

Bloom of *Trichodesmium* species and its impact on coastal water quality and plankton dynamics at Kalpakkam, Southeast coast of India

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A massive bloom of *Trichodesmium* (*T. erythraeum* and *T. thiebautii*) was observed in the coastal waters of Kalpakkam, southeast India. The bloom formed thick and greenish-yellow patches on the sea surface during the post-monsoon season (March 2020). Water and plankton samples were collected in Coastal Near-shore (CNW) and Coastal Offshore Waters (COW) at 12 stations. Nitrate and phosphate concentrations were found distributed evenly in the entire study site. Concentration of ammonia and total nitrogen found increased significantly during the bloom period as compared to non-bloom periods. The blooming species *T. erythraeum* and *T. thiebautii* contributed 53.98 % and 43.82 % to the region's phytoplankton population density. Phytoplankton and zooplankton species richness was relatively low during the study. Results indicated that the higher temperature (≥ 29 °C) and constant salinity (≥ 33 PSU) are the conducive factors for *Trichodesmium* growth. The MODIS Aqua satellite-derived Sea Surface Temperature (SST) and chlorophyll data further supported the in-situ observations.

[**Keywords:** Bay of Bengal, Biomass, Bivalve, Nutrients, *Trichodesmium*, Plankton]

Introduction

Plankton exhibit an unique phenomenon called blooming, and during the bloom, there are chances of discoloration of the water depending on the blooming species, and the bloom patches may extend several kilometers based on its density¹. *Trichodesmium* is nitrogen-fixing, non-heterocystous diazotrophic blue-green algae, which occurs throughout tropical and subtropical regions of world oceans. The morphology of the genus shows cylindrical trichomes². The species is found in stable waters at a depth lower than 50 meters. *Trichodesmium* species are among the most common bloom-forming species and the blooming of these species is exhibited as greenish yellow coloured patches in the open sea³⁻⁶. Generally, the phytoplankton bloom may occur in different seasons based on the causative species. *Trichodesmium* species are worldwide imperative marine cyanobacterium, forming macroscopic colonies that aggregate on the sea surface, an incident referred to as sea sawdust across thousands of square kilometers⁷⁻⁸. *Trichodesmium* exhibit blooms during the summer and spring seasons⁹. During the bloom,

Trichodesmium fixes a large amount of nitrogen (~ 42 Tg N yr⁻¹) when compared to the non-bloom period¹⁰. *Trichodesmium* forms bloom in large patches and this patchy spatial distribution is usually associated with the physical variability of the water¹¹. *Trichodesmium* possesses gas vesicles and nitrogen-fixing enzymes and is vastly adapted to oligotrophic conditions. These blue-green algae prefer warmer temperatures and show abundant growth during the summer season¹². *Trichodesmium* besides being the best nitrogen fixers in the marine environment can maintain their phosphorous levels by producing alkaline phosphates. Alkaline phosphatase is an enzyme capable of removing the inorganic phosphate from the organic phosphates¹³. Since these are blue-green algae, they contain chlorophyll 'a' pigment in considerable quantities and carry on photosynthesis on a large scale during blooms, temporarily increasing productivity on a regional scale.

Bloom formation by the *Trichodesmium* species have been well documented for the past five decades from the west coast^{4,14-24} and east coast of India^{5-6,22,25-31}. In the Indian context, earlier studies during the

1960s and 1970s dealt with very few physicochemical parameters. Studies carried out during the 1990s included the plankton component and recent observations in the past decade included the satellite data³²⁻³⁵. The present study includes all the above components and aims to get a comprehensive picture of the bloom event observed in the coastal waters of Kalpakkam. The study mainly aims to assess the impact of bloom on coastal water quality and plankton community and to study the spatial and temporal extent of the present bloom using satellite imagery.

Materials and Methods

As part of an ongoing monitoring study along the coastal waters off Kalpakkam (Lat. 12°33'55" N and Long. 80°10'54" E) (Fig. 1), sampling was carried out

during the post northeast monsoon period in March 2020. Dense and greenish-yellow patches were spotted on the surface water due to the formation of the phytoplankton bloom (Fig. 2). Samples were collected from twelve different locations in two transects along the nearshore waters in Kalpakkam. The transects were parallel to the shoreline at 1.6 km (Coastal Nearshore Water - CNW) and 5 km (Coastal Offshore Water - COW) from the coast (Fig. 1). The length of each transect (along the coast) was about 20 km. Kalpakkam region is a growing nuclear complex comprising a host of nuclear and allied facilities and the upcoming Prototype Fast Breeder Reactor (PFBR). The Buckingham Canal, which runs parallel to the shore, is connected with two backwaters, namely Edaiyur and Sadras. These two backwaters discharge large quantities of freshwater to the coastal

