

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

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9 **Abstract**

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11 *Trichodesmium* was studied with the purpose of understanding its distribution, organic
12 production and nitrogen fixation in the Arabian Sea. Out of the 143 stations sampled, a
13 total of 93 stations showed the presence of *Trichodesmium* filaments. Two species of
14 *Trichodesmium* namely, *T. thiebautii* and *T. erythraeum* were found. These were
15 distributed on the basis of the physico-chemical conditions of the Arabian Sea. This was
16 the first time that we managed to detect and record the presence of *Trichodesmium*
17 *thiebautii* bloom in the Arabian Sea at depths as deep as 70-80m. Total counts of
18 *Trichodesmium* varied between 0 to 400737 filamentsL⁻¹. *Trichodesmium thiebautii*
19 developed in offshore waters during the fall intermonsoon, when the water temperature
20 was around 28⁰C and nitrate content was as low as 0.34μM. After the northeast monsoon,
21 *Trichodesmium erythraeum* developed in the offshore area and then spread to coastal
22 waters. Both species of *Trichodesmium* together produced a total of 0.263 TgCyear⁻¹ and
23 fixed a total of 0.2976 TgNyear⁻¹ in the Arabian Sea. The study revealed that
24 *Trichodesmium* was a major contributor to the organic matter productivity of the Arabian
25 Sea during the period from November to April. The seasonality of the blooms of
26 *Trichodesmium* is discussed with the help of Ocean Color Monitoring (OCM) data and
27 biogeochemical implication of these findings in the Arabian Sea.

28 **Keywords:** *Trichodesmium*; Primary production; Nitrogen fixation; Monsoon;

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36 **1. Introduction**

37 *Trichodesmium* is a planktonic filamentous cyanobacterium which is known to
38 dwell in tropical and temperate marine environments (Capone et al., 1997; Mulholland
39 and Capone 2009; Subramaniam and Carpenter, 1994). It forms dense blooms which are
40 studied with the purpose of understanding both its biomass as well as its distribution
41 (Carpenter and Prince, 1977; Capone et al., 1997). Since 1950, these blooms have been
42 reported in the Arabian Sea (Ramamurthy et al., 1972; Devassy et al., 1978; Sawant, et
43 al., 1996; Capone et al., 1998; Lugomela et al., 2002; Desa et al., 2005; Parab et al.,
44 2006; Basu et al., 2011), the Lakshadweep Sea (Qasim, 1970), the Andaman Sea
45 (Jyothibabu et al., 2003) and the Bay of Bengal (Jyothibabu et al., 2003; Hegde et al.,
46 2008). The phytoplankton biomass at times exceeds $100\mu\text{gL}^{-1}$ during the blooming
47 period this value is higher than any other biomass value recorded in any other individual
48 species(Parab et al., 2006). The *Trichodesmium* bloom is unique since it can both
49 synthesize organic matter and fix nitrogen (Capone et al., 1998, 2005; Carpenter et al.,
50 1983). The ecological significance of this organism in the Arabian Sea is not very well
51 known, although it does in fact hold the key to the productivity of the Arabian Sea during
52 oligotrophic conditions.

53 The Arabian Sea has certain unique features as far as wind direction, solar
54 insolation, currents, water temperature and upwelling during the NE (Northeast;
55 December to February) and SW (Southwest; June to September) monsoons are

56 concerned. Upwelling during the summer monsoon results in high concentrations of NO_3^-
57 in surface waters, particularly in the north-western reaches of the basin. However during
58 the oligotrophic inter-monsoon period, surface waters are depleted of combined N
59 (nitrogen) thus restricting production of phytoplankton (Bhattathiri et al., 1996).

60 Bio-geochemical estimates and empirical measurements show that N_2 fixation by
61 *Trichodesmium* is a major source of new nitrogen which is of immense importance in
62 supporting the primary production of the oligotrophic environment (Capone, et al., 1997).
63 *Trichodesmium* spp. is considered to be an important source of new nitrogen in the
64 oligotrophic ocean; however more studies on *Trichodesmium* spp. are necessary as there
65 are large loopholes in the understanding of its seasonality in the Arabian Sea. Although
66 this cyanobacterium is common in tropical and sub-tropical seas, its distribution is known
67 to be irregular, however at the same time spatially extensive dense blooms of
68 *Trichodesmium* form when the conditions are appropriate (Eleuterius, et al., 1981;
69 Capone, et al., 1998). Published reports (Capone, et al., 2005) on measurement of N_2 -
70 fixation in various parts of the oceanic environment suggest that *Trichodesmium* is an
71 important source of new nitrogen to the phytoplankton in the ocean. Nitrogen fixation
72 studies have already been conducted and the results are available from the Atlantic
73 (Goering, et al., 1966) as well as the Pacific (Letelier, et al., 1996; Karl, et al., 1997).
74 Studies have also been conducted in the Caribbean Sea (Carpenter and Price, 1977), the
75 China Sea (Saino, et al., 1977; Chen, et al., 2003) and the Sargasso Sea (Orcutt, et al.,
76 2001). It is seen that the presence of new nitrogen significantly amplifies primary
77 production and thus exports carbon into the deeper parts of the ocean. The reports on N_2 -
78 fixation rates by *Trichodesmium* in the Arabian Sea are few despite the fact that,

79 *Trichodesmium* frequently occurs in this region (Capone et al., 1998). Also, these reports
80 have not accounted for the seasonality seen in the *Trichodesmium* blooms in the Arabian
81 Sea nor have they accounted for its diversity. Traditionally it's taken for granted that, in
82 oligotrophic conditions, the level of net biological productivity is sustained by the
83 availability of new nitrogen. This flux of new nitrogen into the euphotic zone which
84 supports primary production is balanced by the concomitant losses suffered due to
85 sinking particles, vertical migration and the mixing of organic nitrogen from the surface
86 waters (Dugdale and Goering, 1967; Eppley and Peterson, 1979; Lewis, et al., 1986;
87 Platt, et al., 1992).

88 Historical data from the Arabian Sea reveal that the cause of the low oxygen zone
89 in the Arabian Sea is partly due to upwelled water and due to respiration of organic
90 matter formed during high biological productivity. Joint Global Ocean Flux Study
91 (JGOFS) indicated high primary productivity in the Western and Central Arabian Sea
92 (Barber et al., 2001) specially during SW monsoon and NE monsoon. However Eastern
93 Arabian Sea values are patchy ($0.18-7.29 \text{ gCm}^{-2}\text{d}^{-1}$), these have been attributed to varying
94 nutrient (specially nitrate) and hydrographic conditions (Naqvi et al., 2006). It must also
95 be noted that the eastern Arabian Sea was not studied during the US JGOFS cruises
96 (Smith 2001, 2005). During the Indian JGOFS study primary productivity of eastern
97 Arabian Sea fluctuated seasonally. During the intermosoon, the area became oligotrophic
98 while during the winter monsoon it was found to be more productive (Bhattathiri et al.,
99 1996). This area is an important site for the blooms of the *Trichodesmium* (Devassy
100 1978). The *Trichodesmium* is important as primary producers and nitrogen fixer where
101 upto 50% of the nitrogen fixed by *Trichodesmium* can be released as nitrogen source to

102 phytoplankton during bloom seasons (Mulholland et al., 2006). This has prompted us to
103 plan study of *Trichodesmium* in the NE Arabian Sea in order to assess seasonality and role
104 of the organism in the Arabian Sea ecosystem with reference to SW monsoon,
105 intermonsoon and NW monsoon seasons.

106

107 **2. Materials and Methods**

108 **2.1. Study area and sampling**

109 The data presented here was collected on board two research vessels the ORV Sagar
110 Kanya (SK) and FORV Sagar Sampada (FORV). This collection of data was done in the
111 months spanning from November to April during cruises SK-152 (30th March to 13th
112 April 2000), SK- 171 (3rd to 17th November 2001); SK 186 (3rd to 19th January 2003);
113 SK214 (4th to 17th December 2004); FORV 212 (27th February to 7th March 2003) and
114 FORV 222 (22nd February to 10th March 2004). While planning the cruises, special
115 emphasis was given to study the distribution of *Trichodesmium* in the Arabian Sea
116 covering 12-22^oN and 65-74^oE (Fig. 1) and seasons (November –fall inter-monsoon (fall
117 IntM); December to February –NE monsoon (NE MoN) and March to April – spring
118 inter-monsoon (spring IntM) so as to include samples from coastal and offshore as well
119 as regions where physical processes such as upwelling and winter cooling, were known to
120 occur. Different cruises during same seasons have been referred as the early NE monsoon
121 - December, mid NE monsoon -January, late NE monsoon-February; early spring
122 intermonsoon-March and late spring intermonsoon-April. Water samples were collected
123 from the euphotic zone with 5L Niskin sampling bottles mounted onto a Sea Bird

124 Electronics[®] conductivity-temperature-density profiler (CTD) rosette. The depth of the
125 euphotic zone was measured using a Secchi Disc.

126

127 **Insert Fig. 1 here**

128

129 **2.2 Physicochemical measurements**

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

134

135 **2.3 Chlorophyll *a* concentration**

136 To obtain the chlorophyll *a* (chl *a*) estimates seawater samples (1 litre) were
137 filtered through GF/F filters and analyzed by HPLC (Wright et al., 1991; Bidigare and
138 Charles, 2002). Prior to the HPLC analysis, the filters were immersed in 90 % acetone,
139 extracted under cold and dark conditions overnight, sonicated and finally filtered through
140 0.2 µm, 13 mm PTFE filters to free the sample from any particulate debris. Aliquots of 1
141 ml of the pigment extract were then mixed with 0.3 ml of distilled water in a 2 ml amber
142 vial and allowed to equilibrate for 5 minutes prior to its injection into an HPLC
143 (Agilent[®] 1100 series) equipped with a diode array detector. Pigments were separated in a
144 C-18 reverse-phase column using the eluent gradient program of Wright, et al. (1991) as
145 adapted by Bidigare and Charles (2002) as detailed in Parab, et al. (2006).

146

147 **2.4. *Trichodesmium* spp. abundance**

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

159

160 **2.5. Primary productivity**

161 For primary productivity analysis, water samples were collected depending upon
162 the euphotic zone that was established using a Secchi Disc. For total phytoplankton
163 measurement, the volume of water samples was transferred in triplicates to 250 ml
164 capacity Nalgene Polycarbonate bottles. One ampoule of ¹⁴C (5µci) was injected to each
165 three light and one dark bottles. These bottles were then incubated for 12 hrs on deck
166 using appropriate light cutoff screens. At the end of the incubation period the water
167 sample (250 ml) was filtered through GF/F filter. All the filters exposed to fuming HCL
168 for 20 minutes in a desiccator in order to dissolve left over bicarbonates. Samples were
169 then placed in a 7 ml mini scintillation vial with scintillation cocktail and activity was

170 determined with a Wallac Scintillation counter (model no. 1409). All counts were quench
171 corrected (UNESCO, 1994).

