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Large-scale latitudinal distribution of *Trichodesmium* spp. in the Atlantic Ocean

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The Atlantic Meridional Transect (AMT) programme is a series of bi-annual cruises between the Falkland Islands (50°S) and the UK (50°N). Measurements of the abundance of the N_2-fixing, colonial cyanobacterium Trichodesmium along this transect in the years 1995–1999 reveal that it is especially abundant between 0 and 15°N, but by contrast almost completely absent between 5 and 30°S. The cruise path between 0 and 15°N lies close to 20°W, on the African (eastern) side of the Atlantic. The maximum colony abundances we observed (~100 000 colonies m^{-2}) are greater than those reported in many other studies. The results of different methods for assessing Trichodesmium abundance are compared. Possible correlations between Trichodesmium abundance and several physical and chemical variables were examined to try and elucidate the factors controlling N_2 fixer occurrence. High Trichodesmium abundance was found to be correlated with shallow mixed layer depth and high estimated iron deposition to the surface ocean, but not with temperature, nitrate or the concentration of total dissolvable iron in sea water.

INTRODUCTION

The filamentous cyanobacteria belonging to the genus *Trichodesmium* represent the major group of N_2-fixing planktonic organisms in the ocean [see the review by Capone *et al.* (Capone *et al.*, 1997)]. *Trichodesmium* occurs at higher abundances in highly stratified, low-nutrient waters at tropical and subtropical latitudes, often forming small- to large-scale blooms which can be seen from space [e.g. (Subramaniam and Carpenter, 1994)], but are difficult to study due to their sparse distribution and ephemeral nature. It has been estimated that N_2-fixation in the oligotrophic ocean may account globally for an annual input of ~80 Tg nitrogen (N) (Capone *et al.*, 1997), although these estimates are subject to a high level of uncertainty, given our limited knowledge on the distribution of *Trichodesmium* and other N_2-fixers in the open ocean.

The magnitude and distribution of N_2-fixation inputs of nitrogen to the ocean are important for a number of reasons. For example, current estimates of nitrogen diffusive fluxes from below the thermocline seem insufficient to sustain the measured rates of primary productivity in the oligotrophic regions of the eastern North Atlantic (Lewis *et al.*, 1986) and the western South Atlantic (Planas *et al.*, 1999). N_2 fixation, where it occurs, has the potential for reconciling such imbalances. N_2-fixation is also the critical feedback in the 'nitrostat', which controls the ocean's fixed nitrogen content over longer time scales (Tyrrell, 1999).

The Atlantic Meridional Transect (AMT) programme is a series of latitudinal transects between the UK (50°N) and the Falkand Islands (50°S), carried out since September 1995 on a bi-annual basis. The scientific work takes advantage of the opportunity presented by a supply ship travelling back and forth between the UK and Antarctica once a year. The length of these cruises, together with the fact that they are carried out during two seasons each year (although even greater frequency would of course be desirable), make them particularly appropriate to characterize the large-scale patterns of distribution of *Trichodesmium* in the open ocean. For instance, little

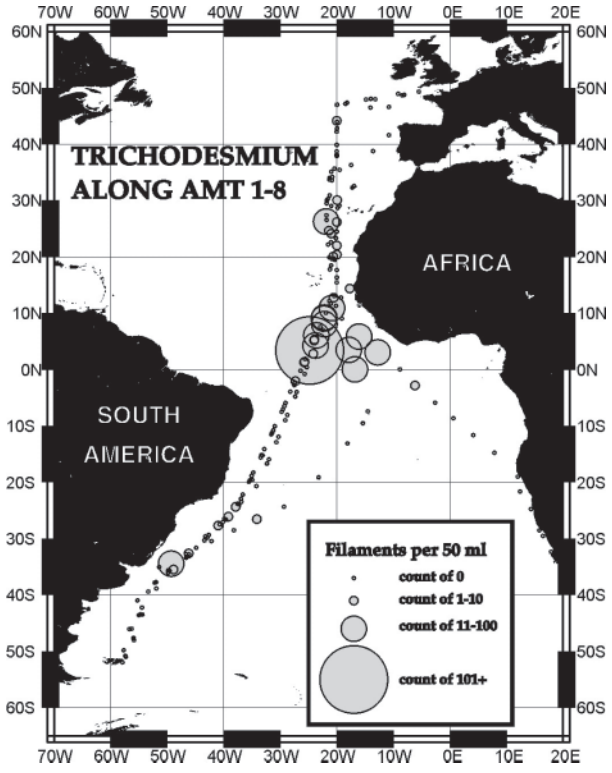

Fig. 1. Concentrations of *Trichodesmium* filaments as measured along eight AMT cruises, as part of standard phytoplankton species assessments. Filament abundances are shown using successively larger circles for every 10-fold increase in concentration. AMT-1, -3, -5 and -7 sailed southwards during September and October 1995–8, while AMT-2, -4, -6 and -8 sailed northwards during April and May 1996–9. AMT-6 unusually left from Cape Town. AMT-7 visited Lisbon and Dakar. AMT-8 called at Ascension Island. All cruises (except AMT-6) called at Montevideo.

previous information is available on the distribution of *Trichodesmium* in the subtropical expanses of the Southern Hemisphere (Carpenter, 1983a).

An additional advantage of the AMT programme is the other measurements carried out on the same cruises. For example, no other study has yet, to our knowledge, addressed the relationship between *Trichodesmium* abundance and the measured concentration of iron in surface waters over such a long transect.

We provide evidence of high abundances of *Trichodesmium* in the eastern low-latitude North Atlantic, but virtual absence of the genus in the tropical and subtropical South Atlantic. We compare the distribution of *Trichodesmium* with that of some other measured variables: total dissolvable iron, nitrate, temperature and mixed layer depth. The distribution of *Trichodesmium* has been compared elsewhere to other biological variables along the transect, including competing phytoplankton groups (Marañón *et al.*, 2000; Poulton, 2002).

