezuela (10°12′N, 67°44′W) with a mean depth of 19 m and a maximum depth of 39 m. Lake stratification occurs during the rainy season (usually May–November, but February–November in 1981), and is characterized by great fluctuations in the thickness of the mixed layer (Lewis, 1983). In most years depth of the upper mixed layer averages about 12 m during lake stratification, but in 1981, the year of our study, it averaged 8 m. Water temperatures in the upper mixed layer range from 26 to 30°C.

For at least 245 years, Lake Valencia has had no outflow (Schubert, 1979). Consequently, the specific conductance of the water is about 2000 μS cm^{-1} and its pH is 8.5–9.5. Due to drainage from urban and agricultural areas, Lake Valencia is heavily loaded with nitrogen (11.2 g m^2 $year^{-1}$ for 1977–78 and 10.3 g m^2 $year^{-1}$ for 1979–81) and phosphorus (2.43 g m^2 $year^{-1}$ for 1977–78 and 3.31 g m^2 $year^{-1}$ for 1979–81) (Lewis & Weibezahn, 1983). Phos-

phorus loading of the lake was augmented in 1979 when additional waters from the city of Valencia were diverted into the lake. The nitrogen:phosphorus supply ratio for Lake Valencia is very low: 4.6:1 from 1977–78 and 3.1:1 from 1979–81. The lake is eutrophic (mean chlorophyll *a* about 40 μg l^{-1}) and sustains large populations of blue-green algae throughout most of the year (Lewis, 1986). The most abundant blue-green taxa in Lake Valencia, *Synechocystis, Microcystis* and *Chroococcus,* do not have a demonstrated ability to fix dinitrogen, but nitrogen fixers of the genera *Anabaena* and *Cylindrosperum* are common and, at times, abundant.

Methods

Insolation was measured continuously during the Lake Valencia study with a Belfort pyheliometer. We divided each day's light record into four 3 h intervals and integrated below the radiation curve for each interval to obtain the total amount of energy for each interval. Because our model requires quantum irradiance rather than energy irradiance, the data were multiplied by a conversion factor derived by calibrating the pyheliometer with a LiCor 180 quantum meter. The vertical extinction of PAR (300–700 nm radiation) at the index station was measured with a submersible quantum sensor whenever water samples were collected.

Water samples were pumped from six depths (0 or 0.5, 1, 3, 5, 10 and 33.5 m) on twenty-nine dates between 13 December 1980 and 15 December 1981. At each depth, some water was preserved with Lugol's solution for later heterocyst enumeration. The remaining water was collected in darkened BOD bottles and used to determine the light response of the populations at the collection depth. Nitrogen fixation was measured with an acetylene reduction technique that uses glass syringes. The mesurements were calibrated periodically with ^{15}N-labelled N_2. The procedures for sample collection, syringe handling, and acetylene analysis are described in Levine & Lewis (1984) and Lewis & Levine (1984). The samples were incubated *in situ* in transparent holders that kept the syringes horizontal. For samples originating at depths of 0–1 m, duplicate syringes were incubated at depths of 0, 0.5, 1, 2 and 5 m. Little light penetrates to depths below 3 m (<1%). Samples from 3 m were therefore incubated only at 2 m and 5 m, where the light intensities were low. Samples from >3 m depth were incubated in the dark, at 7 m. All incubations lasted 4 h (±30 min) and typically begin between 11.00 and 12.00 hours.

Insolation was recorded throughout the incubation period with a LiCor 180 quantum meter and the vertical extinction of PAR at the incubation site was measured just before the incubation. The combined data on light extinction and insolation over the incubation period were used to compute the amount of light reaching each of the sets of syringes at the five different depths of incubation. For modelling, we divide the 3 m euphotic zone into sixty-one layers of 5 cm each. The aphotic zone was not modelled because measurements *in situ* indicated that fixation was negligible in this region.

