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# Seasonal Dynamics of *Trichodesmium* and Phytoplankton Communities in the Eastern Arabian Sea: Winter Vs Spring-inter monsoon

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## Abstract

The filamentous marine cyanobacterium *Trichodesmium* forms extensive blooms in tropical seas, where it plays an important role in nitrogen fixation. This study investigated *Trichodesmium*-associated phytoplankton in the Eastern Arabian Sea (EAS) during bloom and non-bloom conditions. *Trichodesmium* blooms over the continental shelf primarily comprised of *T. erythraeum* and *T. thiebautii* during the Spring Inter Monsoon (SIM) and *T. erythraeum* during the Winter Monsoon (WM). *T. erythraeum* blooms have rarely been reported from the north-east Arabian Sea during WM. Trichomes comprised of 143-1552 cells during the WM, with filaments ranging from 1339 to 13163  $\mu\text{m}$  in length. Non-diazotrophic groups like diatoms and dinoflagellates were associated with *Trichodesmium* during both seasons within the bloom waters. The study found a novel symbiotic relationship between the heterocystous diazotroph *Richelia intracellularis* and *Nitzschia sicula* during WM blooms. This research expands knowledge of lesser-known phytoplankton species and their associations in the EAS.

**Keywords:** Arabian Sea, Phytoplankton associations, *Trichodesmium* bloom

## Introduction

*Trichodesmium*, a marine cyanobacterium is an important nitrogen-fixer in the sea. It is regarded as the most prominent marine diazotroph and has intriguing traits such as nitrogen fixation without heterocyst formation (Bergman *et al.*, 2012). These blue-green algae fix nitrogen, which gets into the marine food web by excretion, grazing, sinking, and decomposition. The marine cyanobacteria's ability to fix nitrogen ( $\text{N}_2$ ) is crucial for the global biogeochemical cycles of nitrogen and carbon. *Trichodesmium* transform  $\text{N}_2$  into bioavailable ammonium ( $\text{NH}_4^+$ ), which can support non-diazotrophic phytoplankton in oligotrophic oceans (Chen *et al.*, 2011; Oyeku and Mandal, 2020) and help primary and secondary production (Carpenter *et al.*, 1999; Sohm *et al.*, 2011). *Trichodesmium* accounts for more than 30 % of algal blooms, making them important players in the global biogeochemical cycle (Dugdale

*et al.*, 1961; Capone *et al.*, 1997). *Trichodesmium* is one of the most common bloom-forming phytoplankton in tropical and subtropical oceans, particularly in the eastern Pacific and Arabian Sea (Dugdale *et al.*, 1961; Capone *et al.*, 1997). It typically forms a prominent cluster or colony, and it regularly produces blooms that are patchy in appearance. The spatial distribution of *Trichodesmium* blooms is often correlated with the physical change of the water body, because the influence of winds can disrupt the organization of bundles which make its distribution uneven and patchy. Warm waters, calm weather conditions, low wind speed, lack of grazers and highly transparent waters are the necessary conditions required for the formation of the *Trichodesmium* blooms (Carpenter and Price, 1976; Lewis *et al.*, 1988; Ganesella-Galvao *et al.*, 1995; Capone *et al.*, 1997; Sellner, 1997; Sarangi *et al.*, 2004; Siqueira *et al.*, 2006; Blondeau-Patissier *et al.*, 2018).

Past literature revealed the co-existence of diatoms like *Rhizosolenia* sp., *Chaetoceros* sp., *Bacteriastrium* sp., *Asterionella glacialis*, *Leptocylindrus danicus*, *Guinardia cylindrus*, *Thalassionema nitzschiodes*, *Nitzschia longissima*, *Thalassiosira eccentrica*, *Hemiaulus hauckii* and *Skeletonema costatum* with *Trichodesmium* during bloom in both the Bay of Bengal and Arabian Sea (Satpathy et al., 2007; Jabir et al., 2013). Additionally, *Trichodesmium* has been found in association with dinoflagellates like *Scripsiella* sp., *Gymnodinium* sp., *Ceratium* sp., and *Gonyaulax pacifica* during blooms in the Arabian Sea (Matondkar et al., 2006). Diazotrophic cyanobacteria are autotrophic, or symbiotically associated with autotrophs like diatoms and dinoflagellates, and live in the upper euphotic region of the sea (Carpenter and Capone, 2008). The cyanobacteria, *Richelia intracellularis* and *Calothrix rhizosoleniae*, were observed in symbiotic association with diatom genera such as *Rhizosolenia*, *Hemiaulus*, *Bacteriastrium*, *Guinardia* and *Chaetoceros* in warm tropical and subtropical oligotrophic water during *Trichodesmium* blooms (Alldredge and Silver, 1982; Villareal et al., 1992; Ferrario et al., 1995; Gomez et al., 2005; Padmakumar et al., 2010; Jabir et al., 2013; Madhu et al., 2013). The Arabian Sea during the Spring Inter Monsoon (SIM) period is known for its stratified state, resulting in oligotrophic water. *Trichodesmium* releases fixed nitrogen in the form of ammonium or dissolved organic nitrogen, which is then available to a community of nutrient-starved non-diazotrophic phytoplankton (Poulton et al., 2009).

Numerous occurrences of *Trichodesmium* blooms in Indian waters between February to May have been reported especially on the west coast (Prabhu et al., 1965; Qasim, 1970; Devassy et al., 1978; Devassy et al., 1987; Shetty et al., 1988; Koya and Kaladharan, 1997; Sarangi et al., 2004; Krishnan et al., 2007; Padmakumar et al., 2010; Parab and Matondkar, 2012; D'Silva et al., 2012; Martin et al., 2013; Jabir et al., 2013) as compared to the east coast (Ramamurthy et al., 1972; Adhakary and Sahu, 1992; Santhanam et al., 1994; Jyothibabu et al., 2003; Mohanty et al., 2010; Shetye et al., 2013). In an attempt to enhance the understanding of the seasonality in *Trichodesmium* and phytoplankton community dynamics, the present study focused on: i) identifying phytoplankton communities within the study area during WM and SIM; ii) quantifying cells per trichome within non-bloom and bloom waters using microscopy; iii) understanding the relationship between *Trichodesmium* and other phytoplankton communities in bloom and non-bloom conditions; and iv) comprehending diazotroph-diatom symbiotic association within blooms.

