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Latitudinal distribution of *Trichodesmium* spp. and N_2 fixation in the Atlantic Ocean

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Abstract. We have determined the latitudinal distribution of *Trichodesmium* spp. abundance and community N_2 fixation in the Atlantic Ocean along a meridional transect from ca. 30° N to 30° S in November–December 2007 and April–May 2008. The observations from both cruises were highly consistent in terms of absolute magnitude and latitudinal distribution, showing a strong association between *Trichodesmium* abundance and community N_2 fixation. The highest *Trichodesmium* abundances (mean = 220 trichomes L^{-1}) and community N_2 fixation rates (mean = 60 µmol m^{-2} d^{-1}) occurred in the Equatorial region between 5° S–15° N. In the South Atlantic gyre, *Trichodesmium* abundance was very low (ca. 1 trichome L^{-1}) but N_2 fixation was always measurable, averaging 3 and 10 µmol m^2 d^{-1} in 2007 and 2008, respectively. We suggest that N_2 fixation in the South Atlantic was sustained by other, presumably unicellular, diazotrophs. Comparing these distributions with the geographical pattern in atmospheric dust deposition points to iron supply as the main factor determining the large scale latitudinal variability of *Trichodesmium* spp. abundance and N_2 fixation in the Atlantic Ocean. We observed a marked South to North decrease in surface phosphate concentration, which argues against a role for phosphorus availability in controlling the large scale distribution of N_2 fixation. Scaling up from all our measurements (42 stations) results in conservative estimates for total N_2 fixation of ∼6 TgN yr^{-1} in the North Atlantic (0–40° N) and ∼1.2 TgN yr^{-1} in the South Atlantic (0–40° S).

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1 Introduction

Biological N_2 fixation represents a major process of new nitrogen supply to the euphotic zone in tropical and subtropical regions of the open ocean (Karl et al., 2002; Mahaffey et al., 2005). In the Atlantic Ocean, recent studies based on both direct measurements of N_2 fixation (Capone et al., 2005) and geochemical approaches (Gruber and Sarmiento, 1997) have resulted in basin-scale estimates of this flux that significantly exceed previously available estimates. The global biogeochemical significance of N_2 fixation stems from the fact that, in conjunction with denitrification, it is a critical flux in the control of the ocean's bioavailable nitrogen inventory. In addition, new production based on N_2 fixation is more effective in atmospheric CO_2 sequestration than that based on NO_3 input from deep waters, because the latter is also coupled to the upward transport of CO_2 through Redfield stoichiometry (Michaels et al., 2001).

The non-heterocystous, bloom-forming, filamentous cyanobacteria *Trichodesmium* spp. is regarded as the dominant planktonic N_2 fixer (Capone et al., 1997) and, as a result, considerable effort has been invested in determining its distribution, abundance and metabolic activity in the sea, together with the factors that control them. *Trichodesmium* spp. is mostly restricted to tropical regions characterised by warm (>22 °C) surface waters and strong vertical stability (Capone et al., 1997; Tyrrell et al., 2003). Due to the very high iron quotas characteristic of *Trichodesmium* (Rueter et al., 1992; Kustka et al., 2003), iron supply has been considered as the most limiting factor for the distribution and metabolic activity of this genus and, by extension, N_2 fixation rates in the ocean (Falkowski, 1997; Berman-Frank et al., 2001). Recently, Moore et al. (2009) demonstrated a

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close association between dissolved iron concentration, in turn related to increased atmospheric deposition of Saharan dust, and N_2 fixation rates in the Atlantic Ocean. In addition, a role for phosphorus availability in the control of both *Trichodesmium* spp. (Sañudo-Wilhelmy et al., 2001) and community (Mills et al., 2004) N_2 fixation rates has also been demonstrated.

As a result of the highly variable distribution of *Trichodesmium* spp. abundance, over both space and time, most studies have so far focused on regions which tend to show higher abundances of this genus (Carpenter et al., 2004; Capone et al., 2005; Mulholland et al., 2006), or have been conducted during blooms (Karl et al., 1992; Capone et al., 1998). There have been few basin-scale surveys of *Trichodesmium* spp. abundance (Tyrrell et al., 2003; Davis and McGillicuddy, 2006) or N_2 fixation (Voss et al., 2004; Staal et al., 2007) and, to the best of our knowledge, only two studies have reported on both *Trichodesmium* spp. abundance and community N_2 fixation over large spatial scales in the open ocean (Kitajima et al., 2009; Moore et al., 2009). Yet, basin-scale studies are essential because they provide estimates of *Trichodesmium* spp. abundance and activity that are representative of 'background' conditions in the open ocean, as opposed to those found during local events of increased abundance and/or growth. In addition, large-scale surveys cross marked environmental gradients and therefore are ideally suited to assess the effect of different controlling factors on distribution patterns and N_2 fixation rates.

Here we report on *Trichodesmium* spp. abundance and community N_2 fixation measured along a meridional transect in the Atlantic Ocean during two contrasting seasons. We describe the latitudinal patterns in *Trichodesmium* spp. abundance and community N_2 fixation in the tropical Atlantic from ca. 30° N to 30° S and show that they are persistent in contrasting seasons. Furthermore, we use the observed latitudinal distributions to assess the relative importance of different environmental factors, such as dust deposition, phosphorus availability and water column structure, in determining the large-scale variability of *Trichodesmium* spp. abundance and community N_2 fixation.