METHOD

Filaments of *Trichodesmium* were counted as part of standard phytoplankton cell counts (all species) on all AMT cruises in the period 1995–1999. However, these standard measurements (using a microscope to count cells in small volumes such as 50 ml) are not reliable for *Trichodesmium* for two reasons: (i) low numbers of filaments, and especially of colonies, in 50 ml volumes lead to a high variability associated with sparse sampling; and (ii) *Trichodesmium* may be able to control its buoyancy and sink or float, in which case a small water sample from the middle of a Niskin sampling bottle may not be representative.

To overcome possible sampling biases from the filament counts, sampling targeted directly at measuring *Trichodesmium* colonies was carried out during the April–May 1999 (northbound) AMT-8 cruise, comprising at each station: (i) a plankton net haul from ~150 m to the surface; (ii) the whole of a Niskin bottle from 15 m depth, a representative depth to sample for *Trichodesmium* [figure 4 in (Capone *et al.*, 1997); figure 1 in (Letelier and Karl, 1996)]; and (iii) a surface bucket.

Filament counts

Counts of *Trichodesmium* filaments, together with other phytoplankton counts, were carried out on samples taken from Niskin bottles using an inverted microscope following the Utermöhl technique and the recommendations contained in the UNESCO manual (Hasle, 1978). Samples (50–100 ml) were allowed to settle overnight and filament counts performed on the full settling chamber.

Net hauls

When the ship stopped once per day for station work (at or close to the time of local solar noon), nets were lowered until 175 or 200 m of wire had been fed out, and then winched to the surface at a speed of ~40 cm s^{-1}, taking 7 or 8 min to ascend. Standard WP-2 zooplankton nets (mesh size 200 μm), or smaller mesh size nets (65 μm), were used. Both mesh sizes were much smaller than colony sizes (measured in millimetres). Problems with flow meters prevented accurate calculation of the volume of water sampled. Once winched to the surface, the nets and cod-end were hosed down with a fine seawater spray to flush out all material. The resulting samples were concentrated by fastening a mesh of pore size 100 μm over the end of a piece of pipe of 4 cm diameter and siphoning water (but not large particles) out through the mesh and pipe. The concentrated samples were then divided, using a sample splitter, and half preserved with 1% acidic Lugol's iodine solution (Throndsen, 1978). Because of the difficulty of microscopy at sea, the untreated half of the

sample was sometimes counted immediately on board, but sometimes not. Counting of samples was carried out using a Bogorov tray of 25 ml volume with a glass slide on top to minimize sway of the suspension, and to prevent the meniscus interfering with the view down the dissecting microscope. The preserved half of the sample was counted later back on land.

Numbers of intact *Trichodesmium* colonies were counted. When high concentrations of colonies were present, counting of only a fraction of the whole sample was sometimes sufficient for a statistically reliable calculation of the concentration (Smayda, 1978). In these cases, counting of subsamples continued until >200 colonies had been counted. It was found that 1% Lugol's solution was insufficient to preserve some of the concentrated samples, which decomposed (as ascertained by odour and the presence of live bacteria), and those results were discarded.

Niskin bottle at 15 m depth

One 30 l Niskin bottle, triggered at 15 m depth at every station, was dedicated solely to sampling for *Trichodesmium* colony abundance. The Niskin bottle was fully emptied through a 9 mm bore tap, with the water right in the bottom of the bottle also being collected by pulling down the bottom cap of the Niskin bottle and catching the outflow. The water was then filtered through an 18 μm, 47 mm polycarbonate filter, and the filter examined under the microscope to count colonies.

Bucket of surface water

A 10 l plastic bucket was lowered into the sea to collect a sample from right at the sea surface. Its contents were filtered and colonies counted as in the previous section.

Total dissolvable iron

Seawater samples for iron were taken from acid-cleaned 10 l Teflon-lined Go-Flo samplers modified for trace metal work, and mounted on an epoxy paint-coated rosette frame deployed on a sheathed hydroline. Samples were collected from typically eight depths through the upper 200 m of the ocean, four of which were typically within the upper mixed layer. Since the depth at which the *Trichodesmium* abundance was measured did not always correspond to the depth of the sample taken for iron analysis, calculation of a mixed layer mean was deemed appropriate. Seawater sub-aliquots for iron analysis were collected in acid-washed 250 ml HDPE bottles immediately upon retrieval of the Go-Flo sampler. Samples were acidified to pH 2.0 in a class 100 laminar airflow bench using sub-boiling, quartz-distilled HCl. An iron(III) reducing agent (Na_2SO_3) was added to acidified samples and allowed to react for at least 8 h. The samples were analysed on board ship using a flow injection–chemiluminescence technique (Bowie *et al.*, 1998). All samples were unfiltered in order to minimize potential contamination from filtration procedures, and hence the iron analysed in these samples is operationally defined as total dissolvable iron (TDFe).

Under our acidification and storage procedures (pH 2.0, ~8 h), the TDFe measurement is expected to include the dissolved phase (inorganic and most organic forms), colloids and labile particulate iron, omitting only acid-resistant forms such as matrix-bound aluminosilicates and unreactive crystalline particles. There remains considerable uncertainty at present as to what constitutes the bioavailable fraction of iron in sea water [(Wells *et al.*, 1995); but see Wu *et al.* (Wu *et al.*, 2001)], and different plankton classes are expected to be able to utilize different forms of iron (Wells *et al.*, 1995). Our TDFe measurements are presumably an overestimate of bioavailable iron. By analogy with nitrogen, the measurements were of the iron equivalent of Σ(DIN + DON + some PON) rather than just DIN, where DIN is dissolved inorganic nitrogen, DON is dissolved organic nitrogen and PON is particulate organic nitrogen.

Temperature, nitrate and chlorophyll profiles

Vertical profiles (0–200 m) of temperature, salinity and fluorescence were obtained with a Neil Brown Mark IIIB CTD. Samples for nutrient analysis were collected from 8–10 depths in the upper 200 m of the water column. The concentration of four inorganic nutrients (nitrate, nitrite, phosphate and silicate) was measured colorimetrically on fresh samples, using a 4-channel Technicon® auto-analyser and standard techniques (Woodward, 1994). Chlorophyll *a* concentration was determined fluorometrically at 5–7 depths on each station, as described by Marañón *et al.* (Marañón *et al.*, 2000).

