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An assessment of nitrogen fixation as a source of nitrogen to the North Atlantic Ocean

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Abstract. The role of nitrogen fixation in the nitrogen cycle of the North Atlantic basin was re-evaluated because recent estimates had indicated a far higher rate than previous reports. Examination of the available data on nitrogen fixation rates and abundance of *Trichodesmium*, the major nitrogen fixing organism, leads to the conclusion that rates might be as high as 1.09 × 10^{12} mol N yr^{-1}. Several geochemical arguments are reviewed that each require a large nitrogen source that is consistent with nitrogen fixation, but the current data, although limited, do not support a sufficiently high rate. However, recent measurements of the fixation rates per colony are higher than the historical average, suggesting that improved methodology may require a re-evaluation through further measurements. The paucity of temporally resolved data on both rates and abundance for the major areal extent of the tropical Atlantic, where aeolian inputs of iron may foster high fixation rates, represents another major gap.

Introduction

The North Atlantic is arguably the most studied region of the world's ocean, including not solely the marine component but also the adjacent coastal, estuarine and atmospheric ecosystems. In addition, the highly populated and industrialized watersheds surrounding the North Atlantic and its relatively small volume compared to other ocean basins suggests that man's impact might be discernible. As part of a basin scale evaluation of the various terms of the nitrogen budget for the North Atlantic (Galloway et al. this volume), a review of the nitrogen cycle of the oceanic component was undertaken to identify the important terms, especially imports and exports (Michaels et al. this volume).

Nitrogen fixation, the conversion of atmospheric dinitrogen to biologically usable ammonium, is one source of nitrogen to the ocean. Studies in the 1970's focused on measuring this input of nitrogen by the most obvious organism, *Trichodesmium* sp., a filamentous cyanobacteria that forms colonial associations approximately 1–1000 mm in size and can aggregate at the surface in extensive blooms (Carpenter & Capone 1992). These studies were extensively reviewed by Carpenter (1983), with the conclusion that fixation in the entire Atlantic contributed 0.94 × 10^{11} mol N yr^{-1} to a global rate of 3.4 × 10^{11} mol N yr^{-1}. On a global basis, this value is a small input of nitrogen to the photic zone compared to other sources such as convective transport and upwelling.

A recent reassessment of the magnitude of nitrogen fixation, however, concluded that nitrogen fixation rates in the Caribbean region were considerably higher than earlier reports (Carpenter & Romans 1991). Using a calculated rate of 10–50 mg N m^{-2} d^{-1}, and applying it over the area of the Caribbean and Atlantic Ocean from 0–30° N of 24 × 10^{12} m^2 implies a source of 6.3 to 31.3 × 10^{11} mol N yr^{-1}, a dramatic upward revision of the nitrogen fixation rate from 1983 to 1991. We therefore examined the literature on nitrogen fixation rates in this region to identify the cause of the increase.

Results and discussion

Methodological considerations

The high fixation rate calculated by Carpenter & Romans (1991) is largely based on data collected as part of tests of the acetylene reduction assay (Carpenter et al. 1987). Martinez et al. (1983) had noted that diver-collected mats of *Rhizosolenia* sp. had much higher rates of nitrogen fixation than mats collected by net tows. In addition, Carpenter & Price (1976) had noted a negative relationship between fixation rates by *Trichodesmium* and turbulence, again suggesting that net tows would underestimate the estimation of nitrogen fixation. However, a comparison of rates between hand and net collected colonies of *Trichodesmium* found no significant difference in several trials in the Caribbean and the Sargasso Sea (Carpenter et al. 1987). Subsequent investigations of nitrogen fixation by *Rhizosolenia* have failed to detect any activity (Villareal & Carpenter 1989).

Realization by the oceanographic community that trace metal contamination could significantly reduce measurements of primary productivity in oligotrophic waters (Fitzwater et al. 1982) had also raised the question whether measurements of nitrogen fixation were too low. *Trichodesmium* is sensitive to metals such as copper (Rueter et al. 1979) and the high requirement of the nitrogen fixation enzyme (nitrogenase) for metals such as Fe (Rueter et al. 1992) and possibly Mo (Howarth & Cole 1985) suggests that contamination could act to either enhance or inhibit fixation. Again, Carpenter et al. (1987) found no significant difference between rates using colonies collected using extremely strict precautions and less stringent, “standard” protocols.