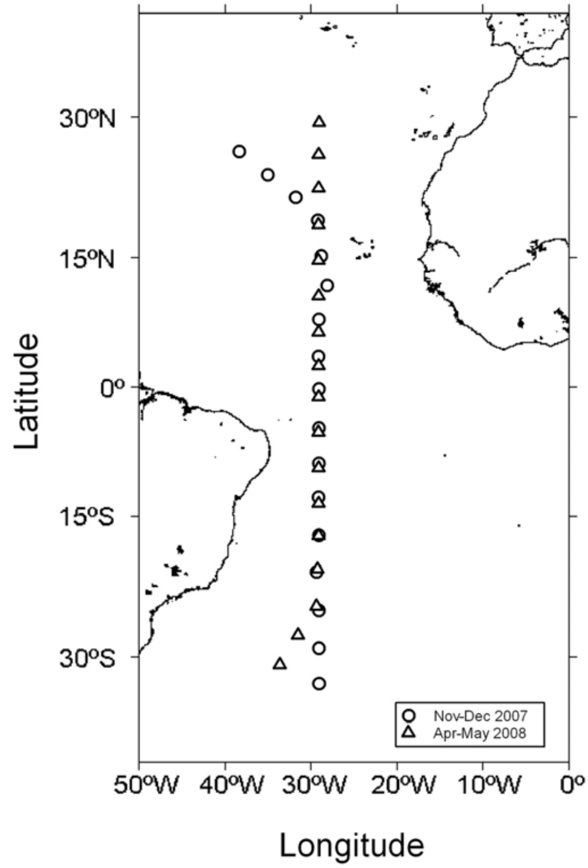

Fig. 1. Map showing the 2007 **(a)** and 2008 **(b)** TRYNITROP cruise tracks. The cruises took place during 16 November–16 December 2007 and 8 April–6 May 2008.

2 Material and methods

2.1 Sampling, hydrography and irradiance

Two oceanographic cruises were conducted on board BIO "Hespérides" in the Atlantic Ocean during 16 November–16 December 2007 and 8 April–6 May 2008 (Fig. 1), as part of the project TRYNITROP (*Trichodesmium* and N_2 fixation in the Atlantic Ocean). The transects took place along 28–29° W from 26° N to 33° S in 2007 and from 29° N to 31° S in 2008. At each sampling station, seawater samples were collected from 0–300 m, just before dawn, using a rosette equipped with 12-L Niskin bottles. The vertical distribution (0–300 m) of temperature, salinity and fluorescence was determined with a CTD SBE911 plus probe attached to the rosette. Samples for nutrient analysis were collected from 14 depths in the upper 300 m. The concentration of nitrate plus nitrite was determined on board on fresh samples with a segmented-flow auto-analyser, using a modified colorimetric protocol that allows to achieve a detection limit of 2 nmol L^{-1} (Raimbault et al., 1990). For the determination of phosphate concentration, samples were stored frozen at −20 °C until analysed in the laboratory following standard colorimetric methods. The detection limit for the analysis of phosphate concentration was 0.02 µmol L^{-1}.

On 16 occasions, vertical profiles of photosynthetically active irradiance (PAR) were obtained at noon with a Satlantic OCP-100FF radiometer. In these occasions, the vertical distribution of fluorescence was also determined at the same locations using the CTD SBE911 plus probe. We found a highly significant relationship between the depth of the 1% PAR level (Z_{eu}) and the depth of the DCM (Z_{DCM}): $Z_{eu} = 9.3 + 0.98 \times Z_{DCM}$, $r^2 = 0.87$, $p < 0.001$, $n = 16$).

2.2 Satellite inference of dust presence in the atmosphere

Aqua-MODIS aerosol optical depth at 550 nm (AOD 550 nm) can be used as an estimator of dust presence in the atmosphere (Kaufman et al., 2005). We obtained seasonal data of AOD 550 nm from the Giovanni online data system of the NASA Goddard Earth Sciences Data and Information Services Center. The data were defined in a grid of 1° of resolution and centered at the closest possible location in the vicinity of each sampling station.

2.3 Chlorophyll-*a* concentration

At each station, 250-mL samples were taken from 6–7 depths covering the whole euphotic layer. Samples were filtered through 0.2 µm pore-size polycarbonate filters using low vacuum pressure. After extraction in 90% acetone overnight, fluorescence was measured on board with a Turner Designs 700 fluorometer, which had been calibrated with pure chlorophyll-*a*.

