

An extensive bloom of the N₂-fixing cyanobacterium *Trichodesmium erythraeum* in the central Arabian Sea

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ABSTRACT: We encountered an extensive surface bloom of the N₂ fixing cyanobacterium *Trichodesmium erythraeum* in the central basin of the Arabian Sea during the spring inter-monsoon of 1995. The bloom, which occurred during a period of calm winds and relatively high atmospheric iron content, was metabolically active. Carbon fixation by the bloom represented about one-quarter of water column primary productivity while input by N₂ fixation could account for a major fraction of the estimated 'new' N demand of primary production. Isotopic measurements of the N in surface suspended material confirmed a direct contribution of N₂ fixation to the organic nitrogen pools of the upper water column. Retrospective analysis of NOAA-12 AVHRR imagery indicated that blooms covered up to 2 × 10⁶ km², or 20% of the Arabian Sea surface, during the period from 22 to 27 May 1995. In addition to their biogeochemical impact, surface blooms of this extent may have secondary effects on sea surface albedo and light penetration as well as heat and gas exchange across the air-sea interface. A preliminary extrapolation based on our observed, non-bloom rates of N₂ fixation from our limited sampling in the spring intermonsoon, including a conservative estimate of the input by blooms, suggest N₂ fixation may account for an input of about 1 Tg N yr⁻¹. This is substantial, but relatively minor compared to current estimates of the removal of N through denitrification in the basin. However, N₂ fixation may also occur in the central basin through the mild winter monsoon, be considerably greater during the fall intermonsoon than we observed during the spring intermonsoon, and may also occur at higher levels in the chronically oligotrophic southern basin. Ongoing satellite observations will help to determine more accurately the distribution and density of *Trichodesmium* in this and other tropical oceanic basins, as well as resolving the actual frequency and duration of bloom occurrence.

KEY WORDS: *Trichodesmium* · Nitrogen fixation · Cyanobacteria · Blooms · Arabian Sea · Remote sensing

INTRODUCTION

The non-heterocystous N₂-fixing cyanobacteria *Trichodesmium* spp. occur through much of the oligo-

trophic waters of the marine tropics and sub-tropics and are often a major component of the planktonic flora in these systems (Carpenter 1983, Capone et al. 1997). They can form conspicuous surface blooms under appropriate conditions, and dense surface accumulations of *Trichodesmium* have been widely reported in oligotrophic seas (Carpenter & Capone 1992). As a N₂ fixer, *Trichodesmium* may provide important inputs of 'new N' into these systems (Dugdale et al. 1964, Capone et al. 1997, Karl et al. 1997).

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While directed studies of the abundance and activities of *Trichodesmium* have established its biogeochemical importance in a few relatively restricted areas of the ocean (Capone et al. 1997), its overall contribution to the oceanic N cycle has generally been thought to be minor (Eppley & Peterson 1979, Capone et al. 1997).

Recent field studies and N budgeting efforts provide strong evidence that the biogeochemical role of *Trichodesmium* spp. in oceanic N₂ fixation is considerably greater than currently believed (Carpenter & Romans 1991, Capone et al. 1997, Karl et al. 1997, Gruber & Sarmiento 1997). Their contribution to oceanic C and N cycling has likely been underestimated due to unique difficulties in quantitatively assessing the *in situ* biomass and activity of *Trichodesmium* by standard methods (Capone et al. 1997). It has been particularly difficult to account for the importance of *Trichodesmium* blooms in CO₂ and N₂ fixation because of the constraints of oceanographic sampling, the infrequency of oceanographic cruises to relevant areas, and the inherent unpredictability of the occurrence of blooms (Carpenter & Capone 1992, Capone et al. 1997).

During 1995, the Arabian Sea was the site of the Joint Global Ocean Flux Study (JGOFS) (Smith et al. 1991). It was chosen because it undergoes major changes in wind direction, speed, solar insolation, currents, water temperature, and upwelling between the NE (December to February) and SW (June to September) monsoons (Madhupratap et al. 1996). Upwelling during the summer monsoon results in high concentrations of NO₃⁻ in surface waters, particularly in the northwest reaches of the basin, thereby precluding N₂ fixation. During the oligotrophic intermonsoon periods, surface waters are depleted of combined N and productivity and biomass are considerably lower.

While there have been numerous reports of large blooms of *Trichodesmium* spp. along the coastal Indian and African coasts during the winter monsoon and the inter-monsoons (Devassy et al. 1978, Devassy 1987, Carpenter & Capone 1992, Kromkamp et al. 1997), there is little documentation of its occurrence in the open reaches of the basin during those periods. Karsten (1907) made qualitative observations of *Trichodesmium* in open waters in the winter and spring during the Tiefsee Expedition in 1898, while Zernova (1962) reported that *Trichodesmium* and *Katagnymene* (another cyanobacterium) concentrations exceeded those of diatoms and dinoflagellates for an extensive area of the Arabian Sea in October and December. Even during the summer (SW) monsoon, when upwelling is most intense along the Somali coast, large portions of the southern stretches of the basin remain highly oligotrophic and *Trichodesmium* may be expected to persist and remain active.

Direct determinations of N₂ fixation in the Arabian Sea are very limited. Dugdale et al. (1964) used ¹⁵N₂ uptake to document relatively high rates of N₂ fixation by *Trichodesmium* at a suite of stations in the northern Arabian Sea in late October and early November 1963. Bryceson (1982), in an annual study off the coast of Dar es Saalam, found *Trichodesmium* biomass and N₂ fixation to be greatest between December and May.

During May 1995 we participated in a JGOFS cruise of the FS 'Meteor' (Germany) on a southward transect along 65°E through the central basin of the Arabian Sea to investigate the importance of this planktonic diazotroph to upper water column C and N dynamics during the spring inter-monsoon.