Results

Heterocystous blue-green algae were present in the euphotic zone of Lake Valencia throughout our year-long study, but were scarce (<200 heterocysts cm^{-3}) during the dry season, when frequent winds thickened the lake's upper mixed layer to >20 m and raised the concentration of dissolved inorganic nitrogen (DIN) in the euphotic zone to >200 μg l^{-1} (Fig. 2). With the beginning of calmer weather in February, Lake Valencia's mixed layer diminished to <10 m and the DIN in the euphotic zone was depleted by phytoplankton. Heterocystous blue-green algae responded to the greater light exposure and lower nitrogen availability with increased heterocyst concentrations. However, heterocyst concentrations did not reach 2000 cm^{-3} until late in the rainy season (September–November). During this period, the depth of the mixed layer increased, but not enough to entrain large amounts of nitrogen-rich water.

Two heterocystous species, *Anabaena spiroides* Kleb. and *Anabaena volzii* Lemm., were abundant in Lake Valencia during our study. *Anabaena spiroides* dominated from late March to late August and *Anabaena volzii* dominated during the remainder of the year

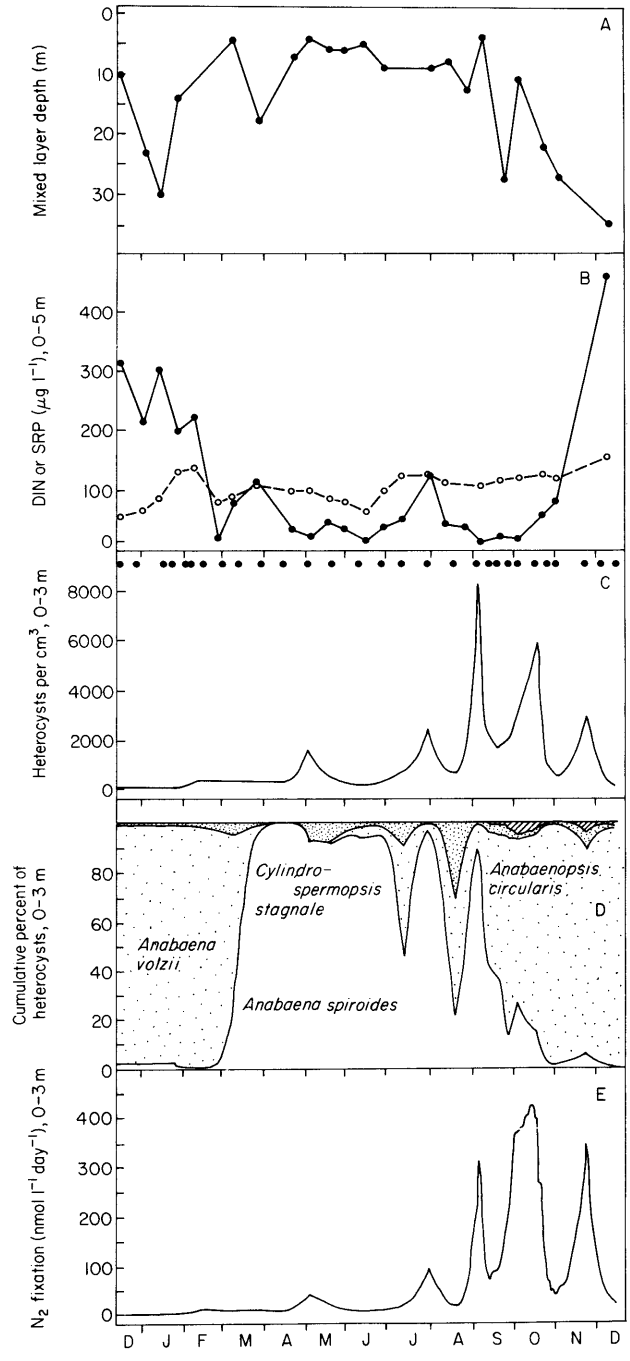

FIG. 2. The seasonal patterns for several variables in Lake Valencia: (A) The depth of the mixed layer, (B) the concentrations of dissolved inorganic nitrogen (DIN, •: $NO_3+NO_2+NH_4$) and soluble reactive phosphorus (SRP, ○) in the euphotic zone, (C) the heterocyst concentration in the euphotic zone, (D) the relative distribution of heterocysts by species, and (E) the mean fixation rate per litre of water in the euphotic zone during daylight. Sampling dates are marked by dots in Panel C.