## Materials and methods

### Study area

The Eastern Arabian Sea (EAS), part of the tropical basin of the northern Indian Ocean, experiences strong seasonality with semi-annually reversing monsoon winds. Therefore, surface circulation along the EAS reverses every six months. The West Indian Coastal Current (WICC) flows poleward during the WM (November to February) and towards the equator during the summer monsoon (June- September) (Shetye et al., 1991). In summer, the WICC transports high-salinity water from the North Arabian Sea southward along the shelf slope region. In winter, the southern EAS is characterized by the occurrence of thermal inversions (Thadathil and Gosh, 1992; Durand et al., 2004), while the northern part of the EAS is affected by winter convection which leads to winter blooms (Madhupratap et al., 1996; Prasanna Kumar and Prasad, 1996). During the spring-summer transition (April-May), a small warm pool develops in the southern EAS, promoting the formation of the gyre with monsoon onset (Joseph, 1990; Hareesh Kumar et al., 2009; Nyadjro et al., 2012).

### Data collection

An oceanographic cruise was conducted in the Arabian Sea during the SIM from April 15<sup>th</sup> to May 5<sup>th</sup> 2017 onboard (FORV-359 Sagar Sampada). Sample collection for microscopic analysis and other parameters was carried out from the southern to the northern Arabian Sea. Massive blooms of *Trichodesmium* sp. were observed in the EAS on May 2<sup>nd</sup> 2017. A Total of 13 stations (named SS1 to SS13) were covered during this SIM cruise. Another oceanographic cruise was carried out during the WM period in the Arabian Sea from December 15<sup>th</sup> 2019-January 6<sup>th</sup> 2020 on board (ORV-364 Sagar Kanya). The cruise track for sample collection started from Goa, moving towards the northern Arabian Sea and further moving southwards up to 4 °N along 64 °W and then diagonally heading towards Goa. A total of 14 sampling points were covered during this cruise named SK1 to SK14. A *Trichodesmium* bloom was also encountered during the WM cruise in the EAS on December 17<sup>th</sup> 2019. The blooms of *Trichodesmium* sp. observed during both cruises were floating on the surface aligned approximately parallel to the shoreline and distributed over the continental shelf of the EAS which made surface waters appear pale brown to green in colour. Samples were collected from bloom and non-bloom stations for microscopic examinations. The cruise tracks with the station locations are shown in Figure 1.

**Hydrographic and meteorological measurements**

Hydrographic measurements, such as temperature, salinity and conductivity were obtained using a Conductivity-Temperature-Depth profiler (CTD Sea-bird 911 plus) equipped with a Niskin rosette sampler used for water sample collection from the surface to euphotic depth. The water samples were analysed for phytoplankton taxonomy. Meteorological parameters like wind speed, wind direction, and air temperature was obtained from Automated Weather Station (AWS) on board respective cruises.

**Diversity and Evenness analysis**

A diversity index is a measure of species diversity in a community that consists of a simultaneous population of several different species, whereas an evenness index shows the relative abundance of species within a selected region. Species richness was calculated using Simpson’s diversity index (Simpson, 1949) and species evenness was calculated using Pielou’s evenness index (Pielou, 1966) for the purpose of understanding the phytoplankton community within the sampled area during both the seasons.

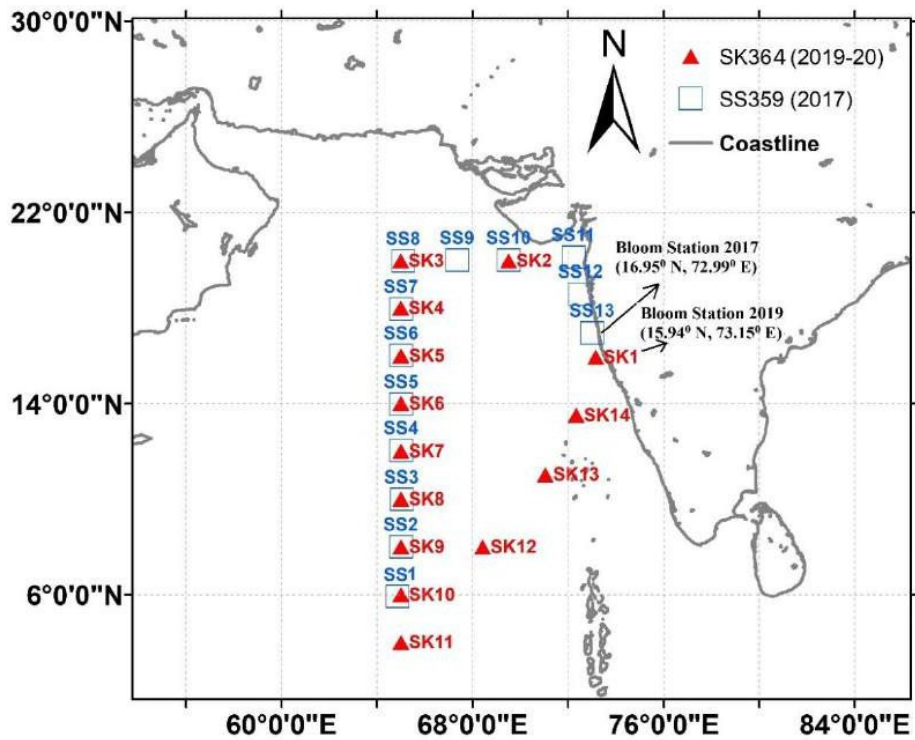


Figure 1. Study area showing the sampling points during SS359 (SS1 to SS13) and SK364 (SK1 to SK14). SS13 and SK1 are the bloom stations in respective seasons.

**Phytoplankton identification and enumeration**

For phytoplankton identification and enumeration, 1-5 litres of water were fixed with 1 % Lugol’s Iodine and preserved with 4 % formaldehyde solution and further stored under dark and cool (4 °C) conditions until microscopic analysis. Samples were concentrated approximately up to 10-15 ml by siphoning the top layer of the sample carefully with a tube. 1ml of concentrated sample was transferred to the Sedgwick-Rafter slide for identification and counting using a Zeiss® Observer A1 AX10 inverted microscope. Phytoplankton samples were enumerated and identified to the lowest possible taxonomic level using a standard taxonomic key (Tomas, 1997).

Simpson’s Diversity Index:

$$D = 1 - \frac{\sum ni(ni - 1)}{N(N - 1)}$$

D: Simpson Diversity Index

ni: Number of individuals belonging to i species

N: Total number of individuals

Pielou’s Evenness Index:

$$J' = H' / H'max$$

J': Pielou evenness index

H': The observed value of Shannon index H'max: lnS

S: Total number of species

## Results

### Hydrographic characteristics of EAS during Spring Inter Monsoon and Winter Monsoon

During the SIM, *in-situ* measured sea surface temperature (SST) was high, ranging from 28-30 °C. The SST at bloom station SS13 was 30 °C. The salinity values ranged from 34.31- 36.73 PSU at the surface with 35.54 PSU at bloom station SS13. Dissolved oxygen (DO) concentration in the surface waters ranged from 3.53-4.13 ml/l. DO value was observed to be highest at the bloom station (4.13 ml/l). During the WM season, SST was relatively lower, ranging from 26-29.52 °C. SST at the bloom station SK1 was observed to be 28.64 °C. Sea surface salinity ranged from 34.73-36.35 PSU, with the lowest value of 34.73 PSU observed at the bloom station SK1. Dissolved oxygen (DO) concentration was comparatively higher during the WM, ranging from 4.19-4.40 ml/l at the surface, with the highest value of 4.40 ml/l observed at the bloom station SK1. During both seasons, the sky appeared to be clear at the bloom stations and wind speeds were observed to be 4 m/s at SS13 and 4.8 m/s at SK1.