Although both of these methodological issues revealed no problem with earlier measurements, the doubling times cited by Carpenter & Romans (1991), from all geographic locales, were considerably higher than previously published values. For example, Carpenter & Price (1977) found values of 45 days for surface colonies from the Caribbean and 105 days for the Sargasso Sea, compared to 1–2 days for the same locations in the 1991 estimate. Since the later doubling time is the basis for the recent re-assessment of the fixation rate (Carpenter & Romans 1991), it is important to understand its provenance. Calculation of the doubling time from rates requires evaluating the biomass. Carpenter et al. (1987) used a biomass of 0.986 ng N trichome^{-1} and a rate of 0.6 ng N trichome^{-1} d^{-1} to calculate a doubling time of 1.13 d (ln 2/0.6/0.986). However, although the biomass of individual colonies does vary somewhat, 2 ug N colony^{-1} or about 10 ng trichome^{-1} (based on 200 trichomes colony^{-1}) seems to be the most commonly reported value (Carpenter & Price 1977; McCarthy & Carpenter 1979; Carpenter et al. 1993). Since the low biomass estimate was utilized by Carpenter et al. (1987), calculated doubling times were tenfold faster than if the higher biomass was utilized. If the doubling times from 1987 were in fact 10–12 days, they are more in line with earlier reports of 10–150 days and suggest an average doubling time longer than the 10 days used by Carpenter & Romans (1991) would be appropriate.

Another factor contributing to the high areal fixation rate is the assumption of depth dependence of abundance and rate as well as the time period of fixation used in the calculation compared to those used in earlier calculations. The rate of nitrogen fixation diminishes rapidly with depth (see for example, Goering et al. 1966; Carpenter & McCarthy 1975; Carpenter & Price 1977), due to a decline in both colony abundance and fixation rate per colony. Carpenter (1983) accounted for this by estimating a mean rate per colony over the photic zone and then halving that rate to account for reduced fixation at the beginning and end of the daylight period (which was assumed to be 12 hrs). Since the majority of estimates for colony abundance are from surface tows, the depth distribution of colony abundance was estimated by assuming a constant abundance from the surface to 15 m and then a linear decrease to 50 m where the abundance was assumed to be 10% of that at the surface (Carpenter 1983). In contrast, the 1991 rate estimate assumed a constant depth distribution of both abundance and rate for colonies present at the surface and a 12 hour period of active fixation. The net effect of these different assumptions are summarized in Table 1 and account for a nearly 10 fold lower areal rate based on the different assumptions. The assumptions employed by Carpenter (1983) still seem realistic and we employ them for an estimate of the basin scale rate of fixation.

Table 1. Effect of various assumptions on calculated areal nitrogen fixation rates.

	Calculations based on Carpenter (1983)			Calculation and rate from Carpenter & Romans (1991)
Parameter	Rate from Carpenter & Romans (1991)	Measured rate from Carpenter et al. (1987)	Mean Photic zone rate from Carpenter (1983)	
Surface rate (ng N colony^{-1} day^{-1})	200	120	17	200
Daylength correction[1] (ng N colony^{-1} day^{-1})	100	60	8.5	200
Mean Photic zone[2] (ng N colony^{-1} day^{-1})	68	41	8.5	200
Colony abundance[2] (Colonies m^{-2})	34,000	34,000	34,000	50,000
Areal Rate (mg N m^{-2} d^{-1})	2.3	1.4	0.3	10

[1] Assuming half the maximal rate over the entire daylight period (Carpenter 1983).

[2] Assuming a constant value from 0–15 m and a linear decrease to 10% of the surface value at 50 m (Carpenter 1983).

Vertical, horizontal and basin-scale distributions

A major requirement for a basin scale estimate of nitrogen fixation is to account for the temporal and horizontal variation in the rates and distribution of the organisms. There is considerable variability in the individual colony rates of nitrogen fixation, ranging from values of 0.4 ng N colony hr^{-1} to values in blooms of 17.4 to 50.4 ng N colony hr^{-1} (Carpenter & Capone 1992). Some of this variation is due to different colony sizes, but even on a per cell basis, the rates are quite variable for reasons not yet understood. A compilation of the extant measurements of fixation rates over the past 20 years reveals the paucity of measurements over the North Atlantic Ocean, arguably the most studied region (Figure 1). The only seasonal series of measurements of nitrogen fixation to define the temporal scale of the variability is not for *Trichodesmium* but for cyanobacteria associated with *Sargassum sp.* off Florida (Phlips et al. 1986). Choosing a representative rate for the entire North Atlantic is therefore admittedly difficult but the data summarized above suggest that the use of just the higher rates of Carpenter & Romans (1991) for the entire basin is currently unwarranted.