RESULTS

Figure 1 shows the paths followed by the first eight AMT cruises, and the concentrations of *Trichodesmium* filaments that were found along those cruises using standard phytoplankton species counts (see Method, Filament counts) of samples collected at 7 m depth. Figure 2 shows the same data as a bar chart for each cruise, together with filament counts from the deep chlorophyll maximum (DCM). The location of the DCM was determined by examining the fluorescence profiles obtained with the CTD. In regions where *Trichodesmium* was abundant (0–15°N), the DCM was located at depths between 20 and 80 m.

Although the actual values of filament concentration changed markedly between cruises during the sampling

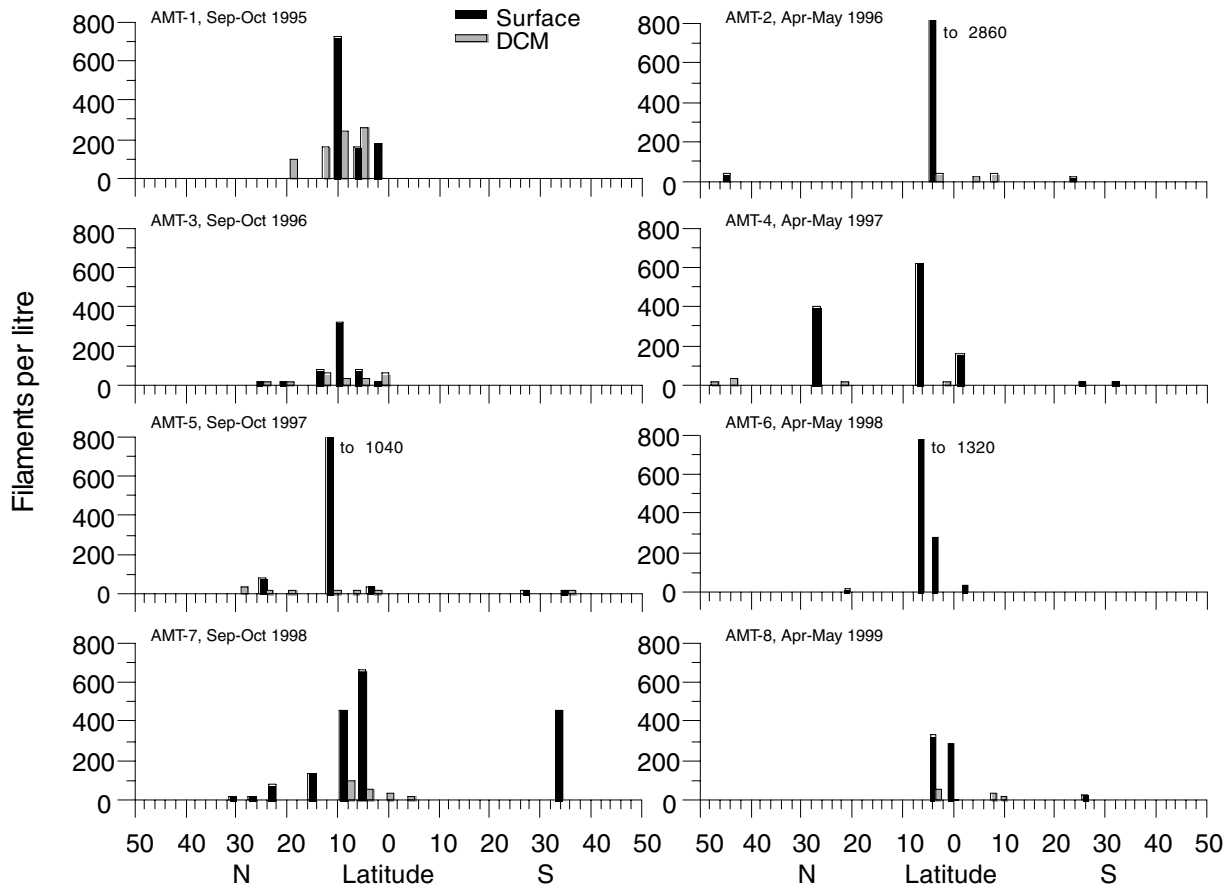

Fig. 2. Latitudinal distribution of *Trichodesmium* filament concentration at the surface (7 m, black bars) and the depth of the DCM (grey bars) during AMT1–8 (September 1995–May 1999). Southbound cruises are on the left, northbound cruises on the right.

period, the observed latitudinal variations depict a very consistent pattern: *Trichodesmium* is present preferentially in the region between 0 and ~15°N (Figure 1). Surprisingly, almost no filaments at all were found in the low-latitude regions of the South Atlantic, with the exception of 34°S on AMT-7 (September–October 1998). Highest filament abundances (>600 filaments l^{-1}) were always measured between 0 and 15°N. In general, *Trichodesmium* was more abundant at the surface rather than at the depth of the DCM (Figure 2). The average (across AMT1–8) filament concentration between 0 and 15°N in the surface layer was 300 ± 101 filaments l^{-1} (average ± SD), whereas the average figure for DCM samples was 39 ± 12 filaments l^{-1}.

Using the average of these two filament concentrations as representative of the mixed layer, we calculate a conservative estimate of ~1.7×10^5 filaments m^{-3} or ~8.5×10^6 filaments m^{-2} for the upper mixed layer (average depth of 50 m in the region, as determined from the density profiles) between 0 and 15°N. In this calculation, only free filaments have been included, because only filament counts were available for all AMT cruises, and because other authors have found that most *Trichodesmium* biomass (>80%) is in the form of free filaments rather than colonies (Letelier and Karl, 1996). Average *Trichodesmium* cell densities (counting only cells within filaments) between 0 and 15°N were ~33 000 cells l^{-1} at the surface and 5000 cells l^{-1} at the DCM. Filament size was quite variable during our study. The average number of cells per filament was 70.

Figure 3a shows the concentrations of colonies found along the AMT-8 transect using net hauls through the upper 100 m or more of the water column (depending on the amount of wire out and line angle). Figure 3b shows colony concentrations obtained using a surface bucket. Figure 3c shows colony concentrations from the same cruise obtained using a Niskin bottle fired at 15 m.