172 To measure *Trichodesmium* productivity, trichomes were first collected in a 202
173 μm mesh 1 m diameter net towed. Trichomes/filaments were picked up and rinsed in
174 filtered seawater. The known numbers of trichomes were then placed in a Nalgene
175 Polycarbonate bottles containing 250 ml of filtered seawater from same station and ^{14}C
176 ($5\mu\text{Ci}$) was added. Further, the same procedure was followed as described for
177 phytoplankton productivity. The phytoplankton and *Trichodesmium*, daily carbon fixation
178 was measured using standard (UNESCO, 1994).

179 **2.6. Nitrogen fixation**

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

184 **2.7. Satellite studies**

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

187 **3. Results**

188 **3.1 Fall Intermonsoon**

189 **3.1.1. Wind, temperature, salinity and nutrients**

190 During the fall inter-monsoon the wind was blowing from the northeast towards
191 the offshore region of the Arabian Sea and wind speed was found to be $5\text{-}6\text{ ms}^{-1}$ (Fig. 2a).
192 These calm conditions supported the dense bloom of the *Trichodesmium thiebautii* at 17°

193 N 70⁰E and 17⁰ N 69⁰E. In this area the water temperature was found to be 28⁰C while
194 mixed layer depth was 5m (coastal) to 70 m (offshore) region (Fig. 3a).

195 The area of *Trichodesmium thiebautii* was marked by occurrence of nitrate and
196 nitrite at non detectable level (Figs. 4a, 4b & 5a). The phosphate and silicate level at
197 these areas was also low, registering at ~ 0.2 μM and ~ 0.5 μM respectively. Other areas
198 (15⁰N 73⁰E and 18⁰N 69⁰E) showed high level of nutrients with high percentage of
199 diatoms and absence of *Trichodesmium*.

200

201 **Insert Fig. 2 here**

202

203 **Insert Fig. 3 here**

204

205 **Insert Fig. 4 here**

206

207 **Insert Fig. 5 here**

208

209

210 **3.1.2. Chlorophyll *a* and *Trichodesmium* distribution**

211 Chl *a* content was high (0.1733 to 5.344 mgm⁻³ ; Fig. 6a) at most of the locations
212 during the fall IntM. The surface Chl *a* maxima observed (Fig. 7a) at areas like 18⁰N
213 70⁰E (0.75 mgm⁻³) and 20⁰N 71⁰E (5.344 mgm⁻³) was on account of the blooms of
214 *Trichodesmium thiebautii* in the offshore region. Similarly at 17⁰N 69⁰E and 18⁰N 70⁰E
215 up to a depth of 30 m, *Trichodesmium* bloom was noticed. Out of the 23 stations
216 sampled 10 stations showed the presence of *Trichodesmium thiebautii*. The highest

217 phytoplankton counts were observed at 18⁰N 70⁰E (15.831 cell nos. x 10⁴L⁻¹) where
218 *Trichodesmium* constituted a major portion. The average total cells counts of
219 phytoplankton was 1.590±3.546 x 10⁴L⁻¹ at the surface and 43.226±95.189 x 10⁶m⁻² in the
220 euphotic zone (Fig. 6b). The number of filaments across transect varied from 0 to
221 10.9570 filaments x 10⁴L⁻¹. The average filament distribution was 6.9993±3.025 x 10⁴L⁻¹
222 at the surface and 9.686±30.720 x 10⁶m⁻² in the euphotic zone (Fig. 6c). At some areas
223 like, 16⁰N 71⁰E, 19⁰N 69⁰E and 20⁰N 70⁰E N the diatom count reached right up to 100 %.
224 However, the *Trichodesmium* stations were invariably marked by low percentages of
225 diatoms and dinoflagellates.

226

227 **Insert Fig. 6 here**

228 **Insert Fig. 7 here**

229

230 ***3.1.3. Primary Production and Nitrogen Fixation***

231 Primary productivity measured during the fall IntM is presented in Fig. 8a. The
232 surface maxima of high primary productivity at 20⁰N 70⁰E and 21⁰N 68⁰E was due to the
233 *Trichodesmium* population. Although, at 21⁰.1N the concentration of Chl *a* was high at
234 40 m due to the presence of the *Trichodesmium* bloom productivity was found to be
235 negligible due to low light at the bottom of the euphotic zone. At other stations, it was
236 observed that the sub-surface Chl *a* maxima due to other phytoplankton rarely coincided
237 with primary productivity maxima. The carbon fixed by *Trichodesmium* varied from 0.43
238 to 20.487 mgCm⁻³d⁻¹. The rate of carbon production was high at 18⁰03.9N where
239 temperature was 29⁰C. The average carbon produced during this season was 8.460±

240 6.504 mgCm⁻³d⁻¹. During our study 12.8 % of the carbon was produced by
241 *Trichodesmium* and the remaining 87.2 % was produced by other phytoplankton as
242 primary producers. The highest value of primary productivity (20.487 mgCm⁻³d⁻¹) was
243 recorded at the surface of 18⁰N 70⁰E, where active growth of *Trichodesmium thiebautii*
244 taking place.

245 The N₂ fixed during this study was 114.110 ± 345.770 μmol Nm⁻³d⁻¹ and
246 varied from 0 to 1252.390 μmolNm⁻³d⁻¹ (Fig. 8b). Higher amounts of nitrogen was fixed
247 at 18⁰N 70⁰E due to the *Trichodesmium* bloom.

248 **Insert Fig. 8 here**

249

250 **3.2 NE Monsoon**

251 ***3.2.1. Wind, temperature and salinity***

252 During the NE Monsoon the wind was blowing from the northwestt and moving
253 along the eastern coast of India (Fig. 2b). The wind speed during this period was found to
254 be <5ms⁻¹. During this season offshore water were showing the effects of winter cooling
255 and it was found that the growth of the *Trichodesmium thiebautii* continued at this time.
256 The temperature data collected, during NE MoN from the NE Arabian Sea concerning
257 temperature is presented in Fig. 3b. The observations and analysis of data made in the
258 present study indicate that the offshore water was largely influenced by the winter
259 cooling lowering the temperatures (Fig. 3b). During this season, *Trichodesmium*
260 *thiebautii* began to appear in the shelf region where the impact of winter cooling had
261 diminished. By the end of the NE MoN it was found that *Trichodesmium erythraeum* had
262 assumed the role of the dominating species of the shelf region.

263 Nutrients concentrations recorded during this season was low (Figs. 4 & 5).
264 However, *Trichodesmium erythraeum* was recorded alongside of *Trichodesmium*
265 *thiebautii* specially in the shelf region. The prevailing calm weather during this period
266 was particularly responsible for the growth of *Trichodesmium* at the sub-surface. The
267 phosphate varied from 0 to 0.35 μM which was low most of the time. The nitrate values
268 ranged from 0 to 0.75 μM and the silicate content recorded was 11.08 μM which was
269 high at the bottom of the euphotic zone, as compared to the surface which was 2.30 μM (
270 Figs. 4d and 5).

271

272 **3.2.2. Chlorophyll *a* and *Trichodesmium* distribution**

273 Phytoplankton biomass in terms of the Chl *a* and total cell counts was reasonably
274 high during this season (Fig. 6a). Average Chl *a* was $0.526 \pm 0.453 \text{ mgm}^{-3}$ at surface and
275 $32.588 \pm 46.851 \text{ mgm}^{-2}$ in euphotic zone (Fig. 6a). Highest Chl *a* was recorded at 21°N
276 69°E and lowest at 12°N 72°E . Similarly average cell density at the surface was
277 $0.112 \pm 0.129 \text{ nos.} \times 10^4 \text{L}^{-1}$ (Fig. 6b). The highest cell counts ($0.606 \text{ nos.} \times 10^4 \text{L}^{-1}$) were
278 recorded at 12°N 74°E and lowest ($0.002 \text{ nos.} \times 10^4 \text{L}^{-1}$) at 21°N 68°E . Filament counts
279 of *Trichodesmium* spp. varied from 0 to 0.616 filaments $\text{nos.} \times 10^4 \text{L}^{-1}$ and average
280 $0.039 \pm 0.119 \text{ filaments} \text{ nos.} \times 10^4 \text{L}^{-1}$ at the surface and $0.214 \pm 0.272 \times 10^6 \text{m}^{-2}$ at the euphotic
281 zone (Fig. 6c).

282 A distinct seasonality was recorded during SK-214, SK-186, FORV-212 and
283 FORV-222 undertaken. During the early NE MoN (SK-214), the concentration of Chl *a*
284 was from 0.187 – 0.507 mgm^{-3} . High concentration of Chl *a* was recorded at 17°N 69°E
285 while low concentration of Chl *a* was found at 15°N 71°E . The sub-surface Chl *a*
286 maxima was found at a depth of 40 m depth at 17°N 69°E , 18°N 67°E , 20°N 66°E , 21°N

287 69°E and 21°N 65°E (Fig. 7b). Out of the 14 stations sampled, 10 samples showed the
288 presence of *Trichodesmium* in the sub-surface waters while others showed its presence at
289 deeper depths (~ 60 m). The total phytoplankton cell counts varied from 0.032 to 0.4352
290 cell nos x 10⁴L⁻¹ at the surface. At two locations (15°N 73°E and 18°N 70°E)
291 *Trichodesmium erythraeum* and *Trichodesmium thiebautii* were found at the depth of 5
292 and 60 m respectively. The highest counts of *Trichodesmium* filaments were found at
293 22°N 67°E (0.0216 filaments x 10⁴L⁻¹) and lowest at 20°N 66°E (0.0022 filaments x 10⁴L⁻¹).
294 During this season diatoms were also recorded in large numbers at 15°N 73°E, 15°N
295 71°E and 18°N 67°E. The *Trichodesmium* percentages in total phytoplankton counts
296 ranged from 0.78 to 35.71 %. The other dominant phytoplankton throughout this season
297 were *Rhizosolenia setigera*, *Nitzschia longissima*, *Thalassiothrix longissima*,
298 *Pyrophaccus horologium* and *Protoperidinium sternii* (Table 1).

