Primary Productivity and Nitrogen fixation by *Trichodesmium* spp. in the Arabian Sea

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Abstract

*Trichodesmium* was studied with the purpose of understanding its distribution, organic production and nitrogen fixation in the Arabian Sea. Out of the 143 stations sampled, a total of 93 stations showed the presence of *Trichodesmium* filaments. Two species of *Trichodesmium* namely, *T. thiebautii* and *T. erythraeum* were found. These were distributed on the basis of the physico-chemical conditions of the Arabian Sea. This was the first time that we managed to detect and record the presence of *Trichodesmium thiebautii* bloom in the Arabian Sea at depths as deep as 70-80m. Total counts of *Trichodesmium* varied between 0 to 400737 filamentsL⁻¹. *Trichodesmium thiebautii* developed in offshore waters during the fall intermonsoon, when the water temperature was around 28°C and nitrate content was as low as 0.34µM. After the northeast monsoon, *Trichodesmium erythraeum* developed in the offshore area and then spread to coastal waters. Both species of *Trichodesmium* together produced a total of 0.263 TgCyear⁻¹ and fixed a total of 0.2976 TgNyear⁻¹ in the Arabian Sea. The study revealed that *Trichodesmium* was a major contributor to the organic matter productivity of the Arabian Sea during the period from November to April. The seasonality of the blooms of *Trichodesmium* is discussed with the help of Ocean Color Monitoring (OCM) data and biogeochemical implication of these findings in the Arabian Sea.

**Keywords:** *Trichodesmium*; Primary production; Nitrogen fixation; Monsoon;
1. Introduction

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Trichodesmium is a planktonic filamentous cyanobacterium which is known to dwell in tropical and temperate marine environments (Capone et al., 1997; Mulholland and Capone 2009; Subramaniam and Carpenter, 1994). It forms dense blooms which are studied with the purpose of understanding both its biomass as well as its distribution (Carpenter and Prince, 1977; Capone et al., 1997). Since 1950, these blooms have been reported in the Arabian Sea (Ramamurthy et al., 1972; Devassy et al., 1978; Sawant, et al., 1996; Capone et al., 1998; Lugomela et al., 2002; Desa et al., 2005; Parab et al., 2006; Basu et al., 2011), the Lakshadweep Sea (Qasim, 1970), the Andaman Sea (Jyothibabu et al., 2003) and the Bay of Bengal (Jyothibabu et al., 2003; Hegde et al., 2008). The phytoplankton biomass at times exceeds 100µgL⁻¹ during the blooming period this value is higher than any other biomass value recorded in any other individual species(Parab et al., 2006). The Trichodesmium bloom is unique since it can both synthesize organic matter and fix nitrogen (Capone et al., 1998, 2005; Carpenter et al., 1983). The ecological significance of this organism in the Arabian Sea is not very well known, although it does in fact hold the key to the productivity of the Arabian Sea during oligotrophic conditions.

The Arabian Sea has certain unique features as far as wind direction, solar insolation, currents, water temperature and upwelling during the NE (Northeast; December to February) and SW (Southwest; June to September) monsoons are
concerned. Upwelling during the summer monsoon results in high concentrations of NO$_3^-$ in surface waters, particularly in the north-western reaches of the basin. However during the oligotrophic inter-monsoon period, surface waters are depleted of combined N (nitrogen) thus restricting production of phytoplankton (Bhattathiri et al., 1996).

Bio-geochemical estimates and empirical measurements show that N$_2$-fixation by \textit{Trichodesmium} is a major source of new nitrogen which is of immense importance in supporting the primary production of the oligotrophic environment (Capone, et al., 1997). \textit{Trichodesmium} spp. is considered to be an important source of new nitrogen in the oligotrophic ocean; however more studies on \textit{Trichodesmium} spp. are necessary as there are large loopholes in the understanding of its seasonality in the Arabian Sea. Although this cyanobacterium is common in tropical and sub-tropical seas, its distribution is known to be irregular, however at the same time spatially extensive dense blooms of \textit{Trichodesmium} form when the conditions are appropriate (Eleuterius, et al., 1981; Capone, et al., 1998). Published reports (Capone, et al., 2005) on measurement of N$_2$-fixation in various parts of the oceanic environment suggest that \textit{Trichodesmium} is an important source of new nitrogen to the phytoplankton in the ocean. Nitrogen fixation studies have already been conducted and the results are available from the Atlantic (Goering, et al., 1966) as well as the Pacific (Letelier, et al., 1996; Karl, et al., 1997). Studies have also been conducted in the Caribbean Sea (Carpenter and Price, 1977), the China Sea (Saino, et al., 1977; Chen, et al., 2003) and the Sargasso Sea (Orcutt, et al., 2001). It is seen that the presence of new nitrogen significantly amplifies primary production and thus exports carbon into the deeper parts of the ocean. The reports on N$_2$-fixation rates by \textit{Trichodesmium} in the Arabian Sea are few despite the fact that,
Trichodesmium frequently occurs in this region (Capone et al., 1998). Also, these reports have not accounted for the seasonality seen in the Trichodesmium blooms in the Arabian Sea nor have they accounted for its diversity. Traditionally it’s taken for granted that, in oligotrophic conditions, the level of net biological productivity is sustained by the availability of new nitrogen. This flux of new nitrogen into the euphotic zone which supports primary production is balanced by the concomitant losses suffered due to sinking particles, vertical migration and the mixing of organic nitrogen from the surface waters (Dugdale and Goering, 1967; Eppley and Peterson, 1979; Lewis, et al., 1986; Platt, et al., 1992).

Historical data from the Arabian Sea reveal that the cause of the low oxygen zone in the Arabian Sea is partly due to upwelled water and due to respiration of organic matter formed during high biological productivity. Joint Global Ocean Flux Study (JGOFS) indicated high primary productivity in the Western and Central Arabian Sea (Barber et al., 2001) specially during SW monsoon and NE monsoon. However Eastern Arabian Sea values are patchy (0.18-7.29 gCm\(^{-2}\)d\(^{-1}\)), these have been attributed to varying nutrient (specially nitrate) and hydrographic conditions (Naqvi et al., 2006). It must also be noted that the eastern Arabian Sea was not studied during the US JGOFS cruises (Smith 2001, 2005). During the Indian JGOFS study primary productivity of eastern Arabian Sea fluctuated seasonally. During the intermossoon, the area became oligotrophic while during the winter monsoon it was found to be more productive (Bhattathiri et al., 1996). This area is an important site for the blooms of the Trichodesmium (Devassy 1978). The Trichodesmium is important as primary producers and nitrogen fixer where upto 50% of the nitrogen fixed by Trichodesmium can be released as nitrogen source to
phytoplankton during bloom seasons (Mulholland et al., 2006). This has prompted us to plan study of *Trichodesmium* in the NE Arabian Sea in order to assess seasonality and role of the organism in the Arabian Sea ecosystem with reference to SW monsoon, intermonsoon and NW monsoon seasons.