In addition to variability in per colony rates, the number of colonies can vary tremendously. Recasting the data summarized previously (Carpenter 1983) to emphasize stations in the North Atlantic (Figure 2) again reveals the lack of information for vast areas of the ocean, especially in view of the

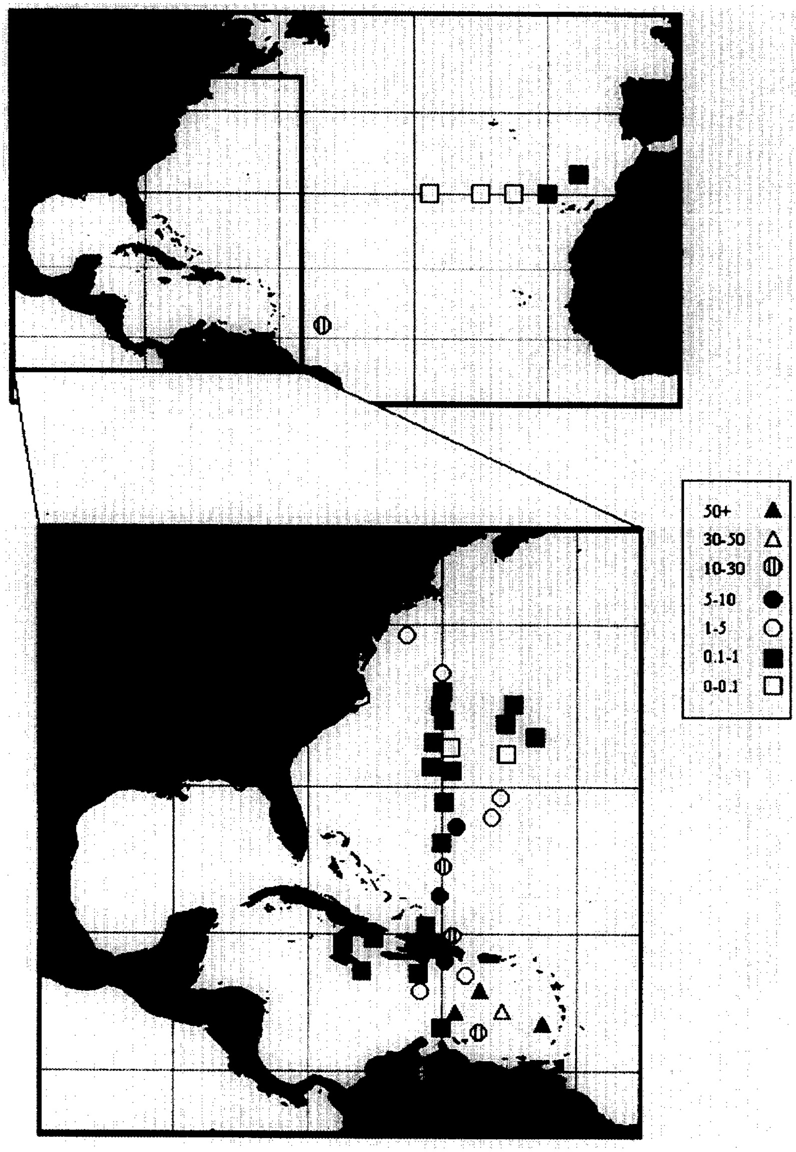

Figure 1. Areal rates of nitrogen fixation (μmol N m^{-2} d^{-1}) measured in the North Atlantic Ocean. Rates based on references cited in Carpenter (1983).

fact that each station represents a single realization of a patchy distribution. For example, there is almost no information in the region from 0° to 30° N and from 20° W to the Caribbean. A basin scale estimate currently requires extrapolation of both rates and abundances from the Caribbean over the entire area.