Taken as a whole, the colony concentrations from the three different techniques agree well in a qualitative sense, that is to say in their estimates of the general area where *Trichodesmium* concentrations are highest or lowest. They also agree with the qualitative distribution obtained from

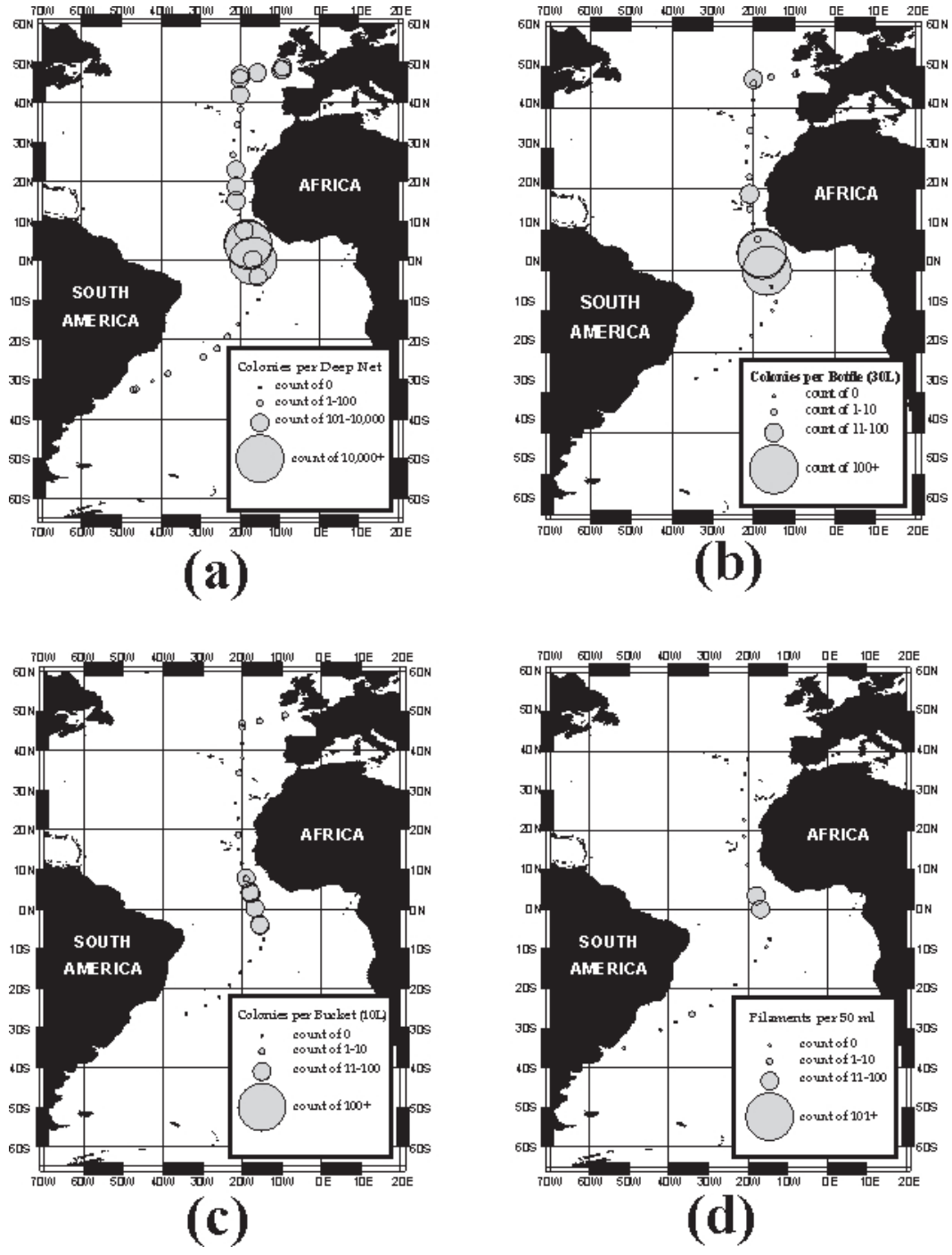

Fig. 3. Distribution of *Trichodesmium* along AMT-8 as measured by several different methods: (**a**) a plankton net hauled through the top 150–200 m; (**b**) a bucket lowered into the water surface; (**c**) a Niskin bottle fired at 15 m depth; and (**d**) counts of filaments in a small water sample taken from a Niskin bottle fired at 7 m depth. See the text for details of each measurement technique.

the filament counts (Figure 3d). All methods agree in identifying a *Trichodesmium* maximum just north of the equator and a barren zone for *Trichodesmium* between 5 and 30°S. There is, however, some slight variation in the latitudes of greatest *Trichodesmium* abundance as indicated by the different methods: the filament counts for AMT-8 suggest 0 and 4°N; the deep nets give 0, 4 and 19°N; the Niskin bottles give 0 and 4°N; and the buckets give 4°S–8°N. Some of the discrepancies will, however, be due to the rather arbitrary nature of the logarithmic ranges

into which measurements are grouped. Other differences may be related to possible active growth of a population in some areas as opposed to senescence in other areas, which could conceivably affect the filament to colony ratio, or the surface to 15 m colony ratio.

Although filament counts were only a by-product of phytoplankton cell counts aimed at enumerating the whole spectrum of different phytoplankton species, and despite the possible biases in such measurements described in Method, these results agree surprisingly well with the targeted colony counts, and the filament patterns are consistent between years.

In terms of other phytoplankton groups, the region of high *Trichodesmium* abundance (0–15°N) showed a considerable degree of inter-cruise variability. The presence of relatively high (30–60%) divinyl chlorophyll *a* to total chlorophyll *a* ratios [e.g. (Gibb *et al.*, 2000)] indicated that prochlorophytes represented an important component of the autotrophic community in the region, although *Synechococcus* spp. were also abundant (Zubkov *et al.*, 1998). Pigment measurements on AMT-8 gave highest zeaxanthin (biomarker for cyanophytes, including *Trichodesmium*) concentrations between 0 and 15°N (A. Poulton, unpublished data). Diatoms and other eukaryotic phytoplankton typically accounted for 20–50% of the total photoautotroph biomass. Between 0 and 15°N, >50% of chlorophyll *a* was found in the picoplankton (<2 μm) size fraction (Marañón *et al.*, 2000).