(Fig. 2D). *Anabaena circinalis* (G. S. West) Wol. and Miller and *Cylindrosperum stagnale* (Wolosz.) Seenayya et Subba Raju were also common, but together these species usually contributed <10% of heterocysts.

Only occasionally, during windy weather, did we measure uniform heterocyst concentrations over the depth of the euphotic zone. More typically, heterocyst concentrations were greatest near the lake surface and declined with depth. The most abrupt gradient in abundance was typically between 0.5 and 1 m depth (Fig. 3). On calm days, a 10–50-fold difference between heterocyst concentrations at the surface and at 3 m depth was not uncommon. However, these profiles were for morning collections; diel studies in Lake Valencia have shown that heterocystous blue-green algae migrate downwards at midday (Levine & Lewis, 1984).

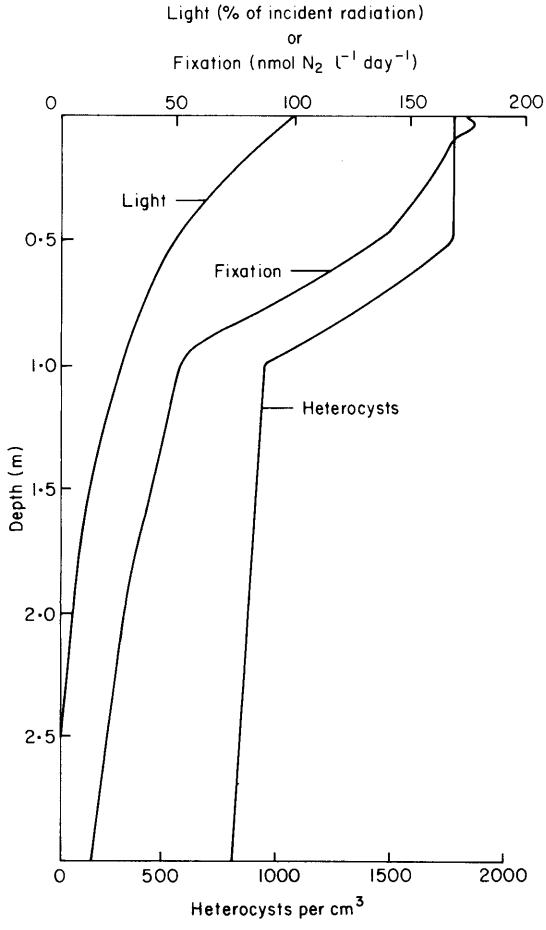

FIG. 3. The average vertical distributions of heterocysts, light (as a percentage of surface irradiance), and diurnal nitrogen fixation in Lake Valencia during 1981.

The parameters of the empirically-determined light–response functions for nitrogen fixation in Lake Valencia varied slightly over time and varied more substantially with depth of sample collection. In general, fixation was very sensitive to light intensity at low light intensities, became saturated at less than full sunlight (surface samples became saturated at about two-thirds full sunlight), and was inhibited at higher light intensities. Characteristics of the functions are described in detail in Lewis & Levine (1984). The light–response functions could only be defined accurately when fixation rates were high. Before September, fixation rates were low; we therefore used curves obtained during early September to calculate fixation throughout the dry season and the early rainy season. Similarly, fixation at 3 m depth was so low that we chose to use the light–response parameters for 1 m depth to calculate fixation between 1 and 3 m depth.