METHODS

Sample collection and analytical methods

Stations were taken each day at intervals of 1 degree of latitude along 65°E. In addition, we carried out intensive studies of water column processes at 3 multiple-day drift stations at 18°N, 10°N, and 3°N. Samples for *Trichodesmium* enumeration were collected at various depths in the upper 100 m of the water column using a conductivity-temperature-depth (CTD)/rosette system equipped with 30 l Niskin bottles. At the northern end of the transect, the shallowest samples were taken at about 2 m depth. At 11°N and further south, surface samples were most often taken at 0.5 and 1 m. Once on deck, 2 to 10 l of water from each bottle were gravity fed through an in-line filter cartridge containing a 45 mm polycarbonate filter with a porosity of 10 µm. After the entire contents of the bottle had drained through the cartridge, the filter was removed, placed on a 75 × 50 mm microscope slide, and a large drop of immersion oil and a coverslip were placed on top of the filter. Trichomes and colonies were identified to species and counted using a Zeiss Axioskop under epifluorescence illumination at a magnification of 160×. Several transects of the filter were counted (usually to a count of at least 500 trichomes or, at low abundance, the whole filter). Free trichomes were enumerated and colonies scored as small (10 trichomes), medium (30 trichomes) or large (100 trichome). Periodic direct determination of the number of trichomes per colony, and the number of cells per trichome were made. At stations with marked surface accumulations of *Trichodesmium*, samples were also collected by bucket and relatively small volumes were filtered (<1 l) and prepared for counting.

Water samples for particulate N and nutrient analyses were also collected with the CTD-rosette system.

Particles were isolated by gentle vacuum filtration onto pre-combusted GF/F filters, dried and stored for analysis ashore. Sinking particles were collected using a drifting Kiel-type sediment trap deployed at 100 to 130 m each day during the extended drift stations. Splits of the material collected were dried and stored for isotopic analysis ashore. Ammonium, nitrate and phosphate concentrations were determined manually by colorimetric methods (Parsons et al. 1984).

The $\delta^{15}\text{N}$ of bulk suspended particulate matter was determined on material collected near the surface (upper 10 m) and throughout the water column. The mean water column $\delta^{15}\text{N}$ in particulate organic nitrogen (PON) was calculated as the mass- and depth-weighted average of the 5 to 10 samples collected between the surface and 100 m depth (Montoya et al. 1992). The $\delta^{15}\text{N}$ of sinking particles was determined on material collected in a drifting sediment trap at the extended stations. All ^{15}N analyses were carried out with a continuous-flow isotope ratio mass spectrometry (IRMS) system and are reported as $\delta^{15}\text{N}$ values relative to atmospheric N_2 .

Ferrous iron [Fe (II)] abundance in the atmosphere was determined by filter collection of aerosol using a High Volume Dichotomous Virtual Impactor (HVDVI) system built of polycarbonate and with a total flow rate of $310 \pm 30 \text{ l min}^{-1}$. This system separates aerosol into 2 size fractions with a cutoff of ca 2 μm . Aerosols were collected on 90 mm Teflon filters (Gelman Zeflour) with a 1 μm pore size. A new set of filters was used each day, providing a series of samples, each of which represented approximately 24 h. Fe (II) abundance was measured on a 47 mm diameter sub-sample cut out of each filter using the colorimetric technique of Fe (II)-Ferrozine complexation. Shipboard analyses were carried out within 1 h of removal from the collection system (R. Siefert, A. Johansen & M. Hoffman unpubl.). Filters and Teflon-coated plasticware were acid-cleaned before each use to minimize iron contamination. Wind speed was recorded from the shipboard meteorological station during each daily filter change.

Rate measurements. Nitrogenase activity was determined by the C_2H_2 reduction method on unconcentrated surface samples (0 to 0.5 m depth samples) and on isolated colonies (>0.5 m) collected by net tows and incubated at simulated light depths, with direct comparisons by $^{15}\text{N}_2$ uptake (Capone 1993, Montoya et al. 1996).

Primary productivity was measured in 250 ml polycarbonate bottles spiked with H^{14}CO_3 (20 $\mu\text{Ci bottle}^{-1}$) and incubated *in situ* for a 4 h period spanning local noon (Steeman Nielsen 1952). Samples were collected by CTD/rosette at either standard depths (e.g. 10, 25, 50, 75, 100, 150, 200 m) or at finer intervals over the top

25 m for high resolution surface samples. At each sample depth, 1 dark bottle treated with 10^{-5} M 3-(3,4-dichlorophenyl)-1, 1-dimethylurea (DCMU) was used to correct the experimental (i.e. light) bottles for nonphotosynthetic incorporation of ^{14}C into particles. After incubation, all samples were treated with DCMU to prevent additional carbon uptake during handling. Size fractionation (post-incubation screening) was performed using 50 ml aliquots from each bottle filtered through polycarbonate filters of 0.2, 0.8, 2.0 and 5.0 μm nominal pore size, as well as Whatman GF/F for comparison. ^{14}C uptake was determined by liquid scintillation counting with quench correction.

Remote sensing. Processed and navigated channel 1 and 2 albedo images acquired by the Advanced Very High-Resolution Radiometer (AVHRR) sensor on board the National Oceanic and Atmospheric Administration's NOAA-14 and NOAA-12 satellites were provided to us by Dr R. Evans, Rosenstiel School of Marine and Atmospheric Science (RSMAS), University of Miami. A total of 12 images from NOAA-14 and 7 images from NOAA-12 covering the study area were available for the period between 20 May and 1 June 1995. Nominal pixel resolution is about 1 km. The processing was done using the DSP image processing software (University of Miami) at RSMAS, where Local Area Coverage (LAC) AVHRR images of the Arabian Sea were archived to support the USJOGFS program. We used the MIA2TIFF procedure of DSP to create TIFF files of the images and used the TIFF_READ procedure of IDL (RSI, Inc) for further analysis of our images. The albedo values were thus scaled from 0 to 255. A classifier for detection of *Trichodesmium* in the water similar to the Gray-McCrary Index (Gray & McCrary 1981) and based on a simple difference between the albedos of channels 1 and 2 had been previously used to identify a *Trichodesmium* bloom near the Great Barrier Reef (Gallegos et al. 1984). Kahru (Kahru et al. 1993) showed that the Normalized Difference Vegetation Index (NDVI) could be used to map surface cyanobacterial blooms in the Baltic Sea. Subramaniam (1995) developed an 'Albedo Vegetation Index' (AVI) consisting of the following procedures to map surface blooms of *Trichodesmium*.

(1) Set all albedo values >200 gray scale units to 0. This removes clouds and other very highly reflective surfaces from further processing.

(2) Determine $\text{AVI} = \text{alb2} - \text{alb1}$ where AVI is the Albedo Vegetation Index used to map *Trichodesmium*, alb1 and alb2 are channel 1 and channel 2 albedos.