2.4 *Trichodesmium* spp. abundance

The ship's non-toxic water supply was used to determine the surface abundance of *Trichodesmium* trichomes. Given that the ship stopped for work station only once every day, the distance between consecutive stations was >400 km. However, the use of the continuous water supply allowed us to obtain samples for *Trichodesmium* spp. abundance at intervals of 55–70 km, thus highly improving the spatial resolution of our measurements.Water was collected from ca. 5 m depth by a Teflon pump and carried to the laboratories through epoxide-free silicone pipes. At each sampling time, between 50–130 L of seawater were filtered by gravity through a 40 µm nylon mesh with a diameter of 15 cm. Particles were then transferred to a 100 mL glass bottle by gently rinsing the mesh with 0.2-µm filtered seawater. Samples were preserved in Lugol's solution and stored in the dark until analysis in the laboratory. Counting of trichomes was carried out with a Nikon Diaphot TMD microscope following the Utermöhl method. During the cruise, we examined regularly under the microscope fresh samples collected both with the underway water supply system and with Niskin bottles at station, and found that the filaments's shape and length were similar. We did not detect the presence of broken or damaged filaments in the samples from the continuous water supply system. These observations suggested that our sampling method resulted in reliable estimates of *Trichodesmium* spp. filament abundance. This was later confirmed when we compared our results with those reported by other studies in the same region (see Sect. 4.1).

2.5 N_2 fixation rates

Rates of N_2 fixation by the whole planktonic community were determined in each station at the surface (5 m), an intermediate depth (30–80 m) and the depth of the deep chlorophyll maximum (DCM). We used the $^{15}N_2$-uptake technique of Montoya et al. (1996) with the modifications described in Rees et al. (2009). Triplicate, 2-L, acid-cleaned clear polycarbonate bottles (Nalgene) were filled directly from the Niskin bottle using acid-washed silicone tubing. After carefully removing all air bubbles, bottles were closed with caps provided with silicone septa, through which 2 mL of $^{15}N_2$ (98 atom%, SerCon) were injected with a gas-tight syringe. The bottles were incubated for 24 h inside on-deck incubators covered with a combination of blue (Mist Blue, Lee filters) and neutral density screens to simulate in situ PAR levels, which were estimated from the location of the DCM. Samples were incubated at a temperature within 2 °C of in situ temperature, using running surface water for the samples from the upper mixed layer, and a system of re-circulating water connected to a refrigerator for the samples collected near the base of the euphotic layer.

Incubations were terminated by filtration through a Whatman GF/F filter (25 mm in diameter). An initial 2-L seawater sample from each depth was also filtered at time zero for the determination of background ^{15}N. After filtration, filters were dried at 40 °C during 24 h and stored at room temperature until pelletization in tin capsules. Measurement of particulate organic nitrogen and ^{15}N atom% was carried out with an elemental analyzer combined with a continuous-flow stable isotope mass-spectrometer (FlashEA112 + Deltaplus, ThermoFinnigan) and using an acetanilide standard as reference. The precision of the analysis, expressed as the standard deviation of the ^{15}N values determined in a series of 10 standards, was 0.15‰. The equations of Weiss (1970) and Montoya et al. (1996) were used to calculate the initial N_2 concentration (assuming equilibrium with atmosphere) and N_2 fixation rates, respectively.

3 Results

3.1 Hydrography and nutrients

The vertical distribution of temperature, in particular the depth of the 16 °C isotherm, allowed us to identify the area affected by the Equatorial upwelling (Fig. 2a, b). Using the location of the 16 °C isotherm above 200 m as a criterion, we divided the latitudinal transects in three different regions: North gyre (29°–15° N), Equatorial region (15° N–10° S) and South gyre (10°–33° S). The rising of isotherms defined the Equatorial upwelling in both cruises over roughly the same latitudinal range. A seasonal change in upper mixed layer (UML) temperatures was found: warmer UML waters occurred in the North gyre in 2007 and in the South gyre in

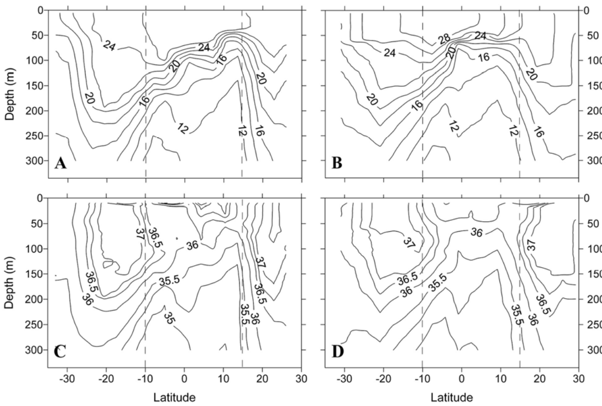

Fig. 2. Latitudinal and vertical distribution of temperature **(a, b)** and salinity **(c, d)**. Left-hand and right-hand plots correspond to the 2007 and 2008 cruises, respectively. Dashed lines define the limits of the three major regions identified by the depth of 16 °C isotherm: North gyre, equatorial upwelling and South gyre.

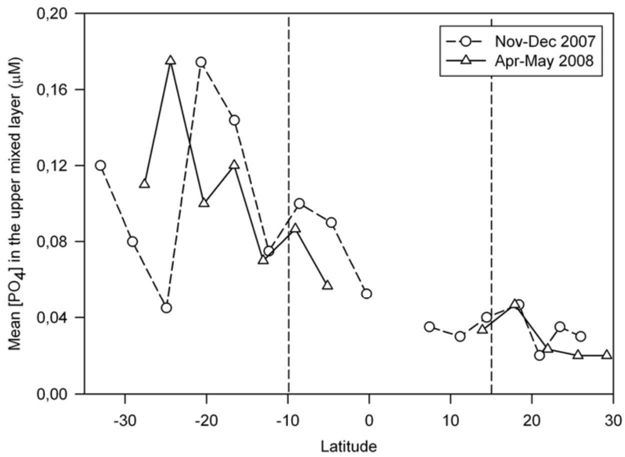

Fig. 4. Latitudinal distribution of mean phosphate concentration in the upper mixed layer during the 2007 (circles) and 2008 (triangles) cruises.

