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Research Article

Nitrogen Uptake Rates during Spring in the NE Arabian Sea

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We present new data on N uptake rates and f-ratios in the north-eastern (NE) Arabian Sea, where significant amounts of *Trichodesmium* were present in spring, 2006. The measured total nitrogen uptake rates ranged from 0.34 to 1.58 mmol N m^{-2} d^{-1}. N_2 fixation associated with *Trichodesmium* varied from 0.002 to 0.54 mmol N $m^{-2}d^{-1}$ estimated from the abundance of *Trichodesmium* and specific N_2 fixation rates of 1.5 pmol N trichome^{-1} h^{-1}. Inclusion of N_2 fixation rates significantly changes f-ratios particularly in the coastal stations. Nitrogen isotopic data of surface suspended particles suggest that recently fixed nitrogen contributes as high as ~79% of the nitrogen in surface suspended particles. In addition, water column gained ~30 mmol N m^{-2} in the form of nitrate, likely due to nitrification of ammonium released by *Trichodesmium*. For better estimations, direct measurement of N_2 fixation is recommended.

1. Introduction

Nitrogenous nutrients are considered to be the major limiting factor of oceanic primary production in many regions [1]. Further, primary production can be partitioned on the basis of the nitrogen source: "new" and "regenerated" production [2]. New production is supported by nitrate from the deeper ocean, rivers, and atmospheric N_2 fixed by diazotrophs. However, ammonium and urea, derived from biological processes occurring within the euphotic zone, sustain regenerated production; these can circulate indefinitely under a quasisteady state or form an ideal closed system if there is no nitrogen loss from the euphotic zone. Losses through the sinking of particulate matter, mixing, and by predation by zooplankton invariably happen in the real ocean, and therefore other sources of nitrogen are needed to sustain productivity. It is important to determine if the sum of the losses, in the form of export production, is balanced by nitrate upwelling and N_2 fixation by diazotrophs, and verify whether on an annual time scale export production is equal to the new production, under steady state [3].

The Arabian Sea (area ~6.2×10^6 km^2), though accounts for only ~1% of the global ocean surface, contributes to ~5% of the global marine primary production [4]. Recent observations based on ocean color show that summer productivity in the western Arabian Sea has been increasing from year 1997 to 2004 [5]. The observed trend in Chl *a* has been attributed to the warming of the Eurasian land mass. However, such claims are not supported by *in situ* hydrographic and chlorophyll measurements as well as a reanalysis of ocean colour data extending to 2009 [6]. Further, such a trend is not observed in the north-eastern (NE) Arabian Sea [7]. Thus, a large spatiotemporal variability exists in the biogeochemical aspects of this basin in response to the climate change. The region is one of the major quasipermanent sites for water column denitrification and loses ~60 Tg N $year^{-1}$ through this process [8]. However, lack of nitrogen fixation measurements in the region increases the uncertainty in the nitrogen balance. Further, *Trichodesmium* blooms have been observed every year during the spring and fall intermonsoons [9, 10] in the NE Arabian Sea region. *Trichodesmium* is an important diazotrophic

plankton that fixes atmospheric N_2 and introduces "new" nitrogen to the euphotic zone [11]. The net loss or gain of nitrogen from the ocean directly influences the carbon budget of the region, which has a bearing on the global carbon budget. Satellite and modeling results have also shown that *Trichodesmium* blooms occur annually more than 30% of the time [12] and sometimes cover more than 20% area of the Arabian Sea during spring and even more during fall [13]. However, such satellite and model results need to be fine-tuned with sea-truth data. Furthermore, ^{15}N-based N uptake rate measurements are also very limited for inter-monsoon periods in the NE Arabian Sea and particularly during *Trichodesmium* blooms.

Here we report the first measurements of ^{15}N-based nitrate, ammonium, and urea uptake rates in the NE Arabian Sea during spring. In the absence of direct measurements of N_2 fixation several authors, for example, Karl et al. [14], Tyrrell et al. [15], and Poulton et al. [16] have used *Trichodesmium* abundance and published values of specific rate of N_2 fixation to estimate the potential magnitude of N_2 fixation associated with it. We too follow a similar approach here. Further, nitrate-based new production has been combined with the estimated N_2 fixation rates to reestimate new production. In addition, we provide a preliminary estimate of nitrogen gained by the water column due to *Trichodesmium* growth.