(3) Set all pixels with values of AVI <-5 or >50 to 0.

(4) Set all pixels with value equal to 0 to 255, a pool which now includes pixels whose channel 1 or 2 albedos were greater than 200 (step 1) or whose AVI value was 0, less than -5 or greater than 50 (step 3).

RESULTS

At the higher latitudes in the transect, *Trichodesmium* populations were sparse, typically less than 10^5 trichomes l^{-1} near the surface (≤ 2 m) and less than 10^6 trichomes m^{-2} in the whole water column (Fig. 1A). This coincided with measurable ($>0.03 \mu M$) NO_3^- concentrations in the surface, and relatively high wind stress (Fig. 1).

Concentrations of trichomes increased at $11^\circ N$ and at several stations to the south with *Trichodesmium*

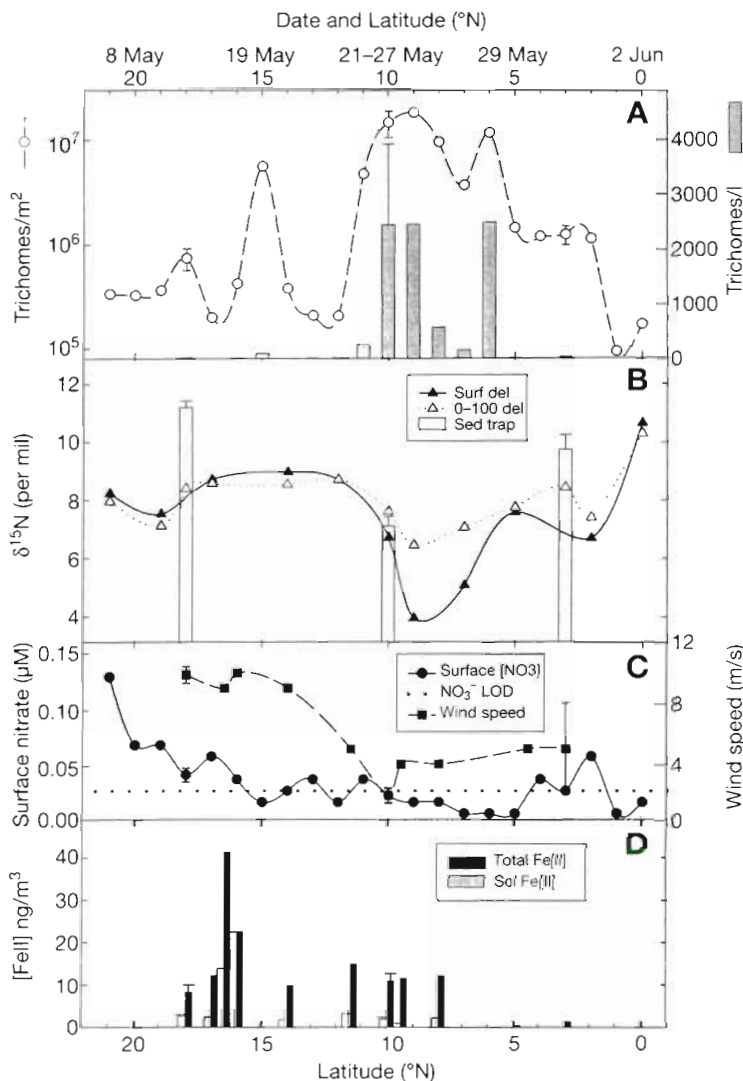


Fig. 1. Latitudinal variation in (A) *Trichodesmium* abundance, (B) natural abundance of ^{15}N ($\delta^{15}N$) in particulate matter, (C) surface NO_3^- concentration and surface wind and (D) total and soluble (sol) aerosol Fe(II) concentration in a transect along $65^\circ E$ in the Arabian Sea in May 1995. Where available, data from multi-day drift stations are presented as means \pm standard errors. Results for *Trichodesmium* abundance (A) are presented as the concentration of samples (l^{-1}) collected in the upper 2 m (o) or integrated over the top 100 m (gray bars) and expressed per m^2 . (B) Isotopic abundance of suspended particulate (Δ , \blacktriangle) and of sediment trap material (open bars). LOD: nominal limit of detection; del: $\delta^{15}N$

found through the upper water column to 50 to 80 m, with very dense populations at the surface. In contrast to more northerly stations, NO_3^- concentrations were near or below the limit of detection, and surface wind stress substantially lower at stations between 11° and $3^\circ N$. Except for 1 station at $6^\circ N$, *Trichodesmium* abundance decreased southward of our station at $10^\circ N$, falling to about 10^6 trichomes m^{-2} at $5^\circ N$, and further decreasing to low levels near the equator. Throughout the transect, the predominant species was *T. erythraeum*. Colony sizes were typically small (about 10 to 30 trichomes per colony) with typically about 100 cells per trichome.

While occupying a multi-day drift station at $10^\circ N$, we encountered extensive surface accumulations of *Trichodesmium erythraeum* during a period of calm winds. The blooms, which we observed for 6 d (22 May through 27 May), were prominent on the surface each morning, and sank slightly (about 0.5 to 1 m) below the surface after midday. Trichome densities in the surface slicks were in excess of 10 000 trichomes l^{-1} (Figs. 1A & 2A). A surface survey on the night of 24 to 25 May, covering two 20 nautical mile transects in a N-S and E-W direction, revealed dense slicks throughout this 400 nautical mile² (about 1300 km²) region (F. Pollehne pers. comm.).

During the bloom, N_2 fixation was readily detected in unconcentrated surface water samples (Fig. 2). A large fraction of the algal biomass and CO_2 fixation, and the bulk of the N_2 fixation, occurred in the upper 0.5 m (Fig. 2B, C). Trichome-specific rates of nitrogenase activity for surface samples averaged about 5-fold greater than comparable samples collected below the surface accumulations (Fig. 2B), demonstrating that the surface slicks were not senescent. Similarly, primary productivity was about $1 \text{ mmol C m}^{-3} \text{ h}^{-1}$ at the surface, $0.1 \text{ mmol C m}^{-3} \text{ h}^{-1}$ at 1 m and $0.01 \text{ mmol C m}^{-3} \text{ h}^{-1}$ at 10 m (Fig. 2D).