2. Materials and Methods

2.1. Study area and sampling

The data presented here was collected on board two research vessels the ORV Sagar Kanya (SK) and FORV Sagar Sampada (FORV). This collection of data was done in the months spanning from November to April during cruises SK-152 (30th March to 13th April 2000), SK-171 (3rd to 17th November 2001); SK 186 (3rd to 19th January 2003); SK214 (4th to 17th December 2004); FORV 212 (27th February to 7th March 2003) and FORV 222 (22nd February to 10th March 2004). While planning the cruises, special emphasis was given to study the distribution of *Trichodesmium* in the Arabian Sea covering 12-22°N and 65-74°E (Fig. 1) and seasons (November –fall inter-monsoon (fall IntM); December to February –NE monsoon (NE MoN) and March to April – spring inter-monsoon (spring IntM) so as to include samples from coastal and offshore as well as regions where physical processes such as upwelling and winter cooling, were known to occur. Different cruises during same seasons have been referred as the early NE monsoon - December, mid NE monsoon -January, late NE monsoon-February; early spring intermonsoon-March and late spring intermonsoon-April. Water samples were collected from the euphotic zone with 5L Niskin sampling bottles mounted onto a Sea Bird
Electronics® conductivity-temperature-density profiler (CTD) rosette. The depth of the euphotic zone was measured using a Secchi Disc.

Insert Fig. 1 here

2.2 Physicochemical measurements

The QUICKSCAT images were downloaded from the SSM/I website at http://www.remss.com/qscat/qscat_browse.html. Temperature and salinity data was taken from CTD. Nutrients were analyzed in an Auto-analyzer using standardized techniques for nutrient analysis in seawater (UNESCO, 1994).

2.3 Chlorophyll a concentration

To obtain the chlorophyll a (chl a) estimates seawater samples (1 litre) were filtered through GF/F filters and analyzed by HPLC (Wright et al., 1991; Bidigare and Charles, 2002). Prior to the HPLC analysis, the filters were immersed in 90 % acetone, extracted under cold and dark conditions overnight, sonicated and finally filtered through 0.2 µm, 13 mm PTFE filters to free the sample from any particulate debris. Aliquots of 1 ml of the pigment extract were then mixed with 0.3 ml of distilled water in a 2 ml amber vial and allowed to equilibrate for 5 minutes prior to its injection into an HPLC (Agilent® 1100 series) equipped with a diode array detector. Pigments were separated in a C-18 reverse-phase column using the eluent gradient program of Wright, et al. (1991) as adapted by Bidigare and Charles (2002) as detailed in Parab, et al. (2006).
2.4. *Trichodesmium* spp. abundance

For the identification and enumeration of the phytoplankton, 500ml of seawater was fixed with 1 % Lugol's iodine and preserved in 3 % buffered formaldehyde solution and then stored under cool and dark conditions until the time of analysis. Prior to microscopic analysis, the samples were concentrated to about 5-10 ml by carefully siphoning the top layer with a tube covered by a 10 µm Nitex filter on one end. Replicates of 1ml sample concentrates were transferred to a Sedgwick-Rafter slide and counted using an Olympus Inverted microscope (Model IX 50) at 200X magnification. The smallest cells enumerated were of ~5µm in diameter. Identifications were based on standard taxonomic keys (Tomas et al., 1997). The results were expressed as the number of cells with the exception of *Trichodesmium* which was expressed as the number of trichomes/filaments.

2.5. Primary productivity

For primary productivity analysis, water samples were collected depending upon the euphotic zone that was established using a Secchi Disc. For total phytoplankton measurement, the volume of water samples was transferred in triplicates to 250 ml capacity Nalgene Polycarbonate bottles. One ampoule of $^{14}\text{C}$ (5µci) was injected to each three light and one dark bottles. These bottles were then incubated for 12 hrs on deck using appropriate light cutoff screens. At the end of the incubation period the water sample (250 ml) was filtered through GF/F filter. All the filters exposed to fuming HCL for 20 minutes in a desiccator inorder to dissolve left over bicarbonates. Samples were then placed in a 7 ml mini scintillation vial with scintillation cocktail and activity was
determined with a Wallac Scintillation counter (model no. 1409). All counts were quench corrected (UNESCO, 1994).

To measure *Trichodesmium* productivity, trichomes were first collected in a 202 μm mesh 1 m diameter net towed. Trichomes/filaments were picked up and rinsed in filtered seawater. The known numbers of trichomes were then placed in a Nalgene Polycarbonate bottles containing 250 ml of filtered seawater from same station and $^{14}$C (5µci) was added. Further, the same procedure was followed as described for phytoplankton productivity. The phytoplankton and *Trichodesmium*, daily carbon fixation was measured using standard (UNESCO, 1994).

2.6. Nitrogen fixation

*Trichodesmium* spp. filaments counted by inverted microscope were further used to calculate the rate of nitrogen fixed per filament using factor developed by Capone et al., 1998 for the Arabian Sea and further validated by C/N content of filaments (for fixed period) using CHN analyzer. Nitrogen fixed was calculated per 10 hrs and then per year.

2.7. Satellite studies

The Chl $a$ images were generated using OC-2 algorithm; ERDAS Imagine 2.5 software was used for image processing.

3. Results

3.1 Fall Intermonsoon

3.1.1. Wind, temperature, salinity and nutrients

During the fall inter-monsoon the wind was blowing from the northeast towards the offshore region of the Arabian Sea and wind speed was found to be 5-6 ms$^{-1}$ (Fig. 2a). These calm conditions supported the dense bloom of the *Trichodesmium thiebautii* at 17°
N 70°E and 17°N 69°E. In this area the water temperature was found to be 28°C while mixed layer depth was 5m (coastal) to 70 m (offshore) region (Fig. 3a).