Because both heterocyst abundance and light decreased with depth, vertical profiles for nitrogen fixation were steep (Fig. 3). For example, the mean nitrogen fixation rate at 3 m depth was just 9% of the value at the lake surface and about 80% of daytime fixation occurred in the surface meter of water. Incubations *in situ* of water from 5, 10 and 33.5 m indicated that the average nitrogen fixation rates at these depths were so low as to be indistinguishable from background: 0.2±2.0 (5 m), −0.4±1.5 (10 m) and 0.9±2.6 (33.5 m) nmol l^{-1} h^{-1}, n=27.

Although insolation and water clarity were greater during the dry season than during the wet season, nitrogen fixation was largely restricted to the wet season (Fig. 2E), because heterocysts were abundant only at this time. Nitrogen fixation rates for daylight hours during the rainy season fluctuated between the extremes of 25 and 400 nmol l^{-1} day^{-1} and were greatest during the last 12 weeks of lake stratification, when >85% of the nitrogen fixation occurred.

Because nocturnal fixation proceeded over the entire mixed layer of Lake Valencia for about 12 h every day, considerable nitrogen

was fixed at night, our estimate is 6.78 kg ha^{-1} $year^{-1}$. By comparison, diurnal nitrogen fixation over the period of study (13 December 1980 to 15 December 1981) was 19.14 kg N ha^{-1} $year^{-1}$. Therefore, about 26 kg N ha^{-1} were fixed in the water column of Lake Valencia during 1981. This value is small compared with the combined external sources, which accounted for 89.3 kg N ha^{-1} $year^{-1}$. Pelagic nitrogen fixation raised the annual nitrogen input to Lake Valencia by about 29% (to 115 kg N ha^{-1}), but did little to change the N:P supply ratio to the lake in 1981: the N:P ratio in allochthonous sources was 2.9:1, whereas the N:P supply ratio of the total nutrient loading (allochthonous inputs plus fixation) was 3.7:1. The nitrogen requirement of the phytoplankton in Lake Valencia during 1981 (1250 kg N ha^{-1} $year^{-1}$, if nitrogen and carbon were incorporated at a ratio of 6:1 by weight (Redfield, 1958); primary productivity was 7500 kg C ha^{-1} $year^{-1}$) was 11 times the total nitrogen loading of the lake and 48 times the amount of nitrogen fixed. Therefore, most of the nitrogen used by the phytoplankton in this lake is supplied through recyling.

Discussion

It is difficult to compare nitrogen fixation rates in Lake Valencia with the fixation rates in other lakes because there are no established procedures for estimating daily and annual nitrogen fixation. Some estimates of daily fixation incorporate allowances for light intensity. For example, daily fixation may be estimated as the product of the fixation rate measured *in situ* and the ratio of daily insolation to light received during the incubation (Leonardson, 1984), or diel studies may be used to determine the proportion of daily fixation that normally occurs during the time of day chosen for incubation (Granhall & Lundgren, 1971; Horne & Goldman, 1972; Leonardson & Bengtsson, 1978; Brownlee & Murphy, 1983). In some instances, daily nitrogen fixation is estimated by multiplying empirically-determined hourly rates by 24 h (Keirn & Brezonik, 1971; Granhall & Lundgren, 1971) or by hours of daylight (Horne & Fogg, 1970). All of these procedures for calculating nitrogen fixation yield inaccurate results for one or both of two reasons: (1) they assume that the light response curve for nitrogen fixation is linear when it is not (Lewis & Levine, 1984), (2) they assume that the distribution of light over time is either constant or regular, when it actually varies substantially.