299 The Chl *a* during the mid NE MoN (SK-186) was much higher at most of stations,
300 compared to early NE MoN. It ranged from 0.173 to 2.6mgm⁻³. Higher concentrations of
301 chl *a* were found at 21°N 69°E where diatoms were dominant (93.94 %) followed by
302 dinoflagellates (4.55 %) and other algae like (1.52 %). Sub-surface Chl *a* maxima was
303 observed (Fig. 7b) at some locations 17°N 72°E, 17°N 70°E, 17°N 67°E, 19°N 66°E, 20°N
304 66°E, 20°N 66°E, and 17°N 68°E during this season. The total phytoplankton cell counts
305 ranged from 0.002 to 0.459 cell nos x 10⁴L⁻¹. Higher counts were found at 17°N 70°E
306 where, diatoms made up 94.44 % and dinoflagellates formed 5.56% of the total
307 phytoplankton population. The presence of *Trichodesmium* (25 to 28.57 %) was found in
308 the 5 out of the 25 stations sampled at the surface. *Trichodesmium erythraeum* was found
309 to be more dominant than *Trichodesmium thiebautii*. The *Trichodesmium* filaments was

310 more (760 filaments L⁻¹) at 18⁰N 69⁰E. The other species that were observed during this
311 period were *Thalassiothrix longissima*, *Chaetoceros dictyaeta*, *Thalassiosira subtilis*,
312 *Coscinodiscus nitidus*, *Navicula* spp., *Nitzschia seriata*, *Nitzschia closterium*,
313 *Rhizosolenia setigera* and *Chaetoceros lorenzianus* (Table 1).

314

315 **Insert Table 1 here**

316

317 During late the NE MoN (part of FORV-212 and FORV-222) it was found that
318 values for Chl *a* varied from 0.132 – 0.960 mgm⁻³ with high values at 17⁰N 69⁰E due to
319 the presence of the *Trichodesmium erythraeum* bloom. The sub-surface Chl *a* maxima
320 was found at a depth of ~ 40-60 m specially at 16⁰N 72⁰E, 10⁰N 74⁰E, 12⁰N 72⁰E and
321 14⁰N 73⁰E. The presence of *Trichodesmium* was observed in 7 out of the 10 stations
322 sampled in this month. The total phytoplankton counts ranged from 0.0078 to 0.2508 cell
323 nosx10⁴L⁻¹. Higher phytoplankton cell counts were found at 17⁰N 69⁰E due to the
324 presence of the *Trichodesmium erythraeum* bloom. The *Trichodesmium* filaments ranged
325 from 0 to 0.6160 filaments x 10⁴L⁻¹. Further a *Noctiluca* bloom was also recorded with
326 the *Trichodesmium* bloom at 10⁰N 64⁰E and 17⁰N 69⁰E. It appears that the *Noctiluca*
327 bloom may have followed the *Trichodesmium* bloom in the Arabian Sea, an idea which
328 provides us with new insights in the study of phytoplankton in the Arabian Sea. A full
329 growth of *Noctiluca miliaris* bloom was stuck at 17⁰N 70⁰E.

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334 **3.2.3. Primary Productivity and Nitrogen Fixation**

335 The primary productivity during this period was high and ranged from 0.907-
336 2572.1 mgCm⁻³d⁻¹ (av.: 217 mgCm⁻³d⁻¹) at surface and 4.284 mgCm⁻²d⁻¹ in the euphotic
337 zone (Fig. 8a).

338 The primary productivity maxima at 18⁰N 70⁰E (40 m) coincided with the
339 *Trichodesmium* bloom in the water column. Similarly, at 19⁰N 70⁰E, high productivity at
340 both, the surface and below 40 m was also due to *Trichodesmium*. The average rate of
341 primary production during the bloom of *Trichodesmium* spp. was 0.356 ± 0.096 mgCm⁻³
342 d⁻¹. At the surface, the carbon production varied from 55.85 to 706.66 mgCm⁻³d⁻¹.
343 Higher rate of primary production was observed at 22⁰N 67⁰E, due to the dense bloom of
344 the *Trichodesmium*. The primary production by *Trichodesmium thiebautii* and
345 *Trichodesmium erythraeum* during the NE monsoon was of the same order i.e. 0.392 and
346 0.378 mgCm⁻³d⁻¹ respectively. When *T. erythraeum* bloom was prominent in the water
347 column however it was found that primary production was high (10.059 mgCm⁻²d⁻¹)
348 compared to the primary production by *T. thiebautii* (6.156 mgCm⁻²d⁻¹). The percentage
349 of primary productivity due to *Trichodesmium* spp. in the total productivity was around
350 0.11 % .

351 During mid NE MoN (SK-186), primary productivity was low at the surface and
352 high at deeper depths. At 15⁰N 72⁰E, the highest primary productivity and Chl *a* was
353 observed at a depth of 50 m due to the *Trichodesmium* bloom. Similarly carbon
354 production was observed at 18⁰N 69⁰E at 60 m due to the bloom of the *Trichodesmium*

355 *thiebautii*. It was observed that *Trichodesmium* played a role of primary producer at the
356 surface like at 22⁰N 68⁰E as well as throughout the water column.

357 The amount of primary production due to *Trichodesmium* during late NE MoN
358 varied from 1.61 to 8.25 mgCm⁻³d⁻¹. The average amount of carbon produced was 7
359 mgCm⁻³d⁻¹. The observations made during this season indicate that *Trichodesmium*
360 contributed a major portion (60 %) to the carbon produced at this time. Higher amount of
361 carbon production (65.85 %) by *Trichodesmium* was seen at area 14⁰N 73⁰E while lower
362 production was recorded at 13⁰N 70⁰E (0.14 %).

363 The N₂ fixation during this season ranged from 0 -13.598 μmolNm⁻³d⁻¹ at the
364 surface and 0 - 31.597 μmolNm⁻²d⁻¹ at the euphotic zone and depended upon the
365 intensity of the bloom. The average N₂ fixed during this season was 4.432±13.598
366 μmolNm⁻³d⁻¹ (Fig. 8b). The rate of N₂ fixation also varied species wise. The amount of
367 nitrogen fixed by *T. erythraeum* varied from 0 to 2.4 μmol Nm⁻³d⁻¹. In the column, the
368 nitrogen fixed by *T. erythraeum* was found to be much higher (23 ± 4.77 μmol Nm⁻²d⁻¹)
369 than that fixed by *T. thiebautii* (14.09 ± 4.074 μmol Nm⁻²d⁻¹). During the late NE MoN
370 the total nitrogen fixed by *Trichodesmium* spp. varied from 0 to 70.409 μmolNm⁻³d⁻¹
371 with an average of 14.002 ± 23.772 μmolNm⁻³d⁻¹ (n=8). Higher amount of nitrogen was
372 fixed at 12⁰N 74⁰E and lower amount of it was fixed at 16⁰N 72⁰E. The amount of N₂
373 fixed by *T. erythraeum* varied from 1.25 to 37.25 μmolNm⁻³d⁻¹ which was much higher
374 than that fixed by *T. thiebautii* (0 to 32.67 μmolNm⁻³d⁻¹) during late the NE MoN period.

375

376 **3.3. Spring Intermonsoon**

377 **3.3.1. Wind, Temperature and Salinity**

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

386

387 **3.3.2. Chlorophyll *a* and *Trichodesmium* distribution**

388 During the spring IntM the Chl *a* highly ranged from 0.074 -5.905 mgm^{-3} . The
389 average Chl *a* was $0.759\pm 1.025 \text{ mgm}^{-3}$ at the surface and $14.749\pm 13.828 \text{ mgm}^{-2}$ in the
390 euphotic zone (Fig. 6a). At the surface high Chl *a* was found at $20^{\circ}\text{N } 70^{\circ}\text{E}$ and low at
391 $15^{\circ}28.76\text{N}$. The total phytoplankton cell counts ranged from 0.025-41.992 cell nos. \times
392 10^4L^{-1} . The average cell counts were $2.033\pm 7.302 \text{ cell nos. } \times 10^4\text{L}^{-1}$ at the surface and
393 $16.929\pm 26.176 \text{ cell nos. } \times 10^6\text{m}^{-2}$ (Fig. 6b) Similarly *Trichodesmium* filaments were also
394 high at the same position as the total cell counts. The filaments varied from 0-40.074 nos.
395 $\times 10^4\text{L}^{-1}$ at the surface and 0.021-100.301 nos. $\times 10^6\text{m}^{-2}$. The average *Trichodesmium*
396 filaments were 2.381 ± 8.313 at surface and 6.115 ± 20.737 at the column (Fig. 6c).

397 In the early spring IntM the concentration of Chl *a* varied from 0.169 – 2.741
398 mgm^{-3} . The high Chl *a* was found at $19^{\circ}\text{N } 66^{\circ}\text{E}$ (2.741 mgm^{-3}) was mainly due to the
399 bloom of *Noctiluca miliaris*. The phytoplankton counts ranged from 0.0252 to 1.1164 cell

400 nos. $\times 10^4 L^{-1}$. The high cell count found at $19^0 N 66^0 E$ was also due to the *Noctiluca*
401 *miliaris bloom*. During this month a total of 13 stations were studied out of which only 4
402 stations showed the presence of *Trichodesmium*. The observations indicate that part of
403 the NE Arabian Sea, where the winter cooling affect (low temperature and high
404 nutrients), supports *Noctiluca* and the other part of the Sea, where the nutrient
405 concentration was low and high temperatures prevail, is for *Trichodesmium* area (Table
406 1).

407 During late spring IntM concentration of Chl *a* varied from 0.074 to $5.905 \mu g L^{-1}$
408 with the highest values recorded at $20^0 N 70^0 E$ and the lowest values recorded at $15^0 N$
409 $70^0 E$. Phytoplankton cell counts ranged from 0.033 to 41.991 cell nos. $\times 10^4 L^{-1}$. The
410 phytoplankton cell density showed peak values in coastal waters ($21^0 N 69^0 E$, $20^0 N 70^0 E$
411 and $15^0 N 73^0 E$) mostly north of $20^0 N$ (Fig. 7c). *Trichodesmium* was the major component
412 of the phytoplankton averaging 3.8063 ± 10.3463 filaments $\times 10^4 L^{-1}$ (n=29) with high
413 concentrations (40.0737 filaments $\times 10^4 L^{-1}$) at $20^0 N 70^0 E$ in the coastal waters off
414 Gujarat (Fig. 6c). In general, diatoms and dinoflagellates were less numerous, averaging
415 0.2936 and 0.0630 cells L^{-1} respectively. However at some locations, like $20^0 N 70^0 E$ to
416 $20^0 N 72^0 E$ the domination of diatoms was noticed. The dominant diatom, *Nitzschia* sp.
417 (2.3025 cells $\times 10^4 L^{-1}$) was found at $20^0 N 70^0 E$. Dinoflagellates reached a maximum of
418 1.1666 cells $\times 10^4 L^{-1}$ at $20^0 N 70^0 E$, which was adjacent to the diatom dominated stations
419 indicating succession of groups. The area between $16-18^0 N$ in coastal waters was
420 characterized by domination of dinoflagellates. For example, at areas like $16^0 N 73^0 E$,
421 $18^0 N 72^0 E$ and $17^0 N 72^0 E$ dinoflagellates like *Ceratium* spp., *Peridinium* spp., and
422 *Prorocentrum* spp. were dominant organisms. At the edge of the shelf, a mixed

423 community of diatoms, dinoflagellates and *Trichodesmium* dominated the flora specially
424 at 21⁰N 69⁰E, 20⁰N 70⁰E, 15⁰N 73⁰E which was in coastal as well as offshore waters
425 (Fig. 6c). The other areas like 21⁰N 69⁰E, 18⁰N 72⁰E and 17⁰N 72⁰E also supported high
426 counts of *Trichodesmium erythraeum*. The *Trichodesmium erythraeum* was well
427 distributed during this time of year and mostly in succession to the dinoflagellates (south
428 of 18⁰S) and the diatoms (north of 18⁰N). Diatoms were the second most important
429 group of organisms that were encountered during the present study, they were also the
430 most diverse in nature.