### Phytoplankton community structure of EAS during SIM and WM

During the SIM, 432 phytoplankton species were identified in the EAS using microscopy. A total of 217 species of diatoms, 198 species of dinoflagellates and 17 species belonging to other algal communities, including *Trichodesmium sp.* were observed. The phytoplankton diversity in the EAS was relatively higher during the WM. Overall, 513 phytoplankton species were identified out of which 280, 212 and 21 species were the respective contributions of diatoms, dinoflagellates and other algal groups including *Trichodesmium sp.* Microscopic analysis showed the dominance of diatoms during both the seasons within the study area except for the bloom stations SS12, SS13 and SK1, where approximately 75-90 % was contributed by *Trichodesmium sp.* Tables 1 and 2 summarize the distribution of the most abundant phytoplankton species observed within the study area during both seasons. During the SIM pennate diatoms such as *Pseudo-nitzschia sp.*, *Nitzschia sp.*, *Asterionellopsis sp.*, *Thalassionema sp.*, *Fragillariopsis sp.* and *Navicula sp.* were dominating phytoplankton species. However, centric diatoms such as *Chaetoceros sp.*, *Bacteriastrium sp.*, *Dactyliosolen sp.*, *Hemiaulus sp.*, *Rhizosolenia sp.*, *Guinardia sp.* and *Leptocylindrus sp.* were the major contributing phytoplankton during the WM throughout the study area.

### Taxonomic study of *Trichodesmium sp.* in bloom waters

Massive blooms of *Trichodesmium sp.* were observed to be floating on the surface aligned approximately parallel to the shoreline and distributed over the continental shelf off Ratnagiri during SIM (Fig. 2a) and the continental shelf off Malvan during the WM (Fig. 2b). Surface waters of the bloom station SS13 appeared pale brown to green in colour during the SIM while superficial brownish patches were observed in the surface waters of SK1 during the WM. Microscopic analysis revealed a mixed bloom of *T. erythraeum* and *T. thiebautii* during the SIM contributing 75 % of the total phytoplankton population with cell density  $9.13 \times 10^6$  trichomes  $l^{-1}$  at the bloom station SS13, and the remaining 25 % phytoplankton population were predominantly composed of diatoms, dinoflagellates and other algae. *T. erythraeum* was observed to be the major constituent of the bloom out of these two species with cell density  $7.86 \times 10^6$  trichomes  $l^{-1}$ , whereas *T. thiebautii* contributed  $1.27 \times 10^6$  trichomes  $l^{-1}$  at the bloom station. Two types of colonies were observed; *T. erythraeum* trichomes with parallel straight tuft colonies with attenuated end cell (Fig. 3a), which were composed of 12-55 trichomes, and *T. thiebautii* with radial puff colonies (Fig. 3b), composed of 27-168 trichomes per colony. Each trichome had a length range of 55.55-1209.9  $\mu m$  and was formed by cells ranging from 12-98 per trichome. During the WM it was observed that the bloom was caused only by *T. erythraeum* with cell density  $4.26 \times 10^6$  trichomes  $l^{-1}$ . *T. erythraeum* contributed 67 % of total phytoplankton population at the bloom station SK1 whereas diatoms constituted 31 %, and dinoflagellates and other algae both contributed 1 % of the total phytoplankton population. Results showed that the bloom was comprised of both individual trichomes (Fig. 3c) and the colonial form (Fig. 3d). Colonies were composed of 25-30 trichomes. It was observed that individual trichomes were found to be more numerous as compared to the colonial form with the very long trichome with length ranging from 1339-13163.49  $\mu m$  and width of 35-38  $\mu m$ . Trichomes were found to be comprised of 143-1552 cells per trichome. Thus, the comparative analysis between the seasons show that the bloom waters of the WM were comprised of longer trichomes and the number of trichomes existing individually were higher.

### Diazotroph-diatom symbiotic association within blooms

Diazotrophs-diatoms symbiotic association (DDAs) were more diverse during the WM bloom. However, it was observed that during the SIM *Richelia*