Nutrient concentrations in the very surface layers also reflected the influence of the bloom (Fig. 3). Ammonium concentrations at 10 m remained steady at about $0.2 \mu M$ throughout the bloom, while transients of higher ammonium concentrations (up to $0.9 \mu M$) were found in the uppermost 0.5 m. In contrast, there were no discernible differences in absolute phosphate concentrations between the very surface waters and 10 m. There was a possible trend of general decrease over the period of the bloom at both depths which was somewhat stronger at the surface.

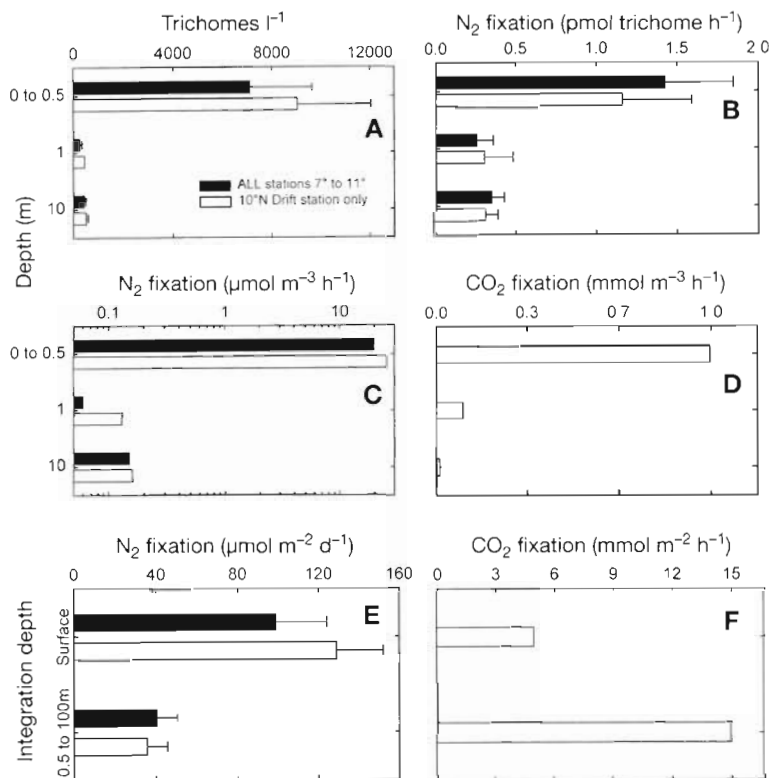


Fig. 2. Depth distributions of (A) cell abundance, (B) trichome specific N_2 fixation, and volumetric and areal rates, respectively, of (C, E) N_2 and (D, F) CO_2 fixation, at stations between 7° and $11^\circ N$ on a transect along $65^\circ E$. Samples collected for *Trichodesmium* abundance (A) are as described for Fig. 1. N_2 fixation results are expressed on a per trichome (B), volumetric (C) and depth-integrated (E) basis. Primary productivity is presented on a volumetric (D) and depth-integrated (F) basis

Size fractionation studies of $^{14}CO_2$ uptake revealed C fixation rates in the surface layer to be primarily associated with the largest size fractions ($>5 \mu m$), presumably *Trichodesmium* spp. (Fig. 4). Pre-filtration of bloom waters through $20 \mu m$ mesh to remove *Trichodesmium* filaments also removed most ($>80\%$) of the

$^{14}CO_2$ uptake activity (data not shown). Hence, much of the C and N input would have been completely missed using standard sampling protocols that call for pre-filtration of samples to remove zooplankton.

N_2 fixation by *Trichodesmium* in the surface 0.5 m at the drift station exceeded that occurring through the rest of the upper water column. Areal rates of N_2 fixation in the upper 0.5 m averaged $129 \pm 23 \mu mol N m^{-2} d^{-1}$ ($\pm SE, n = 5$), about 3-fold greater than that occurring between 0.5 to 40 m [about $40 \pm 10 \mu mol N m^{-2} d^{-1}$ ($\pm SE, n = 10$)] (Fig. 2). Mean depth-integrated primary production on days preceding the bloom ranged from 13 to 17 $mmol C m^{-2} d^{-1}$ (F. Pollehne & C. Humborg pers. comm.). Depth-integrated C fixation on 22 May was about $20 mmol C m^{-2} d^{-1}$ with 25% of this occurring in the upper 0.5 m.

The $\delta^{15}N$ of suspended particles varied between about 4 and 11‰, with a broad minimum in the upper water column in the region of the *Trichodesmium* spp. bloom (Fig. 1B). Sinking particles collected at $10^\circ N$ had an isotopic composition similar to that of suspended particles in the upper water column and significantly lower than the $\delta^{15}N$ of sinking particles collected at the other 2 drift stations (5° and $18^\circ N$). At the northern and southern drift stations, sinking particles collected in the sediment trap had a $\delta^{15}N$ markedly higher than suspended particles in the upper water column but similar to the suspended particles below the mixed layer, which averaged about 10‰ with little variation through the transect (data not shown).

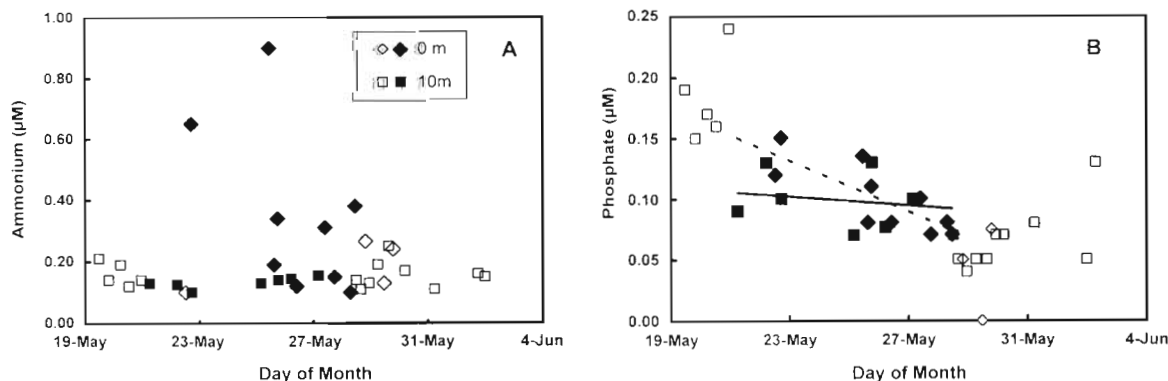


Fig. 3. Concentrations of (A) ammonium and (B) phosphate in surface waters ($<0.5 m$) and at 10 m at stations between $15^\circ N$ (19 May) and $0^\circ N$ (4 June). For the period 21 to 28 May 1995, the 'Meteor' was on station at $10^\circ N$. Trend lines indicate first order regression slopes for either surface (dashed lines) or 10 m (solid lines) for the $10^\circ N$ drift station. Solid data points represent measurements taken at the drift station