431

432 **3.3.3. Primary Production and Nitrogen Fixation**

433 During the spring IntM primary productivity estimated was 1.056-3489.104
434 mgCm⁻³d⁻¹ which coincided with the *Trichodesmium* bloom area. The average primary
435 productivity was 255.095±668.570 mgCm⁻³d⁻¹ (n=32) at the surface and
436 2046.857±3810.722 mgCm⁻²d⁻¹ (n=35) at the euphotic zone (Fig. 8a).

437 In the early spring IntM, at location 22⁰N 66⁰E the *Trichodesmium* was found
438 aggregated at the surface. The primary production due to *Trichodesmium* during this
439 season varied from 0.69 to 0.88 mgCm⁻³d⁻¹. The average was found to be 0.79 ± 0.09
440 mgCm⁻³d⁻¹ (n=3). About 29 %, out of the total carbon production recorded, was produced
441 by *Trichodesmium*.

442 In the late spring IntM at 21⁰N 69⁰E and 15⁰N 73⁰E, the high values of Chl *a* and
443 primary productivity were on account of the *Trichodesmium* bloom throughout the water
444 column. *Trichodesmium erythraeum* was the only species found during this season. The
445 average carbon production at surface was 131.150 ± 80.67 mgCm⁻³d⁻¹ (n=29). Higher

446 rates of primary production in the water column were recorded at locations 17⁰N 72⁰E,
447 21⁰N 69⁰E, 16⁰N 71⁰E and 15⁰N 73⁰E. During this season *Trichodesmium* contributed
448 nearly 30 % to the total primary production.

449 Nitrogen fixation rate during the spring IntM was reasonably high
450 (271.814±950.263 $\mu\text{molNm}^{-3}\text{d}^{-1}$) at the surface and 720.348±2405.996 $\mu\text{molNm}^{-2}\text{d}^{-1}$ in
451 the column (Fig. 8b). The average amount of nitrogen fixed was 1.2±1.1 $\mu\text{molNm}^{-3}\text{d}^{-1}$
452 (n=3). The average nitrogen fixed by *T. thiebautii* was higher (1.75± 0.25) than that fixed
453 by *T. erythraeum*. At 20⁰N 68⁰E and 22⁰N 66⁰E, higher amount of nitrogen was fixed by
454 *T. thiebautii* whereas, at 22⁰N 66⁰E the major contributor to N₂-fixation was *T.*
455 *erythraeum*.

456 During late spring IntM the average N₂-fixed by *T. erythraeum* was 299.81 ±
457 995.54 $\mu\text{molNm}^{-3}\text{d}^{-1}$ (n=29). At the surface it varied from 0 to 4580.42 $\mu\text{molNm}^{-3}\text{d}^{-1}$. The
458 rate of nitrogen fixation was high at 20⁰N 70⁰E and at column level N₂-fixated was in the
459 range of about 9.49 to 11471.50 $\mu\text{mol Nm}^{-3}\text{d}^{-1}$.

460

461 **4. Discussion**

462 The Arabian Sea experiences hydrographic changes, which are related to the
463 monsoon system (Shetye, et al., 1990, Brock and McClain, 1992, Banse and English,
464 1993, 2000, Madhupratap, et al., 1996). The region of study undertaken fall under the
465 influence of both the NE and the SW monsoon. During the onset of the SW monsoon
466 season, i.e. June, the west coast of India experiences intense upwelling, which is first
467 visible off the southern tip of India. During this period, continental slope waters begin to
468 shoal upward into the shelf region causing substantial cooling, which is observed in the

469 satellite sea surface temperature imagery (Sreejith and Shenoi, 2002; Vinayachandran et
470 al., 2004). As the season advances the upwelling signatures migrate northward, covering
471 the entire coast of India by late July (Shetye, et al., 1990). This process is responsible for
472 bringing in the much needed new nutrients (DeSouza, et al., 1996) that help to trigger
473 large phytoplankton blooms by early August (Goes, et al., 1992) and continue upto
474 October.

475 The NE monsoon, marks a period wherein the offshore region receives a
476 substantial amount of new nutrients (Kumar et al., 2009). Satellite derived measurements
477 of Chl *a* concentrations in the region of the NE Arabian Sea start to increase by
478 December and tend to reach peak values by February (Banse and English, 2000). The
479 data collected during early NE MoN showed that, the nitrate concentrations were
480 undetectable at 18^o05.98, 18^o10.47N and 21^o17.81N where as low (<0.97 μM) at most of
481 the NE Arabian Sea, presumably because a significant fraction of nutrients had already
482 been used by phytoplankton (Parab, et al., 2006), whereas other nutrients such as
483 phosphate and silicate were present. Considering the nutrients enrichment during NE
484 MoN the phytoplankton growth in the water column appears to be reduced by an active
485 grazing by zooplankton (Landry, et al., 1998; Caron and Dennet, 1999) a notion that is
486 reinforced by the elevated level of ammonium concentration found in the water column
487 during early NE MoN estimated at the order of 0.57-6.13 μM of ammonia.

488 In our study, we found that during low wind speeds (< 5 ms⁻¹), thick blooms of
489 *Trichodesmium* spp. were observed (Fig. 2). However wind speed >6 knot resulted in
490 disappearance of the *Trichodesmium* bloom. Earlier studies (Chang et al., 2000) have
491 reported that besides wind and water temperature, low nutrients were also factors that

492 favoured growth of the *Trichodesmium*. In the Arabian Sea, during the non monsoonal
493 period, the upper layers of the water were devoid of nutrients. In such a situation,
494 *Trichodesmium* had an advantage over other phytoplankton, as it could fix nitrogen and it
495 could make use of phosphate from subsurface layers. The stratification of the water
496 column during low wind conditions (as seen during mid and late NE MoN and early
497 spring IntM) was also an important factor for the *Trichodesmium* blooms to develop and
498 persist in the Arabian Sea. Associations between abundance of *Trichodesmium* and
499 vertical stratification have been reported in the North Pacific sub-tropical gyre (Capone,
500 1983). The average mixed layer depth during our study was 10-40m, during
501 *Trichodesmium* bloom.

502 The bloom of *Trichodesmium thiebautii* observed during the fall intermonsoon
503 continued during the early NE MoN where out of the 15 stations sampled 13 showed the
504 presence of a *Trichodesmium thiebautii* bloom. The filaments were distributed
505 throughout the water column in the euphotic zone. Deep Chl *a* maxima was noticed at a
506 *Trichodesmium thiebautii* concentrations were also observed during mid NE MoN. Out of
507 the 18 stations sampled, 7 stations showed the presence of a mixed population of
508 *Trichodesmium erythraeum* and *Trichodesmium thiebautii*. Surface Chl *a* maxima was
509 observed at 15^o14.21N and was largely attributed to *Trichodesmium thiebautii* and
510 *Trichodesmium erythraeum*.

511 During late NE MoN and early spring IntM, mixed populations of *Trichodesmium*
512 *erythraeum* and *Trichodesmium thiebautii* were noticed at 20^o29.1N, 19^o3.7N and
513 15^o8.57N. However, in the late spring IntM, 29 stations out of the 35 stations sampled
514 supported *Trichodesmium erythraeum* blooms. The rates of primary production during

515 the *Trichodesmium* bloom were considerably higher than those recorded during non
516 bloom time in the North Atlantic Ocean , which usually ranged from 804 to 1080 mgCm⁻²
517 d⁻¹(Carpenter, et al., 2004). Several observations have been made in the eastern
518 equatorial Atlantic during *Trichodesmium* bloom where Bauerfeind (1987) noted a mean
519 rate of production was 247 mgCm⁻²d⁻¹ between January and May, 1979 over ten sections
520 between 2⁰S and 3⁰N at the 22⁰W meridian. In March and April of 1989, at 18⁰N and
521 30⁰W (NW of Cape Verde Islands) primary production over an 11 days period averaged
522 about 500 mgCm⁻²d⁻¹ (Jochme, et al., 1993). Claustre and Marty (1995) measured
523 primary production at 20⁰N, 31⁰W in autumn 1991 and spring 1992 and where rates
524 averaged 352 ± 68 and 267 ± 53 mgCm⁻²d⁻¹ respectively. At the oligotrophic EUMELI
525 JGOFS at 22⁰N and 32⁰W, rate of the primary production were ranged from 289 to 276
526 mgCm⁻²d⁻¹ (Morel, et al., 1996). Steven (1971) reported an annual average of 288 mgCm⁻²
527 d⁻¹ for a station off the NW coast of Barbados. Beers, et al. (1968) found an annual mean
528 of 110 mgCm⁻²d⁻¹ for a station in the Caribbean off Jamaica. Chang, et al. (2000)
529 reported that *Trichodesmium* contribution was in the range of 0.003 to 2.27 % of primary
530 productivity in the Kuroshio.

531 We have observed difference in the contributions made by *Trichodesmium*
532 *erythraeum* and *Trichodesmium thiebautii* towards the organic productivity during our
533 study. In the fall inter-monsoon season about 12 % of total surface primary production
534 was due to only *T. thiebautii* whereas during the spring inter-monsoon it was 30 %
535 because of the presence of *Trichodesmium erythraeum*. Capone, et al., 1998 reported 23
536 % of total surface primary production was due to *Trichodesmium erythraeum*. The
537 explanation for the high primary production rates could be partially due to the NE

538 monsoon, which generates substantial convective mixing, resulting in deep mixed layers
539 in the northern Arabian Sea and growth of diatom population (Lee, et al., 2000; Weller,
540 et al., 1998).