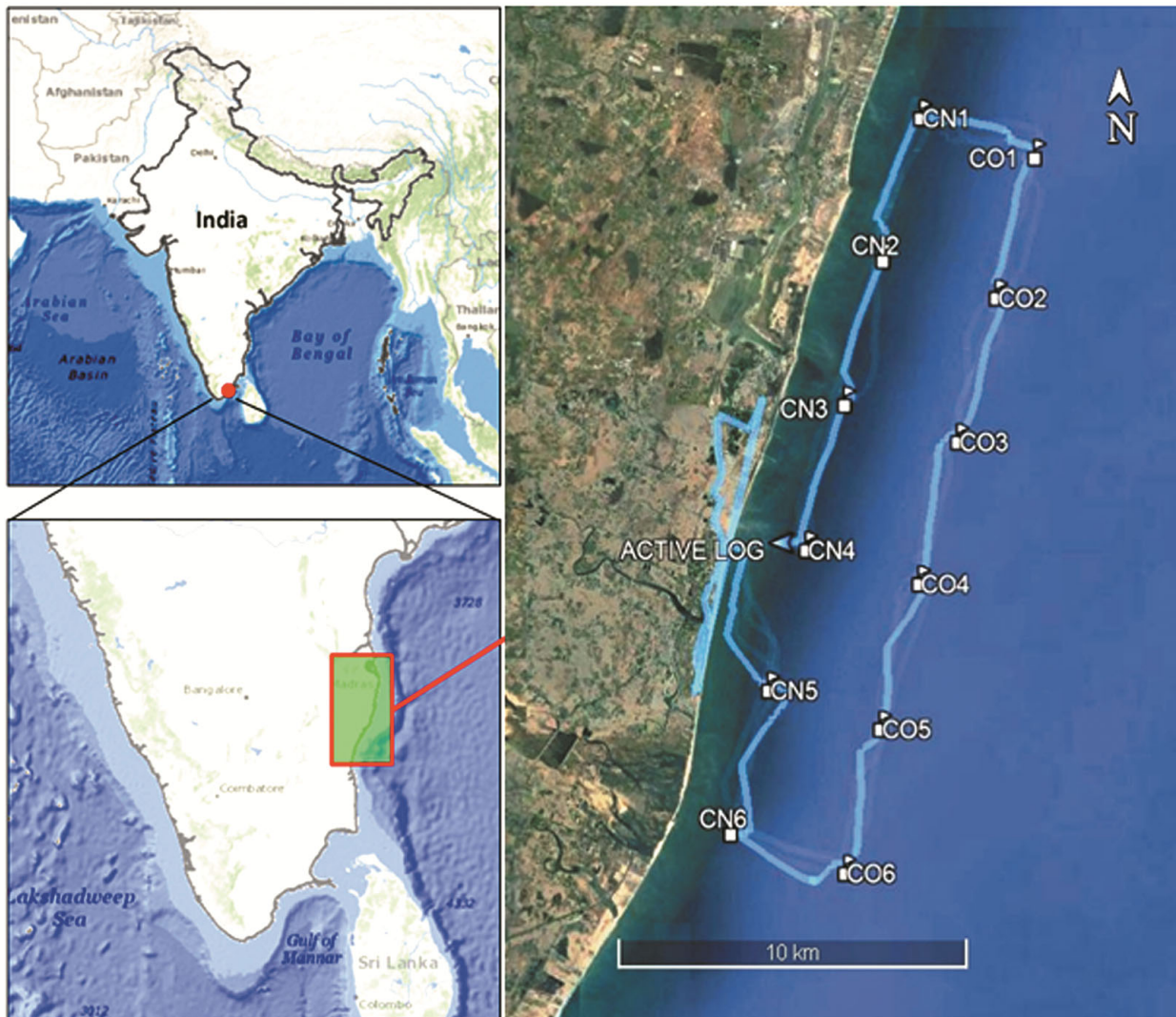


Fig. 1 — Map showing the study area and sampling location

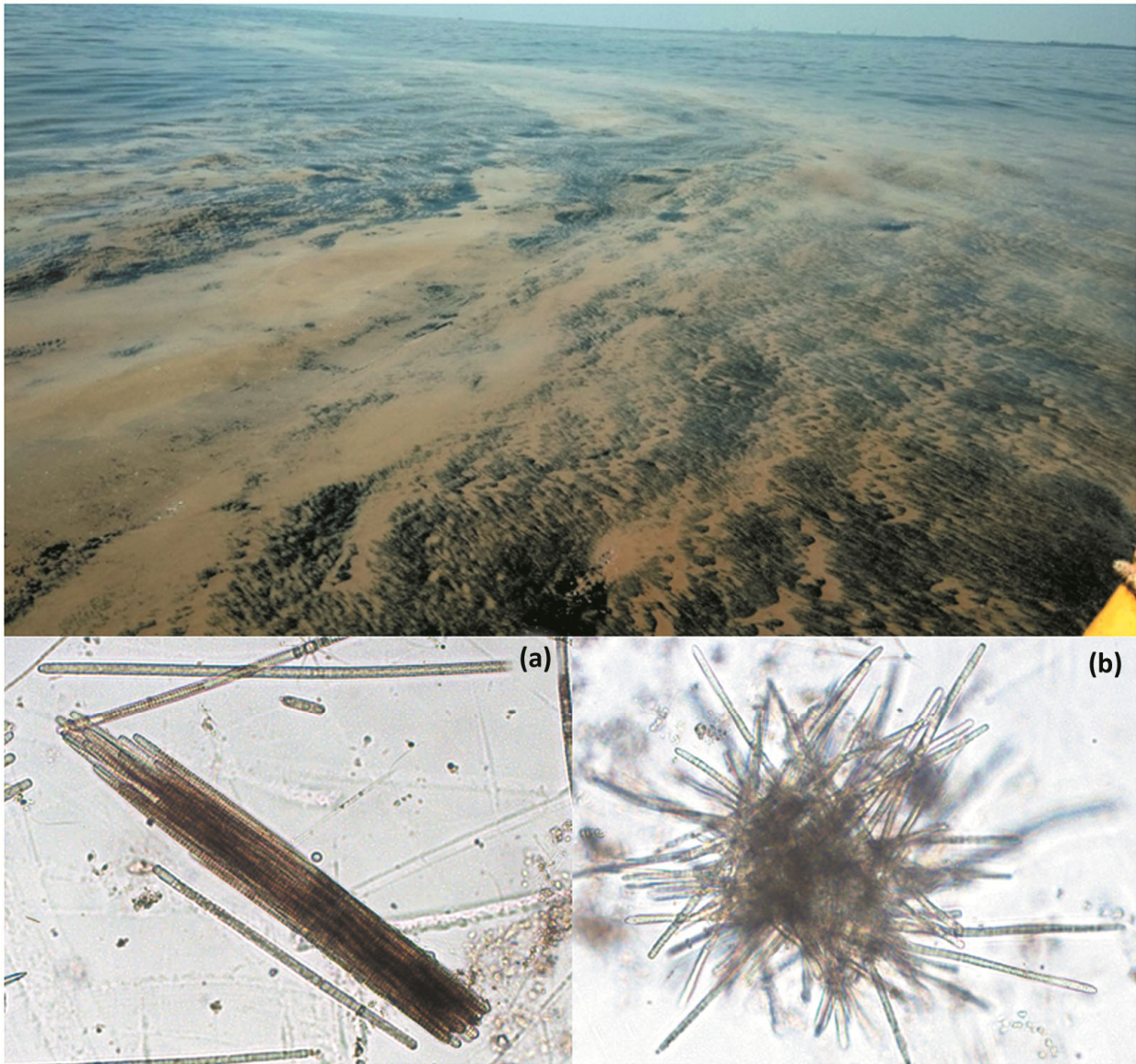


Fig. 2 — Bloom patches (*Trichodesmium* spp.) observed on the sea surface and microphotographs of the blooming species: (a) *T. erythraeum*, and (b) *T. thiebautii*

environment for a period of 2 to 3 months (October – December) during the North-East Monsoon (NEM) and occasionally during South-West Monsoon (SWM) (July – September). The annual precipitation at Kalpakkam is ~1300 mm, of which the bulk of precipitation (~65 %) is derived in the NE monsoon³⁶. Due to its geographic location, it experiences monsoon wind reversal and consequently, the current reversal takes place. The coastal current direction remains towards the north from March to September and it changes towards the south during October to February with the onset of SWM and NEM, respectively. The change in the coastal water current

pattern also brings oceanic water or the diluted coastal water from the north-eastern Bay of Bengal depending upon the northerly or southerly current.

The surface water samples were collected using pre-cleaned polypropylene containers for analysis of physicochemical and biological parameters. The parameters such as temperature, pH, salinity, dissolved oxygen, and turbidity were measured in-situ using a portable multi-parameter probe (HANNA instruments). Nutrients such as nitrate, phosphate, silicate, ammonia, total nitrogen, and total phosphates were analyzed using SKALAR SAN++ continuous flow analyzer following methods based on Parsons