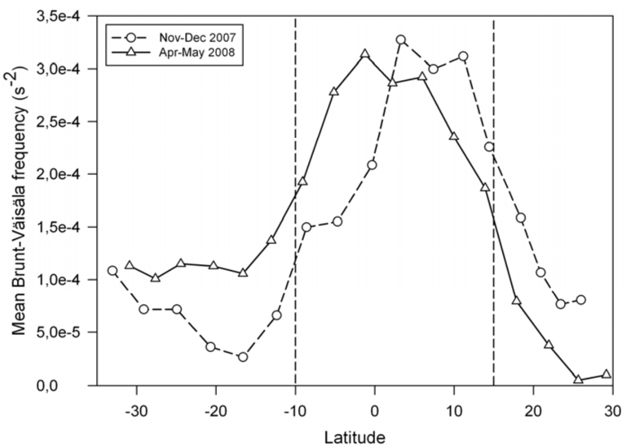

Fig. 3. Mean Brunt-Väisäla frequency (s^{-2}) over the upper 125 m of the water column during the 2007 **(a)** and 2008 **(b)** cruises.

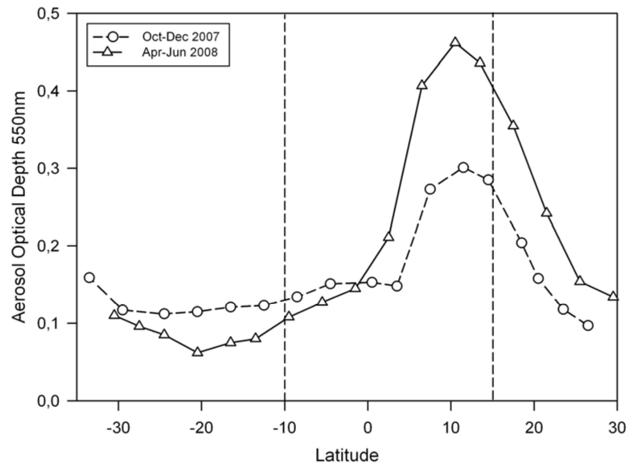

Fig. 5. Latitudinal distribution of seasonal aerosol optical depth at 550 nm (AOD 550 nm) derived from Aqua-MODIS satellite during the 2007 (circles) and 2008 (triangles) cruises.

2008, although warm waters (>26 °C) were always present in the Equatorial region. The latitudinal distribution of salinity also illustrated the effect of the Equatorial upwelling, which was associated with lower salinity in subsurface waters (Fig. 2c, d). Both subtropical gyres were characterised by higher salinities, particularly in the upper 150 m. The Brunt-Väisäla frequency, averaged over the upper 125 m, exhibited approximately the same distribution on each cruise (Fig. 3). The highest values were measured in the Equatorial region, where a relatively shallow and steep thermocline led to enhanced stability in the upper water column.

Nitrate concentration in the UML ranged between 30–150 nM without any clear latitudinal pattern (data not shown). In contrast, phosphate concentration showed a consistent decreasing trend from South to North in both cruises: values around or higher than 0.1 µM were measured in the Southern gyre, whereas values <0.04 µM were measured in the North gyre (Fig. 4). As a result, the nitrate to phosphate ratio increased markedly from South to North in both cruises.

3.2 Estimated dust presence in the atmosphere

The Aqua-MODIS AOD 550 nm index indicated that, on both cruises, the atmospheric content of aerosols was higher between the Equator and 20° N (Fig. 5). This increase in estimated dust presence in this region was particularly marked during the 2008 cruise, conducted in April–May.

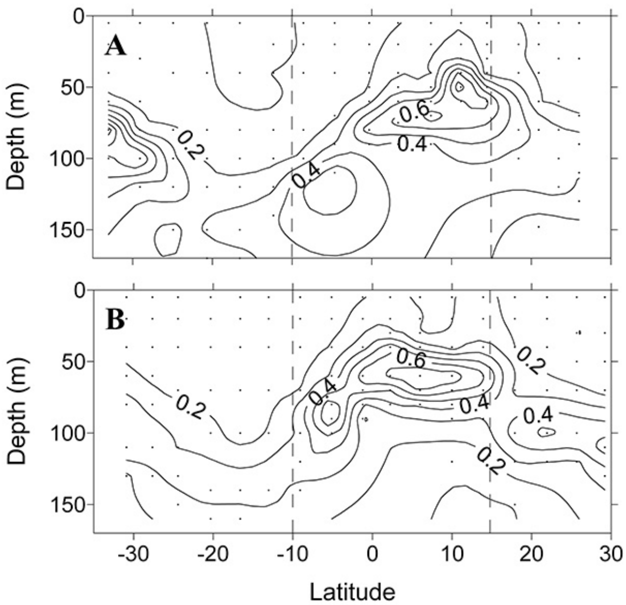

Fig. 6. Latitudinal and vertical distribution of chlorophyll-*a* concentration during the 2007 **(a)** and 2008 **(b)** cruises.