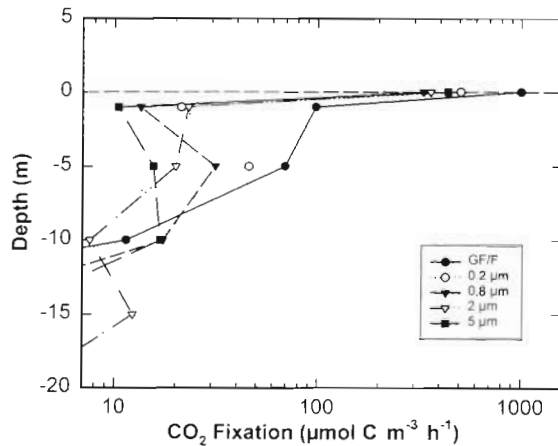


Fig. 4. Depth distribution of size-fractionated $^{14}\text{CO}_2$ uptake in the upper water column during a *Trichodesmium* bloom

Spatial extent of the bloom

We performed a retrospective analysis of the NOAA-12 and 14 AVHRR derived images of the Arabian Sea from 20 May to 1 June 1995. NOAA-14 passes occur in the afternoon and did not detect surface plant biomass in the region of the bloom. Two images from overpasses of the center of the basin (23 and 27 May) as well as 2 more along the western side of the basin (20 and 25 May, Subramaniam et al. in press b) revealed extensive surface blooms (Fig. 5A, C), with accumulations apparently intensifying from the first to the second overpass in each sector. Surface accumulations were not detected in images obtained from either satellite immediately after 27 May (for example on 28 or 29 May, or on 1 June). The western basin bloom on 25 May and the central basin bloom on 27 May were each observed over a span of about $5^\circ \times 15^\circ$, for a total area of at least $2 \times 10^6 \text{ km}^2$.

DISCUSSION

Trichodesmium abundance at the surface and in the water column varied by several orders of magnitude along the transect. The spring intermonsoon of 1995 was relatively brief, with the winter monsoon sustained until mid-April (M. Roman pers. comm.) and an early arrival of the summer monsoon. Thus, the low *Trichodesmium* abundance in the northern portion of our transect was likely a result of the relatively high wind speeds and elevated concentrations of dissolved inorganic nitrogen in the surface mixed layer in that region (Fig. 1C).

In contrast to the northern portion of the transect which is most affected by the monsoons, much greater concentrations of *Trichodesmium*, including dense surface aggregations, were encountered between roughly

12° and 6° N (Fig. 1A). This region was characterized by very low surface nutrient concentrations and wind speed (Fig. 1C) and relatively high concentrations of Fe(II) in atmospheric aerosols (Fig. 1D).

Iron availability has been proposed as an important factor limiting *Trichodesmium* populations in the open ocean (Rueter et al. 1992, Capone et al. 1997). On our transect, the relatively high atmospheric Fe(II) found at stations between 21 and 8° N (Fig. 1D) decreased substantially at stations located further to the south and therefore more distant from continental sources. This pattern suggests that low Fe availability may partially account for the reduced population density of *Trichodesmium* in the most southern portion of the transect.

While the bloom density at 10° N was sufficient to be observed as surface slicks, densities observed at the surface, of up to $17\,000$ trichomes l^{-1} , were far below those reported for areas along the west coast of India. For instance, Devassy et al. (1978) noted bloom densities as high as 39×10^6 trichomes l^{-1} (see Carpenter & Capone 1992). In fact, the pixel we were in did not register a bloom on either 23 or 27 May, while nearby pixels did register. Nonetheless, we did observe slicks each morning from the 22nd through the 27th, which indicates a relatively high threshold for the algorithm and, therefore, greater densities of *Trichodesmium* in pixels recording a response. Also, as mentioned above, a survey over a 20×20 nautical mile survey the night of 24 to 25 May revealed slicks throughout a much larger region (about 1300 km^2) centered on our drift station and overlapping regions of positive returns from the AVI.

Standard sampling protocols for upper water column processes, which may span 100 m between the surface and the base of the euphotic zone, generally obtain 'surface' samples from depths >1 m, and often at 10 m depth. Such sampling would omit populations of phytoplankton, such as *Trichodesmium*, which can concentrate in the upper 1 m or less under bloom conditions. Furthermore, pre-filtration through a coarse mesh (e.g. 100 to 150 μm) is regularly employed in CO_2 fixation studies to remove macrozooplankton grazers (e.g. Strickland & Parsons 1972). This procedure would also remove large colonial phytoplankton such as *Trichodesmium* from the incubation, potentially leading to a significant underestimate of total primary production in the water column.

Relationship to total and export production

Trichodesmium is primarily dependent upon N_2 fixation for its nitrogen requirement (Capone et al. 1997, Carpenter et al. 1997). However, assuming a C:N ratio of 5.2 for new cyanobacterial biomass, N_2 fixation