The area of *Trichodesmium thiebautii* was marked by occurrence of nitrate and nitrite at non detectable level (Figs. 4a, 4b & 5a). The phosphate and silicate level at these areas was also low, registering at ~ 0.2 µM and ~ 0.5 µM respectively. Other areas (15°N 73°E and 18°N 69°E) showed high level of nutrients with high percentage of diatoms and absence of *Trichodesmium*.

3.1.2. Chlorophyll *a* and *Trichodesmium* distribution

Chl *a* content was high (0.1733 to 5.344 mgm⁻³; Fig. 6a) at most of the locations during the fall IntM. The surface Chl *a* maxima observed (Fig. 7a) at areas like 18°N 70°E (0.75 mgm⁻³) and 20°N 71°E (5.344 mgm⁻³) was on account of the blooms of *Trichodesmium thiebautii* in the offshore region. Similarly at 17°N 69°E and 18°N 70°E up to a depth of 30 m, *Trichodesmium* bloom was noticed. Out of the 23 stations sampled 10 stations showed the presence of *Trichodesmium thiebautii*. The highest
phytoplankton counts were observed at 18°N 70°E (15.831 cell nos. x 10^4 L^-1) where 
Trichodesmium constituted a major portion. The average total cells counts of 
phytoplankton was 1.590±3.546 x 10^4 L^-1 at the surface and 43.226±95.189 x 10^6 m^-2 in the 
euphotic zone (Fig. 6b). The number of filaments across transect varied from 0 to 
10.9570 filaments x 10^4 L^-1. The average filament distribution was 6.9993±3.025 x 10^4 L^-1 
at the surface and 9.686±30.720 x 10^6 m^-2 in the euphotic zone (Fig. 6c). At some areas 
like, 16°N 71°E, 19°N 69°E and 20°N 70°E N the diatom count reached right up to 100 %. 
However, the Trichodesmium stations were invariably marked by low percentages of 
diatoms and dinoflagellates.

Insert Fig. 6 here

Insert Fig. 7 here

3.1.3. Primary Production and Nitrogen Fixation

Primary productivity measured during the fall IntM is presented in Fig. 8a. The 
surface maxima of high primary productivity at 20°N 70°E and 21°N 68°E was due to the 
Trichodesmium population. Although, at 21°.1N the concentration of Chl a was high at 
40 m due to the presence of the Trichodesmium bloom productivity was found to be 
negligible due to low light at the bottom of the euphotic zone. At other stations, it was 
observed that the sub-surface Chl a maxima due to other phytoplankton rarely coincided 
with primary productivity maxima. The carbon fixed by Trichodesmium varied from 0.43 
to 20.487 mgCm^-3 d^-1. The rate of carbon production was high at 18°03.9N where 
temperature was 29°C. The average carbon produced during this season was 8.460±
6.504 mgCm\(^{-3}\)d\(^{-1}\). During our study 12.8 % of the carbon was produced by *Trichodesmium* and the remaining 87.2 % was produced by other phytoplankton as primary producers. The highest value of primary productivity (20.487 mgCm\(^{-3}\)d\(^{-1}\)) was recorded at the surface of 18\(^{0}\)N 70\(^{0}\)E, where active growth of *Trichodesmium thiebautii* taking place.

The N\(_2\) fixed during this study was 114.110 ± 345.770 µmol Nm\(^{-3}\)d\(^{-1}\) and varied from 0 to 1252.390 µmolNm\(^{-3}\)d\(^{-1}\) (Fig. 8b). Higher amounts of nitrogen was fixed at 18\(^{0}\)N 70\(^{0}\)E due to the *Trichodesmium* bloom.

*Insert Fig. 8 here*

### 3.2 NE Monsoon

#### 3.2.1. Wind, temperature and salinity

During the NE Monsoon the wind was blowing from the northswestt and moving along the eastern coast of India (Fig. 2b). The wind speed during this period was found to be <5ms\(^{-1}\). During this season offshore water were showing the effects of winter cooling and it was found that the growth of the *Trichodesmium thiebautii* continued at this time. The temperature data collected, during NE MoN from the NE Arabian Sea concerning temperature is presented in Fig. 3b. The observations and analysis of data made in the present study indicate that the offshore water was largely influenced by the winter cooling lowering the temperatures (Fig. 3b). During this season, *Trichodesmium thiebautii* began to appear in the shelf region where the impact of winter cooling had diminished. By the end of the NE MoN it was found that *Trichodesmium erythraeum* had assumed the role of the dominating species of the shelf region.
Nutrients concentrations recorded during this season was low (Figs. 4 & 5). However, *Trichodesmium erythraeum* was recorded alongside of *Trichodesmium thiebautii* specially in the shelf region. The prevailing calm weather during this period was particularly responsible for the growth of *Trichodesmium* at the sub-surface. The phosphate varied from 0 to 0.35 µM which was low most of the time. The nitrate values ranged from 0 to 0.75 µM and the silicate content recorded was 11.08 µM which was high at the bottom of the euphotic zone, as compared to the surface which was 2.30 µM (Figs. 4d and 5).

### 3.2.2. Chlorophyll a and *Trichodesmium* distribution

Phytoplankton biomass in terms of the Chl *a* and total cell counts was reasonably high during this season (Fig. 6a). Average Chl *a* was 0.526±0.453 mgm⁻³ at surface and 32.588 ±46.851 mgm⁻² in euphotic zone (Fig. 6a). Highest Chl *a* was recorded at 21⁰N 69⁰E and lowest at 12⁰N 72⁰E. Similarly average cell density at the surface was 0.112±0.129 nos.x10⁴L⁻¹ (Fig. 6b). The highest cell counts (0.606 nos.x10⁴L⁻¹) were recorded at 12⁰N 74⁰E and lowest (0.002 nos.x10⁴L⁻¹) at 21⁰N 68⁰E. Filament counts of *Trichodesmium* spp. varied from 0 to 0.616 filaments nos.x10⁴L⁻¹ and average 0.039±0.119 filaments nos.x10⁴L⁻¹ at the surface and 0.214±0.272 x10⁶m⁻² at the euphotic zone (Fig. 6c).