Table 1. Mean *Trichodesmium* spp. surface abundance and integrated N_2 fixation rate on each region during the 2007 and 2008 cruises. Standard deviation is indicated in brackets.

	Trichodesmium spp. (trichomes L^{-1})		N_2 fixation (µmol N m^{-2} d^{-1})	
	2007	2008	2007	2008
North Gyre	31 [52]	8 [11]	25 [6]	11 [4]
Equator	222 [351]	222 [174]	66 [15]	55 [21]
South Gyre	0.5 [0.5]	1 [1]	3 [1]	10 [2]

3.3 Chlorophyll-*a* concentration

Surface chlorophyll-*a* concentration was low in both transects (<0.2 mg m^{-3}) and its vertical distribution was characterized by a deep chlorophyll maximum (DCM), associated with the thermocline, with concentrations above 0.3–0.4 mg m^{-3} (Fig. 6). The DCM was shallower and more intense in the region affected by the Equatorial upwelling. The euphotic layer-integrated chlorophyll-*a* concentration ranged between 19–31 mg m^{-2} (data not shown) across the latitudinal range and did not show any marked differences between cruises.

3.4 *Trichodesmium* spp. abundance and N_2 fixation

Trichodesmium was particularly abundant in the Equatorial region, whereas it was rare or absent in the South gyre (Fig. 7a, b). The region of highest (>100–200 trichomes L^{-1}) surface abundance extended from 15° N to the Equator in 2007 and from 15° N to 10° S in 2008. The highest abundances were measured near 7° N in 2007 (1600 trichomes L^{-1}) and near 3° S in 2008 (800 trichomes L^{-1}). Although there was some inter-cruise variability, the regional differences in *Trichodesmium* abundance were consistent (Table 1). Cruise-averaged abundances were ca. 220 trichomes L^{-1} in the Equatorial region, compared with 8–31 trichomes L^{-1} in the North gyre and 0.5–1 trichomes L^{-1} in the South gyre.

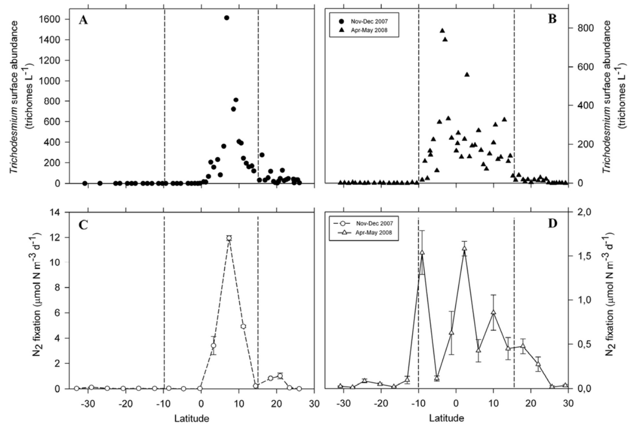

Fig. 7. Latitudinal distribution of mean surface N_2 fixation and surface *Trichodesmium* spp. abundance during the 2007 (left-hand plots) and 2008 (right-hand plots) cruises. Bars in the N_2 fixation plots represent the standard deviation of the mean ($n = 3$).

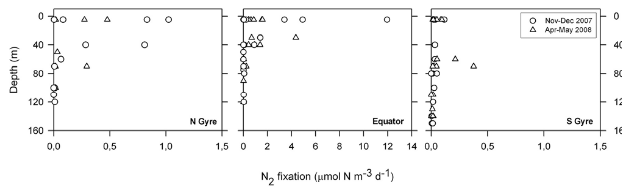

Fig. 8. Vertical distribution of N_2 fixation during the 2007 (triangles) and 2008 (circles) cruises in each latitudinal region.

The latitudinal distribution of N_2 fixation rates at the surface closely resembled that of *Trichodesmium* abundance (Fig. 7c, d). These two variables were highly correlated in our study (Pearson's $r = 0.74$, $p < 0.01$, Table 2). The highest N_2 fixation rates were measured in the Equatorial region. In this region, the mean surface N_2 fixation during the 2007 cruise was more than 3-fold higher than during 2008 (2.94 versus 0.80 µmol N m^{-3} d^{-1}). Diazotrophic activity was mostly restricted to the North Atlantic during 2007, whereas it extended all over the Equatorial region in 2008.

N_2 fixation was detectable in all stations, although not at all depths, and the highest rates were commonly measured in the upper 50 m of the water column (Fig. 8). The vertical distribution of N_2 fixation rates in the North gyre and in

Table 2. Correlation coefficients (Pearson's r) between euphotic-layer integrated N_2 fixation and surface *Trichodesmium* spp. abundance and selected variables computed for all the stations sampled during the 2007 and 2008 cruises.