541 Both biomass and productivity of *Trichodesmium* showed large seasonality.
542 Primary productivity due to *Trichodesmium* was as low as 8-15 mgCm⁻³d⁻¹ during NE
543 MoN (8-15 mgCm⁻²d⁻¹). Another important factor for the success of *Trichodesmium* in
544 the Arabian Sea may be the iron input brought about through upwelling and /or
545 atmospheric deposition and land runoff (Witter, et al., 2000). In the present study, large
546 seasonality was also observed in the nitrogen fixation. High N₂-fixation rate values were
547 recorded during the fall IntM (1108 ± 3511 μmolNm⁻²d⁻¹; n=13) followed by spring IntM
548 (720 ± 2406 μmolNm⁻²d⁻¹; n=32), however lower values were observed during NE MoN
549 (24 ± 32 μmolNm⁻²d⁻¹; n=28). Previous studies on the rates of N₂-fixation by
550 *Trichodesmium* in the sub-tropical North Atlantic were generally much lower (< 10
551 μmolNm⁻²d⁻¹) typically because of the low biomass of the *Trichodesmium* spp.
552 (Carpenter, et al., 2004). Published report (Goering, et al., 1966) did indicate the volume
553 specific rates of N₂-fixation from two cruises off the north-eastern coast of South
554 America. However, they did not provide areal estimates, on the other hand, in south-
555 western N. Atlantic they reported the mean rate to be 108 μmolNm⁻²d⁻¹. Carpenter and
556 Romans (1991) postulated rates of N₂-fixation for *Trichodesmium* of 710 to 3600
557 μmolNm⁻²d⁻¹ based on the high abundance of *Trichodesmium* encountered in the tropical
558 portion of a transect through the Atlantic. In contrast to the above studies, Lipschultz and
559 Owens (1996) produced a much smaller estimate for the contribution of *Trichodesmium*
560 in the same region. Capone, et al. (2005) reported the average N₂-fixation rate (898

561 $\mu\text{molNm}^{-2}\text{d}^{-1}$) in the same study area. In the Southern East China Sea, Chang, et al.
562 (2000) reported that the N_2 -fixation rate varied from 0.1 to $59.4 \mu\text{molNm}^{-2}\text{d}^{-1}$. This was
563 much lower than the results obtained during the our study in the NE Arabian Sea (Table
564 2). The Arabian Sea is known as an active site for nitrogen fixation (Devassy, et al.,
565 1978, Capone, et al., 1998). One factor that favors the establishment of N_2 -fixers in the
566 Arabian Sea is the NO_3^- deficit arising from local and far-field denitrification. The NO_3^- :
567 PO_4^{3-} ratio was lower than 15 at all depths in the Arabian Sea (Morrison, et al., 1998). As
568 the N- deficient sub-surface waters were brought to the surface through upwelling and
569 vertical mixing, the nutrients were taken up by the phytoplankton in a (Redfield) ration of
570 15 (by atoms), and this led to a surplus of PO_4^{3-} in surface waters. This excess PO_4^{3-} is
571 observed most strikingly within the coastal anoxic zone where PO_4^{3-} concentrations in
572 excess of $3 \mu\text{M}$ occur when denitrification removes all dissolved NO_3^- . The organisms
573 that fix N_2 also require relatively large amount of iron (Fe), which could be supplied by
574 atmospheric deposition, mobilization from shelf and slope sediments and upwelling.
575 Consequently, blooms of *Trichodesmium* spp. occur over large parts of the Arabian Sea
576 mostly during the spring inter-monsoon season when surface waters are NO_3^- depleted.
577 The calmness of the sea during this season allows the establishment of warm surface
578 waters, reduced turbulence and high euphotic zone light intensities, conditions that also
579 favour nitrogen fixation (Devassy, et al., 1978, Capone, et al., 1997, Capone, et al.,
580 1998). Apart from the experimentally measured N_2 -uptake rates (Dugdale, et al., 1964,
581 Capone, et al., 1998), evidence for N_2 -fxation in the Arabian Sea has been provided by
582 data on natural isotope abundance in NO_3^- (Brandes, et al., 1998). The estimated N_2 -

583 fixation rate for the region is 3.3 TgNyr^{-1} (Bange, et al., 2000) which is speculated to play
584 an important role in understanding biogeochemistry of the region.

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

589
590 **Insert Table 2 here**
591
592

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

603 **Insert Fig. 9 here**

604 Another important feature observed during the NE MoN was that *Trichodesmium*
605 *thiebautii* occurred as deep as 70 – 80 m in the water column. Phosphate availability may
606 be an important factor for *Trichodesmium* to appear (Karl, et al., 1992). In the NE
607 Arabian Sea, the contribution of *Trichodesmium* to total phytoplankton counts varied

608 from 1% to 95 %, with the highest counts being observed in the spring IntM. The
609 dominant phytoplankton species in the *Trichodesmium* bloom were *Trichodesmium*
610 *erythraeum*, *Trichodesmium thiebautii*, *Navicula* spp., *Nitzschia closterium*, *Nitzschia*
611 *seriata*, *Rhizosolenia setigera*, *Rhizosolenia shrubsolei*, *Chaetoceros curvisetus*,
612 *Noctiluca miliaris*, *Melosira moniliformis*, *Chaetoceros decipiens*, *Rhizosolenia hebetata*
613 and *Thalassiothrix frauenfeldii*.

614 Another noteworthy observation made during the present investigation was the
615 occurrence of mixed blooms of *Trichodesmium erythraeum* and *Noctiluca miliaris* from
616 late NE MoN and early spring IntM in the shelf region, whereas, in the offshore region,
617 *Noctiluca* dominated the bloom, this coincided with a reduction in the density of the
618 *Trichodesmium* filaments. Further, unique occurrence of isolated patches of decomposed
619 filaments in combination with *Noctiluca* at a few stations coupled with elevated nutrient
620 suggests that, the post *Trichodesmium* bloom triggers the *Noctiluca miliaris* bloom in the
621 Arabian Sea. It is a well known fact that the Arabian Sea becomes oligotrophic during
622 the late NE MoN, which supports the occurrence of a *Noctiluca miliaris* (Gomes et al.,
623 2008; 2009). Winter convection (February-March) that brings high nutrients to surface
624 water in the NE Arabian Sea triggers blooms of the *Noctiluca miliaris*. Subsequently, in
625 the Arabian Sea *Noctiluca* and *Trichodesmium* blooms coexist with high counts of
626 *Navicula* sp., *Nitzschia closterium*, *Nitzschia seriata* and *Thalassiosira subtilis*. However
627 *Trichodesmium* spp. which contributes 0.11 to 60 % of total primary production of the
628 Arabian Sea remains important.

629 It appears that a sizable portion of nitrogen will be brought back to the surface
630 layer, (may be NO_3), which could support phytoplankton productivity (new production)

631 in the Arabian Sea. On analyzing the data we collected from all the stations, we found
632 that the organic carbon produced by *Trichodesmium* in the region was about
633 0.263TgCyear^{-1} , this value was, in fact very close to the amount of nitrogen fixed by the
634 *Trichodesmium* in the region during same period, which was estimated to be about
635 $0.2976\text{TgNyear}^{-1}$. At times large amounts of biomass get accumulated at surface during
636 *Trichodesmium* bloom in the Arabian Sea. This cyanobacteria is effective for N_2 fixation,
637 but not as primary producer and hence is responsible for the matching carbon fixation and
638 nitrogen fixation quantity ratio nearing one. Thus the presence of *Trichodesmium* spp.
639 recorded from November to April in the Arabian Sea (Fig. 9) is a important factor
640 responsible for maintaining the ecosystem of the Arabian Sea during oligotrophic
641 conditions.

642
643

644 **5. Conclusions**

645
646

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

655

656 **Acknowledgment**

657 We deeply appreciate the encouragement and support received from our Director, Dr. S.
658 R. Shetye while conducting this study. This study was carried out under the Ocean Color
659 Project with financial assistance from the Space Application Centre (SAC), Ahmedabad.
660 A DST Fellowship to S. G. Parab is also gratefully acknowledged.

661

662

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898

899 **List of Tables**

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902

1. Dominant phytoplankton in the Arabian Sea
2. Historical data of N₂ fixation by *Trichodesmium* studies in the world ocean

903

Table(s)

904 **Table 1** Dominant phytoplankton in the Arabian Sea.
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| | Surface | | | Column | | |
|------------------------|--|---------------------------------|-------------------------------------|--|--|---------------------------------------|
| Fall IntM | <i>Trichodesmium thiebautii</i> | <i>Nitzschia Closterium</i> | <i>Amphora Hyaline</i> | <i>Chaetoceros socialis</i> | <i>Melosira moniliformis</i> | <i>Chaetoceros Danicus</i> |
| NE MoN | <i>Gymnodinium gracile</i> | <i>Prorocentrum minimus</i> | <i>Noctiluca milaris</i> | <i>Trichodesmium thiebautii</i> | <i>Nitzschia longissima</i> | <i>Noctiluca miliaris</i> |
| Spring IntM | <i>Trichodesmium erythraeum</i> | <i>Noctiluca miliaris</i> | <i>Coscinodiscus marginatus</i> | <i>Navicula delicatula</i> | <i>Trichodesmium erythraeum</i> | <i>Rhizosolenia stolterfothii</i> |

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Table 2

| Location | Sampling period | Mean Rate ($\mu\text{molN m}^{-2}\text{d}^{-1}$) | SE | n | Method | Source |
|---|------------------------|--|-----------|----------|-------------------|---------------------------|
| Southwestern N. Atlantic | Nov 1964 | 41 | 7.6 | 19 | $^{15}\text{N}_2$ | Goering et al., 1966 |
| 0-24 ⁰ N, 45-66 ⁰ N | May 1965 | 108 | 24 | 17 | uptake | |
| Carribbean, 12-22 ⁰ N | | 161 | 20 | 12 | AR | Carpenter and Price, 1977 |
| Bermuda Atlantic | 1995-1997 | 41 | | 14 | $^{15}\text{N}_2$ | Orcutt et al., 2001 |
| Time-Series studies | | | | | uptake | |
| N. Pacific, 21 ⁰ N, 159 ⁰ W | 1972 | 134 | | 2 | AR | Gunderson, 1976 |
| East China Sea, 10-25 ⁰ N | | 126 | 49 | 32 | AR | Saino, 1977 |
| Hawaii Ocean Time-Series/station ALOHA | 1990-1992 | 84 | 43 | 8 | AR | Karl et al., 1997 |
| Arabian Sea, 7-10 ⁰ N | May 1995 | 35 | 7.4 | 9 | AR | Capone et al., 1998 |
| Arabian Sea, 10 ⁰ N bloom | May 1995 | 99 | 25 | 9 | AR | Capone et al., 1998 |
| Coastal Tanzania (bloom-upper 0.5m) | 1975-1999 | 59 | | | AR | Lugomela et al., 2002 |
| Gulf of Mexico | July 2000 | 85 | 18 | 4 | $^{15}\text{N}_2$ | Holl et al., 2007 |
| | | | | | uptake | |
| Western North Pacific | Nov-Dec 2007 | 538 | | 4 | AR | Kitajima et al., 2009 |
| 0-12 ⁰ N | May-June 2008 | 939 | | 3 | | |
| 16-24.5 ⁰ N | | | | | | |
| Atlantic Ocean | Nov-Dec 2007 | | | | AR | Fernandez et al., 2010 |
| 30 ⁰ N to 30 ⁰ S | April-May 2008 | | | | | |
| North Gyre, | | 25 | | | | |
| Equator | | 66 | | | | |
| South Gyre | | 3 | | | | |
| Arabian Sea (12-22 ⁰ N and 65-72 ⁰ E) | | | | | | |
| Fall Intermonsoon | Nov 2001 | 1108.15 | 973.8 | 13 | Trichome based | Present study |
| NE monsoon | Jan-Feb | | | | | |
| | 2003,2004; | 24.75 | 5.9 | 28 | (Capone et. al., | Present study |
| | Dec 2004 | | | | 1998) | |
| Spring Intermonsoon | April 2000; | 720.35 | 425.3 | 32 | | Present study |
| | March 2003, 2004 | | | | | |