2. Materials and Methods

As discussed earlier, *Trichodesmium* bloom occurs regularly during spring in the eastern Arabian Sea, an attempt was made to study chemical and biological properties in the coastal as well as open ocean waters during such bloom conditions. To cover both coastal and open ocean regions water samples were collected for biological and chemical studies at fifteen locations during 15–28 April 2006 in the NE Arabian Sea (Figure 1). Due to the limited ship time, ^{15}N-based new and total productivity measurements were made only at eight stations (four coastal and four open ocean stations). The vertical profiles of temperature and salinity for the sampling locations were obtained using a CTD-Seabird Electronics Sea sat, SBE 911 Plus, USA. Mixed layer depth (MLD) is defined as the depth where the water temperature is 1°C less than the surface value [17]. Onboard-automated weather station was used to monitor the winds. A hyperspectral radiometer (Satlantic Inc.) was used for the measurement of depth variation of light and the depth of euphotic zone (depth of 1% intensity of the surface irradiance) at each station. Water samples were collected using a CTD rosette fitted with Niskin bottles. Six sampling depths were chosen to cover the euphotic zone. These depths were chosen to correspond to 100%, 80%, 64%, 20%, 5%, and 1% of surface irradiance. 100 mL of each sample was separately collected for nutrient measurement. Nutrients were measured using a SKALAR autoanalyzer. 1 litre of water sample from each depth was also collected for Chl *a* measurement and filtered on 47 mm GF/F 0.7 μm pore size filters under low vacuum. Chl *a* was then extracted using 10 mL of 90% acetone (AR grade) and was measured using Turner Design fluorometer [18]. We might have lost some picoplankton (size range 0.2–2 μm) by using GF/F filters of pore size 0.7 μm. Campbell et al. [19] reported that picoplankton contribute 1% to 25% and 2% to 39% to the total biomass in the coastal and off-shore Arabian Sea during spring. In the present study, picoplankton of size less than 0.7 μm were only missed out. Therefore, the degree of underestimation in the measured Chl *a* is much less than 25% and 39% in the coastal and open ocean locations, respectively. Bell and Kalff [20] report that the importance of picoplankton drops significantly to less than 20% when the total chl *a* concentration exceeds 1 mg m^{-3} in the oligotrophic (tropical) oceans. Therefore, at some coastal locations, where Chl *a* concentration exceeds 1 mg m^{-3}, the degree of underestimation in the measured Chl *a* could be still lower.

Phytoplankton identification and enumeration were also carried out simultaneously by the National Institute of Oceanography, Goa and the experimental details are published [21]. Briefly, 1 litre (L) of seawater was fixed with 3% Lugol's iodine and stored in dark and cool condition until analysis. Prior to microscopic analysis, samples were concentrated to 5–10 mL by carefully siphoning the top layer with a tube covered with a 10 μm Nytex filter on one end. Replicates of 1 mL sample concentrates were transferred to a Sedgwick-Rafter and counted using an Olympus-Inverted microscope (Model IX 50) at 200x magnification. The smallest cells enumerated were of ~5 μm in diameter. Identifications were based on standard taxonomic keys [22]. The results are expressed as numbers of cells L^{-1} except for *Trichodesmium* which are expressed as number of trichomes L^{-1}. Total cell counts include *Trichodesmium* (in the unit of trichomes L^{-1}) and no conversion is made to get *Trichodesmium* abundance in the unit of cells L^{-1}.

At each station, 2 L surface seawater was collected for measuring the nitrogen isotopic composition of natural particulate organic nitrogen (PON), before the commencement of ^{15}N tracer measurements. Water samples were collected in 2-L polycarbonate bottles (procured from Nalgene, USA) in duplicate for nitrate and ammonium uptake rate measurements at each depth. While 1-L bottles were used for urea uptake rate measurements at each depth in duplicate. Prior to incubation at 10.00 Hrs local time, tracers containing 99 atom% ^{15}N ($Na^{15}NO_3$, $^{15}NH_4Cl$ and urea, obtained from SIGMA-ALDRICH, USA) were added to the bottles, nitrate was added at less than 10% of the ambient concentration, a very small, constant amount of ammonium and urea were added for all depths (0.01 μM), following Watts and Owens [23]. The added amount was fairly low in comparison to the earlier reported values of ammonium (0.1–0.5 μM) from the region proximal to the present study area [24]. For the calculation of uptake rate for ammonium and urea it was assumed that tracers added were the only sources for the plankton. Tracer-added bottles, which were covered with neutral density filters to simulate the irradiance at the depths from which they were collected, were kept in an on-deck water bath for incubation. Temperature of the water bath was maintained by flowing seawater from 6 m depth. Incubation

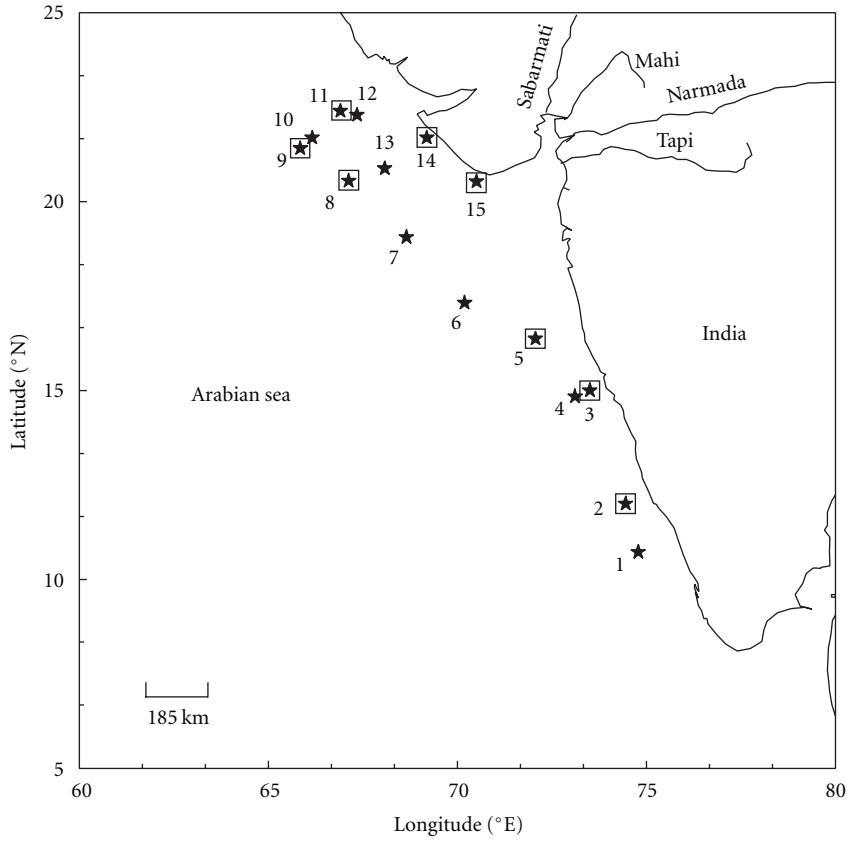

Figure 1: Sampling locations (filled stars) in the NE Arabian Sea. ^{15}N tracer experiments were done at eight stations (rectangles). Station numbers (1 to 15) represent the chronological order in which sampling was done. Rivers (Sabarmati, Mahi, Narmada and Tapi) debouching in to the Arabian Sea are also shown.