A district seasonality was recorded during SK-214, SK-186, FORV-212 and FORV-222 undertaken. During the early NE MoN (SK-214), the concentration of Chl *a* was from 0.187 – 0.507 mgm⁻³. High concentration of Chl *a* was recorded at 17⁰N 69⁰E while low concentration of Chl *a* was found at 15⁰N 71⁰E. The sub-surface Chl *a* maxima was found at a depth of 40 m depth at 17⁰N 69⁰E, 18⁰N 67⁰E, 20⁰N 66⁰E, 21⁰N
Out of the 14 stations sampled, 10 samples showed the presence of *Trichodesmium* in the sub-surface waters while others showed its presence at deeper depths (~ 60 m). The total phytoplankton cell counts varied from 0.032 to 0.4352 cell nos x 10^4 L^-1 at the surface. At two locations (15°N 73°E and 18°N 70°E) *Trichodesmium erythraeum* and *Trichodesmium thiebautii* were found at the depth of 5 and 60 m respectively. The highest counts of *Trichodesmium* filaments were found at 22°N 67°E (0.0216 filaments x 10^4 L^-1) and lowest at 20°N 66°E (0.0022 filaments x 10^4 L^-1). During this season diatoms were also recorded in large numbers at 15°N 73°E, 15°N 71°E and 18°N 67°E. The *Trichodesmium* percentages in total phytoplankton counts ranged from 0.78 to 35.71 %. The other dominant phytoplankton throughout this season were *Rhizosolenia setigera*, *Nitzschia longissima*, *Thalassiothrix longissima*, *Pyrophaccus horologium* and *Protoperidinium sternii* (Table 1).

The Chl *a* during the mid NE MoN (SK-186) was much higher at most of stations, compared to early NE MoN. It ranged from 0.173 to 2.6 mg m^-3. Higher concentrations of chl *a* were found at 21°N 69°E where diatoms were dominant (93.94 %) followed by dinoflagellates (4.55 %) and other algae like (1.52 %). Sub-surface Chl *a* maxima was observed (Fig. 7b) at some locations 17°N 72°E, 17°N 70°E, 17°N 67°E, 19°N 66°E, 20°N 66°E, 20°N 66°E, and 17°N 68°E during this season. The total phytoplankton cell counts ranged from 0.002 to 0.459 cell nos x 10^4 L^-1. Higher counts were found at 17°N 70°E where, diatoms made up 94.44 % and dinoflagellates formed 5.56% of the total phytoplankton population. The presence of *Trichodesmium* (25 to 28.57 %) was found in the 5 out of the 25 stations sampled at the surface. *Trichodesmium erythraeum* was found to be more dominant than *Trichodesmium thiebautii*. The *Trichodesmium* filaments was
more (760 filaments L\(^{-1}\)) at 18\(^{0}\)N 69\(^{0}\)E. The other species that were observed during this period were *Thalassiothrix longissima*, *Chaetoceros dichaeta*, *Thalassiosira subtilis*, *Coscinodiscus nitidus*, *Navicula* spp., *Nitzschia seriata*, *Nitzschia closterium*, *Rhizosolenia setigera* and *Chaetoceros lorenzianus* (Table 1).

**Insert Table 1 here**

During late the NE MoN (part of FORV-212 and FORV-222) it was found that values for Chl *a* varied from 0.132 – 0.960 mgm\(^{-3}\) with high values at 17\(^{0}\)N 69\(^{0}\)E due to the presence of the *Trichodesmium erythraeum* bloom. The sub-surface Chl *a* maxima was found at a depth of ~ 40-60 m specially at 16\(^{0}\)N 72\(^{0}\)E, 10\(^{0}\)N 74\(^{0}\)E, 12\(^{0}\)N 72\(^{0}\)E and 14\(^{0}\)N 73\(^{0}\)E. The presence of *Trichodesmium* was observed in 7 out of the 10 stations sampled in this month. The total phytoplankton counts ranged from 0.0078 to 0.2508 cell nosx10\(^{4}\)L\(^{-1}\). Higher phytoplankton cell counts were found at 17\(^{0}\)N 69\(^{0}\)E due to the presence of the *Trichodesmium erythraeum* bloom. The *Trichodesmium* filaments ranged from 0 to 0.6160 filaments x 10\(^{4}\)L\(^{-1}\). Further a *Noctiluca* bloom was also recorded with the *Trichodesmium* bloom at 10\(^{0}\)N 64\(^{0}\)E and 17\(^{0}\)N 69\(^{0}\)E. It appears that the *Noctiluca* bloom may have followed the *Trichodesmium* bloom in the Arabian Sea, an idea which provides us with new insights in the study of phytoplankton in the Arabian Sea. A full growth of *Noctiluca miliaris* bloom was stuck at 17\(^{0}\)N 70\(^{0}\)E.
3.2.3. Primary Productivity and Nitrogen Fixation

The primary productivity during this period was high and ranged from 0.907-2572.1 mgCm⁻³d⁻¹ (av.: 217 mgCm⁻³d⁻¹) at surface and 4.284 mgCm⁻²d⁻¹ in the euphotic zone (Fig. 8a).

The primary productivity maxima at 18⁰N 70⁰E (40 m) coincided with the *Trichodesmium* bloom in the water column. Similarly, at 19⁰N 70⁰E, high productivity at both, the surface and below 40 m was also due to *Trichodesmium*. The average rate of primary production during the bloom of *Trichodesmium* spp. was 0.356 ± 0.096 mgCm⁻³d⁻¹. At the surface, the carbon production varied from 55.85 to 706.66 mgCm⁻³d⁻¹. Higher rate of primary production was observed at 22⁰N 67⁰E, due to the dense bloom of the *Trichodesmium*. The primary production by *Trichodesmium thiebautii* and *Trichodesmium erythraeum* during the NE monsoon was of the same order i.e. 0.392 and 0.378 mgCm⁻³d⁻¹ respectively. When *T. erythraeum* bloom was prominent in the water column however it was found that primary production was high (10.059 mgCm⁻²d⁻¹) compared to the primary production by *T. thiebautii* (6.156 mgCm⁻²d⁻¹). The percentage of primary productivity due to *Trichodesmium* spp. in the total productivity was around 0.11%.