DISCUSSION

Distribution of *Trichodesmium*

The four different techniques used to measure the abundance of *Trichodesmium* all yielded a similar qualitative picture [see Chang (Chang, 2000) for a comparison in a different location]. High abundances were detected between the equator and ~15°N, and absence or low abundance was always found between 5 and 30°S. Elsewhere on the transect, abundances were intermediate or more variable in concentration. This general picture of *Trichodesmium* abundance was consistent between different years in the period 1995–1999, according to the filament counts, and was also repeated on both northbound and southbound cruises (Figure 2).

Compared with other regions, the abundances we observed were very high. The highest colony abundance on AMT8, as measured in Niskin bottles fired at 15 m, was 11 000 colonies m^{-3} [≡2200 filaments l^{-1} within colonies, if each colony is assumed to possess 200 filaments (McCarthy and Carpenter, 1979; Letelier and Karl, 1996)]. The five highest free (solitary) filament abundances from the phytoplankton cell counts (AMT1–8) were 2860, 1320, 1040, 720 and 660 filaments l^{-1}. When plotting distributions, Carpenter (Carpenter, 1983a) separated the global ocean into five different categories of filament concentration: 0.1, 1, 10, 100 and 1000 l^{-1}, and our high values therefore fall into the highest category. A table [table 1 in (Carpenter and Romans, 1991)] of observed abundances of *Trichodesmium* in the North Atlantic lists densities of between 10 and 5500 filaments l^{-1}. Recent studies have found an average of 46 filaments l^{-1} at the HOTS station near Hawaii (Karl *et al.*, 1995), up to ~500 filaments l^{-1} in the northern Indian Ocean (up to 17 000 l^{-1} in surface slicks) (Capone *et al.*, 1998), several hundred to 10 000 filaments l^{-1} in surface slicks near New Caledonia and Fiji (Dupouy *et al.*, 2000), and up to 600 filaments l^{-1} in the East China Sea (Chang, 2000). The *Trichodesmium* filaments found during our study, however, while quite variable in length, tended on average to be somewhat smaller (average for the whole transect of 70 cells per filament) than typically reported in the literature [100 cells per filament (Capone *et al.*, 1997)].

Reports of *Trichodesmium* abundance in the scientific literature back to the 1800s were listed and analysed by Carpenter (Carpenter, 1983a), and the historical measurements in the area of our transect are in broad agreement with our results. The historical data along our transect measured highest abundances at ~0–10°N (~10^4 filaments l^{-1} in summer and autumn, ~10^6 filaments l^{-1} in winter and spring), lower abundances at 0–30°S, and a complete absence south of 30°S. The historical data agree on average with our observation (from filaments) of an asymmetry across the equator (difference between north and south subtropical Atlantic). Our occasional high colony counts north of 30°N agree with historical observations [see references cited in Carpenter (Carpenter, 1983a), p. 76]. The global distribution of *Trichodesmium* has more recently been plotted and described by Capone *et al.* (Capone *et al.*, 1997). While acknowledging incomplete data coverage, their figure 2 shows higher numbers to the western sides of ocean basins, with a general lack of *Trichodesmium* on the eastern sides of ocean basins. In contrast to this overall trend, we found high abundances [comparable in magnitude to those observed on the western side of the North Atlantic, table 1 in (Carpenter and Romans, 1991)] of *Trichodesmium* near to the eastern edge of the Atlantic (although our sampling was always >200 miles offshore due to economic exclusion zones). Gruber and Sarmiento analysed the distribution of the quasi-conservative tracer N* [(= N – 16P + 2.90 μmol kg^{-1}) × 0.87] along isopycnal surfaces in the Atlantic (Gruber and Sarmiento, 1997). This tracer, indicative of N_2-fixation, shows strong latitudinal variation between ~0 and 15°N at 20°W

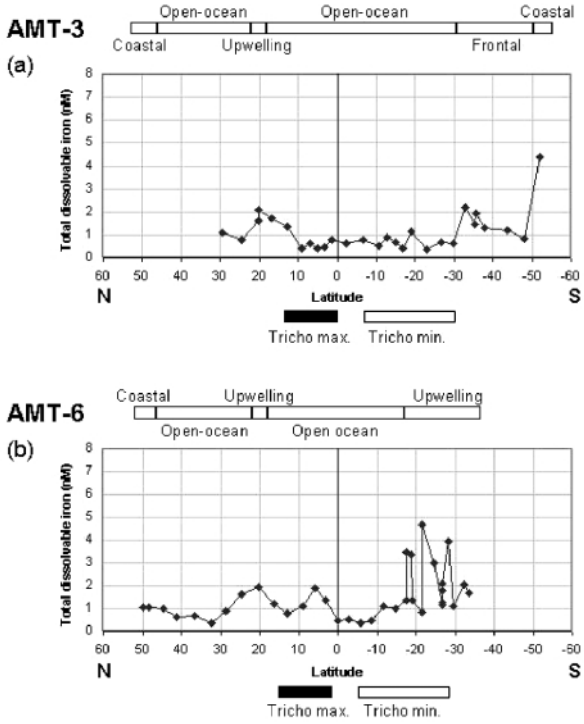

Fig. 4. Latitudinal distribution of the mean mixed layer concentration of TDFe along (**a**) AMT-3, September–October 1996 and (**b**) AMT-6, May–June 1998. The horizontal bars above the figures indicate the type of environment along the cruise track. AMT-6 unusually departed from South Africa rather than South America. These TDFe concentrations of ~1–2 nM in the tropical North Atlantic and ~0.5–0.9 nM in the South Atlantic oligotrophic gyre regions agree reasonably well with recent literature data (Powell *et al.*, 1995; Helmers, 1996; Vink and Measures, 2001) using similar sampling and analytical techniques. See Bowie *et al.* (Bowie *et al.*, 2002) for a more detailed presentation of the data.