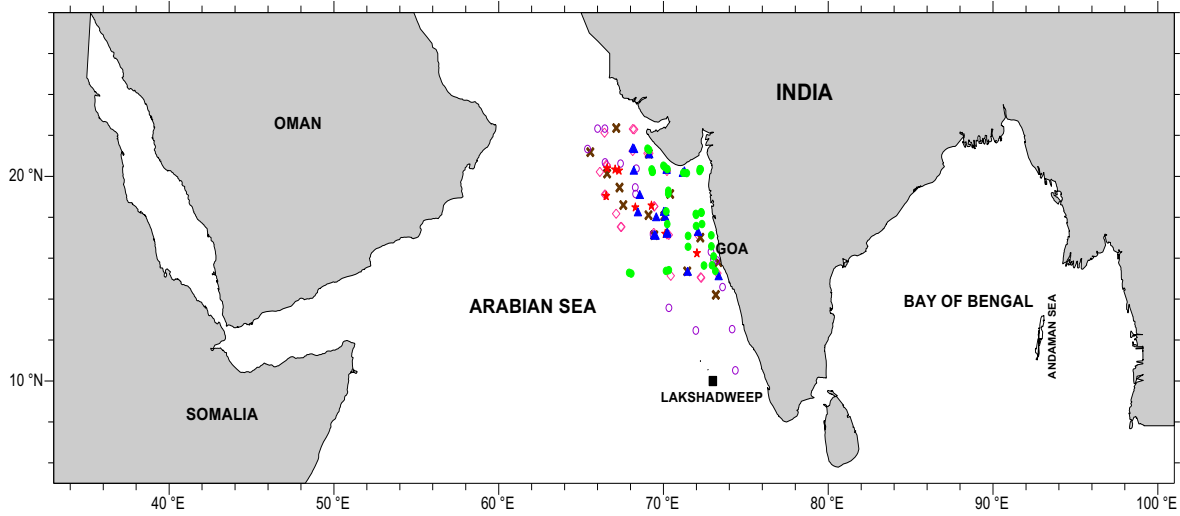
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Figure captions

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1. Study area showing sampling positions.
2. The pattern of wind direction during (a) fall intermonsoon (b) NE monsoon and (c) Spring intermonsoon.
3. Variations in water temperature ($^{\circ}\text{C}$) and salinity (psu) during (a) fall intermonsoon (b) NE monsoon and (c) Spring intermonsoon.
4. Variations in nutrients during different seasons (a) Nitrate (b) Nitrite (c) Phosphate and (d) Silicate.
5. Vertical profiles of nutrients during (a) fall intermonsoon (b) NE monsoon and (c) Spring intermonsoon.
6. Seasonal distribution of (a) Chlorophyll *a* (b) Phytoplankton cell density and (c) *Trichodesmium* filaments. The sets of panels at the left side are surface and right side are column.
7. Seasonal distribution of (a) Primary Productivity and (b) Nitrogen fixation during *Trichodesmium* bloom. The sets of panels at the left side are surface and right side are column.
8. Depth wise distribution of Chlorophyll *a* and Phytoplankton cell counts (including *Trichodesmium* spp.) during *Trichodesmium* bloom.
9. Chlorophyll *a* from OCM in the Arabian Sea during different months.

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▲ SK 171 ✕ SK 214 ○ FORV 222

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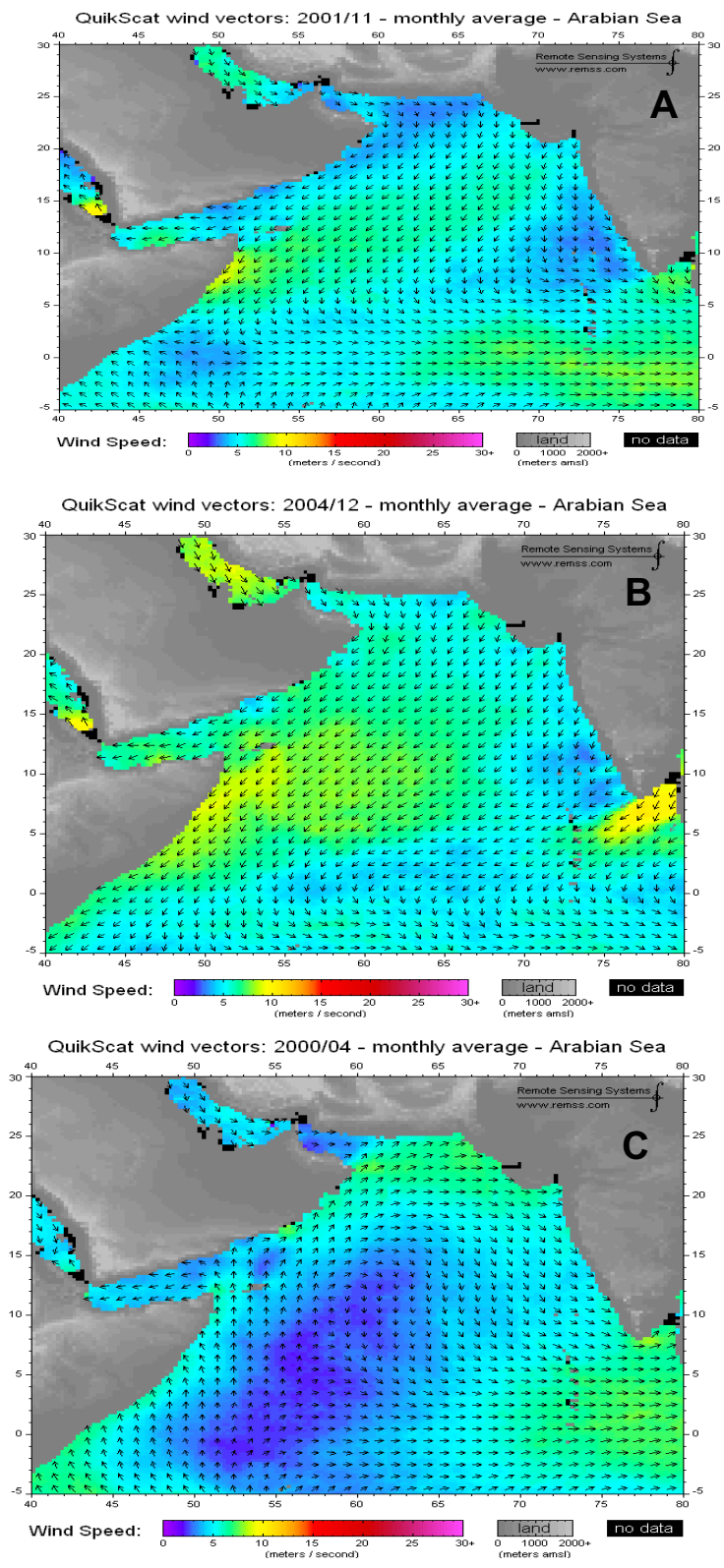
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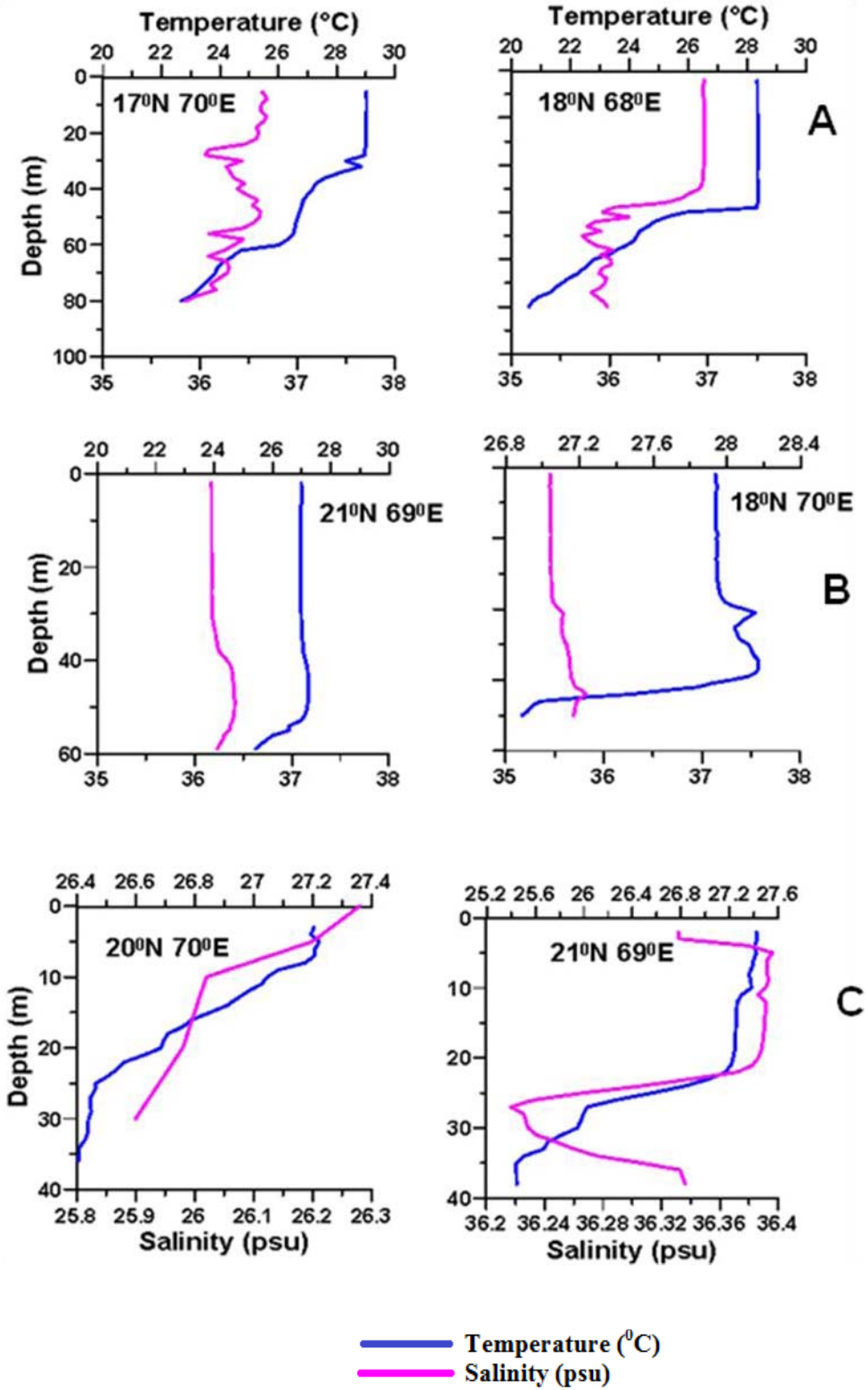
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Fig. 1