During mid NE MoN (SK-186), primary productivity was low at the surface and high at deeper depths. At 15⁰N 72⁰E, the highest primary productivity and Chl *a* was observed at a depth of 50 m due to the *Trichodesmium* bloom. Similarly carbon production was observed at 18⁰N 69⁰E at 60 m due to the bloom of the *Trichodesmium*
thiebautii. It was observed that *Trichodesmium* played a role of primary producer at the
surface like at 22°N 68°E as well as throughout the water column.

The amount of primary production due to *Trichodesmium* during late NE MoN varied from 1.61 to 8.25 mgCm⁻³d⁻¹. The average amount of carbon produced was 7 mgCm⁻³d⁻¹. The observations made during this season indicate that *Trichodesmium* contributed a major portion (60%) to the carbon produced at this time. Higher amount of carbon production (65.85%) by *Trichodesmium* was seen at area 14°N 73°E while lower production was recorded at 13°N 70°E (0.14%).

The N₂ fixation during this season ranged from 0 - 13.598 µmolNm⁻³d⁻¹ at the surface and 0 - 31.597 µmolNm⁻²d⁻¹ at the euphotic zone and depended upon the intensity of the bloom. The average N₂ fixed during this season was 4.432±13.598 µmolNm⁻³d⁻¹ (Fig. 8b). The rate of N₂ fixation also varied species wise. The amount of nitrogen fixed by *T. erythraeum* varied from 0 to 2.4 µmol Nm⁻³d⁻¹. In the column, the nitrogen fixed by *T. erythraeum* was found to be much higher (23 ± 4.77 µmol Nm⁻²d⁻¹) than that fixed by *T. thiebautii* (14.09 ± 4.074 µmol Nm⁻²d⁻¹). During the late NE MoN the total nitrogen fixed by *Trichodesmium* spp. varied from 0 to 70.409 µmolNm⁻³d⁻¹ with an average of 14.002 ± 23.772 µmolNm⁻³d⁻¹ (n=8). Higher amount of nitrogen was fixed at 12°N 74°E and lower amount of it was fixed at 16°N 72°E. The amount of N₂ fixed by *T. erythraeum* varied from 1.25 to 37.25 µmolNm⁻³d⁻¹ which was much higher than that fixed by *T. thiebautii* (0 to 32.67 µmolNm⁻³d⁻¹) during late the NE MoN period.
3.3. Spring Intermonsoon

3.3.1. Wind, Temperature and Salinity

During this season the wind was blowing from the northeast and moving along the east coast of India (Fig. 2c), the wind speed during this period was found to be <5 ms\(^{-1}\). This period is the transitional period during which *Trichodesmium* spp. and *Noctiluca miliaris* co-existed. These blooms were related to the deepening of the thermocline in this area (Fig. 3c). During this season, the nitrogenous nutrients were low at the surface which varied from 0.0 to 0.39 µM (Figs. 4a & 5c). During this time, high (1.66 – 3.38 µM) silicate content was noticed (Fig. 5c), which suggests an inadequate uptake and coincides with the low density of diatom.

3.3.2. Chlorophyll a and *Trichodesmium* distribution

During the spring IntM the Chl \(a\) highly ranged from 0.074 -5.905 mgm\(^{-3}\). The average Chl \(a\) was 0.759±1.025 mgm\(^{-3}\) at the surface and 14.749±13.828 mgm\(^{-2}\) in the euphotic zone (Fig. 6a). At the surface high Chl \(a\) was found at 20\(^0\)N 70\(^0\)E and low at 15\(^0\)28.76N. The total phytoplankton cell counts ranged from 0.025-41.992 cell nos. x 10\(^4\)L\(^{-1}\). The average cell counts were 2.033±7.302 cell nos. x 10\(^4\)L\(^{-1}\) at the surface and 16.929±26.176 cell nos. x 10\(^6\)m\(^{-2}\) (Fig. 6b) Similarly *Trichodesmium* filaments were also high at the same position as the total cell counts. The filaments varied from 0-40.074 nos. x 10\(^4\)L\(^{-1}\) at the surface and 0.021-100.301 nos. x 10\(^6\)m\(^{-2}\). The average *Trichodesmium* filaments were 2.381±8.313 at surface and 6.115±20.737 at the column (Fig. 6c).

In the early spring IntM the concentration of Chl \(a\) varied from 0.169 – 2.741 mgm\(^{-3}\). The high Chl \(a\) was found at 19\(^0\)N 66\(^0\)E (2.741 mgm\(^{-3}\)) was mainly due to the bloom of *Noctiluca miliaris*. The phytoplankton counts ranged from 0.0252 to 1.1164 cell
The high cell count found at 19°N 66°E was also due to the *Noctiluca miliaris* bloom. During this month a total of 13 stations were studied out of which only 4 stations showed the presence of *Trichodesmium*. The observations indicate that part of the NE Arabian Sea, where the winter cooling affect (low temperature and high nutrients), supports *Noctiluca* and the other part of the Sea, where the nutrient concentration was low and high temperatures prevail, is for *Trichodesmium* area (Table 1).

During late spring IntM concentration of Chl *a* varied from 0.074 to 5.905 µgL⁻¹ with the highest values recorded at 20°N 70°E and the lowest values recorded at 15°N 70°E. Phytoplankton cell counts ranged from 0.033 to 41.991 cell nos. x 10⁴L⁻¹. The phytoplankton cell density showed peak values in coastal waters (21°N 69°E, 20°N 70°E and 15°N 73°E) mostly north of 20°N (Fig. 7c). *Trichodesmium* was the major component of the phytoplankton averaging 3.8063±10.3463 filaments x 10⁴L⁻¹ (n=29) with high concentrations (40.0737 filaments x 10⁴L⁻¹) at 20°N 70°E in the coastal waters off Gujarat (Fig. 6c). In general, diatoms and dinoflagellates were less numerous, averaging 0.2936 and 0.0630 cells L⁻¹ respectively. However at some locations, like 20°N 70°E to 20°N 72°E the domination of diatoms was noticed. The dominant diatom, *Nitzschia* sp. (2.3025 cells x 10⁴L⁻¹) was found at 20°N 70°E. Dinoflagellates reached a maximum of 1.1666 cells x 10⁴L⁻¹ at 20°N 70°E, which was adjacent to the diatom dominated stations indicating succession of groups. The area between 16-18°N in coastal waters was characterized by domination of dinoflagellates. For example, at areas like 16°N 73°E, 18°N 72°E and 17°N 72°E dinoflagellates like *Ceratium* spp., *Peridinium* spp., and *Prorocentrum* spp. were dominant organisms. At the edge of the shelf, a mixed
community of diatoms, dinoflagellates and *Trichodesmium* dominated the flora specially at 21°N 69°E, 20°N 70°E, 15°N 73°E which was in coastal as well as offshore waters (Fig. 6c). The other areas like 21°N 69°E, 18°N 72°E and 17°N 72°E also supported high counts of *Trichodesmium erythraeum*. The *Trichodesmium erythraeum* was well distributed during this time of year and mostly in succession to the dinoflagellates (south of 18°S) and the diatoms (north of 18°N). Diatoms were the second most important group of organisms that were encountered during the present study, they were also the most diverse in nature.