was carried out for four hours symmetrical to local noon at each station. At the end of incubation, all samples were filtered sequentially through precombusted (4 hrs at 400°C) 47 mm diameter and 0.7 μm pore size Whatmann GF/F filters, washed with filtered sea water, dried in an oven at 50°C overnight and stored for further mass spectrometric analysis.

For the present study, a *CarloErba* elemental analyzer interfaced via Conflo III to a *Finnigan Delta Plus* mass spectrometer was used to measure PON and atom% ^{15}N in the samples. The technique for submicrogram level ^{15}N determination [25] was followed. The agreement between the measured PON of duplicate samples was better than 12%. The coefficient of variation in atom% ^{15}N measurement was <1%. Two standards IAEA-NO_3 (KNO_3, #213) and IAEA-N-2($[NH_4]_2SO_4$, #342) were used to check the accuracy of the measurements. Uptake rates were calculated using the equation of Dugdale and Wilkerson [26] after correcting for blanks. The equation used for the calculation ensures that there is no effect of material, detrital or otherwise, which has not fixed ^{15}N during the experiment, on the estimates of uptake rates. Daily uptake rates were calculated by multiplying hourly values by 12 for nitrate and by 18 for ammonium and urea [26, 27]. Column integrated uptake rates were calculated using the trapezoidal integration from the surface to the euphotic depth. Here we follow the approach of Eppley and Peterson [3], where new production is equivalent to nitrate uptake rate in the absence of N_2 fixation. Yool et al. [28] suggested, on the basis of specific nitrification rates measurements, that a substantial, up to about half of the nitrate present could be generated *in situ* through recent, near surface, nitrification. However, in the present study, surface nitrate concentrations were generally below or near detection limits. In addition, for short incubations (~4 h) there is no need to make corrections for isotopic dilution, and also the nitrification effect is minimal. Therefore, the measured nitrate uptake rates can reasonably be treated as a part of new production, apart from nitrogen fixed by *Trichodesmium*.

As *Trichodesmium* was present in the study area, it is required to incorporate N_2 fixation associated with the *Trichodesmium* with the measured nitrate uptake rates to calculate new production. Direct measurement of N_2 fixation was not performed, so the potential magnitude of N_2 fixation associated with the *Trichodesmium* was estimated based on the observed *Trichodesmium* abundance and the reported cell-specific N_2 fixation rate. There exist some data on cell-specific N_2 fixation rates from field and laboratory experiments; for example, Fu and Bell [29] reported N_2 fixation rate 2 pg N cell^{-1} h^{-1} from cultured strain of *Trichodesmium* sp. (GBRTRLI101) from the Great Barrier Reef Lagoon, McCarthy and Carpenter [30] measured N_2 fixation

rates (1.9 pg N trichome^{-1} h^{-1}) for *Oscillatoria thiebautii* (Gom.) in the subtropical north Atlantic Ocean. Capone et al. [13] observed an extensive bloom of *Trichodesmium* N_2 fixation in the central Arabian Sea and measured specific N_2 fixation rate (1.5 pmol N trichome^{-1} h^{-1}). We use the specific N_2 fixation rates given by Capone et al. [13] as their measurements are from the Arabian Sea and the abundance of *Trichodesmium* in both the studies are also comparable. Therefore, here, we have estimated the potential magnitude of N_2 fixation associated with *Trichodesmium* from their abundance and a nitrogen-specific N_2 fixation rate of 1.5 pmol N trichome^{-1} h^{-1} with a 12 h period [15] of N_2 fixation. The estimated N_2 fixation rate is then used with the measured nitrate uptake rates for calculating the new production. Here the *f*-ratio [3] is calculated in two ways:

(i) $f = \rho NO_3/(\rho NO_3 + \rho NH_4 + \rho \text{urea})$, (hereafter referred as f_1),

(ii) $f = (\rho NO_3 + \rho N_2)/(\rho NO_3 + \rho N_2 + \rho NH_4 + \rho \text{urea})$, (hereafter referred to as f_2),

where, ρNO_3, ρNH_4, ρurea are the uptake rates of nitrate, ammonium, and urea, respectively, and ρN_2 is the estimated N_2 fixation rate.

We have subdivided our sampling locations based on water depths: coastal stations (<200 m) and open ocean stations (>200 m).