[figures 13a and b, and 14a and b in (Gruber and Sarmiento, 1997)].

Ecology of *Trichodesmium*

The similarity between distributions of *Trichodesmium* obtained using different sampling techniques (Figure 1), and in different years (Figure 2), raises the question of the cause of this consistent pattern. Why is *Trichodesmium* so much more successful just to the north of the equator than to the south of it? The environmental determinants of *Trichodesmium* success or failure in competition with other phytoplankton are not yet well established (Hood *et al.*, 2000). Here we take advantage of other measurements made during the AMT cruises to make a preliminary evaluation of correlations between *Trichodesmium* abundance and several environmental parameters.

Rate of iron supply from the atmosphere to the sea surface

Nitrogenase, the universal enzyme for N_2-fixation, contains iron atoms within the molecule. This has been thought to imply a very high iron requirement for N_2-fixers (Raven, 1988; Rueter, 1988), although this requirement has recently been revised significantly downwards to only slightly higher than that required for taking up nitrate (Sañudo-Wilhelmy *et al.*, 2001). On the basis of the higher iron requirement, it has been suggested (Brand, 1991; Falkowski, 1997) that variability in dissolved iron may limit the distribution and activity of N_2-fixers in the ocean, if they are outcompeted by other phytoplankton when iron availability is low. This suggestion is strongly supported by higher abundances of *Trichodesmium* downwind of iron-laden dust sources in North Africa and Asia (Capone *et al.*, 1997) [for a map of estimated iron supply from the atmosphere to the ocean surface, see figure 8 of Duce and Tindale (Duce and Tindale, 1991)]. The (sub-)tropical North Atlantic Ocean underlies the path of trade winds blowing westwards from the Sahara desert region. Here, some of the highest particulate deposition on the surface of the ocean occurs, bringing with it very high iron inputs of up to 1000 mg m^{-2} $year^{-1}$ [(Duce and Tindale, 1991); see also (Tegen and Fung, 1995; Mahowald *et al.*, 1999)]. This region of high dust flux corresponds reasonably well to the areas of highest abundance of *Trichodesmium* along the AMT transects.

TDFe in surface sea water

The episodic nature of dust supply from the atmosphere over the low-latitude North Atlantic, combined with the short residence time of iron in surface waters (Jickells, 1999), leads us to expect that the in-water iron concentrations measured on a single cruise need not agree with the annually averaged atmospheric supply. Johnson *et al.* also noted a more general lack of correlation between the rate of atmospheric dust supply and surface water iron concentration (Johnson *et al.*, 1997).

The concentration of TDFe in the surface mixed layer (Figure 4), measured on AMT-3 and AMT-6, did not correspond closely to the dust supply (Duce and Tindale, 1991). During the AMT transects, we observed elevated TDFe concentrations at high latitudes, and also between 18 and 34°S on AMT-6 (a series of inshore/offshore transects in the Benguela upwelling system). This was due to a release of iron from the continental shelf sediments (Johnson *et al.*, 1999; Bowie *et al.*, 2002). However, there was also no close correlation between TDFe and *Trichodesmium* abundance when only the open-ocean stations are considered, and little difference between TDFe concentrations where *Trichodesmium* is abundant and where it is scarce. However, our poor understanding of the relationship between TDFe and bioavailable iron (Method) complicates a direct comparison. Luxury uptake could potentially provide phytoplankton with adequate iron from episodic dust inputs, despite generally

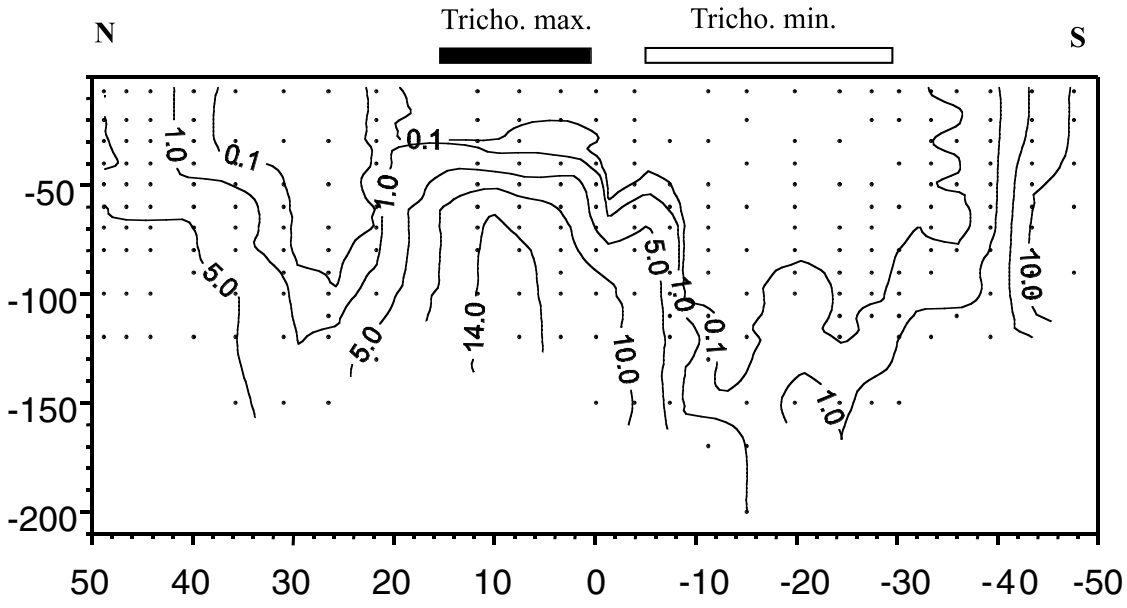

Fig. 5. Contour plot of the concentration of nitrate (μmol NO_3 kg^{-1}) against depth and latitude on the second AMT cruise, April–May 1996.

low concentrations. A high iron demand by *Trichodesmium* would also have the potential to reduce iron concentrations within blooms, as suggested for the West Florida shelf following a dust storm (Lenes *et al.*, 2001). Capone *et al.* (Capone *et al.*, 1998) and Sañudo-Wilhelmy *et al.* (Sañudo-Wilhelmy *et al.*, 2001) found a general lack of correlation between surface water iron (total or dissolved) and *Trichodesmium* abundance in the Arabian Sea and in the low-latitude North Atlantic, respectively. However, both of these latter cruises remained within high-iron regions for their whole length, in contrast to the much longer AMT cruises.