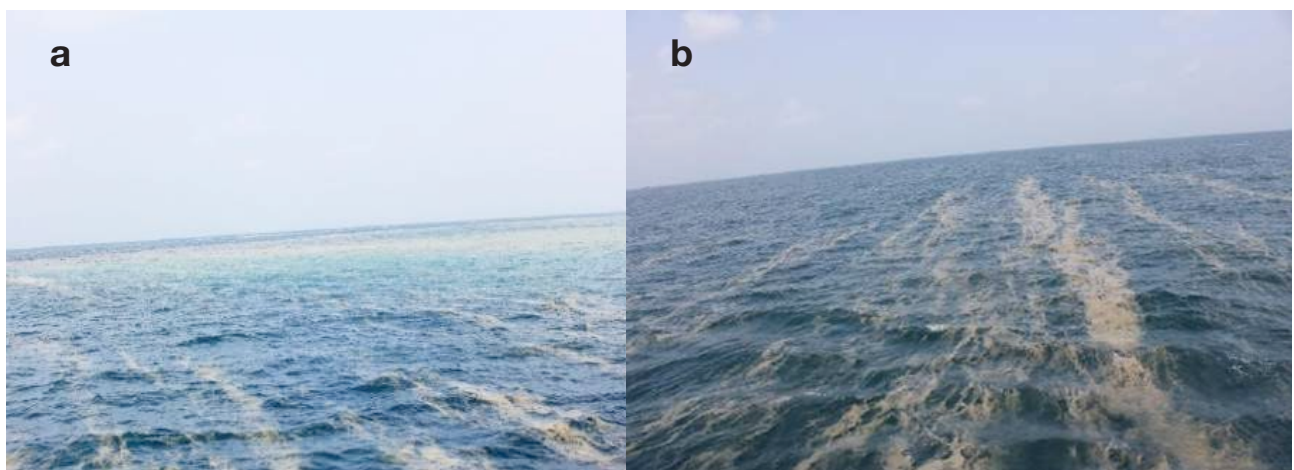




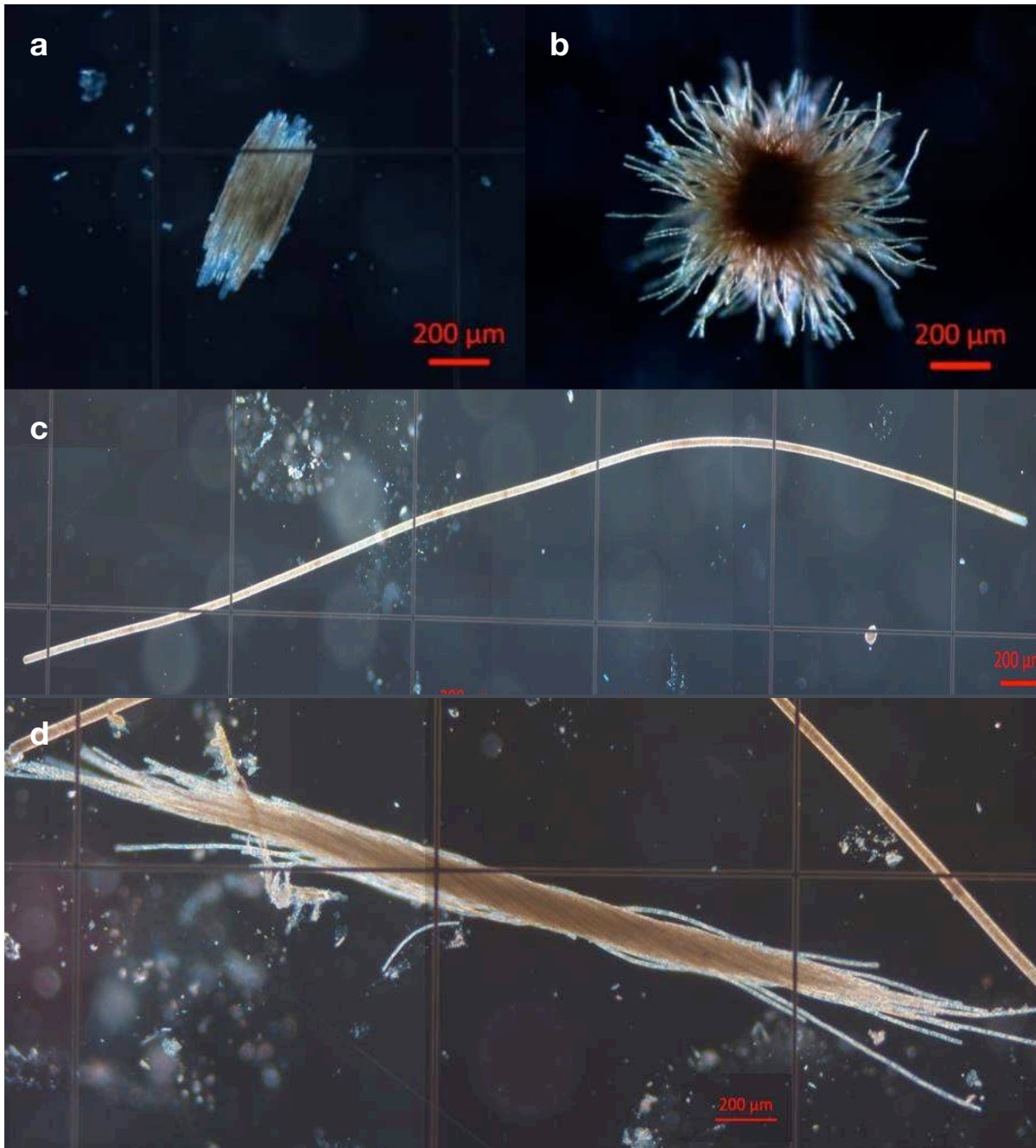
	SK1	SK2	SK3	SK4	SK5	SK6	SK7	SK8	SK9	SK10	SK11	SK12	SK13	SK14
<i>Podolampas bipes</i>	✓	✓	x	✓	✓	✓	x	✓	✓	✓	✓	✓	✓	✓
<i>Prorocentrum micans</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Prorocentrum gracile</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Oxytoxum scolopax</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Protoperdinium divergens</i>	✓	x	✓	✓	✓	x	✓	x	✓	✓	✓	✓	✓	✓
<i>Scrippsiella trochoidea</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	x	✓	✓
<b>Other Algae</b>														
<i>Trichodesmium erythraeum</i>	✓	✓	x	✓	x	✓	✓	x	✓	✓	x	x	✓	✓
<i>Trichodesmium thiebautii</i>	✓	✓	x	✓	x	✓	✓	x	✓	✓	x	✓	✓	✓
<i>Dictyocha fibula</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Dictyocha octanaria</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Octatis octanaria</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Dictyocha speculum</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Hillea fusiformis</i>	x	✓	✓	✓	✓	x	✓	✓	✓	x	✓	✓	✓	✓
<i>Phaeocystis globosa</i>	✓	✓	x	✓	x	✓	✓	✓	✓	✓	x	✓	✓	✓
<i>Meringosphaera</i>	x	✓	✓	✓	✓	✓	✓	x	✓	✓	✓	x	✓	✓
<i>Richelia intracellularis</i>	✓	✓	✓	✓	x	x	✓	x	x	x	x	x	✓	x

*intracellularis* was associated endosymbiotically with *Guinardia cylindrus* (Fig. 4a) with two trichomes per cell and a single trichome in *Rhizosolenia hebetata* (Fig. 4b) at the bloom station SS13. Trichomes of *R. intracellularis* were made up of 9-17 vegetative cells, with one terminally located heterocyst in *G. cylindrus* and at both ends of the trichomes in *R. hebetata* which was spherical and wider than vegetative cells. While it was noted that during the WM, *R. intracellularis* was living as an endosymbiont inside *R. hebetata* (Fig. 4c-4e), *R. styliformis* (Fig. 4f), *Hemiaulus hauckii* (Fig. 4g), *H. sinensis* (Fig. 4h) and *G. cylindrus* (Fig. 5a) was found in the bloom waters SK1 and non-bloom waters (SK2, SK3, SK4, SK7, SK13, SK14). *R. intracellularis* was observed to be associated endosymbiotically with *Nitzschia sicula* (Fig. 5b-5c) only at the bloom station.

Moreover, *R. intracellularis* was observed to be associated epiphytically with *Chaetoceros decipiens* (Fig. 5d) at SK1. *Calothrix rhizosoleniae* was observed to be associated epiphytically with *Chaetoceros compressus* (Fig. 5e-5f) at non bloom stations like SK3, SK7. Bunches of free living and solitary trichomes of *R. intracellularis* were also observed at SK1 (Fig. 5g). 1-3 trichomes of *R. intracellularis* were observed inside *R. styliformis* cells, which occurred in single or double form at one or both ends of the host. A single trichome was observed inside *N. sicula*, located at the centre of the valve. The endosymbiotic association between *R. intracellularis* and *N. sicula* has not been reported earlier. Trichomes of *R. intracellularis* were made up of 6 - 16 vegetative cells, with a terminally located heterocyst at one end or both ends of the trichomes, which were



**Figure 2.** Field photograph of *Trichodesmium* bloom (a) off Ratnagiri during Spring Inter Monsoon (May 2<sup>nd</sup> 2017) captured on-board FORV-Sagar Sampada 359, and (b) during the Winter Monsoon (December 17<sup>th</sup> 2019) captured on-board ORV-SK 364.