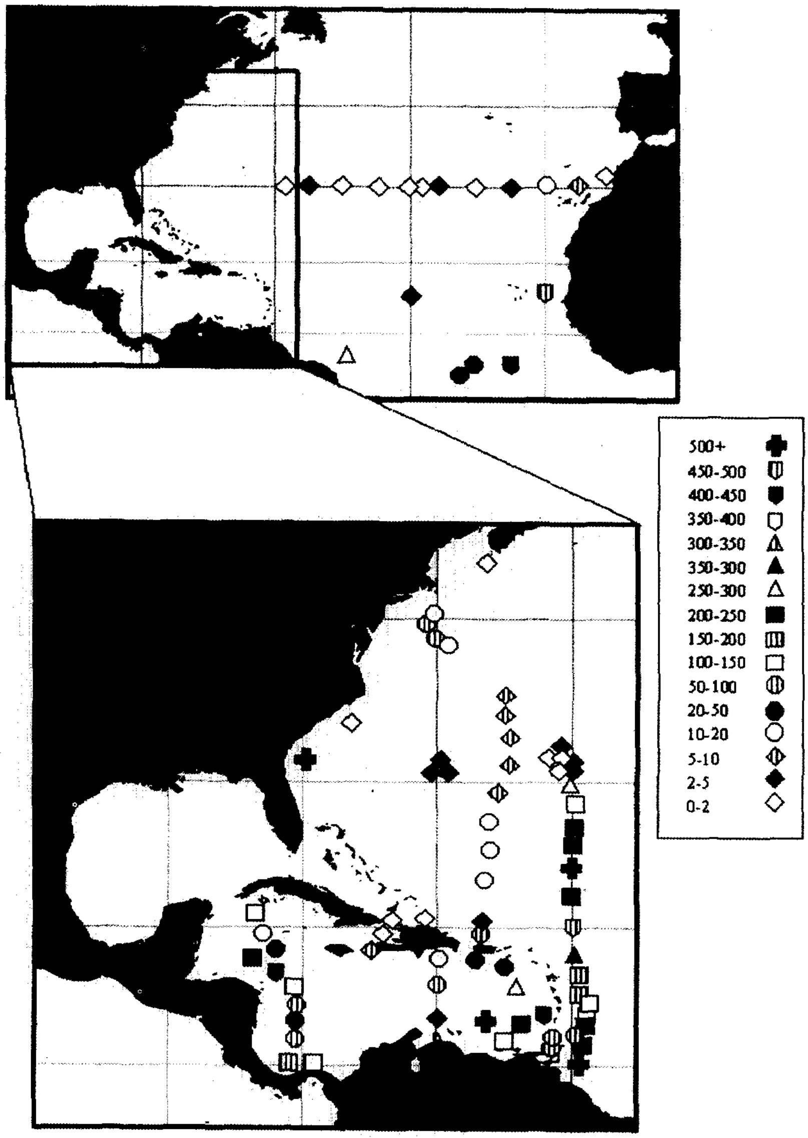

Figure 2. Surface distribution of *Trichodesmium* trichomes (trichomes $m^{-3} \times 10^{-3}$) in the North Atlantic Ocean. Data based on references cited in Carpenter (1983) with the addition of Carpenter & Romans (1991).

In addition to re-examining specific studies on nitrogen fixation, we examined the extensive Continuous Plankton Recorder (CPR) survey data for the northern region of the basin (Edinburgh, Oceanic Laboratory 1967). The CPR survey is a plankton distribution study using instruments towed at a