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Fig. 2



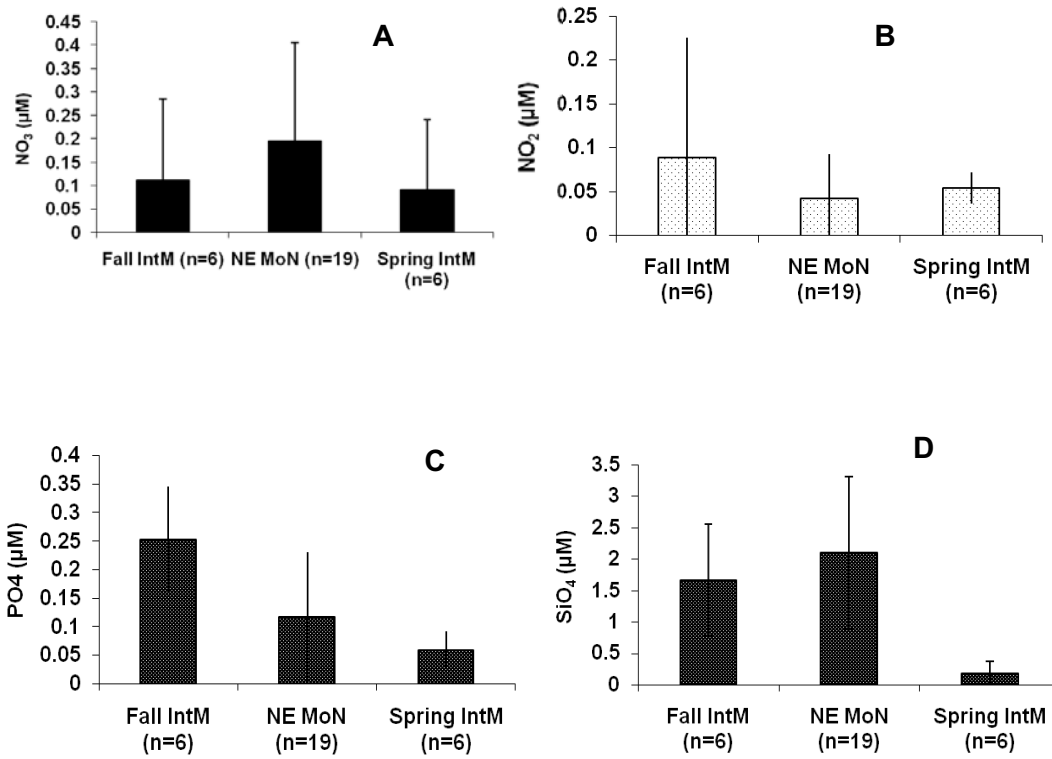
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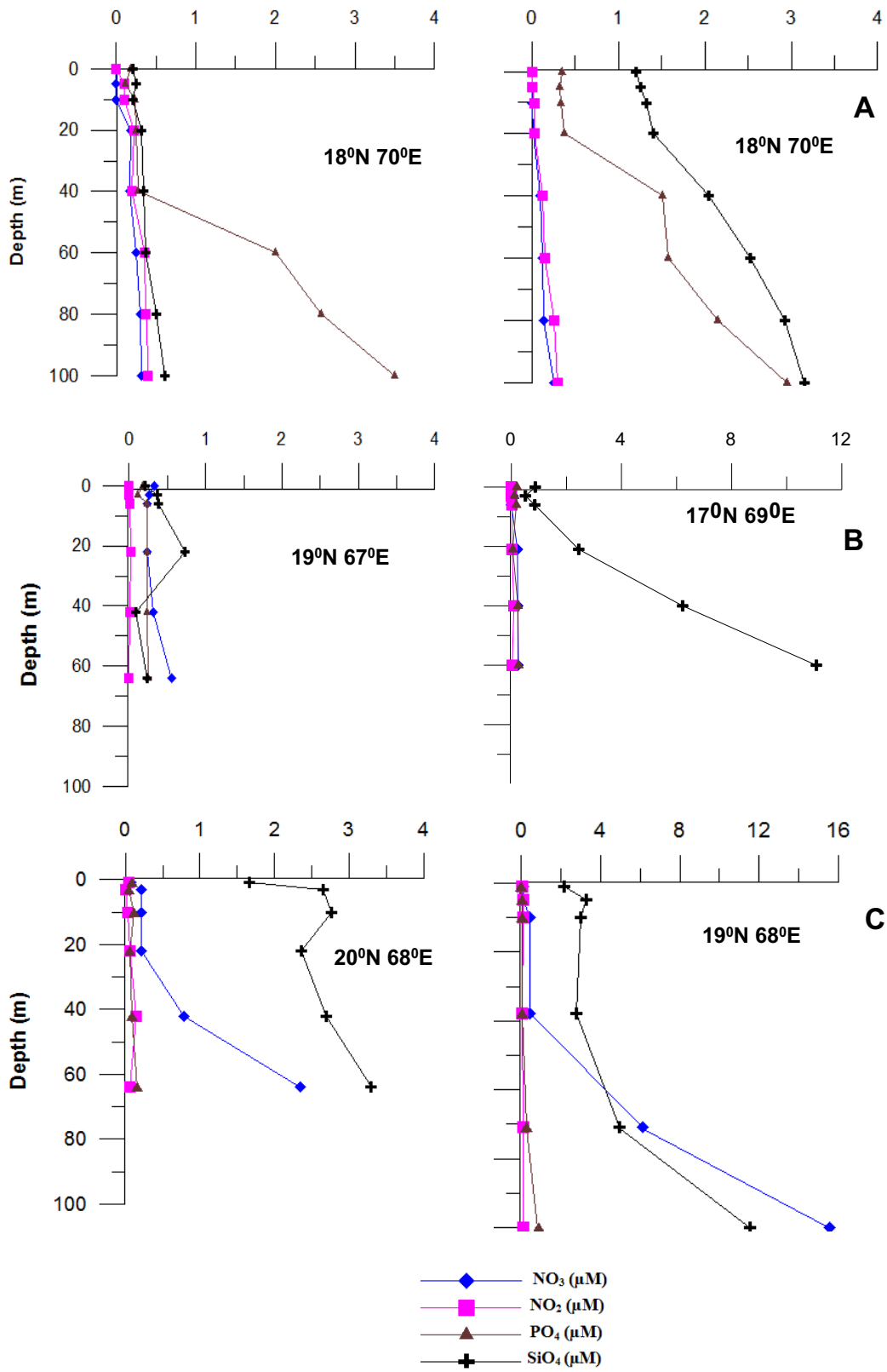
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Fig. 3



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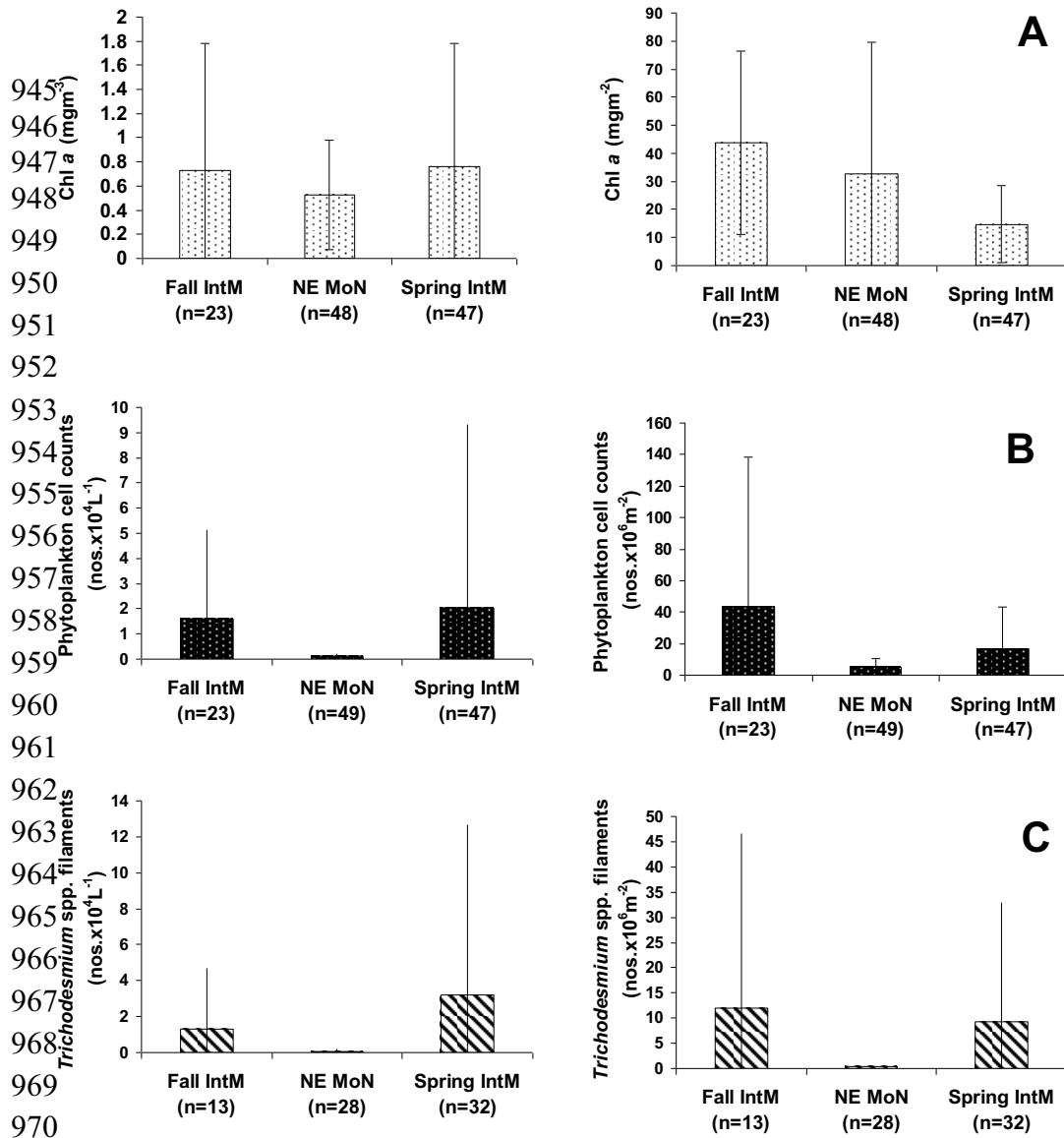
Fig. 4