**Figure 3.** (a) *T. erythraeum* tuft colony, (b) *T. thiebautii* puff colony, (c) Single trichome of *T. erythraeum*, (d) Tuft colony of *T. erythraeum* (a,b – SIM; c,d – WM).

spherical and wider than vegetative cells. Free living trichomes were observed to have one terminally located heterocyst.

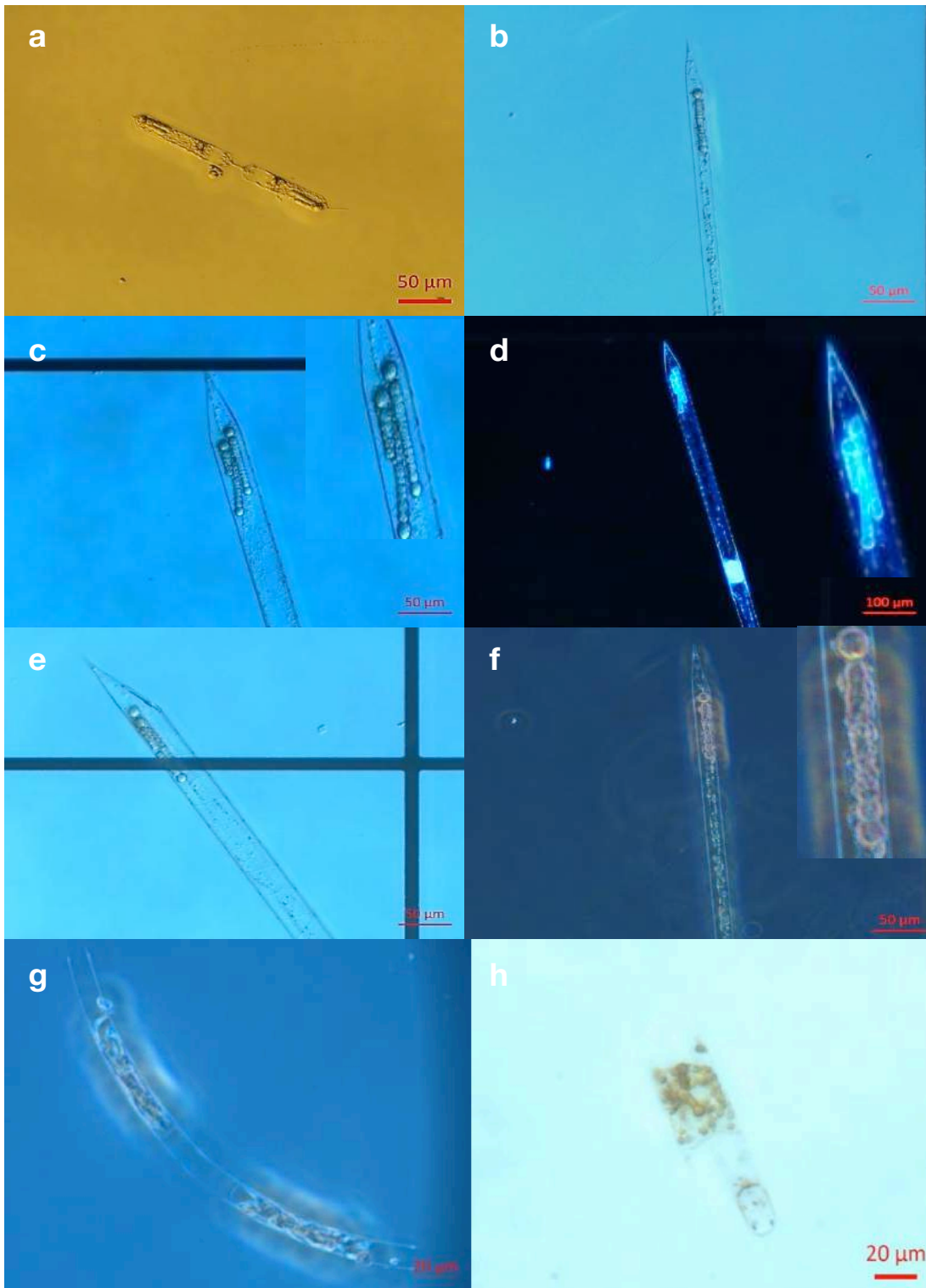
#### ***Trichodesmium* sp. versus other phytoplankton community**

Phytoplankton community structure showed variability with respect to the abundance of *Trichodesmium* sp. It is observed from Figure 6 that the diatoms and dinoflagellate abundance increased with the increase in number of *Trichodesmium* trichomes until it exceeds

the limit and form blooms. The abundance of other algal communities followed irregular trends with respect to the number of *Trichodesmium* trichomes (Fig. 6d).

Table 3 shows that in general during the SIM, the number of species of diatoms, dinoflagellates and other algae increased with the increase in the number of *Trichodesmium* trichomes. Simpson's diversity index showed maximum species diversity ( $D=0.95$ ) at station SS5 which is in open waters and minimum





**Figure 4.** *Richelia intracellularis* as an endosymbiont (a) in *Guinardia cylindrus*, (b-e) in *Rhizosolenia hebetata*, (f) in *R. styliformis*, (g) in *Hemiaulus hauckii*, and (h) in *Hemiaulus sinensis*. (a-b – during SIM; c-h – during WM).

Simpson's index ( $D=0.41, 0.46$ ) was found in the eastern part of continental shelf at SS12 and SS13 where the bloom was encountered. Species evenness was observed to be highest at SS10 ( $J'=0.94$ ), SS3 ( $J'=0.93$ ), and SS5 ( $J'=0.9$ ) while minimum evenness

was noticed at SS12 ( $J'=0.38$ ) and SS13 ( $J'=0.31$ ) which were the bloom stations.

Table 4 summarizes the diversity of phytoplankton species during the WM. The highest species diversity



**Figure 5.** DDAs during the WM - *Richelia intracellularis* as an endosymbiont (a) in *Guinardia cylindrus*, (b-c) in *Nitzschia sicula*, (d) *R. intracellularis* epiphytically attached to *Chaetoceros decipiens*, (e-f) *Calothrix rhizosoleniae* epiphytically attached to *Chaetoceros compressus*, (g) free trichomes of *R. intracellularis*.

according to Simpson's diversity index was observed at SK7 and the lowest was encountered at SK1, which was the bloom station. Overall the species diversity of phytoplankton in terms of Simpson's index (D) ranged between 0.54- 0.98. Pielou's species evenness

( $J'$ ) ranged between 0.42-0.86, which shows that the phytoplankton species were evenly distributed throughout the study area during the WM with an exception at the bloom station SK1 ( $J'$  = 0.42).