3. Results

3.1. Hydrographic Conditions. Surface temperature, salinity, winds, mixed layer depth (MLD), and euphotic depth (EPD) data are listed in Table 1 for all the stations. Surface winds were low during the sampling period in the study area, ranged from 2.9 to 7.4 ms^{-1} with an average ~5.5 ms^{-1}. Sea surface temperatures (SST) were high, and ranged from 27 to 30°C. A decreasing trend was observed in SST from the south to the north, whereas surface salinity showed the opposite trend (Table 1). These trends are statistically different from zero, as the Student's *t*-test showed, at 0.01 levels. Surface water was highly stratified at all the stations. Prasanna Kumar and Narvekar [17] reported the similar environment conditions, which led to a shallow mixed layer in the region. This was also seen in the present study as MLD varied from 11 to 33 m. No significant difference was observed in MLD values between coastal (stations 2–4 and 14–15) and open ocean (stations 1 and 5–13) locations (Table 1). The deepest and the shallowest EPD were observed at the stations 2 and 15 (both coastal). Overall, it varied from 48 to 58 m and 18 to 67 m for the open ocean and coastal stations, respectively. EPD was deeper than MLD at all stations (Table 1).

3.2. Inorganic Nutrients and Chl a Distribution. Surface inorganic nutrients (nitrate, nitrite and phosphate) and Chl *a* data are given in Table 2. Surface nitrate was mostly near or below to detection limit (<0.01 μM) at all stations except stations 14 and 15. Nitrite concentration was below 0.1 μM at all the locations. However, phosphate concentration in surface was significant (>0.2 μM) in the study area (Table 2). The mixed layer was generally devoid of nitrate except at station 15, whereas nitrate was higher below the mixed layer (0.6 to 8.3 μM) (Figures 2(a) and 2(b)). Surprisingly, nitrate was >0.8 μM throughout the euphotic zone at station 15 (Figure 2(b)). Such high concentrations were not seen even at the nearby station 14. Surface Chl *a* was generally low (0.11 to 0.85 mg m^{-3}) at all the stations except at station 15 (6.63 mg m^{-3}). At the coastal and the open ocean locations it varied from 0.15 to 6.63 mg m^{-3} (average 1.38 mg m^{-3}) and 0.11 to 0.23 mg m^{-3} (average 0.16 mg m^{-3}), respectively. Unlike nitrate, Chl *a* was lower throughout the euphotic zone (Figures 2(a) and 2(b)) and showed a slight increase below mixed layer, at all stations but 15.

3.3. Phytoplankton Cells. Total phytoplankton (including *Trichodesmium*) cell counts and *Trichodesmium* abundance are shown in Table 2. Total plankton cell counts varied from 180 to 8338 cells L^{-1}. In the coastal region the average cell counts were 3291 cells L^{-1}, whereas, in the open ocean it was 766 cells L^{-1}. The presence of diatoms, dinoflagellates and cyanobacteria were observed at all the locations with varying proportions. Over all, diatoms were dominated plankton population in the region (more than 50%) and its species were *Navicula sp*., *Thalassiothrix frauenfeldii, Skeletonema costatum, and Rhizosolenia setigera.* After diatoms, cyanobacteria was most abundant plankton and mainly dominated in coastal region. *Trichodesmium erythraeum* and *Trichodesmium thibautii* both were found in the region with the slight dominancy of the former. *Scrippsiella trachoidea* was the main dinoflagellate found in the region. *Trichodesmium* abundance varied from 0 to 4004 trichomes L^{-1}. *Trichodesmium* was generally abundant in coastal stations, however, at two open ocean stations (station 5 and 6) significantly higher *Trichodesmium* cells (374 and 192 trichomes L^{-1}) were found in surface water. More than 1000 trichomes L^{-1} were observed at stations 4, 14, and 15 with the highest found at 15. Unlike the other stations, *Trichodesmium* were present throughout the euphotic zone at stations 4 and 15 (Figures 2(a) and 2(b)).

3.4. $\delta^{15}N$ of Surface Natural PON. Natural isotopic composition of nitrogen ($\delta^{15}N$) of PON data are shown in Table 2. A large variation was observed in the $\delta^{15}N$ of surface PON, ranged from 2.5‰ to 11.4‰. *Trichodesmium* fixes nitrogen of an isotopic composition (~0‰) close to that of atmospheric N_2 [31], thus, it has the lowest $\delta^{15}N$ among the marine phytoplankton. $\delta^{15}N$ of PON varied with the abundance of *Trichodesmium* in the surface waters and its minimum value was found at station 15 (*Trichodesmium* bloom station). $\delta^{15}N$ of PON in the coastal water ranged from 2.5‰ to 7.4‰ (average 5.1‰). Whereas in the open ocean it ranged from 5.5‰ to 11.4‰ (average 8.0‰). The difference in $\delta^{15}N$ of PON between coastal and open ocean is mainly because of the difference in the abundance of *Trichodesmium* between both regions. *Trichodesmium* was an order of magnitude more abundant in the coastal region (average abundance = 1387 trichomes L^{-1}) than in the open ocean (average abundance = 134 trichomes L^{-1}).