	Euphotic layer-integrated N_2 fixation	Surface *Trichodesmium* spp. abundance
Euphotic layer-integrated N_2 fixation	–	0.75**
Surface N_2 fixation	0.91**	0.74**
Surface chlorophyll-*a*	0.61**	0.68**
Brunt-Väisälä frequency (0–125 m)	0.58**	0.74**
Surface temperature	0.36*	0.45**
Seasonal AOD 550 nm	0.37*	0.40*

* $p < 0.05$; ** $p < 0.01$

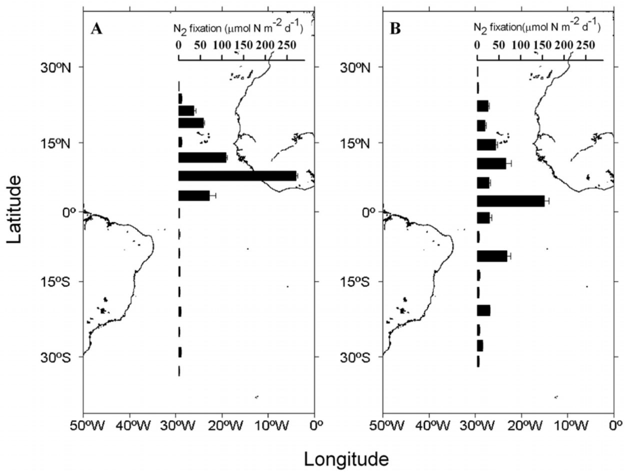

Fig. 9. Latitudinal distribution of euphotic layer-integrated N_2 fixation (µmol N m^{-2} d^{-1}) during the 2007 **(a)** and 2008 **(b)** cruises.

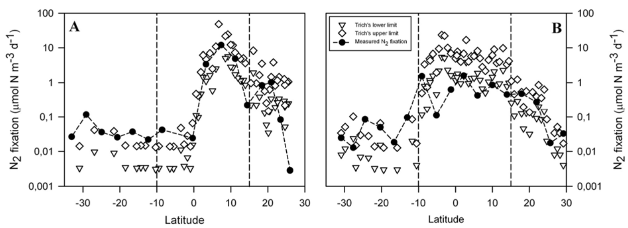

Fig. 10. Comparison of the latitudinal distribution of measured surface N_2 fixation (black circles) with the estimated lower (open triangles) and upper (open diamonds) limit for N_2 fixation due to *Trichodesmium* spp. during the 2007 **(a)** and 2008 **(b)** cruises.

the Equatorial region was characterized by a clear tendency to decrease with depth. In the South gyre, however, N_2 fixation was distributed more uniformly over the euphotic layer. There was a strong correlation between surface N_2 fixation rate and euphotic layer-integrated N_2 fixation rate (Pearson's $r = 0.91$, $p < 0.01$, Table 2). In both cruises, the highest integrated rates (ca. 250 and 150 µmol N m^{-2} d^{-1} in 2007 and 2008, respectively) were measured at stations located within the Equatorial region (Fig. 9). The mean N_2 fixation rate in the Equatorial region was 66 and 55 µmol N m^{-2} d^{-1} in 2007 and 2008, respectively (Table 1). The North gyre, with mean rates of 25 and 11 µmol N m^{-2} d^{-1} in 2007 and 2008, respectively, showed higher diazotrophy than the South gyre (3.4 and 9.7 µmol N m^{-2} d^{-1}). While N_2 fixation south of the Equator was almost undetectable during the 2007 cruise, substantial rates were measured in the Southern Hemisphere in 2008.

3.5 Relative contribution of *Trichodesmium* spp. to community N_2 fixation

We applied an indirect approach to assess whether *Trichodesmium* spp. could account for the measured surface N_2 fixation rates. We used the large dataset collected by Mulholland et al. (2006), which provides in situ measurements of the filament-specific rate of N_2 fixation by *Trichodesmium*. We determined the 25th and 75th percentiles of this dataset in order to estimate a lower and an upper limit for the filament-specific rate of N_2 fixation by *Trichodesmium*. Multiplying these rates by the measured filament abundances, we obtained an upper and a lower estimate for the surface rate of N_2 fixation that could be attributed to *Trichodesmium*, which we then compared with the measured surface community diazotrophy rates (Fig. 10). We found that *Trichodesmium* spp. abundance was sufficient to explain the measured rates of N_2 fixation in the North gyre and Equatorial upwelling regions. However, the measured rates in most of the Southern Hemisphere stations clearly exceeded the maximal rates that, according to our estimates, could be sustained by *Trichodesmium*.

4 Discussion

4.1 Latitudinal distribution of *Trichodesmium* spp.

Our measurements, obtained with high spatial resolution, indicate that *Trichodesmium* spp. is most abundant (>200 trichomes L^{-1}) in the Equatorial Atlantic region between 5° S–15° N, has modest abundances in the North Atlantic subtropical gyre and is virtually absent from the South Atlantic gyre. These patterns agree with those identified by Tyrrell et al. (2003) and Moore et al. (2009), who reported on surface abundances obtained at longer distance intervals, and are also suggested by the analysis of ocean color data by Westberry and Siegel (2006). The mean abundances we measured between 5° S–15° N are similar to the highest abundances reported by Moore et al. (2009) for the same region. These authors found a close association between iron concentration and both *Trichodesmium* abundance and community N_2 fixation along a transect conducted in the Atlantic Ocean in October–November 2005. Our own observations, carried out during contrasting seasons, support this association and suggest that the observed latitudinal patterns are persistent over seasonal scales.