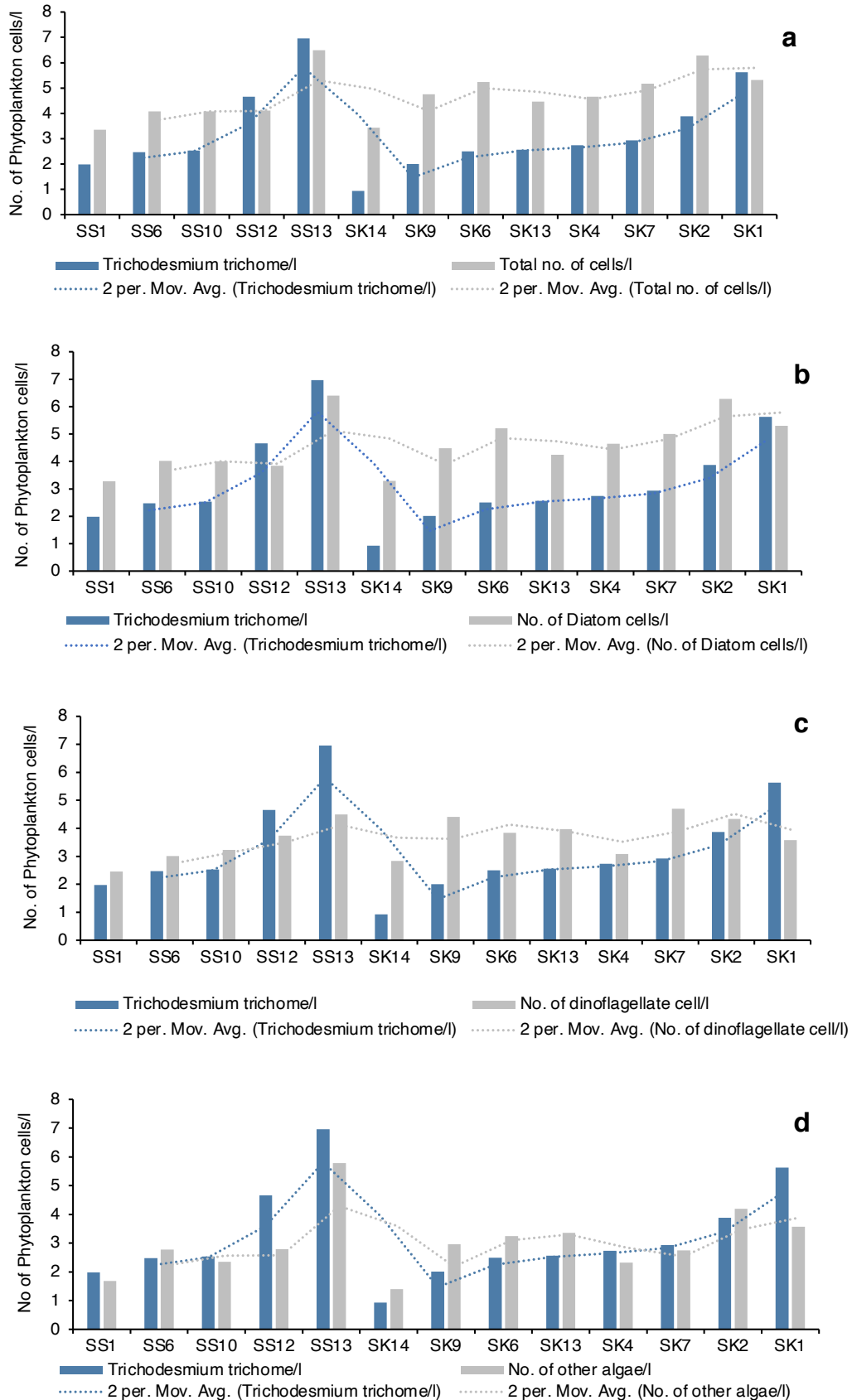


Figure 6. Comparison of number of *Trichodesmium* trichomes with (a) total number of cells/l, (b) No of diatoms cells/l, (c) no of dinoflagellates, and (d) no of other algal groups.

**Table 3.** Comparison of *Trichodesmium*, diatoms, dinoflagellate and other algal abundance along with Evenness and Richness index at various sampling sites during the Spring Inter Monsoon.

Station ID.	<i>Trichodesmium</i> trichomes/l	No. of Diatom sp./l	No. of Dinoflagellate Sp./l	No. of Other algae sp./l	Simpson's diversity index (D)	Pielou's evenness index (J')
SS1	9.52x10 <sup>1</sup>	1.8x10 <sup>1</sup>	1.5x10 <sup>1</sup>	8	0.79	0.74
SS2	0	1.8x10 <sup>1</sup>	0	4	0.81	0.84
SS3	0	1.7x10 <sup>1</sup>	0	2	0.84	0.93
SS4	0	2.1x10 <sup>1</sup>	1.1x10 <sup>1</sup>	5	0.72	0.71
SS5	0	2.9x10 <sup>1</sup>	1.4x10 <sup>1</sup>	0	0.9	0.9
SS6	2.96x10 <sup>2</sup>	3.0x10 <sup>1</sup>	1.4x10 <sup>1</sup>	8	0.81	0.74
SS7	0	3.5x10 <sup>1</sup>	1.8x10 <sup>1</sup>	0	0.84	0.73
SS8	0	5.1x10 <sup>1</sup>	2.0x10 <sup>1</sup>	0	0.87	0.88
SS9	0	4.8x10 <sup>1</sup>	2.5x10 <sup>1</sup>	0	0.87	0.89
SS10	3.36x10 <sup>2</sup>	6.7x10 <sup>1</sup>	2.7x10 <sup>1</sup>	7	0.95	0.94
SS11	0	8.2x10 <sup>1</sup>	2.5x10 <sup>1</sup>	0	0.88	0.74
SS12	4.53x10 <sup>4</sup>	1.01x10 <sup>2</sup>	2.9x10 <sup>1</sup>	1.1x 10 <sup>1</sup>	0.41	0.38
SS13	9.13x10 <sup>6</sup>	1.19x10 <sup>2</sup>	3.0x10 <sup>1</sup>	1.3x10 <sup>1</sup>	0.46	0.31