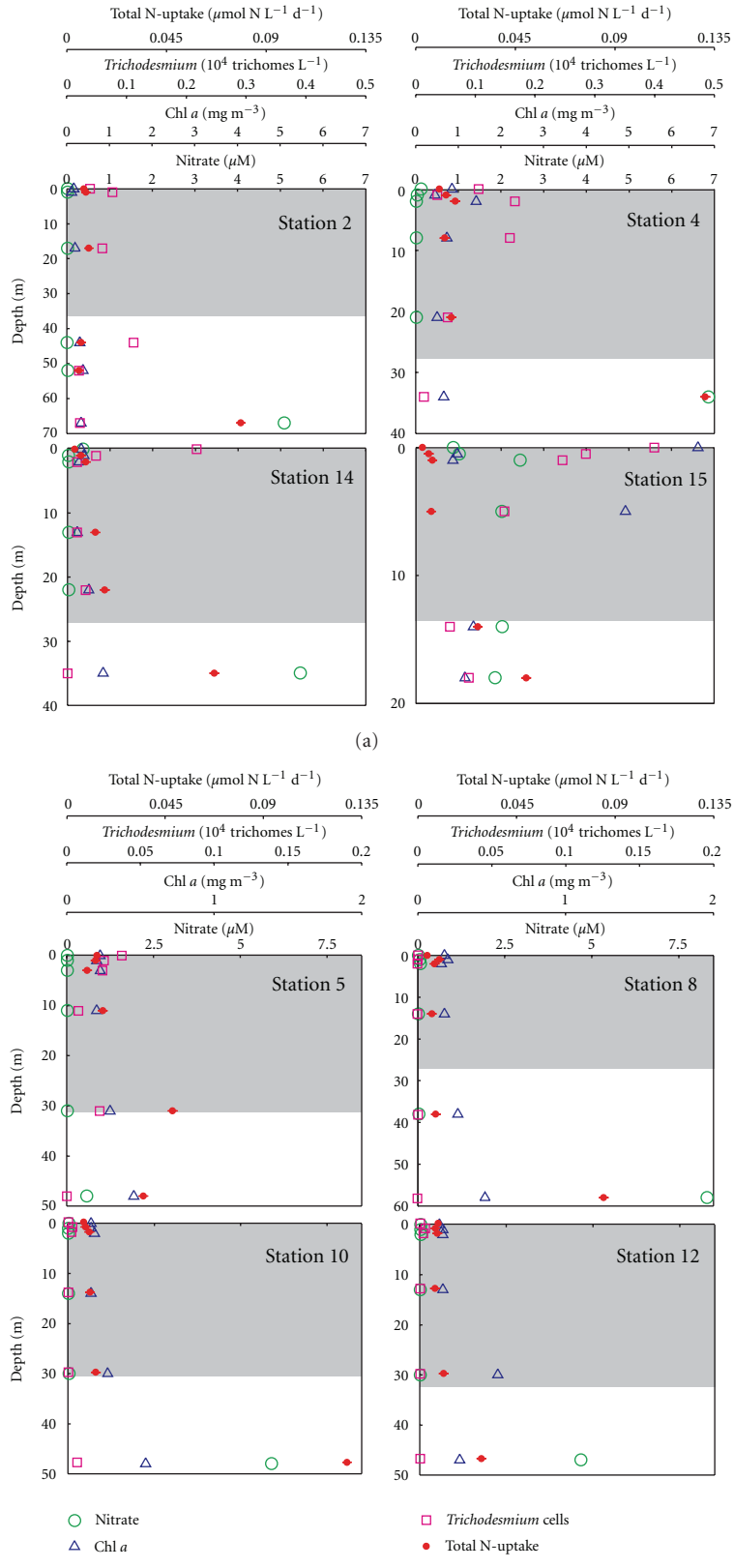

Figure 2: Vertical profiles of nitrate, Chl *a*, measured total N uptake rates (sum of ρNO_3, ρNH_4, and ρurea), and *Trichodesmium* abundance. The shaded area represents the mixed layer. (a) refers to coastal stations 2, 4, 14, and 15 (water depth <200 m) and (b) open ocean stations 5, 8, 10, and 12 (water depth >200 m). Error bars represent the 1-sigma (standard deviation) in the measured N uptake rates.

Table 1: Sampling date, station number, temperature, salinity at the surface and wind speed (V_w), mixed layer depth (MLD), and euphotic depth (EPD) data at different sampling stations.

Sampling Date	Station no.	Temp. (°C)	Salinity	V_w (ms^{-1})	MLD (m)	EPD (m)
16 Apr 2009	1[b]	30.28	33.92	2.9	19	—
17 Apr 2009	2[a,#]	30.28	34.04	3.1	29	67
18 Apr 2009	3[a]	29.15	34.88	4.9	25	—
19 Apr 2009	4[a,#]	29.30	35.38	5.7	26	34
20 Apr 2009	5[b,#]	28.88	34.99	6.6	28	48
21 Apr 2009	6[b]	28.70	35.60	4.8	25	—
22 Apr 2009	7[b]	28.83	35.45	4.3	11	—
23 Apr 2009	8[b,#]	28.21	35.86	6.0	20	58
23 Apr 2009	9[b]	28.02	36.48	6.0	23	—
24 Apr 2009	10[b,#]	27.52	36.60	5.8	27	48
24 Apr 2009	11[b]	28.02	36.58	5.8	33	—
25 Apr 2009	12[b,#]	27.38	36.47	7.4	29	47
25 Apr 2009	13[b]	27.63	36.46	7.4	26	—
26 Apr 2009	14[a,#]	27.41	36.39	6.5	24	35
27 Apr 2009	15[a,#]	27.22	36.23	7.0	15	18

a: denotes coastal locations (water depth <200 m).
b: denotes open ocean locations (water depth >200 m).
#: denotes stations at which nitrate, ammonium and urea uptake rates measurements were carried out.
—: no data available.

Table 2: Station number, nitrate, nitrite, phosphate, Chl *a*, total cell counts (including *Trichodesmium*), and abundance of *Trichodesmium* at the surface and δ^{15}N of surface natural PON data at different sampling stations.