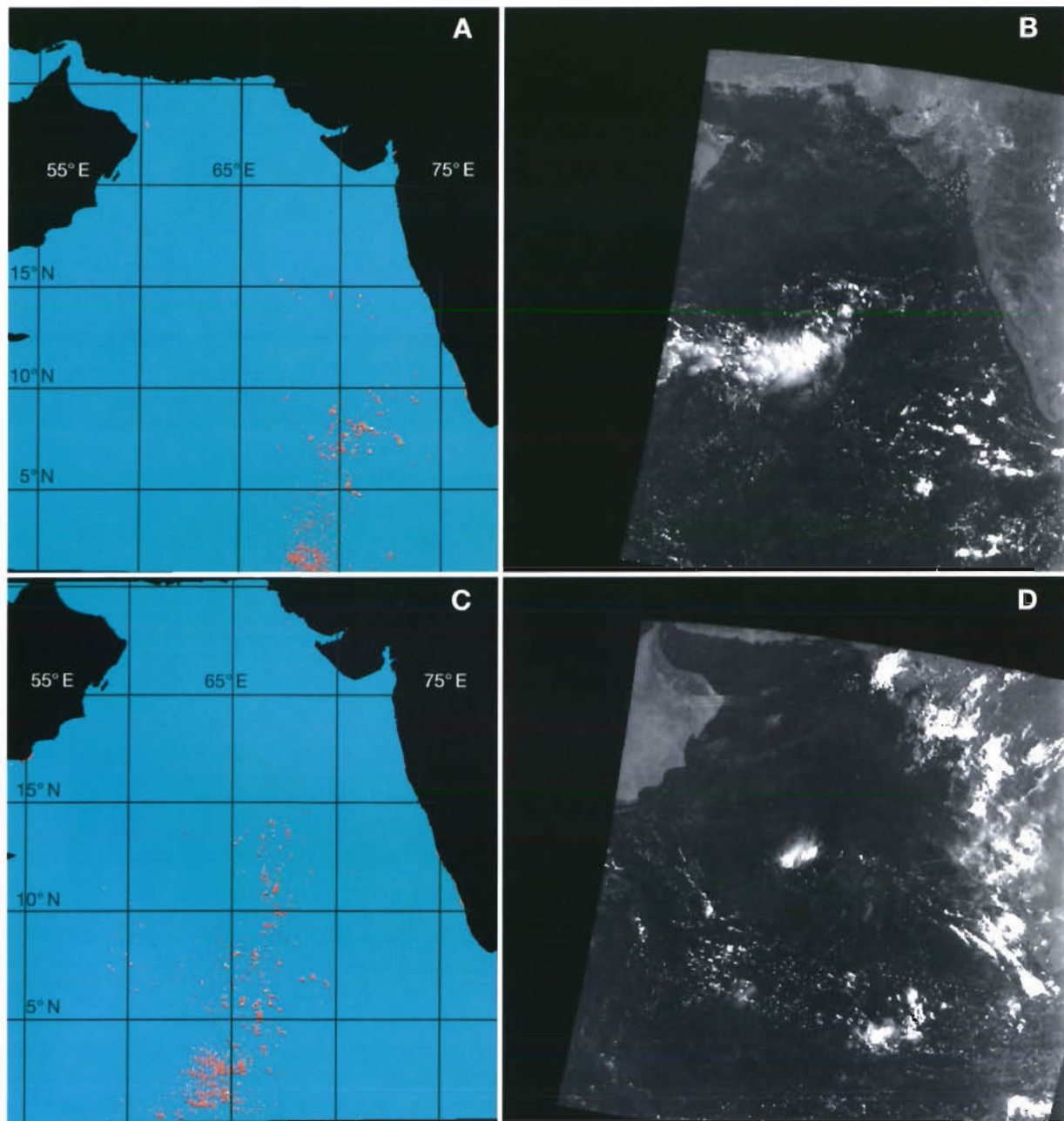


Fig. 5. Surface distributions of *Trichodesmium* in the Arabian Sea based on a vegetation index derived from the NOAA-12 AVHRR channels 1 and 2. During the period 20 to 27 May 1995, 'Meteor' was on station at 65°E, 10°N. (A) Processed image and (B) raw image for 23 May, 06:34 h; (C) processed image and (D) raw image, 27 May, 06:48 h

satisfied only about 13.5% of the total N demand associated with the very high rates of primary production in the very surface layer (Table 1). Interestingly, the rate of disappearance of phosphate in the surface waters could support fixation of $1.14 \text{ mmol C m}^{-3} \text{ d}^{-1}$, or about 23% of total surface primary production. These 2 independent estimates of the rate of production of new biomass clearly indicate that N_2 -fixation made a significant contribution to the local N budget, though the

bulk of primary production was supported by recycled nutrients during our period of observation. Total (depth-integrated) N_2 fixation during the bloom could directly support primary production of about $1 \text{ mmol C m}^{-2} \text{ d}^{-1}$. This represents about 6% of depth-integrated production, a value close to that typically given for the contribution of new N to total primary production in highly oligotrophic ocean waters (Eppley & Peterson 1979, cf. Platt et al. 1989). The upward vertical flux of

Table 1. Estimate of the contribution of N_2 fixation to the N demand of planktonic CO_2 fixation in the upper water column at the drift station at $10^\circ N$, $65^\circ E$ during the period 20 to 27 May 1995. N demand based on a C:N elemental ratio of 5.2 for the surface, and 6.6 for 0.5 to 100 m. PON: particulate organic nitrogen

	C productivity ($mmol\ C\ m^{-2}\ d^{-1}$)	N demand ($mmol\ N\ m^{-2}\ d^{-1}$)	N_2 fixation ($mmol\ N\ m^{-2}\ d^{-1}$)	N_2 fix/total N demand (%)	PON from N_2 fixation ^a (%)
Surface	5	0.962	0.13	13.5	60
0.5–100	15	2.264	0.036	1.6	
Sediment trap					20
Total	20	3.019	0.166	5.5	

^aFrom $\delta^{15}N$

NO_3^- through the thermocline is often assumed to satisfy this demand (Dugdale & Goering 1967, Eppley & Peterson 1979, cf. Lewis et al. 1986).

Nitrogen stable isotope measurements provided independent direct evidence of the contribution of *Trichodesmium* to the N budget of the upper water column. N_2 fixation is accompanied by relatively little isotopic fractionation, producing organic matter with an isotopic composition very close to that of atmospheric N_2 and therefore significantly depleted in ^{15}N relative to average marine sources of nitrogen (Delwiche & Steyn 1970, Carpenter et al. 1997). In the Arabian Sea, this effect is accentuated by the isotopic fractionation that accompanies denitrification in the midwater oxygen minimum zone, which discriminates against ^{15}N resulting in an increase in the abundance of the heavy isotope in the residual pool of NO_3^- at depth. Samples of bulk suspended PON collected from the upper 10 m of the water column within the bloom showed a marked depletion in ^{15}N relative to near surface PON samples collected at sites north and south of the bloom (Fig. 1B). Over the course of bloom development, the $\delta^{15}N$ of surface PON fell from 6.7‰ on 22 May to 3.9‰ on 28 May. Although *Trichodesmium* biomass was most concentrated near the surface, our vertical profiles of the $\delta^{15}N$ of PON indicate that N_2 fixation had a measurable effect on the entire upper water column (Fig. 1B). The broad ^{15}N minimum of surface suspended particles and in the mean water column ^{15}N in the region of the *Trichodesmium* bloom demonstrate that N_2 fixation made a significant contribution to the overall N budget of this region.