### Correlation between hydrographic parameters and phytoplankton groups

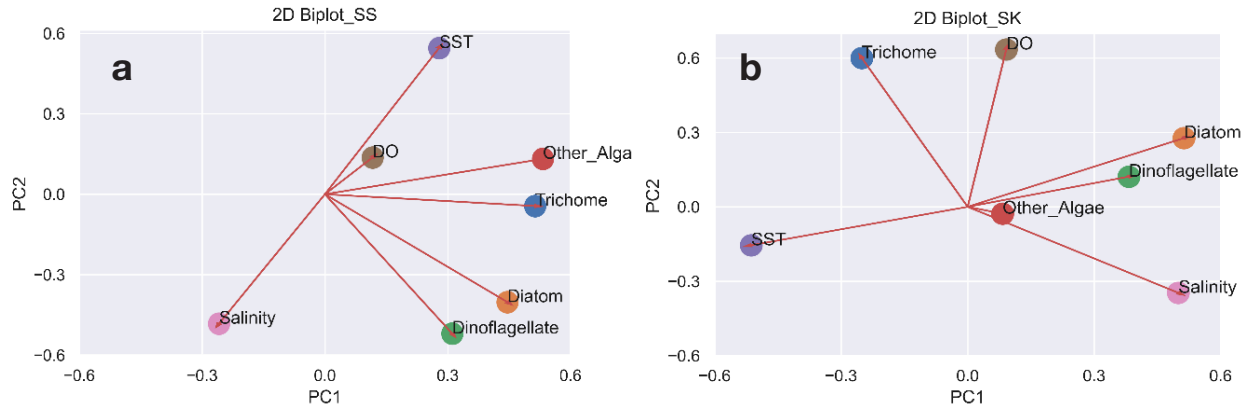
Principal Component Analysis (PCA) was performed to understand the relation between different hydrographic parameters and the phytoplankton groups. The results of PCA for the SIM and the WM are depicted in Fig. 7a and 7b. During the SIM, it was observed that other algae (excluding *Trichodesmium*) and *Trichodesmium* trichomes were positively correlated with SST and negatively correlated with salinity (Fig. 7a). Diatoms and dinoflagellates were positively correlated with DO and salinity and negatively

correlated with SST (Fig. 7a). Also, it was observed from Fig. 7a that the *Trichodesmium* trichomes and other algae (that excludes *Trichodesmium*) had a very strong positive correlation with DO.

During the WM, *Trichodesmium* trichomes were positively correlated with SST and DO, while it had a negative correlation with salinity (Fig. 7b). Diatom and dinoflagellates showed a strong negative correlation with SST and a positive correlation with salinity and DO (Fig 7b).

**Table 4.** Comparison of *Trichodesmium*, diatoms, dinoflagellate and other algal abundance along with Evenness and Richness index at various sampling sites during the Winter Monsoon.

Station ID.	<i>Trichodesmium</i> trichomes/l	No. of diatom sp./l	No. of dinoflagellate sp./l	No of Other algal sp. /l	Simpson's diversity index (D)	Pielou's evenness index (J')
SK1	4.26x10 <sup>6</sup>	6.9x10 <sup>1</sup>	1.2x10 <sup>1</sup>	1.0x10 <sup>1</sup>	0.54	0.42
SK2	7.50x10 <sup>3</sup>	9.0x10 <sup>1</sup>	2.2x10 <sup>1</sup>	7	0.97	0.82
SK3	0	8.7x10 <sup>1</sup>	1.1x10 <sup>1</sup>	9	0.98	0.86
SK4	5.40x10 <sup>2</sup>	8.9x10 <sup>1</sup>	4.2x10 <sup>1</sup>	4	0.96	0.75
Sk5	0	6.1x10 <sup>1</sup>	1.9x10 <sup>1</sup>	8	0.93	0.74
SK6	3.14x10 <sup>2</sup>	7.0x10 <sup>1</sup>	3.4x10 <sup>1</sup>	1.0x10 <sup>1</sup>	0.96	0.79
SK7	8.45x10 <sup>2</sup>	9.7x10 <sup>1</sup>	7.4x10 <sup>1</sup>	1.0x10 <sup>1</sup>	0.98	0.81
SK8	0	8.4x10 <sup>1</sup>	3.6x10 <sup>1</sup>	1.4x10 <sup>1</sup>	0.95	0.74
SK9	1.01x10 <sup>2</sup>	3.7x10 <sup>1</sup>	2.5x10 <sup>1</sup>	8	0.93	0.72
SK10	0	5.4x10 <sup>1</sup>	3.0x10 <sup>1</sup>	1.0x10 <sup>1</sup>	0.97	0.83
SK11	0	3.1x10 <sup>1</sup>	2.5x10 <sup>1</sup>	6	0.92	0.73
SK12	0	4.1x10 <sup>1</sup>	8	6	0.96	0.86
SK13	3.60x10 <sup>2</sup>	2.6x10 <sup>1</sup>	2.5x10 <sup>1</sup>	8	0.95	0.82
SK14	8.48	5.0x10 <sup>1</sup>	2.2x10 <sup>1</sup>	1.2x10 <sup>1</sup>	0.97	0.86



**Figure 7.** Principal Component Analysis (PCA) showing the inter-relationship between different hydrographic parameters and the phytoplankton groups during the SIM (a) and the WM (b).

## Discussion

The EAS is a highly dynamic basin, where seasonal variations in the biological and physico-chemical characteristics has been a recurring phenomenon. The hydrographical features observed during the SIM and WM reveals the seasonality within the study area. Phytoplankton biodiversity is mainly affected by the sea water temperature and salinity (Sugie *et al.*, 2020). The observations from this study shows that water temperature was higher in the bloom regions during both the seasons. Temperature has been recognized as a key factor that controls *Trichodesmium* blooms (Marumo and Nagasawa, 1976; Carpenter, 1983; Satpathy *et al.*, 2007; Oyeku and Mandal, 2020). Usually, blooms of non-heterocystous filamentous cyanobacteria occur during the warm season (Ramamurthy *et al.*, 1972), as cyanobacteria need comparatively high temperatures for their optimal growth compared to other phytoplankton (Suva-pepant, 1992; Sellner, 1997). *Trichodesmium* is a stenohaline cyanobacteria, which requires salinity greater than 33 PSU for optimum growth and abundance and cannot withstand low salinity (Ramamurthy *et al.*, 1972; Krishnan *et al.*, 2007). The study also revealed that the salinity in the bloom waters were higher than 34 PSU. Also, it was observed that DO values at the bloom stations were higher during both the seasons which might be because of photosynthetic release of oxygen by the dense blooms of *Trichodesmium* filaments. Similar observations have also been reported on the east and west coast of India (Satpathy *et al.*, 2007; Mohanty *et al.*, 2010; Capone *et al.*, 1997; Padmakumar *et al.*, 2010) during *Trichodesmium* blooms.