Although iron concentration data are not available in the present study, the satellite data of aerosol optical depth obtained during the time period of our surveys do suggest enhanced rates of atmospheric dust deposition between the Equator and 20° N, where the highest *Trichodesmium* abundances were found. In our study, we found a significant correlation between aerosol optical depth at 550 nm and *Trichodesmium* abundance (Pearson's $r = 0.40$, $p < 0.05$, Table 2). The available climatologies of dust and iron deposition in the central Atlantic show a region of persistent, albeit varying seasonally, high deposition rates between roughly 10° S–30° N (Gao et al., 2001; Mahowald et al., 2005), coinciding with the region of increased *Trichodesmium* abundances. Given the very high iron requirements of *Trichodesmium* (Kutska et al., 2003) and the demonstrated relationship between iron availability and *Trichodesmium* growth rate (Berman-Frank et al., 2007), it is likely that atmospheric deposition of dust is the main process controlling the distribution of this genus in the central Atlantic Ocean. Additional factors which may have also favoured the presence of *Trichodesmium* in the Equatorial region include the shallowing of the upper mixed layer and the increase in water column stability, which in our study was reflected in the higher values of the Brunt-Väisäla frequency encountered between 10° S–20° N. In fact, we found a highly significant correlation between the Brunt-Väisäla frequency and *Trichodesmium* spp. abundance (Pearson's $r = 0.74$, $p < 0.01$, Table 2). The shallowing of the upper mixed layer may result in a reduction in the energetic expenditure involved in the vertical migrations carried out by *Trichodesmium* spp., which allow them to take up nutrients, phosphate in particular, from below the nutricline (Karl et al., 1992).

The latitudinal range of distribution of *Trichodesmium* extended further south during the 2008 cruise, conducted in April–May, than during the 2007 cruise, conducted in November–December. Although our data are not sufficient to establish seasonal patterns, these differences are consistent with a role of atmospheric deposition in determining the abundance of *Trichodesmium* spp., given that aerosol deposition in the Eastern North Atlantic is more intense and occurs over a larger area during spring than during winter (Gao et al., 2001; Kaufman et al., 2005). In addition, the increased stability of the water column south of the Equator may have also contributed to extend further south the range of distribution of *Trichodesmium* during the 2008 cruise.

4.2 Latitudinal distribution of N_2 fixation

We have shown that N_2 fixation rates in the central Atlantic are higher between 5° S–15° N during two contrasting seasons, and that *Trichodesmium* is likely to account for most of the N_2 fixation in this region. Our observations support the results of Moore et al. (2009), who found increased N_2 fixation in the same latitudinal range, where higher iron concentrations were measured, and concluded that iron rather than phosphorus supply explain the North-South differences in diazotrophy in the Atlantic Ocean. As described before for *Trichodesmium* spp. abundance, we found a clear association between the region of increased N_2 fixation rates and the latitudinal range of enhanced atmospheric dust presence in the Eastern central Atlantic. These two variables were significantly correlated (Pearson's $r = 0.37$, $p < 0.05$, Table 2). Together, these results strongly suggest that iron supply through atmospheric deposition is a major determinant of planktonic N_2 fixation in the Atlantic Ocean, as has also been shown for the North Pacific (Shiozaki et al., 2009).

The role of phosphorus, which has been found to limit N_2 fixation in the central Atlantic (Sañudo-Wilhelmy et al., 2001; Mills et al. 2004) must also be considered. During our surveys, PO_4 concentration showed a clear decreasing trend from South to North, a recurrent pattern in the Atlantic Ocean (Mather et al., 2008; Moore et al., 2009). The highest rates of N_2 fixation thus occurred in waters with low (<0.05 µM) PO_4 levels, whereas little N_2 fixation took place in the more phosphorus-rich waters of the South gyre. Although *Trichodesmium* and other phytoplankton can obtain P from the pool of dissolved organic phosphorus, P availability is still very low in the North Atlantic, as evidenced in the enhanced alkaline phosphatase activity (APA) measured there (Mather et al., 2008). APA is well known to increase in response to P limitation in phytoplankton. In spite of increased P limitation in the North Atlantic, as compared with the South Atlantic, N_2 fixation is higher in the North, which indicates that the large-scale latitudinal distribution of N_2 fixation in the Atlantic is not controlled by P availability. Current evidence indicates that iron-mediated stimulation of N_2 fixation in the Equatorial and North Atlantic draws the surface phosphate pool to very low concentrations (Mather et al., 2008; Moore et al., 2009), but nitrogen remains the proximate limiting nutrient for primary production (Mills et al., 2004; Moore et al., 2008).