Sediment trap data provide additional evidence for the vertical flux of recently fixed nitrogen and its importance in the region of the *Trichodesmium* bloom. The $\delta^{15}N$ of sinking particles from sediment trap deployments at $18^\circ N$ and $5^\circ N$ (Fig. 1B) was similar to the mean ^{15}N of bulk PON in the deep waters of the Arabian Sea (ca 10‰; J. Montoya & M. Voss unpubl. data), suggesting that these stations represent typical, non-bloom conditions in this region. In contrast, the ^{15}N of sinking particles collected at our extended drift station

at $10^\circ N$ during the bloom was markedly lower. These $\delta^{15}N$ values were not significantly different from the ^{15}N of PON in the upper water column and were much lower than the mean for deep PON, demonstrating that organic matter derived from N_2 fixation was a major component of the vertical flux of organic matter to the deep sea during the bloom. Additionally, the low $\delta^{15}N$ of sinking material allows us to rule out preferential export of isotopically heavy material by zooplankton (Checkley & Miller 1989) as a mechanism for generating the low $\delta^{15}N$ at the surface within the bloom. Thus, our isotopic data provide unambiguous evidence that N_2 -fixation within the surface bloom made a significant contribution to the local N budget.

A simple mass balance calculation can be used to provide a first-order estimate of the contribution of recently fixed nitrogen to the surface pool of suspended particles as well as to the sinking organic matter collected in the sediment trap. Diazotroph organic matter typically has a $\delta^{15}N$ near or slightly less than 0‰ (Carpenter et al. 1997). Although we did not measure the $\delta^{15}N$ of NO_3^- below the mixed layer, the consistent isotopic signature of suspended particles in deep water ($\delta^{15}N = ca\ 10\text{‰}$) as well as preliminary analyses of NO_3^- samples obtained elsewhere in the Arabian Sea (M. Altabet pers. comm., J. Brandes pers. comm.) suggest that the NO_3^- entering the mixed layer has a $\delta^{15}N$ of approximately 10‰. Given these constraints, our isotopic data suggest that recently fixed nitrogen contributed up to 60% of the nitrogen in suspended particles at the surface during the bloom and as much as 20% of the nitrogen in sinking organic matter collected by our drifting sediment trap (Table 1).

Since more than 80% of surface primary production was associated with *Trichodesmium*, the relatively small fraction (13.5%) of the instantaneous N demand supplied by N_2 fixation at the very surface initially appears to conflict with the larger (60%) estimate of the contribution of N_2 fixation to near surface biomass based on ^{15}N natural abundance measurements (Table 1). This mismatch implies that other sources of inorganic or organic N, e.g. recycled N, were being

used by the bloom to support production. While earlier tracer studies have reported a low capacity for ammonium assimilation by *Trichodesmium* (see Capone et al. 1997), some of our recent results using ^{15}N tracers at near ambient levels indicate that *Trichodesmium* can effectively assimilate ammonium at high rates relative to N_2 fixation when available (M. Mulholland & D. Capone unpubl.). During the course of a bloom, inorganic N and, in particular, ammonium pools can build up to significant concentrations (Fig. 3; Karl et al. 1992). Although no measurements of the isotopic composition of the surface ammonium pool during the bloom are available, with time this ammonium pool should be derived increasingly from the bloom itself (i.e. largely N_2 -derived) and therefore have an isotopic signature similar to that of recently fixed N. Thus, uptake of ammonium represents a mechanism for retaining recently fixed N in the upper part of the water column, thereby contributing to the large fraction of surface biomass derived from N fixation (ca 60%).

Remote sensing

The areal extent of the 2 blooms detected by remote sensing could represent upwards of 20% of the surface of the Arabian Sea. A positive response within a pixel indicates a surface abundance above a threshold, and not necessarily uniform surface coverage. However, as noted above, the response appears to have a relatively high threshold as we observed extensive, but patchy, distributions of slicks in a pixel without a positive response. Thus, our estimate of surface coverage is conservative and this may therefore be one of the largest surface phytoplankton blooms yet recorded.

The inability to detect surface blooms by satellite in the afternoon concurred with our observations at sea level (see above) and is consistent with studies examining the *in situ* behavior of *Trichodesmium* (Villareal & Carpenter 1990). *Trichodesmium* colonies have gas vesicles that render them buoyant, but they undergo a regular daily change in buoyancy and depth distribution. Typically, a large fraction of the population is positively buoyant in the early morning and, if wind stress is low, rises to the sea surface. Accumulation of photosynthate results in a large fraction of the population becoming negatively buoyant throughout the day as this ballasting overcomes the positive buoyancy derived from internal gas vacuoles. This behavior, which has general relevance for the normal depth distribution of the population (Capone et al. 1997), resulted in striking regional-scale effects during blooms as evidenced by the AVHRR imagery, which is only capable of detecting phytoplankton at the very surface of the sea.

Although our shipboard observations provide direct evidence that *Trichodesmium* was the dominant component of the bloom, Brock & McClain (1992) have suggested that high reflectance surface features in the Arabian Sea could also be due to coccolithophorid blooms. There is, however, little evidence of near-surface coccolithophorid blooms visible to shipboard observers or satellite-based sensors surveying this region. For example, Brown & Yoder (1994) mapped the global occurrence of coccolithophorid blooms using data from the Coastal Zone Color Scanner (CZCS) and commented that 'The paucity of blooms in the Arabian Sea and the Indian Ocean is in agreement with findings of several older phytoplankton studies...'. We are aware of only 1 report of a coccolithophorid bloom in the Arabian Sea, but that bloom occurred in the upwelling region near the Oman margin during the southwest monsoon (Kleijne et al. 1989). While surface blooms of *Trichodesmium* can have the same absolute reflectance value as a coccolithophorid bloom, their spectral signatures are extremely different. Coccolithophorid blooms are blue or milky white, with maximal reflectance around 500 nm. In contrast, *Trichodesmium* blooms are brown or straw-colored and have a low reflectance around 500 nm (due to absorption by phycoerythrin) and a high reflectance around 560 nm and in the near infra-red around 750 nm (Subramaniam et al. in press a). Thus, we conclude that our analysis of satellite-derived images provides a direct measure of the spatial extent of the *Trichodesmium* bloom we encountered during our cruise.