### 3.3.3. Primary Production and Nitrogen Fixation

During the spring IntM primary productivity estimated was 1.056-3489.104 mgCm⁻³d⁻¹ which coincided with the *Trichodesmium* bloom area. The average primary productivity was 255.095±668.570 mgCm⁻³d⁻¹ (n=32) at the surface and 2046.857±3810.722 mgCm⁻²d⁻¹ (n=35) at the euphotic zone (Fig. 8a).

In the early spring IntM, at location 22°N 66°E the *Trichodesmium* was found aggregated at the surface. The primary production due to *Trichodesmium* during this season varied from 0.69 to 0.88 mgCm⁻³d⁻¹. The average was found to be 0.79 ± 0.09 mgCm⁻³d⁻¹ (n=3). About 29 %, out of the total carbon production recorded, was produced by *Trichodesmium*.

In the late spring IntM at 21°N 69°E and 15°N 73°E, the high values of Chl *a* and primary productivity were on account of the *Trichodesmium* bloom throughout the water column. *Trichodesmium erythraeum* was the only species found during this season. The average carbon production at surface was 131.150 ± 80.67 mgCm⁻³d⁻¹ (n=29). Higher
rates of primary production in the water column were recorded at locations 17°N 72°E, 21°N 69°E, 16°N 71°E and 15°N 73°E. During this season *Trichodesmium* contributed nearly 30% to the total primary production.

Nitrogen fixation rate during the spring IntM was reasonably high (271.814±950.263 µmolNm\(^{-3}\)d\(^{-1}\)) at the surface and 720.348±2405.996 µmolNm\(^{-3}\)d\(^{-1}\) in the column (Fig. 8b). The average amount of nitrogen fixed was 1.2±1.1 µmolNm\(^{-3}\)d\(^{-1}\) (n=3). The average nitrogen fixed by *T. thiebautii* was higher (1.75±0.25) than that fixed by *T. erythraeum*. At 20°N 68°E and 22°N 66°E, higher amount of nitrogen was fixed by *T. thiebautii* whereas, at 22°N 66°E the major contributor to N\(_2\)-fixation was *T. erythraeum*.

During late spring IntM the average N\(_2\)-fixed by *T. erythraeum* was 299.81 ± 995.54 µmolNm\(^{-3}\)d\(^{-1}\) (n=29). At the surface it varied from 0 to 4580.42 µmolNm\(^{-3}\)d\(^{-1}\). The rate of nitrogen fixation was high at 20°N 70°E and at column level N\(_2\)-fixated was in the range of about 9.49 to 11471.50 µmol Nm\(^{-3}\)d\(^{-1}\).

### 4. Discussion

The Arabian Sea experiences hydrographic changes, which are related to the monsoon system (Shetye, et al., 1990, Brock and McClain, 1992, Banse and English, 1993, 2000, Madhupratap, et al., 1996). The region of study undertaken fall under the influence of both the NE and the SW monsoon. During the onset of the SW monsoon season, i.e. June, the west coast of India experiences intense upwelling, which is first visible off the southern tip of India. During this period, continental slope waters begin to shoal upward into the shelf region causing substantial cooling, which is observed in the
satellite sea surface temperature imagery (Sreejith and Shenoi, 2002; Vinayachandran et al., 2004). As the season advances the upwelling signatures migrate northward, covering the entire coast of India by late July (Shetye, et al., 1990). This process is responsible for bringing in the much needed new nutrients (DeSouza, et al., 1996) that help to trigger large phytoplankton blooms by early August (Goes, et al., 1992) and continue upto October.

The NE monsoon, marks a period wherein the offshore region receives a substantial amount of new nutrients (Kumar et al., 2009). Satellite derived measurements of Chl $a$ concentrations in the region of the NE Arabian Sea start to increase by December and tend to reach peak values by February (Banse and English, 2000). The data collected during early NE MoN showed that, the nitrate concentrations were undetectable at $18^0.05.98$, $18^0.10.47N$ and $21^0.17.81N$ where as low (<0.97 µM) at most of the NE Arabian Sea, presumably because a significant fraction of nutrients had already been used by phytoplankton (Parab, et al., 2006), whereas other nutrients such as phosphate and silicate were present. Considering the nutrients enrichment during NE MoN the phytoplankton growth in the water column appears to be reduced by an active grazing by zooplankton (Landry, et al., 1998; Caron and Dennet, 1999) a notion that is reinforced by the elevated level of ammonium concentration found in the water column during early NE MoN estimated at the order of 0.57-6.13 µM of ammonia.

In our study, we found that during low wind speeds ($< 5$ ms$^{-1}$), thick blooms of *Trichodesmium* spp. were observed (Fig. 2). However wind speed $> 6$ knot resulted in disapperance of the *Trichodesmium* bloom. Earlier studies (Chang et al., 2000) have reported that besides wind and water temperature, low nutrients were also factors that
favoured growth of the *Trichodesmium*. In the Arabian Sea, during the non monsoonal period, the upper layers of the water were devoid of nutrients. In such a situation, *Trichodesmium* had an advantage over other phytoplankton, as it could fix nitrogen and it could make use of phosphate from subsurface layers. The stratification of the water column during low wind conditions (as seen during mid and late NE MoN and early spring IntM) was also an important factor for the *Trichodesmium* blooms to develop and persist in the Arabian Sea. Associations between abundance of *Trichodesmium* and vertical stratification have been reported in the North Pacific sub-tropical gyre (Capone, 1983). The average mixed layer depth during our study was 10-40m, during *Trichodesmium* bloom.