Nitrate

Using dissolved N_2 as the source of N atoms for cellular construction is a last resort, despite the very high concentrations (hundreds of micromoles) of N_2 in sea water. Uptake of NO_3 or NH_4 molecules is energetically cheaper, and the respective enzymes are not deactivated by exposure to oxygen, as is nitrogenase. When grown in the laboratory under different conditions, even N_2-fixers have been found to obtain most of their N from NH_4 and NO_3 when they are available, rather than (or as well as) from N_2 [(Mulholland and Capone, 1999) and references therein].

Although facultative N_2-fixers such as *Trichodesmium* are not obliged to fix N_2 if other nitrogen sources are present, the constraints of being adapted to a N_2-fixation lifestyle probably mean that they can compete successfully with other phytoplankton only in conditions favouring N_2-fixation. This implies that they will be competitively excluded in the presence of high nitrate or ammonium concentrations [figure 1 in (Capone *et al.*, 1998)]. Figure 5 shows that the high abundances of *Trichodesmium* do indeed occur in nitrate-depleted surface waters, although nitrate is, if anything, more depleted (certainly to a greater depth) in the area of minimum *Trichodesmium*.

Since all phytoplankton share a common need for light and for nutrients such as phosphorus, as well as for nitrogen, the most favourable niche for N_2-fixers is likely to be one in which N is present only as N_2, but yet other needs such as light and phosphate are abundantly satisfied [see figure 2b in (Sañudo-Wilhelmy *et al.*, 2001) for an estimate of the phosphorus requirement for N_2-fixer growth]. In low- and mid-latitude oceans, nutrients normally limit phytoplankton growth in surface waters more strongly than does light. Nitrate deficit ($16 \times [PO_4] - [NO_3]$) is, therefore, a potential indicator of the favourability of the environment for N_2-fixers such as *Trichodesmium*, assuming that all phytoplankton require ~16 atoms of N for every atom of P (Copin-Montegut and Copin-Montegut, 1983). However, the main latitudinal and vertical patterns in the distribution of phosphate along the transect (not shown) are the same as those reported for nitrate. Therefore, determination of nitrate deficit would require very accurate determinations of both $[NO_3]$ and $[PO_4]$, which are difficult to obtain at the low nutrient concentrations in the *Trichodesmium* maximum and minimum areas. For that reason, nitrate deficit is not plotted here.

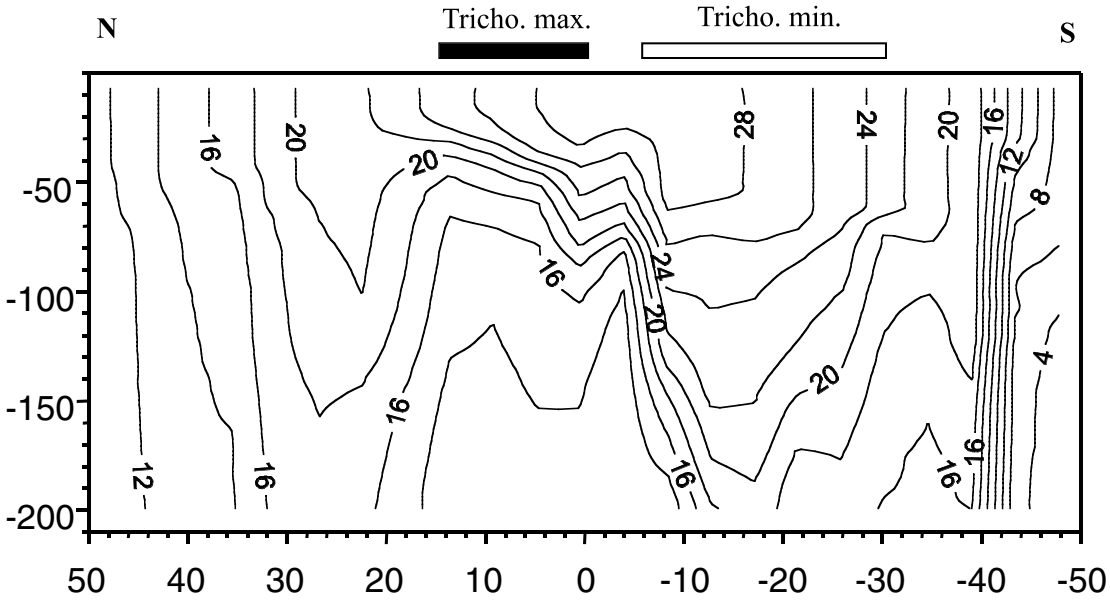

Fig. 6. Contour plot of water temperature (°C) against depth and latitude on the second AMT cruise, April–May 1996.

Temperature

Warm waters have been suggested as a factor in controlling where and when *Trichodesmium* can flourish (Carpenter, 1983a,b). Chang *et al.* found water temperature to be of some use as a predictor of *Trichodesmium* abundance in the East China Sea, but could not use it to explain all aspects of the distribution (Chang *et al.*, 2000). However, Figure 6 shows that there is little correspondence between *Trichodesmium* and water temperature along the AMT transect. Temperature is more or less symmetrical across the equator.

Mixed layer depth

It has been suggested that active buoyancy regulation may allow *Trichodesmium* to migrate vertically (Villareal and Carpenter, 1990) and take up ('mine') phosphate from below the nutricline (Karl *et al.*, 1992). Internal storage of phosphorus-rich compounds and the ability to fix N_2 upon return to the well-illuminated upper layer would then give *Trichodesmium* competitive advantage over other phytoplankton. Such a strategy would be favoured by a shallowing of the pycnocline, which would reduce the energy investment required for this migratory movement. Associations between *Trichodesmium* abundance and vertical stratification (shallow upper mixed layer) have been found in (i) time series in the North Pacific subtropical gyre (Karl *et al.*, 1995) and (ii) two transects in the central North Atlantic (Sañudo-Wilhelmy *et al.*, 2001).