Comparisons of nitrogen fixation in lakes are also complicated by inaccuracies in the conversion of acetylene reduction to nitrogen fixation. Early researchers often used a theortetical value, 3:1, for the molar ratio of acetylene reduced to nitrogen fixed. However, simultaneous measurements of $^{15}N_2$ fixation and acetylene reduction have shown that the ratio of acetylene reduction to nitrogen fixation actually varies with season and depth and is usually >3:1 (Graham, Hamilton & Campbell, 1980). To calculate fixation in Lake Valencia, we used empirically-determined depth-specific conversion ratios (Levine & Lewis, 1984).

Our estimates of nitrogen fixation in Lake Valencia may be low because our model assumes that the vertical distribution of heterocysts is similar throughout the day, even though heterocystous blue-green algae actually undergo diel migrations (Levine & Lewis, 1984). We sampled in the morning when heterocystous blue-green algae are concentrated near the lake surface. At midday, surface populations may migrate down, avoiding the photoinhibition that is included in our model.

Our model results also are influenced by the use of one sampling site to characterize the heterocyst abundance and the light–response function over the entire lake. Synoptic studies of Lake Valencia have shown that the variability of nitrogen fixation and heterocyst abundance along a horizontal plane is even greater than the temporal variability of these parameters (Levine & Lewis, 1985). This finding suggests that our model does not accurately estimate nitrogen fixation in Lake Valencia on any particular date. However, the spatial variability of heterocysts and nitrogen fixation in Lake Valencia is highly ephemeral, rather than fixed. Therefore, repeated observations at any given site are an unbiased estimator of the lake mean through time.

The annual nitrogen fixation rate in Lake Valencia per unit area (26 kg ha^{-1} $year^{-1}$) is comparable to fixation measured in temperate

lakes with long-term summer blue-green algal blooms. For example, Clear Lake, California, has a mean nitrogen fixation rate of 18 kg ha^{-1} $year^{-1}$ (Horne & Goldman, 1972), Lake Södra Bergundasjön, Sweden, has a fixation rate of 22 kg ha^{-1} $year^{-1}$ (Leonardson & Bengtsson, 1978), Lake Mize, Florida, has a mean fixation rate of 23 kg ha^{-1} $year^{-1}$ (Keirn & Brezonik, 1971), and the nitrogen fixation rate for Lake 885, Manitoba, is 27 kg ha^{-1} $year^{-1}$ (Brownlee & Murphy, 1983). On the other hand, Lake Valencia fixed substantially less nitrogen in 1981 than some shallow tropical lakes fix in a year. For example, nitrogen fixation brought 44 kg N ha^{-1} into Lake George, Uganda in 1968 (Horne & Viner, 1971) and nitrogen fixation has contributed as much as 175 kg ha^{-1} $year^{-1}$ to Rietvlei Dam, South Africa, during dry years when the lake has been shallow (Ashton, 1981). Significantly, during a year when Rietvlei Dam was deep, annual nitrogen fixation was only 5 kg ha^{-1}. These observations suggest that annual nitrogen fixation is influenced more by lake depth than by mean annual temperature. In deep lakes, fixers may be mixed to depths where light limits nitrogen fixation. In addition, lake stratification may reduce the amounts of trace metals in the euphotic zone. Trace metals such as molybdenum and iron are essential for nitrogen fixation (Carr & Whitton, 1982).

The seasonal trends of nitrogen fixation in Lake Valencia are reminiscent of those described for warm monomictic and dimictic lakes in temperate regions: fixation was low during lake mixing and high at the end of the stratification period. For temperate lakes, the annual pattern in blue-green algal abundance is sometimes attributed to seasonal trends in temperature; the fixers are supposedly favoured by warm temperatures (Wetzel, 1983). This explanation does not hold for lake Valencia, however, because the lake has an almost constant temperature.