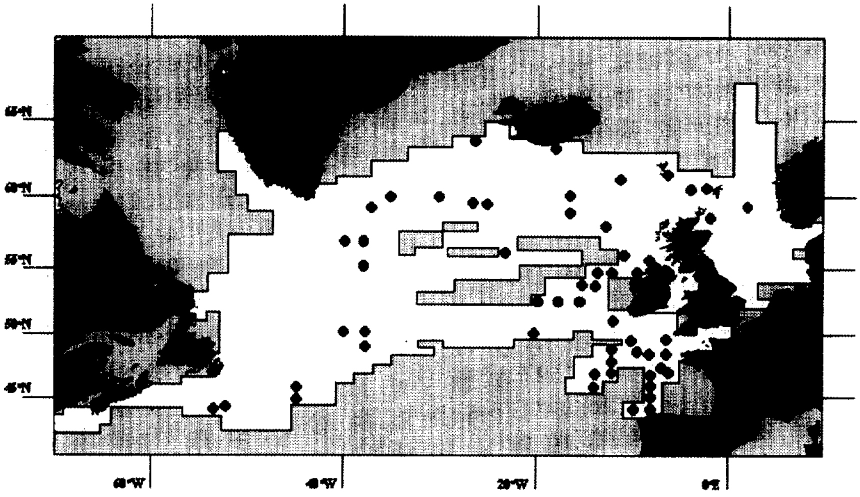

Figure 3. Occurrence of *Trichodesmium* spp in the northern North Atlantic. Dots represent presence in 1° latitude 2° longitude squares pooled for all months for the years 1958–1968 inclusive. Hatched oceanic areas represent no data. Data source: Continuous Plankton Survey, UK (The Oceanic Laboratory, Edinburgh, 1973).

fixed depth of 10 m, and carried out by ships of opportunity. Although the extent of the survey has varied since its introduction in the 1930's, there has been reasonable coverage over the northern North Atlantic basin. Figure 3 summarizes the locations where *Trichodesmium* has been recorded. Given the general view that *Trichodesmium* is a tropical or sub-tropical species, it is notable that the genus has been found in many parts of the central and eastern regions of the basin, clearly indicating that it is not confined to the lower latitudes. However, the general pattern of the distribution suggests that the *Trichodesmium* may be passively transported by the Gulf Stream/North Atlantic Drift, rather than growing *in situ*. Unfortunately, because of its nature the CPR survey data merely indicate presence or absence, thus no abundance information can be inferred. Even assuming the (unlikely) case of similar cell densities as in the tropics in all the regions indicated by the CPR data, the question remains whether the individual colonies were active and capable of nitrogen fixation. Carpenter (1983) concluded that 20 °C was the minimum temperature for fixation activity by *Trichodesmium* and thus, given the low average temperatures of the northern North Atlantic basin, we assume that rates of fixation would be relatively low. A low rate combined with the small areal extent of the northern region compared to the southern region, leads us to conclude that nitrogen fixation in this area of the basin makes a small contribution to the nitrogen cycle. Nevertheless, the widespread distribution and potential activity of the genus warrants more attention than hitherto displayed.

Given the paucity of data on the distribution and activity of *Trichodesmium* over much of the Atlantic basin, is it possible that under-sampling could result in a major underestimate of its importance, and thus account, in part at least, for the apparent imbalance in the nitrogen budget? As pointed out by others, the presence of relatively rare blooms can dramatically increase the input of nitrogen to the surface ocean, yet our ability to quantify their occurrence is limited to chance encounters on scattered cruises (Carpenter & Capone 1983; Carpenter & Capone 1992; Karl et al. 1992). One of the major gaps in our understanding of *Trichodesmium* physiology is knowledge of the requirements for bloom formation.

Formation of a bloom *de novo* rather than merely a surface aggregation of a vertically dispersed population would seem to require a faster growth rate than the average values measured for nitrogen. The highest turnover rates of about 10 d for nitrogen (Carpenter et al. 1987) are still slow compared to what one might expect to overcome physical dispersion. However turnover times of 1–8 d for carbon (Lewis et al. 1988; Carpenter et al. 1993; Carpenter & Roenneberg 1995) and for cellular chlorophyll (Prufert-Bebout et al. 1993) are certainly sufficient for bloom formation but are inconsistent with balanced growth of the cells.

There are few contemporaneous measurements of carbon and nitrogen turnover times. Carpenter & Price (1977) measured both rates for Caribbean populations, from which turnover times of 44.8 d for nitrogen and 14.5 - 29 d for carbon can be calculated. More recently, Carpenter et al. (1993) reported carbon doubling times of 3–3.8 d. For comparison, nitrogen doubling times of 17–33 d can be calculated based on acetylene reduction rates of 0.5 nmol ethylene colony^{-1} hr^{-1} for *T. erythraeum* and 1.0 nmol colony^{-1} hr^{-1} for *T. thiebautii* and measured N content per colony of 2.1–2.4 ug. Applying a 6.3:1 conversion factor from acetylene to dinitrogen as measured by Carpenter & Price (1977), rather than a 3:1 ratio, would proportionally increase the nitrogen doubling time and exacerbate the difference. Use of alternate nitrogen sources such as inorganic nitrogen would provide nitrogen to support high carbon-based growth rates but assimilation of both NH_4^+ and NO_3^- has been shown to be negligible compared to fixation (Carpenter & McCarthy 1975). Resolving the nutrient demands of balanced growth clearly requires more contemporaneous measurements both nitrogen and carbon utilization but should also include use of phosphorus (see below).