According to Prabhu *et al.*, 1965; Qasim, 1970; Devassy *et al.*, 1978; Devassy *et al.*, 1987; Shetty *et al.*, 1988; Koya and Kaladharan, 1997; Sarangi *et al.*, 2004; Krishnan *et al.*,

2007; Padmakumar *et al.*, 2010; Parab and Matondkar, 2012; D'Silva *et al.*, 2012; Martin *et al.*, 2013; Jabir *et al.*, 2013; Jyotibabu *et al.*, 2017; Ahmed *et al.*, 2017; Dias *et al.*, 2020; Ramesh *et al.*, 2021, *Trichodesmium* blooms usually occur every year between February-May along the west coast of India when temperature is elevated with intense sunlight and when salinity is more stable (Jyothibabu *et al.*, 2003). However, during this study, blooms were also witnessed in the WM. High SST (28.64) favours water column stratification, probably leading to nutrient-poor environments that support the existence of extensive blooms of filamentous *T. erythaeum* in the study area during the WM. *Trichodesmium* bloom occurrence during WM in the Arabian Sea is not often observed so can be considered quite unusual. Also, the observed length of *Trichodesmium* filaments or trichomes and number of cells per trichome within this study are of great interest as this long filamentous *Trichodesmium* has not been recorded earlier from the Arabian Sea (Length: 1339-13163.49  $\mu\text{m}$ ). As *Trichodesmium* blooms occur in a nutrient poor environment (Devassy *et al.* 1978; Padmakumar *et al.*, 2010), the long filaments and great numbers of cells per trichome observed during the study period could possibly occur to optimize the nutritional and other physiological requirements.

As a diazotrophic cyanobacteria, *Trichodesmium* fix atmospheric nitrogen and make this available for other phytoplankton communities in a usable form. This study suggests that non-diazotrophic community growth increased with an increase in the number of *Trichodesmium* filaments. However, the abundance of other phytoplankton decreased when the number of *Trichodesmium* cells surpassed the normal limits, i.e., under bloom condition (Fig. 6). This phenomenon

was observed during both cruises, in spite of its occurrence during different seasons. Thus, it clearly indicates the positive relationship between *Trichodesmium* and other phytoplankton species unless it overconsumes the available nutrients and flourishes to form blooms. Similar trends of abundance were observed for diatoms and dinoflagellates (Fig. 6b-6c), but variability was noted in the abundance of other algal groups (Fig. 6d).

Symbiotic association of diazotrophs-diatoms helps diatoms to fix atmospheric nitrogen in oligotrophic waters with the help of epiphytic or endosymbiotic diazotrophs, as they are the only organisms capable of converting molecular N<sub>2</sub> into NH<sub>4</sub>, a more readily assimilated form of dissolved nitrogen (Karl et al., 2002). Diazotrophs are significant in environments where nitrogen limits primary production. In the present study, it was observed that the diazotroph, *Richelia intracellularis* was found to be endosymbiotically associated with diatoms (DDAs) restricted within the bloom waters of the EAS during the SIM, while such associations were found in bloom and non-bloom regions during the WM. Past studies also emphasized the importance of DDAs on phytoplankton nutrient and energy budgets in the Palk Bay (Madhu et al., 2013) as well as in the oligotrophic waters of the Arabian Sea (Jabir et al., 2013) during the SIM. Additionally, DDAs were more abundant within the bloom waters of the EAS during the WM as well as with varying diatom species. Therefore, bloom waters with diazotrophs like *Trichodesmium* and *Richelia* not only support the proliferation of a non-diazotrophic phytoplankton community through regenerated ammonium produced from these nitrogen fixers (Kulkarni et al., 2010), but also through a significant contribution to the nitrogen cycle and the budget of oligotrophic seas during blooms.

Phytoplankton community composition showed distinct variation in bloom and non-bloom stations. At the bloom stations, certain phytoplankton species were observed to be abundant. These include *Trichodesmium erythraeum*, *Chaetoceros curvisetus*, *Bacteriastrum elongatum*, *Chaetoceros dictyota*, *Pseudo-nitzschia liniola*, *Chaetoceros compressus*, *Richelia intracellularis*, *Protoperdinium parthenopes*, *Ceratium furca*, *Chaetoceros decipiens*, and *Gonyaulax spinifera*. This suggests that these species thrive and are present in significant quantities during phytoplankton blooms. On the other hand, at the non-bloom stations, different phytoplankton species were observed in higher numbers. These include

*Pseudo-nitzschia pungens*, *Pseudo-nitzschia delicatissima*, *Chaetoceros lorenzianus*, *Chaetoceros messanensis*, *Bacteriastrum delicatulum*, *Dactyliosolen fragilissimus*, *Chaetoceros compressus*, *Nitzschia longissima*, *Navicula delicatula*, *Thalssiothrix gibberula*, *Lioloma pacificum*, *Protoperdinium conicum*, *Protoperdinium oceanicum*, *Gymnodinium breve*, and *Podolampas palmipes*. This indicates that these species exhibit higher population densities in environments that are not experiencing phytoplankton blooms. Overall, the study provides insights into the distribution and abundance of phytoplankton species in different ecological contexts, highlighting the variations between bloom and non-bloom stations.

During the SIM, it was observed that pennate diatoms such as *Pseudo-nitzschia* sp., *Nitzschia* sp., *Asterionellopsis* sp., *Thalassionema* sp., *Thalssiothrix* sp., *Fragillariopsis* sp., and *Navicula* sp. were the dominant phytoplankton species. This means that these types of diatoms were the most abundant and influential in the phytoplankton community during this period. In contrast, during the WM, centric diatoms such as *Chaetoceros* sp., *Bacteriastrum* sp., *Dactyliosolen* sp., *Hemiaulus* sp., *Rhizosolenia* sp., *Guinardia* sp., and *Leptocylindrus* sp. took over as the major contributing phytoplankton throughout the study area. This implies that these centric diatoms became the most significant and impactful contributors to phytoplankton composition during the WM period, replacing the previously dominant pennate diatoms.

## Conclusions

*Trichodesmium* sp. association with other phytoplankton communities during the SIM and WM were studied within the EAS. Similar trends were observed between *Trichodesmium* trichomes and other phytoplankton community abundance except at bloom stations. Microscopic analysis revealed that a mixed bloom of *T. erythraeum* and *T. thiebautii* occurred during the SIM period in the EAS off the coast of Ratnagiri, while the bloom witnessed during WM on the continental shelf off Malvan comprised only of *T. erythraeum*. The observed length of *Trichodesmium* trichomes and number of cells per trichome during WM have not been observed before in the EAS. Symbiotic associations of *Richelia intracellularis* with diatoms like *G. cylindrus*, *R. hebetata*, *R. styliiformis*, *N. sicula* and *C. decipiens* were observed during bloom period. Free living trichomes were also reported during the WM bloom at the bloom station. Endosymbiotic association of *R. intracellularis* with *N. sicula* is a novel observation at the bloom station during the WM. Overall,

the distribution of diatoms and dinoflagellates were observed to have a negative correlation with SST while an inverse relation was found for *Trichodesmium*.

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