Low fixation in Lake Valencia during the dry season may be explained by light-limited phytoplankton growth. Light limitation is suggested by deep mixing of surface waters and the accumulation of DIN and SRP in the mixed layer. Nitrogen fixation and heterocyst production are energy-expensive processes that usually are terminated when ammonium and nitrate are introduced (Carr & Whitton, 1982). The explanation for low nitrogen fixation in Lake Valencia during early lake stratification is more elusive. Mixed layer depth appeared to be more stable early than late in the stratification period, and throughout stratification DIN concentrations were normally $<50 \mu g\ l^{-1}$ and DIN:SRP ratios were <2:1. At such low N:P ratios the phytoplankton succession models of Tilman, Kilham & Kilham (1982) and Smith (1983) predict nitrogen limitation and blue-green algal dominance. The paradox may stem from our inability to resolve short-term changes in mixed layer depth with bi-weekly measurements. We believe that the occurrence of large populations of nitrogen fixers near the surface coincides with very low dissolved inorganic nitrogen concentrations ($\ll 50 \mu g\ l^{-1}$), and that this intense depletion of inorganic nitrogen occurs only when exceptionally calm weather causes layering of high stability. This stability, which is interrupted frequently by temporary deep mixing due to unseasonally windy weather (atelomixis: Lewis, 1983), may be missed by bi-weekly measurements of mixed-layer thickness. Towards the end of the stratification interval, the entire water column becomes depleted of inorganic nitrogen. Atelomixis then brings less DIN to the surface and shorter periods of high-stability layering are required for severe DIN depletion. Nitrogen fixation is thus more likely during late stratification.

An alternative explanation for the delay in fixation until late in the stratification interval is that a factor necessary for fixation may have been depleted in the upper mixed layer early in the season and only reintroduced in quantity late in the season during episodes of atelomixis. Frequency of atelomixis seems to have increased after August (Fig. 2A). There are several reports of nitrogen fixation being stimulated by the introduction of small amounts of phosphorus (Stewart & Alexander, 1971; Mague, Weare & Holm-Hansen, 1974), but it is unlikely that phosphorus stimulated nitrogen fixation in Lake Valencia in 1981; the SRP concentrations that we measured in the upper mixed layer of this lake were among the highest on record for surface waters. Goering & Ness (1964) have found that ammonium occasionally stimulates fixation, but its usual effect is depression of nitrogenase synthesis (Carr & Whitton, 1982). Iron and molybde-

num are better candidates for stimulants of fixation because both are essential elements for fixation and are often depleted from the epilimnia of lakes during sustained stratification (Morton & Lee, 1974; Howarth & Cole, 1985).

It has been suggested that nitrogen fixation ultimately compensates for nitrogen shortages in lakes with low N:P supply ratios, bringing these lakes to phosphorus limitation (Schindler, 1977; Kilham & Kilham, 1980). Our calculations indicated that in 1981 only about 23% of the nitrogen input to Lake Valencia was due to pelagic nitrogen fixation. We did not measure nitrogen fixation in sediments. However, since most of Lake Valencia's sediment surface is below the euphotic zone, nitrogen fixation is this habitat must be heterotrophic. Estimates of nitrogen fixation in dark lacustrine sediments have ranged from 0.03 to 2.7 kg ha^{-1} $year^{-1}$ (Howarth *et al.*, 1987), values an order of magnitude lower than the rate of pelagic nitrogen fixation in Lake Valencia. Because much of the small amount of nitrogen fixed in sediments may never be released into the water column, sediment-based nitrogen fixation is probably insignificant to the nitrogen loading of Lake Valencia. To alleviate nitrogen limitation in Lake Valencia (i.e. to raise the N:P supply ratio for the lake to that required by algae, 7:1), nitrogen fixation would have had to be 2 times greater in 1977–78 and an average of 5 times greater in 1979–81 than it was in 1981. Such rates are possible under ideal conditions, as measurements of fixation in Lake George and Rietvlei Dam confirm, and they may sometimes occur in Lake Valencia. However, under Lake Valencia's mixing regime, nitrogen fixation appears to be an unreliable 'fix' for the lake's nitrogen shortages.

Acknowledgments

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