Even if filaments or colonies do not regulate their buoyancy, then deep mixed layers could still be unfavourable. The high energy requirements of N_2-fixation would be hard to satisfy in deep mixed layers, in which average light intensities for passively mixed phytoplankton are low. Figure 5 shows that mixed layer depth may explain why *Trichodesmium* occurs in the region 0–15°N (generally quite shallow mixed layer depths), but not between 5 and 30°S (typically very deep mixed layers). This contrast in mixed layer depths between the two regions is repeated on the other AMT cruises, AMT-3 and AMT-5 being partial exceptions [figure 3.6 in (Poulton, 2002)]. Average regional mixed layer depth is always (for every cruise) shallower for the region 0–15°N (10–40 m) than for the region 5–30°S (60–130 m), but on AMT-3 and AMT-5 the mixed layer depth is shallower than 40 m at one or two of the stations between 5 and 30°S [figure 3.6 in (Poulton, 2002).]

Biogeochemical implications

Fixed nitrogen (also known as reactive nitrogen or combined nitrogen or DIN) is the sum of all dissolved inorganic nitrogen except N_2, and is the nutrient that is proximately most scarce, relative to phytoplankton requirements, over most of the ocean's surface. Understanding its cycling and distribution is, therefore, of considerable importance for biological oceanography. One of the larger fluxes in the oceanic nitrogen cycle is due to N_2-fixation [table 8.5 in (Pilson, 1998)], although its global magnitude is rather uncertain and has been subjected to much revision over the last 30 years [figure 4

in (Karl *et al.*, 2002)]. Model results (Tyrrell, 1999) strongly suggest that, particularly over longer time scales, the amount of N_2-fixation in the oceans is controlled by a feedback response whereby it balances the N cycle and keeps N levels tied relative to P levels. However, this does not preclude other factors from controlling the amount of N_2-fixation over shorter time scales, or from controlling where it occurs.

Another hypothesis suggests a controlling role of iron on the variation of N_2-fixation over time, and suggests that variability in continental aridity, and in atmospheric dust transport to oceans far from land, controls how much N_2-fixation occurs there (Brand, 1991; Falkowski, 1997). This would entail increased N_2-fixation during the drier ice ages and, it is suggested, extra drawdown of atmospheric CO_2 by phytoplankton whose N limitation is reduced. The match between *Trichodesmium* abundance along the AMT transect and iron supply from the atmosphere agrees with this hypothesis, but the lack of a clear correlation with seawater TDFe concentration does not agree with it. However, this latter comparison is complicated by several factors, discussed above in the context of TDFe.

If the distribution of N_2-fixers is influenced instead by the need for a shallow mixed layer, in agreement with our results, climate change could stimulate increased N_2-fixation as the oceans become more strongly stratified (Karl *et al.*, 1995).

We estimated (see the Appendix) the extent to which the *Trichodesmium* populations observed between 0 and 15°N affect the input of new N to the surface mixed layer, deriving a N_2-fixation rate of 0.2 mmol N m^{-2} day^{-1}. This estimate is based on assumed, not measured, N_2 fixation rates, and needs to be confirmed by measurements along the AMT transect. Planas *et al.* calculated upwards nitrate diffusive supply for 3–13°N to be 0.93 mmol N m^{-2} day^{-1} (Planas *et al.*, 1999). Our estimate of N_2-fixation therefore represents >20% of total new nitrogen input to the region. This is a conservative estimate, though, given that it does not take into account the occurrence of blooms, during which *Trichodesmium* abundance and activity can be several orders of magnitude higher. The region where *Trichodesmium* is abundant coincides with an area of enhanced phytoplankton growth rates (Marañón *et al.*, 2000), suggesting that N_2-fixation and the subsequent DON release (Vidal *et al.*, 1999) may play an important role in stimulating primary production in the low-latitude eastern North Atlantic.

CONCLUSIONS

Four different ways of measuring *Trichodesmium* abundance give similar results along long (100° of latitude) transects in the open Atlantic: abundances are highest in the region 0–15°N (near to the west coast of North Africa), but extremely low or absent in the region 5–30°S, with more variable intermediate amounts elsewhere. While we were able to conclusively determine the *Trichodesmium* distribution along the transect, it was not possible to achieve such certainty about the ecological factors responsible for it. Attempts to match the high and low abundances of *Trichodesmium* with other parameters measured on the same cruises were successful for estimated iron deposition and for mixed layer depth (high iron deposition and shallow mixed layer depth being correlated with high *Trichodesmium* abundance), but less successful for seawater iron concentration, nitrate concentration and water temperature.

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APPENDIX

Taking into account the average abundance of *Trichodesmium* observed between 1995 and 1999 (8.5×10^6 filaments m^{-2}; see Results), and assuming (i) a nitrogen content of 100 pg N $cell^{-1}$ [10 ng N per filament for a 100 cell filament; (Carpenter and Romans, 1991; Rueter *et al.*, 1992; Letelier and Karl, 1996)], (ii) an average cell per filament ratio of 70 and (iii) a nitrogen-specific N_2-fixation rate of 4 μmol N (mmol cell-N)$^{-1}$ h^{-1} (Carpenter, 1983b; Mulholland *et al.*, 1999) for 12 h a day, we estimate an average N_2-fixation rate in that area of 0.2 mmol N m^{-2} day^{-1}. While there are many uncertainties in this calculation, such as the omitted contribution of both filaments within colonies and cells not in filaments, our estimate is similar in magnitude to some others. Other estimates are: (i) 0.166 mmol N m^{-2} day^{-1} for a station with abundant *Trichodesmium* in the Indian Ocean (Capone *et al.*, 1998); (ii) 0.0001–0.06 mmol N m^{-2} day^{-1} in the Kuroshio Current (Chang *et al.*, 2000); and (iii) ~0.14 mmol N m^{-2} day^{-1} calculated in a similar manner by Karl *et al.* [(Karl *et al.*, 1995), table 1] for the HOTS station in the North Pacific, although we believe their value should be halved due to an incorrect assumption of 24 rather than 12 h of N_2-fixation day^{-1}.