Station no.	NO_3^- (μM)	NO_2^- (μM)	PO_4^{2-} (μM)	Chl *a* (mg m^{-3})	Total cell counts (cells L^{-1})*	*Trichodesmium* (trichomes L^{-1})	δ^{15}N (‰)
1[b]	—	—	—	0.15	1840	240	—
2[a,#]	nd	0.02	0.24	0.17	840	768	6.5
3[a]	—	—	—	0.18	1376	96	7.4
4[a,#]	0.1	0.03	0.43	0.85	8338	1056	4.3
5[b,#]	nd	0.02	0.23	0.23	1428	374	8.8
6[b]	—	—	—	0.14	672	192	5.5
7[b]	—	—	—	0.11	180	90	7.2
8[b,#]	nd	0.02	0.23	0.18	616	44	10.5
9[b]	—	—	—	0.14	972	72	—
10[b,#]	nd	0.03	0.36	0.16	756	nd	7.9
11[b]	—	—	—	0.16	728	26	—
12[b,#]	nd	0.03	0.38	0.14	1188	nd	11.4
13[b]	—	—	—	0.17	812	nd	—
14[a,#]	0.33	0.03	0.48	0.32	3099	2160	4.6
15[a,#]	0.88	0.09	0.68	6.63	4256	4004	2.5

a: denotes coastal locations (water depth <200 m). b: denotes open ocean locations (water depth >200 m). #: denotes stations at which nitrate, ammonium and urea uptake rates measurements were carried out. —: no data available. nd: not detectable (below analytical limit of detection). *: total cell counts include all the phytoplankton including *Trichodesmium*. Phytoplankton, other than *Trichodesmium*, are in the unit of cells L^{-1}. *Trichodesmium* counts (trichomes L^{-1}) are not converted into cells L^{-1}.

3.5. Nitrogen Uptake Rates. Nitrate, ammonium, and urea uptake rates data are shown in Table 3. Euphotic-depth-integrated nitrate uptake rates varied from 0.22 to 1.29 mmol N m^{-2} d^{-1}. Similar to Chl *a*, mostly nitrate uptake was limited to below the mixed layer at all the stations (Figures 2(a) and 2(b)). Euphotic nitrate uptake rates were 0.22 to 0.56 mmol N m^{-2} d^{-1} (with an average 0.52 mmol N m^{-2} d^{-1}) and 0.39 to 1.29 mmol N m^{-2} d^{-1} (with an average 1.07 mmol N m^{-2} d^{-1}) for coastal and open ocean stations, respectively. Interestingly, the lowest nitrate uptake was observed at station 15 at which the highest abundance of *Trichodesmium* was observed. Overall, average euphotic nitrate uptake rate was twice higher at open ocean stations than that at coastal stations.

Table 3: Station number, euphotic depth-integrated uptake rates (mmol N m^{-2} d^{-1}) of nitrate (ρNO_3), ammonium (ρNH_4), and urea (ρNO_3), N_2 fixation rates (ρN_2) and *f*-ratios (f_1 and f_2) data at different sampling stations. Errors associated with the values are 1-sigma standard deviation.

Station No.	ρNO_3	ρNH_4	ρurea	ρN_2[a]	f_1	f_2
2	0.55 ± 0.04	0.39 ± 0.01	0.11 ± 0.01	0.54	0.52 ± 0.03	0.69 ± 0.03
4	0.90 ± 0.03	0.23 ± 0.01	0.13 ± 0.01	0.36	0.71 ± 0.02	0.78 ± 0.02
5	1.00 ± 0.02	0.35 ± 0.01	0.15 ± 0.05	0.10	0.67 ± 0.03	0.69 ± 0.03
8	0.94 ± 0.03	0.13 ± 0.02	0.13 ± 0.01	0.008	0.78 ± 0.02	0.78 ± 0.02
10	1.29 ± 0.01	0.19 ± 0.02	0.10 ± 0.01	0.008	0.82 ± 0.02	0.82 ± 0.02
12	0.39 ± 0.01	0.10 ± 0.01	0.08 ± 0.01	0.002	0.68 ± 0.01	0.69 ± 0.01
14	0.56 ± 0.01	0.14 ± 0.02	0.09 ± 0.01	0.08	0.71 ± 0.02	0.74 ± 0.02
15	0.22 ± 0.05	0.07 ± 0.01	0.05 ± 0.01	0.35	0.65 ± 0.08	0.83 ± 0.08

a: N_2 fixation rates = *Trichodesmium* abundance × 1.5 pmol N trichome^{-1} h^{-1} × 12 h.