The bloom of *Trichodesmium thiebautii* observed during the fall intermonsoon continued during the early NE MoN where out of the 15 stations sampled 13 showed the presence of a *Trichodesmium thiebautii* bloom. The filaments were distributed throughout the water column in the euphotic zone. Deep Chl *a* maxima was noticed at a *Trichodesmium thiebautii* concentrations were also observed during mid NE MoN. Out of the 18 stations sampled, 7 stations showed the presence of a mixed population of *Trichodesmium erythraeum* and *Trichodesmium thiebautii*. Surface Chl *a* maxima was observed at 15°14.21N and was largely attributed to *Trichodesmium thiebautii* and *Trichodesmium erythraeum*.

During late NE MoN and early spring IntM, mixed populations of *Trichodesmium erythraeum* and *Trichodesmium thiebautii* were noticed at 20°29.1N, 19°3.7N and 15°8.57N. However, in the late spring IntM, 29 stations out of the 35 stations sampled supported *Trichodesmium erythraeum* blooms. The rates of primary production during
the *Trichodesmium* bloom were considerably higher than those recorded during non-bloom time in the North Atlantic Ocean, which usually ranged from 804 to 1080 mgCm\(^{-2}\)d\(^{-1}\) (Carpenter, et al., 2004). Several observations have been made in the eastern equatorial Atlantic during *Trichodesmium* bloom where Bauerfeind (1987) noted a mean rate of production was 247 mgCm\(^{-2}\)d\(^{-1}\) between January and May, 1979 over ten sections between 2\(^{\circ}\)S and 3\(^{\circ}\)N at the 22\(^{\circ}\)W meridian. In March and April of 1989, at 18\(^{\circ}\)N and 30\(^{\circ}\)W (NW of Cape Verde Islands) primary production over an 11 days period averaged about 500 mgCm\(^{-2}\)d\(^{-1}\) (Jochme, et al., 1993). Claustre and Marty (1995) measured primary production at 20\(^{\circ}\)N, 31\(^{\circ}\)W in autumn 1991 and spring 1992 and where rates averaged 352 ± 68 and 267 ± 53 mgCm\(^{-2}\)d\(^{-1}\) respectively. At the oligotrophic EUMELI JGOFS at 22\(^{\circ}\)N and 32\(^{\circ}\)W, rate of the primary production were ranged from 289 to 276 mgCm\(^{-2}\)d\(^{-1}\) (Morel, et al., 1996). Steven (1971) reported an annual average of 288 mgCm\(^{-2}\)d\(^{-1}\) for a station off the NW coast of Barbados. Beers, et al. (1968) found an annual mean of 110 mgCm\(^{-2}\)d\(^{-1}\) for a station in the Caribbean off Jamaica. Chang, et al. (2000) reported that *Trichodesmium* contribution was in the range of 0.003 to 2.27 % of primary productivity in the Kuroshio.

We have observed difference in the contributions made by *Trichodesmium erythraeum* and *Trichodesmium thiebautii* towards the organic productivity during our study. In the fall inter-monsoon season about 12 % of total surface primary production was due to only *T. thiebautii* whereas during the spring inter-monsoon it was 30 % because of the presence of *Trichodesmium erythraeum*. Capone, et al., 1998 reported 23 % of total surface primary production was due to *Trichodesmium erythraeum*. The explanation for the high primary production rates could be partially due to the NE

Both biomass and productivity of *Trichodesmium* showed large seasonality. Primary productivity due to *Trichodesmium* was as low as 8-15 mgCm\(^{-3}\)d\(^{-1}\) during NE MoN (8-15 mgCm\(^{-2}\)d\(^{-1}\)). Another important factor for the success of *Trichodesmium* in the Arabian Sea may be the iron input brought about through upwelling and/or atmospheric deposition and land runoff (Witter, et al., 2000). In the present study, large seasonality was also observed in the nitrogen fixation. High N\(_2\)-fixation rate values were recorded during the fall IntM (1108 ± 3511 µmolNm\(^{-2}\)d\(^{-1}\); n=13) followed by spring IntM (720 ± 2406 µmolNm\(^{-2}\)d\(^{-1}\); n=32), however lower values were observed during NE MoN (24 ± 32 µmolNm\(^{-2}\)d\(^{-1}\); n=28). Previous studies on the rates of N\(_2\)-fixation by *Trichodesmium* in the sub-tropical North Atlantic were generally much lower (< 10 µmolNm\(^{-2}\)d\(^{-1}\)) typically because of the low biomass of the *Trichodesmium* spp. (Carpenter, et al., 2004). Published report (Goering, et al., 1966) did indicate the volume specific rates of N\(_2\)-fixation from two cruises off the north-eastern coast of South America. However, they did not provide areal estimates, on the other hand, in south-western N. Atlantic they reported the mean rate to be 108 µmolNm\(^{-2}\)d\(^{-1}\). Carpenter and Romans (1991) postulated rates of N\(_2\)-fixation for *Trichodesmium* of 710 to 3600 µmolNm\(^{-2}\)d\(^{-1}\) based on the high abundance of *Trichodesmium* encountered in the tropical portion of a transect through the Atlantic. In contrast to the above studies, Lipschultz and Owens (1996) produced a much smaller estimate for the contribution of *Trichodesmium* in the same region. Capone, et al. (2005) reported the average N\(_2\)-fixation rate (898...
µmol Nm$^{-2}$d$^{-1}$) in the same study area. In the Southern East China Sea, Chang, et al. (2000) reported that the N$_2$-fixation rate varied from 0.1 to 59.4 µmol Nm$^{-2}$d$^{-1}$. This was much lower than the results obtained during the our study in the NE Arabian Sea (Table 2). The Arabian Sea is known as an active site for nitrogen fixation (Devassy, et al., 1978, Capone, et al., 1998). One factor that favors the establishment of N$_2$-fixers in the Arabian Sea is the NO$_3^-$ deficit arising from local and far-field denitrification. The NO$_3^-$: PO$_4^{3-}$ ratio was lower than 15 at all depths in the Arabian Sea (Morrison, et al., 1998). As the N- deficient sub-surface waters were brought to the surface through upwelling and vertical mixing, the nutrients were taken up by the phytoplankton in a (Redfield) ration of 15 (by atoms), and this led to a surplus of PO$_4^{3-}$ in surface waters. This excess PO$_4^{3-}$ is observed most strikingly within the coastal anoxic zone where PO$_4^{3-}$ concentrations in excess of 3 µM occur when denitrification removes all dissolved NO$_3^-$. The organisms that fix N$_2$ also require relatively large amount of iron (Fe), which could be supplied by atmospheric deposition, mobilization from shelf and slope sediments and upwelling.