4.3 N_2 fixation in the South Atlantic

The fact that filamentous diazotrophs such as *Trichodesmium* are rare in the South Atlantic gyre (Tyrrell et al., 2003; Moore et al., 2009; our study), together with the low or even negative values of the N* tracer observed in subsurface waters (Gruber and Sarmiento, 1997), could lead us to expect that N_2 fixation does not take place in this region. However, we were able to detect N_2 fixation in all the stations during our cruises. The average rates measured in the South gyre were substantial (ca. 4 and 10 µmol N m^{-2} d^{-1} in 2007 and 2008, respectively), given the extreme oligotrophy of this region, and some peak values were comparable to those measured in the Equatorial region. Our estimates of the rates of N_2 fixation that could be sustained by the extremely low (<1 trichome L^{-1}) *Trichodesmium* abundances measured in the South gyre strongly suggest that other diazotrophs were the main contributors to N_2 fixation in this region. The same conclusion was reached by Moore et al. (2009), who reported relatively constant rates of diazotrophy in the <20 mum size fraction across the Atlantic Ocean. These results suggest that the large scale geographical distribution of unicellular diazotrophs in the open ocean is more uniform than that of *Trichodesmium*, contributing a background of modest but persistent N_2 fixation rates.

Montoya et al. (2004) pointed out that the vertical distribution of unicellular diazotrophs is relatively uniform over the euphotic layer, in contrast with that of *Trichodesmium*, which tends to concentrate in the shallower portions of the water column (Carpenter et al., 2005). In agreement with this observation, we found that N_2 fixation rates tended to peak at or near the surface in the Equatorial and North gyre regions, whereas a more uniform vertical distribution was found in the South gyre. This pattern is consistent with an increased contribution of unicellular diazotrophs to community N_2 fixation in the South gyre. However, nitrogenase is a highly conserved enzyme across microbial phylogenetic groups (Zehr et al., 2000), and therefore the elevated costs of N_2 fixation, both in terms of energetic expenditure and iron requirements, must also be present in unicellular diazotrophs. One can therefore ask why unicellular diazotrophs carry on fixing N_2 in environments that are very impoverished in iron. It has been shown that N_2 fixation in a unicellular cyanobacterium such as *Cyanothece* is much less depressed under low iron concentrations than it is in *Trichodesmium* (Berman-Frank et al., 2007). These authors concluded that the small cell size and rapid intracellular Fe recycling capacity of unicellular diazotrophs make them relatively resistant to low iron concentrations, which would give them advantage in low-iron waters. These factors can, therefore, explain the persistence of N_2 fixation in a region that experiences very low atmospheric deposition such as the South Atlantic subtropical gyre.

4.4 Biogeochemical significance of N_2 fixation

The mean rates of N_2 fixation we measured in the Equatorial and North gyre regions (55–66 and 11–25 µmol m^{-2} d^{-1}, respectively) are similar to those recently reported by Moore et al. (2009), who studied also the eastern region of the Atlantic, but lower than the mean rates observed in other studies more focused on the western tropical Atlantic (Capone et al., 2005; Montoya et al., 2007). As a rough calculation, we scaled up from all our measurements (42 stations) to the whole Atlantic Ocean (40° N–40° S) by multiplying the measured daily rates by 365 and using the location of the continental shelf to define the region's longitudinal limits. We estimate an annual N_2 fixation of ∼6 TgN yr^{-1} in the North Atlantic (0–40° N) and ∼1.2 TgN yr^{-1} in the South Atlantic (0–40° S). These are rather conservative estimates because they do not take into account the occurrence of *Trichodesmium* blooms and also because our surveys did not cover the Western tropical Atlantic, where higher *Trichodesmium* abundances have been reported (Capone et al., 2005; Montoya et al., 2007). In addition, a substantial fraction of the N_2 fixed by diazotrophs can be released as dissolved organic nitrogen (DON), whose subsequent remineralization represents an additional source of new nitrogen for the ecosystem (Glibert and Bronk, 1994). Geochemical estimates of N_2 fixation, which integrate over wide spatial and temporal scales and take into account also the production of DON, are in the range 15–56 TgN yr^{-1} for the whole Atlantic Ocean (Knapp et al., 2008).

To assess the biogeochemical significance of measured N_2 fixation rates, it is particularly useful to compare them with the diffusive flux of nitrate from below the thermocline, which represents the other main input of new nitrogen into the euphotic layer. Available estimates of vertical nitrate diffusivity are subject to a large degree of uncertainty, mainly because of a lack of direct measurements of the vertical diffusivity coefficient (K_z). For the tropical North Atlantic, estimates of this flux range widely between 100–1000 µmol m^{-2} d^{-1} (see review in Capone et al., 2005). These authors estimated that N_2 fixation can represent between 50–180% of the vertical diapycnal flux of nitrate. However, given that N_2 fixation and vertical nitrate diffusion exhibit large spatial and temporal variability, concurrent and direct measurements of both fluxes are needed to determine their relative importance. During the 2008 cruise, we were able to obtain direct measurements of vertical diffusivity, which we then combined with data of nitrate nanomolar concentration in order to calculate vertical fluxes of nitrate (Mouriño-Carballido et al., 2010). We found that the contribution of N_2 fixation to the total input of new nitrogen (the sum of N_2 fixation and vertical diffusion of nitrate) in the North gyre, the equatorial region and the South gyre was 2, 22 and 44%, respectively. These contributions would be lower, at least in the Equatorial region, if atmospheric nitrogen input were taken into account. In addition, it can be expected that these contributions will change seasonally, mainly because of variability in vertical diffusivity associated with changes in the vertical density gradient. Our results highlight the quantitative importance of N_2 fixation and demonstrate that even in regions of low absolute rates of diazotrophy this process may represent a major source of nitrogen to sustain new production in the upper ocean.

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