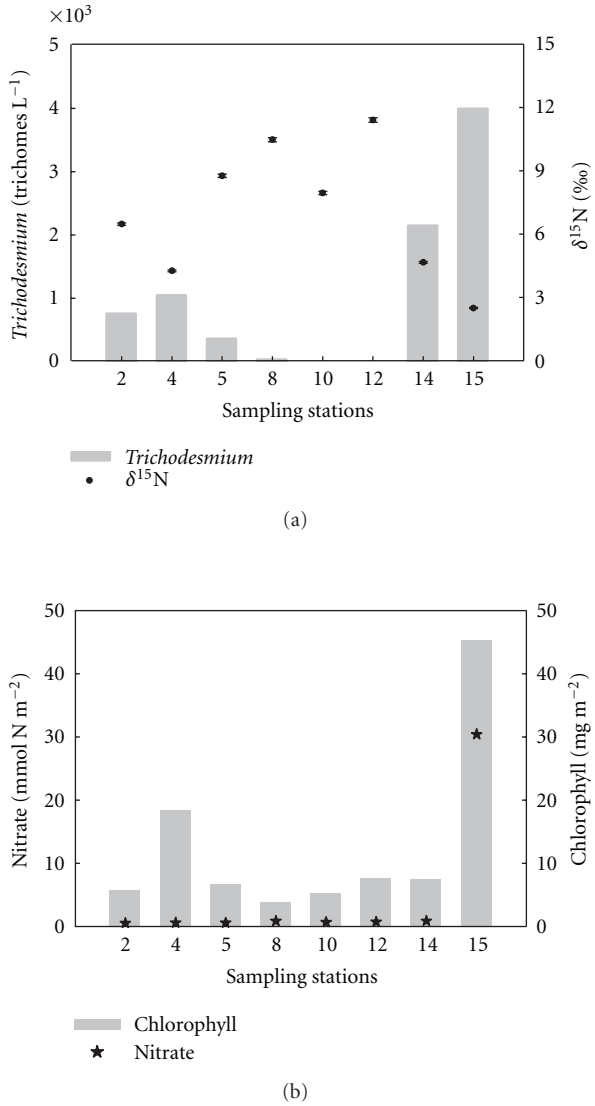

Figure 3: Stationwise variation of (a) surface *Trichodesmium* abundance and $\delta^{15}N$ values of natural PON for zero time incubation, (b) mixed layer depth-integrated nitrate and Chl *a* concentrations. Error bars represent the 1-sigma (standard error) associated with the isotopic measurements of $\delta^{15}N$.

Euphotic-depth-integrated ammonium uptake rates varied from 0.07 to 0.39 mmol N m^{-2} d^{-1} (with an average 0.19 mmol N m^{-2} d^{-1}) and 0.10 to 0.19 mmol N m^{-2} d^{-1} (with an average 0.14 mmol N m^{-2} d^{-1}) for coastal and open ocean stations, respectively. Euphotic urea uptake rates varied from 0.05 to 0.15 mmol N m^{-2} d^{-1} (with an average 0.11 mmol N m^{-2} d^{-1}) and 0.08 to 0.13 mmol N m^{-2} d^{-1} (with an average 0.10 mmol N m^{-2} d^{-1}) for coastal and open ocean stations, respectively. Mostly, ammonium uptake rates were higher than urea uptake rates at all stations. Similar to the nitrate uptake rate, the lowest (euphotic depth) ammonium and urea uptake rates were also associated with station 15. The measured total nitrogen (sum of nitrate, ammonium and urea) uptake rates integrated over the euphotic depth, ranged from 0.34 to 1.58 mmol N m^{-2} d^{-1} (Table 3). The highest rate was measured at station 10 and the lowest at 15.

3.6. N_2 Fixation Rates. Depth-integrated N_2 fixation associated with *Trichodesmium* (estimated from their abundance and cell specific uptake rate) for euphotic zone are shown in Table 3. Depth-integrated N_2 fixation rates varied from 0.002 to 0.54 mmol N m^{-2} d^{-1}. Euphotic N_2 fixation rates were 0.08 to 0.54 mmol N m^{-2} d^{-1} (average 0.33 mmol N m^{-2} d^{-1}) and 0.002 to 0.10 mmol N m^{-2} d^{-1} (average 0.02 mmol N m^{-2} d^{-1}) for coastal and open ocean stations, respectively. Although the surface abundance of *Trichodesmium* at station 15 was nearly 4 times than that at station 2, the N_2 fixation was more at the latter station than the former. The integrated rate depends on the abundance of *Trichodesmium* cells as well as the depth up to which the integration was done. Therefore, the rate was more at station 2 (EPD = 67 m) than that at station 15 (EPD = 18 m).

3.7. f-Ratios. The *f*-ratios (f_1 and f_2), integrated over euphotic zone for all stations, are shown in Table 3. Overall, both f_1 and f_2 ranged from 0.52 to 0.82 and 0.69 to 0.83, respectively. For coastal stations, f_1 and f_2 were found 0.52 to 0.71 and 0.69 to 0.83, respectively. Inclusion of N_2 fixation related to the *Trichodesmium* significantly changed (increased) the *f*-ratio in the coastal stations, as

Trichodesmium was more abundant in the coastal stations. However, no significant difference was observed between f_1 and f_2, which ranged from 0.67 to 0.82 and 0.69 to 0.82, respectively, for open ocean stations as *Trichodesmium* was not as abundant as in the coastal stations.

4. Discussion

Trichodesmium abundance in the present study was comparable to that previously reported from central Arabian Sea (between 1000 and 4000 trichomes L^{-1}, [13]) but lower than that reported from the west coast of India ($>10^7$ filaments L^{-1} [9]). N_2 fixation rates estimated from their abundance are comparable to the measured uptake rates of other forms of nitrogen (nitrate, ammonium and urea), particularly in the coastal stations. Therefore, a significant difference is seen between f_1 and f_2 for coastal stations. Nitrate uptake rates were higher below the mixed layer, where nitrate and Chl *a* concentrations were also higher (Figures 2(a) and 2(b)). However, N_2 fixation was confined to the mixed layer as most of *Trichodesmium* was confined to the surface layers. The above observations suggest that N_2 fixation and nitrate uptake dominates as a major factor of new production in the surface and below the mixed layer, respectively, at least in the coastal region.