Other nitrogen fixing organisms

Traditionally, *Trichodesmium* has been considered the primary nitrogen fixing organism in the pelagic ocean. There are other organisms that can also contribute but our knowledge of their impact is limited. For instance, *Hemiaulus* sp., a marine diatom, frequently contains a cyanobacterial symbiont that fixes nitrogen (Villareal 1991). Villareal (1991) estimated that *Hemiaulus*, assuming a cell density of 100 l^{-1} ,would contribute 4.8 ug-at N m^2 d^{-1} but noted that densities of 10^5 cells l^{-1} have been reported off Florida. Although not all cells contained symbionts, the majority (91–100%) in the Caribbean did (Villareal 1994), suggesting that these organisms could also be important if blooms were frequent. Unfortunately, our knowledge of their distribution or activity is extremely limited so that a basin scale assessment of the contribution of *Hemiaulus* sp. to the nitrogen cycle of the North Atlantic is premature.

Basin scale speculation

The motivation for these deliberations sprang from a desire to independently evaluate the value of 6–31 × 10^{11} mol N yr^{-1} as compared to the earlier value of 1 × 10^{11} mol N yr^{-1} for nitrogen fixation in the North Atlantic. Using an historically high rate (rather than a turnover time) of 0.060 ng N $trichome^{-1}$ hr^{-1} (Carpenter et al. 1987) for the entire region and trichome densities from Carpenter (1983), we roughly calculate an input of about 10.7 × 10^{11} mol N yr^{-1} to the region (Table 2). Based on the available evidence summarized above (other than the additional data in 1987, nearly as limited today as in 1983) we are forced to conclude that Carpenter & Romans (1991) somewhat overstated the role of nitrogen fixation in the North Atlantic.

Interestingly, several lines of geochemical evidence imply an even higher fixation rate than we calculate can be supported by available evidence. There is a puzzling mismatch in the central Sargasso Sea between the depth of appearance of nitrate (nitracline) and the deeper depth of detectable levels of phosphate (Michaels et al. 1994b). Combining the residence time of different depth layers in the volume from 15° N to 45° N with the amount of "excess" nitrate compared to phosphate leads to a calculated production rate of 34 to 61 × 10^{11} mol N yr^{-1} required to sustain the anomaly (Michaels et al. this volume) and they argue that nitrogen fixation is required to sustain the observed NO_3^-:$PO_4^=$ anomaly. A second puzzle is the net depletion of dissolved inorganic carbon from the surface waters near Bermuda during a period when the water column is stratified and fully oligotrophic (Michaels et al. 1994a). The amount of new nitrogen required to balance the observed net community fixation of carbon is comparable to that required to sustain the NO_3^-:$PO_4^=$ anomaly and again, high rates of nitrogen fixation would resolve the puzzle.

Other potential sources of new nitrogen such as atmospheric inputs of ammonium and nitrate in wet or dry deposition have been evaluated for the waters around Bermuda and found to supply small amounts of nitrogen compared to internal processes such as convective transport of nitrate from

Table 2. Basin scale assessment of the nitrogen fixation rate.

Region	Fixation rate[1] (pmoles N col^{-1} hr^{-1})	Days[2] (d yr^{-1})	Depth interval (m)	Colony density (colonies m^{-3})	Area (10^{12} m^2)	Area rate[3] (10^{12} mol N yr^{-1})
Southern (0–30° N)	800	365	50	1000	18	1.05
mid-Atlantic (31–50° N)	400	250	50	200	14	0.036
Northern (>50° N)	80	100	25	20	6	7×10^{-5}

[1] The southern rate is based on the Carpenter at al. (1987) rate of 6 pmole C_2H_4 $trichome^{-1}$ h^{-1}, 200 trichomes $colony^{-1}$ and a 3:1 ratio. The mid-Atlantic and northern rates are estimates.

[2] The number of days of active fixation are diminished northward to account for the winter period of high turbulence and reduced light intensity.