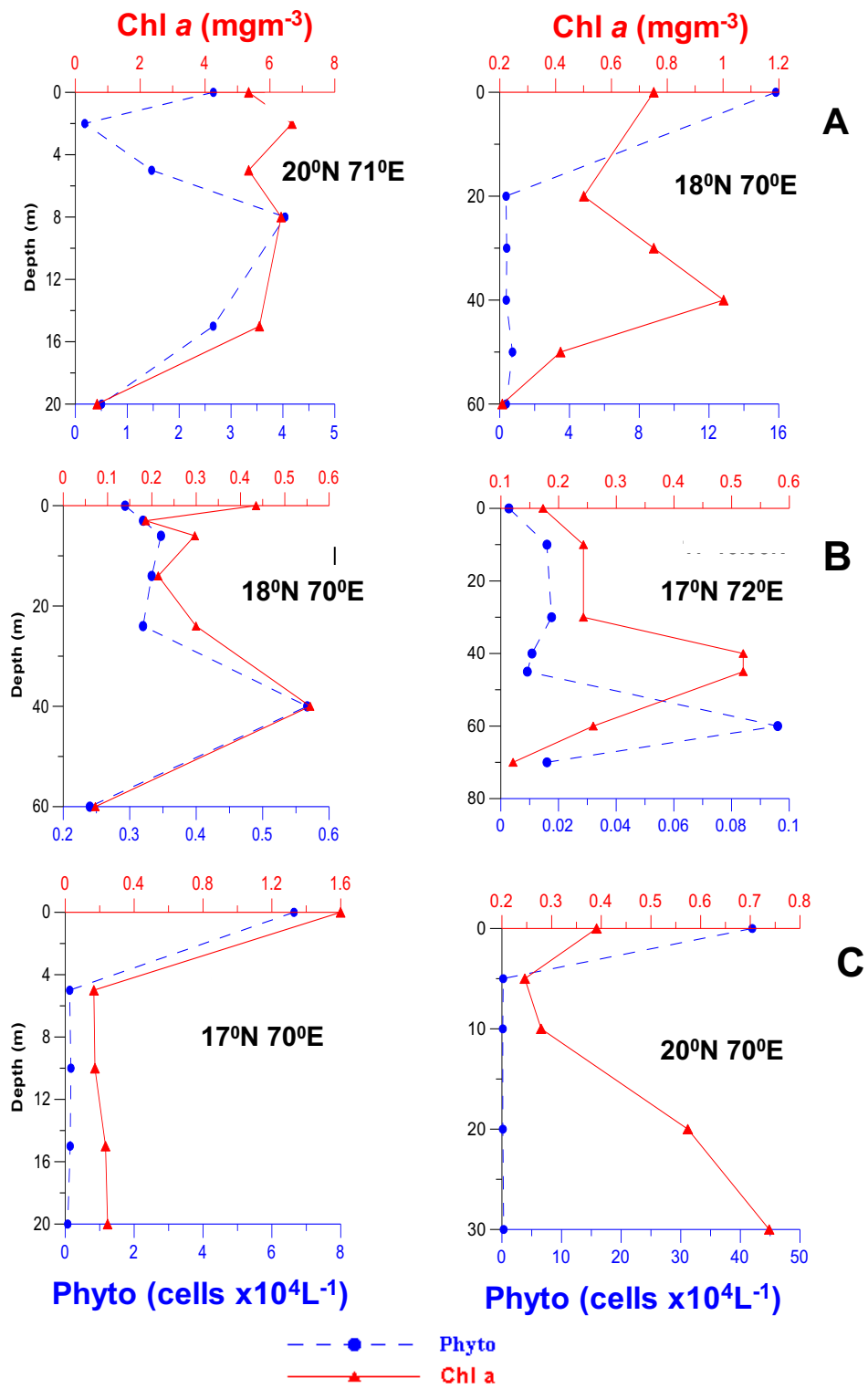
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944 **Fig. 5**

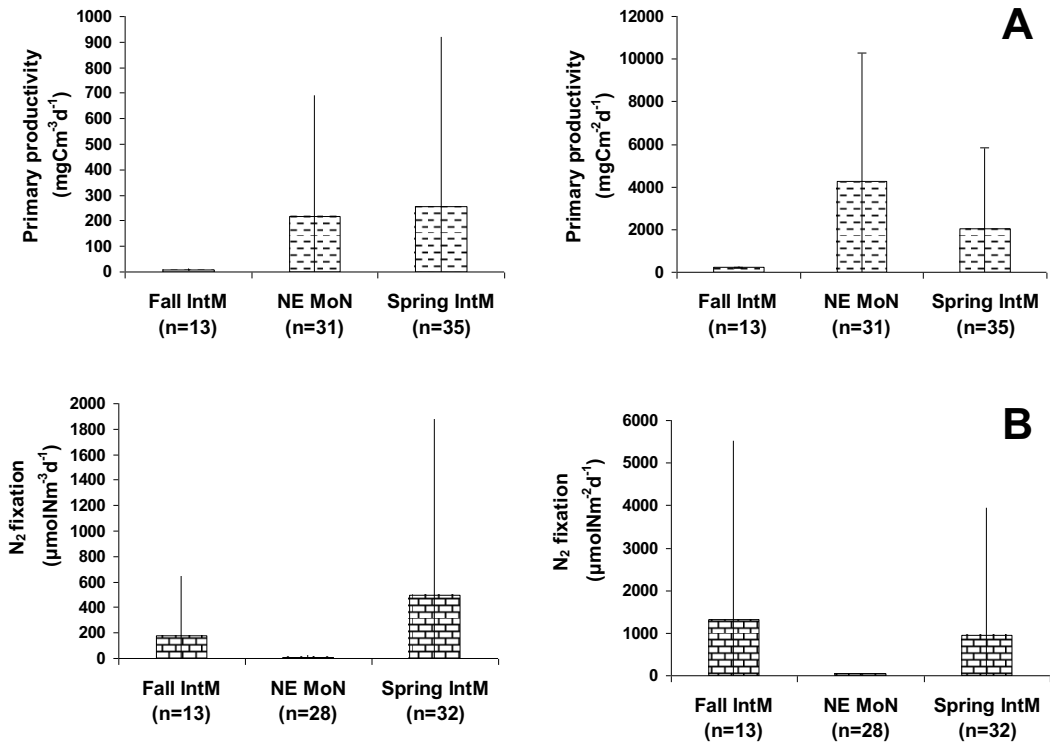


984 **Fig. 6**



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986 **Fig. 7**

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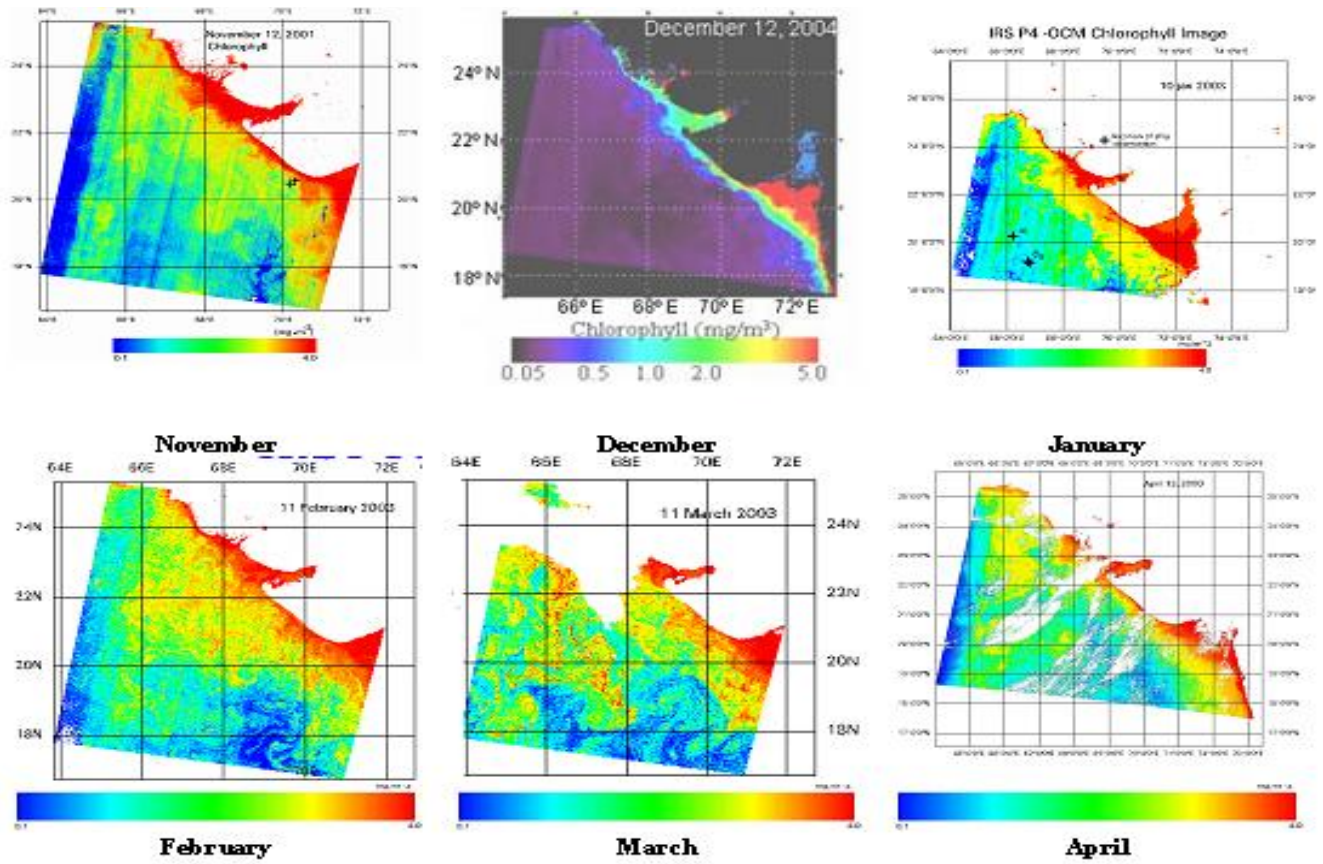
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Fig. 8



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Fig. 9