Capone et al. [13] used simple mass balance to estimate the contribution of recently fixed nitrogen to the surface pool of suspended particles as well to the sinking organic matter collected by sediment traps. They used the nitrogen isotopic composition of natural surface PON in their calculation. They assumed nitrogen isotopic composition of *Trichodesmium* ($\delta^{15}N = 0‰$) and nitrate below mixed layer ($\delta^{15}N = 10‰$). In a similar way, our isotopic data suggest that the recently fixed nitrogen contributes to as high as ~79% of the nitrogen in surface PON.

Trichodesmium were generally abundant in the low nitrate waters (Figures 2(a) and 2(b)). However, at station 15 *Trichodesmium* were detected with higher concentrations of nitrate (Figure 2(a)). Figure 3 shows the $\delta^{15}N$ of natural surface PON and *Trichodesmium* abundance (a) along with the mixed layer depth-integrated nitrate and Chl *a* (b) at different stations. The lowest $\delta^{15}N$ of PON coincides with the highest *Trichodesmium* abundance in the surface at station 15, a clear indication of the dominance of *Trichodesmium* in the total phytoplankton population. Further, the highest mixed layer integrated Chl *a* is also observed here showing the intensity of *Trichodesmium* bloom. Similar abundance of *Trichodesmium* bloom was observed by Capone et al. [13] in the central Arabian Sea with very low concentrations of nitrate in the water column. Devassy et al. [9] also observed developments of such blooms under a low nitrate environment. However, we have observed a significantly higher concentration of nitrate in the mixed layer at station 15. Atmospheric deposition, river discharge, upwelling/deep mixing, supply from the western Arabian sea through advection or nitrification of NH_4^+ released by *Trichodesmium* [32] could be considered as other possible sources of the observed nitrate at station 15. No simultaneous observations are available for the atmospheric deposition during the study period. However, any atmospheric contribution should be observable over a wide region, but no other station, not even the nearby station 14, showed measurable concentration of nitrate at the surface. This indicates that contribution of atmospheric aerosols is minor to the higher concentration of NO_3 observed at station 15. There are some rivers, for example, Mahi, Narmada and Tapi (major rivers; annual mean discharge $>300\,m^3s^{-1}$), and Sabarmati (smaller river; annual mean discharge $<50\,m^3s^{-1}$) debouch into the region (Figure 1). However, all the rivers have very low discharge, <5% of the summer monsoon discharge, during the month of April (http://www.grdc.sr.unh.edu/). Further, river water (salinity ~0 psu) lowers the salinity of seawater. However, no such signature was observed at station 15. Salinity was high (>36 psu; Table 1) at station 15 and similar to the nearby stations. It is also known that significant amounts of nutrients are removed during the passage of the river through the estuarine ecosystem. Therefore, the contribution from river discharge is likely to be negligible. It is possible that a short term upwelling had occurred in the area before the sampling time. Winds were also low during the period (Table 1). To the best of our knowledge, neither a cyclone passed through the area nor any rough sea conditions were reported from the region just before and during sampling. Furthermore, no earlier evidence is available for upwelling/deep mixing in the region during this time of the year. Nutrients supply from the western Arabian Sea through advection is limited to the open waters of western and central Arabian Sea, and its effect in the eastern Arabian Sea has ruled out by Jyothibabu et al. [33]. Therefore, nitrification of the released ammonium could be the most likely source of the observed higher concentration of nitrate at station 15. Devassy et al. [9] also reported a progressive accumulation of dissolved inorganic nitrogen with increase in *Trichodesmium* abundance in surface water during 1975 and 1977. If *Trichodesmium* is indeed the source of the observed nitrate, it can be termed as new nitrogen input to the water column. This input is scaled to ~ $30\,mmol\,N\,m^{-2}$ after normalizing with the column nitrate of the nearest station 14. Higher *Trichodesmium* was observed at other stations as well, for example, stations 2, 4, and 14 but such accumulation of nitrate was not observed at these stations. At stations 2 and 14 higher abundance was limited to the surface but at station 4 *Trichodesmium* was present significantly throughout the water column. Therefore, it is suggested that this preliminary evidence of significant new nitrogen addition must be verified by future experiments; similar experiments along with the direct measurements of N_2 fixation.

5. Conclusions

^{15}N-based productivity and N uptake rate measurements were carried out in the NE Arabian Sea during April-2006. Both the open ocean and coastal stations showed very low nitrate, ammonium, and urea uptake rates in the shallow mixed layers, due possibly to strong stratification and low nutrient supply. During spring, the NE Arabian Sea was

well stratified and most of the nitrate uptake took place below the mixed layer. Inclusion of N_2 fixation associated with *Trichodesmium* significantly changes (increase) the *f*-ratio, particularly in the coastal stations. Nitrate uptake and N_2 fixation dominates as a major factor of new production below mixed layer and surface layers, particularly in coastal stations, respectively. The lowest $\delta^{15}N$ of surface PON coincides with the highest *Trichodesmium* abundance in surface, suggesting *Trichodesmium* fixes atmospheric N_2 ($\delta^{15}N$ = 0‰) and adds new nitrogen to the ocean. $\delta^{15}N$ of surface PON suggests that the recently fixed nitrogen contributes to as high as ~79% to the nitrogen in surface suspended particles. Higher nitrate observed during *Trichodesmium* bloom could be as much as $\sim 30\,\text{mmol N m}^{-2}$. The uncertainty in this estimate may be reduced by future measurements of N_2 fixation.

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