A mesoscale sea-surface feature of this temporal and spatial extent likely affects the *in situ* light field and heat and gas exchange across the ocean-atmosphere interface. For example, *Microcystis*, another gas vacuolate cyanobacteria, has been shown to act as a canopy species, reducing the irradiance available to non-buoyant species deeper in the water column (Oliver & Ganf 1988). The absorption of incident light by surface blooms of cyanobacteria can also make a significant contribution to the heat budget of the upper water column. The dominant source of variability in absorption of short-wave (visible) radiation in the open ocean is phytoplankton pigment, and it has been speculated that episodic phytoplankton blooms could contribute to a biogeochemically mediated feedback to the warm water pool in the Pacific (Siegel et al. 1995). Cyanobacterial blooms in the Baltic Sea have been shown to increase sea surface temperature locally by 1.5°C (Kahru et al. 1993). *Trichodesmium*, with its UV absorbing compounds and phycobilipigments, displays higher absorption than eukaryotic phytoplankton in the UV and blue regions of the spectrum (Subramaniam et al. in press a). An increase in the local surface temperature due to the presence of *Trichodesmium*

was noted during the bloom. The average surface temperature until 18 May was 30.5°C. It increased to 31.5°C from the 20 to 26 of May and reached a maximum of about 35°C on 26 May, coinciding with the maximum observed light attenuation and *Trichodesmium* biomass. There was no change in the incident surface irradiance during this period (H. Siegel pers. comm.). As positively buoyant colonies accumulate near the surface during periods of calm conditions and minimal mixing energy, a positive feedback for further warming may occur as the population absorbs heat, thus adding stability to the upper water column. The biologically mediated heating of the surface waters could modify the ocean-atmosphere heat exchange processes and should be taken into account in thermodynamic models of air-sea interaction. For example, Sathyendranath et al. (1991) have speculated that phytoplankton biomass could influence the flux of moisture through the air-sea boundary and have an impact on the formation of tropical storms and the monsoons in the Arabian Sea.

Extrapolations and biogeochemical comparisons

The dramatic changes in the nutrient status of the Arabian Sea over the year, and particularly in the northwestern portions of the basin, are well documented. In contrast, the extent of spatial and seasonal variation in the abundance and activity of *Trichodesmium* and other N_2 fixing cyanobacteria is currently unknown. We lack direct information on the intensity of N_2 fixation during the winter monsoon, and on whether the summer monsoon substantially represses *Trichodesmium* populations in the more southern and central reaches of the basin which are remote from the areas of strong monsoonally induced upwelling. Finally, the frequency of blooms remains to be determined. The next generation of ocean color sensors [e.g. Sea-viewing Wide Field-of-view Sensor (SeaWiFS) and Moderate Resolution Imaging Spectroradiometer (MODIS)] may provide the resources necessary to better determine the spatial extent and temporal frequencies of these phenomena, as well as a means of inferring their biogeochemical impact in the N and C cycles.

Our observations were made during a relatively brief spring intermonsoon period in a single meridional transect consisting of about 22 stations. Because of the limited temporal and spatial extent of our determinations of *Trichodesmium* N_2 fixation rate, we can only make tentative extrapolations of our results to the Arabian Sea basin as a whole. Depth-integrated rates for the stations extending southward from 11° N varied between 14 and 97 $\mu\text{mol N m}^{-2} \text{d}^{-1}$ and averaged about

40 $\mu\text{mol N m}^{-2} \text{d}^{-1}$. If we assume these are typical of rates of N_2 fixation in the northern and western basin during intermonsoon periods, this could account for about 0.24 Tg N yr^{-1} (Table 2). Assuming similar rates through the southern/central areas throughout the whole year, input by N_2 fixation would amount to about 0.71 Tg N (Table 2). Finally, if we assume that the blooms we encountered are not atypical, but occur twice per intermonsoon season over an extent of sea surface comparable to that which we observed, this could account for an additional input of 0.07 Tg N, summing to a total of about 1 Tg N yr^{-1} (Table 2).

External nitrogen inputs to the Arabian Sea are thought to be about 3 Tg N yr^{-1} (Somasunder et al. 1990). Thus, N_2 fixation can account for a considerable fraction of new inputs to the basin.

The Arabian Sea is a major oceanic site of denitrification and is generally considered to be a net sink for combined N (Naqvi et al. 1992). Annual water column denitrification is estimated to be about 30 Tg, far greater than our current estimate of all inputs into the basin. The source of input which sustains this large N sink is not yet clearly delineated, but the bulk of nitrate appears to arrive by deep water advection from the south (Naqvi et al. 1992). Thus, while N_2 fixation may be of direct importance as a source of fixed N to the phytoplankton populations of the upper water column during oligotrophic periods, it (and other inputs) appear to be only relatively minor sources of fixed N in the basin relative to denitrification.

However, our extrapolation of annual N_2 fixation in the upper water column is likely conservative. The spring intermonsoon of 1995 was relatively brief and rate of N_2 fixation may have been relatively low in comparison to levels that are achieved after a more prolonged intermonsoon. Similarly, areas of the basin less affected by the monsoonal influence may have rates more similar to those we have reported for the chronically oligotrophic open tropical Atlantic Ocean (Capone et al. 1997). Furthermore, the surface population densities we encountered may have been at the lower end of those occurring at nearby sites as evidenced by the AVI.

Table 2. Estimate of annual input of N by N_2 fixation in the Arabian Sea

	Area ($\text{km}^2 \times 10^6$)	Areal N_2 fixation ($\mu\text{mol N m}^{-2} \text{d}^{-1}$)	Days	N (Tg)
Blooms	2	129	20	0.07
Background				
N. Arabian Sea	3.5	40	120	0.24
S. Arabian Sea	3.5		360	0.71
Total N fixation				1.01

We conclude that large populations and, at times, dense surface blooms, of *Trichodesmium* spp. do occur in the central areas of the Arabian Sea. The populations can provide an important input of new N during oligotrophic periods and can have a marked effect on the isotopic abundance of the particulate nitrogen pool of the upper water column. In addition, N₂ fixation in the upper water column may be an important episodic source of combined N and organic matter to fuel denitrification in the extensive oxygen minimum zone at depth.

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