Consequently, blooms of *Trichodesmium* spp. occur over large parts of the Arabian Sea mostly during the spring inter-monsoon season when surface waters are NO$_3^-$ depleted. The calmness of the sea during this season allows the establishment of warm surface waters, reduced turbulence and high euphotic zone light intensities, conditions that also favour nitrogen fixation (Devassy, et al., 1978, Capone, et al., 1997, Capone, et al., 1998). Apart from the experimentally measured N$_2$-uptake rates (Dugdale, et al., 1964, Capone, et al., 1998), evidence for N$_2$-fixation in the Arabian Sea has been provided by data on natural isotope abundance in NO$_3^-$ (Brandes, et al., 1998). The estimated N$_2$-
fixation rate for the region is 3.3 TgNyr\(^{-1}\) (Bange, et al., 2000) which is speculated to play an important role in understanding biogeochemistry of the region.

Thus our present study illustrates the seasonal distribution of *Trichodesmium* and its ability to fix carbon and nitrogen in the Arabian Sea. A large part of the Arabian Sea tends to become oligotrophic during a major part of the year (6-7 months) where primary productivity is impacted by the nitrogen fixed by the *Trichodesmium*.

Insert Table 2 here

During the present study, a total of 143 stations were sampled in the NE Arabian Sea in order to study the *Trichodesmium* bloom. Majority of these stations (93 stations) showed the presence of *Trichodesmium* i.e. 65 % of the total stations were represented by *Trichodesmium*. A significant finding of the present study was the occurrence of *T. thiebautii* in the offshore part of the Arabian Sea, just after the SW monsoon, as early as November (Fig. 9). This was largely attributed to the low temperatures (22-27\(^{0}\)C) and low nitrate levels in the euphotic zone; *Trichodesmium erythraeum* began appearing in February in the coastal water and spread to offshore water during the months of April and May, when temperatures generally high and nitrate concentrations are low and so *Trichodesmium erythraeum* thrives in this environment.

Insert Fig. 9 here

Another important feature observed during the NE MoN was that *Trichodesmium thiebautii* occurred as deep as 70 – 80 m in the water column. Phosphate availability may be an important factor for *Trichodesmium* to appear (Karl, et al., 1992). In the NE Arabian Sea, the contribution of *Trichodesmium* to total phytoplankton counts varied
from 1% to 95 %, with the highest counts being observed in the spring IntM. The dominant phytoplankton species in the *Trichodesmium* bloom were *Trichodesmium erythraeum*, *Trichodesmium thiebautii*, *Navicula* spp., *Nitzschia closterium*, *Nitzschia seriata*, *Rhizosolenia setigera*, *Rhizosolenia shrubsolei*, *Chaetoceros curvisetus*, *Noctiluca miliaris*, *Melosira moniliformis*, *Chaetoceros decipiens*, *Rhizosolenia hebetata* and *Thalassiothrix frauenfeldii*.

Another noteworthy observation made during the present investigation was the occurrence of mixed blooms of *Trichodesmium erythraeum* and *Noctiluca miliaris* from late NE MoN and early spring IntM in the shelf region, whereas, in the offshore region, *Noctiluca* dominated the bloom, this coincided with a reduction in the density of the *Trichodesmium* filaments. Further, unique occurrence of isolated patches of decomposed filaments in combination with *Noctiluca* at a few stations coupled with elevated nutrient suggests that, the post *Trichodesmium* bloom triggers the *Noctiluca miliaris* bloom in the Arabian Sea. It is a well known fact that the Arabian Sea becomes oligotrophic during the late NE MoN, which supports the occurrence of a *Noctiluca miliaris* (Gomes et al., 2008; 2009). Winter convection (February-March) that brings high nutrients to surface water in the NE Arabian Sea triggers blooms of the *Noctiluca miliaris*. Subsequently, in the Arabian Sea *Noctiluca* and *Trichodesmium* blooms coexist with high counts of *Navicula* sp., *Nitzschia closterium*, *Nitzschia seriata* and *Thalassiosira subtilis*. However *Trichodesmium* spp. which contributes 0.11 to 60 % of total primary production of the Arabian Sea remains important.

It appears that a sizable portion of nitrogen will be brought back to the surface layer, ( may be N0₃), which could support phytoplankton productivity (new production)
in the Arabian Sea. On analyzing the data we collected from all the stations, we found that the organic carbon produced by *Trichodesmium* in the region was about 0.263 TgC year\(^{-1}\), this value was, in fact very close to the amount of nitrogen fixed by the *Trichodesmium* in the region during same period, which was estimated to be about 0.2976 TgN year\(^{-1}\). At times large amounts of biomass get accumulated at surface during *Trichodesmium* bloom in the Arabian Sea. This cyanobacteria is effective for N\(_2\) fixation, but not as primary producer and hence is responsible for the matching carbon fixation and nitrogen fixation quantity ratio nearing one. Thus the presence of *Trichodesmium* spp. recorded from November to April in the Arabian Sea (Fig. 9) is an important factor responsible for maintaining the ecosystem of the Arabian Sea during oligotrophic conditions.

5. Conclusions

The two species of the *Trichodesmium* form blooms in the Arabian Sea, these blooms depend upon environmental conditions. Accordingly blooms appear in the coastal water or open ocean. *Trichodesmium thiebautii* blooms were noticed just after monsoon in the low nutrient offshore environment and low temperature. Similar conditions extend in the coastal water during January where *T. thiebautii* was noticed. March onwards offshore waters are marked with *T. erythraeum* blooms and April onwards coastal waters. These blooms synthesize 0.263 TgC year\(^{-1}\) and fix 0.2976 TgN year\(^{-1}\). The nitrogen fixed help the productivity of the Arabian Sea which is otherwise limited due to the depletion of nitrogenous nutrients, between the two monsoon systems.
Acknowledgment

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Figure(s)

Fig. 6
Fig. 7
Fig. 9