[3] Includes 6 hrs of daylight to account for diminished fixation at the beginning and end of the daylight period (Carpenter 1983), a factor of 0.7 to reduce the number density of surface colonies with depth (Carpenter 1983) and another factor of 0.7 to replicate the depth dependence of fixation activity

deeper water to the euphotic zone (Knap et al. 1986; Michaels et al. 1993). A basin scale assessment of atmospheric inputs from North America and Europe reached a similar conclusion for the pelagic regime, although in certain coastal waters an anthropogenic influence can be documented (Prospero et al. this volume).

These geochemical arguments for high fixation rates in the North Atlantic also imply a difference from other basins where similar evidence is not present. Nitrogen fixation rates in the tropical Atlantic might actually be stimulated by large inputs of Fe from atmospheric dust (Prospero et al. this volume). Limited numbers of modern evaluations of Fe concentrations in the Atlantic find higher concentrations (1 nM Fe) in the Northern Atlantic (T. Church, pers. comm.), which receives aeolian inputs from Africa, than in the Pacific (0.01 nM Fe) where dust storms from Asia are infrequent (Martin et al. 1991). Release from iron limitation might therefore foster higher fixation in parts of the Atlantic (0°–30° N) where (conveniently for such speculation) there are no measurements! This difference might also explain the lack of a $NO_3^-:PO_4^=$ anomaly in the Pacific Ocean.

In addition to iron, phosphorus is also required for balanced growth. Phosphorus is in limited supply in the oligotrophic waters of the Atlantic, raising the interesting question of the source of phosphorus to balance nitrogen fixation. Carpenter & Price (1977) suggested that increased phosphorus concentrations as oceanic water entered the Caribbean fostered higher numbers and greater rates of fixation by *Trichodesmium*. Phosphorus limitation might therefore reduce fixation rates over the tropical Atlantic region compared to extrapolation from the Caribbean rates. However, abundances along a transect from the Caribbean to Bermuda can be quite constant (Carpenter & Romans 1991) and fixation rates between the Caribbean population and Sargasso Sea population varied only from 92 to 120 ng N colony day^{-1} (Carpenter et al. 1987) and hence do not lend support to such a limitation.

Karl (1992) suggested that the ability of *Trichodesmium* to vertically migrate (Villareal & Carpenter 1990) permitted acquisition and storage of required phosphorus at the nutricline to support carbon and nitrogen fixation at the surface. Such a mechanism would help explain the anomalous distribution of nitrate and phosphorus in the Sargasso Sea (Michaels et al. this volume) by providing a mechanism to remove phosphorus and leave nitrate below the euphotic zone. In addition to migration, Trichodesmium also has the capacity for high rates of alkaline phosphatase activity (McCarthy and Carpenter 1979; Elardo et al. 1994) which would permit utilization of organic phosphorus in the surface waters and alleviate the phosphorus constraint but would not provide a sink in the nitracline. In this scenario, remineralization of high N:P (125) *Trichodesmium* sp. (Karl et al. 1992) at depth would provide "excess" nitrate compared to phosphate. Either mechanism has major implications for the phosphorus cycle in the same way that high rates of nitrogen fixation have for the nitrogen cycle and ultimately the carbon cycle of the North Atlantic.

Conclusions

The primary conclusion from this investigation is that although the most recent basin estimate of nitrogen fixation (Carpenter & Romans 1991) is of the order required by a basin scale budget of nitrogen, such high rates cannot be supported on current evidence. However, both our assessment and the 1991 estimate are based on very limited information. The new basin-scale nitrogen budget (Michaels et al. this volume) dramatically illustrates the inadequacy of our knowledge of ocean scale nitrogen fixation and clearly points to the need for a major re-assessment. The consequences for biogeochemical cycling of a nitrogen fixation rate of the suggested magnitude are profound, and would lead to a major re-adjustment of our concepts of global biogeochemical cycles.

To provide a better constraint on the fixation rate over the basin, future research directions must begin to address not only spatial and temporal variability, but also the physiology of the organisms. For instance Karl et al. (1995) attribute major ecosystem changes to changes in abundance of *Trichodesmium* trichomes rather than colonies. The JGOFS time series station at Bermuda and the newly established German-Spanish station in the Canary Islands represent two important platforms from which to launch studies of the temporal variation and more importantly, the mechanisms behind the variability such as the causal factor(s) permitting bloom formation. Spatial variation would also be partially addressed by such a fundamental understanding but some form of remote sensing would seem to be required to deal with the scales of variability (Borstad et al. 1992; Subramaniam & Carpenter 1994).

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