*et al.*³⁷. The Suspended Particulate Matter (SPM) estimation was made by filtering 500 ml of water samples on pre-weighed 0.45 micron polycarbonate filters (Millipore) and reweighed after desiccating at 40 °C for 48 h. The initial and final weight of the filter paper was taken to calculate SPM (mg L⁻¹). Chlorophyll-*a* was estimated by spectrophotometric method following Parsons *et al.*³⁷. Phytoplankton and zooplankton samples were collected using conical plankton nets of mesh sizes 55 µm and 200 µm, and the collected samples were preserved immediately using buffered formalin (4 %) for further analysis. For the quantitative study of phytoplankton, the samples were collected in 1 L bottles and preserved in Lugol's iodine solution (1 %). A detailed procedure mentioned in Sahu *et al.*²⁹ was followed for preservation to counting. The phytoplankters were identified following standard taxonomic monographs³⁸⁻⁴³ and zooplankton were identified up to the species level based on standard literature⁴⁴⁻⁴⁶ and were counted using the standard procedure⁴⁷ and expressed as nos. m⁻³. The quantitative analysis of both phyto- and zoo-plankton was done by standard procedures using an inverted microscope (Zeiss Axiovert 40). Correlation and Principal Component Analysis (PCA) with Varimax rotation of the data was carried out with help of XLSTAT Pro.

Results and Discussion

Physicochemical properties of water

Values recorded for physicochemical properties during the study are given in Table 1. Temperature plays a significant role in controlling the *Trichodesmium* abundance in the marine environment⁵. These filamentous algae bloomed most frequently during hot weather seasons, as cyanobacteria demand a higher temperature for optimal growth than other phytoplankton⁶. The sea-surface temperature was

almost constant, with an average of 29.93±0.58 °C and 29.95±0.31 °C at CNW and COW, respectively. The results corroborated the general criterion that *Trichodesmium* blooms were restricted to seas with greater than 20 °C SST^{3,48}. Previous studies also recorded a similar temperature range (≥ 29 °C) in various coastal waters of India during the bloom of *Trichodesmium*^{4,18,27,49}. The present findings also agree with earlier reported *Trichodesmium* bloom events from the same location^{5-6,50}. Furthermore, temperature tolerance of the cultured strains of *Trichodesmium* spp. (*T. erythraeum* IMS101, *T. erythraeum* BRTRL101 and *T. tenue* H94) has been reported to be 20 to 34 °C with optimal temperatures being 24 – 30 °C for their growth and N₂ fixation⁵¹⁻⁵². Temperature developed a negative correlation ($r = -0.591$, $p \leq 0.05$) with *Trichodesmium erythraeum* in the present stud (Table 2) indicating the adverse impact of elevated water temperature on the species after the bloom formation. This observation is further confirmed from the PCA analysis where Temperature was found to be negatively loaded with *Trichodesmium erythraeum* abundance in PC 3 (Table 3).

The MODIS Aqua satellite-derived SST and chlorophyll data (Fig. 3a-j) for the sampling period (5th March to 13th April 2020) showed some interesting results. The different SST gradient-based water masses were observed in the weekly SST images (Fig. 3f-j). The weekly SST image of 5-12th March showed that the changes in SST pattern and the occurrence of SST front (temperature-based different water masses) merging might have induced the phytoplankton bloom in the study region. The sudden SST front due to the commencement of summer and movement of warmer (28.5 – 29 °C) water mass towards northwards (off Kalpakkam and Chennai region) and its merging with cooler water mass (28 – 28.5 °C) might be the probable reasons for

Table 1 — Hydrographic and physicochemical conditions during the bloom event (Mar 2020) in the coastal waters of Kalpakkam, Southeast coast India

Sampling region	Coastal Near-shore									Coastal Offshore								
	CN1	CN2	CN3	CN4	CN5	CN6	Max	Min	Avg ± SD	CO6	CO5	CO4	CO3	CO2	CO1	Max	Min	Avg ± SD
Station code	30.20	30.30	30.30	30.40	29.10	29.30	30.40	29.10	29.93 ± 0.58	29.70	29.90	29.50	30.10	30.30	30.20	30.30	29.50	29.95 ± 0.31
Temp (°C)	8.22	8.22	8.23	8.25	8.32	8.31	8.32	8.22	8.26 ± 0.05	8.30	8.33	8.32	8.29	8.32	8.31	8.33	8.29	8.31 ± 0.01
pH	33.02	33.04	33.15	33.65	33.21	33.15	33.65	33.02	33.20 ± 0.23	34.03	33.98	34.06	34.01	34.03	33.96	34.06	33.96	34.01 ± 0.04
Salinity (PSU)	4.14	4.63	5.73	4.98	5.55	5.82	5.82	4.14	5.14 ± 0.67	5.82	5.11	4.73	5.34	5.05	5.57	5.82	4.73	5.27 ± 0.39
DO (mg L ⁻¹)	22.92	13.64	15.24	9.50	28.60	10.82	28.60	9.50	16.79 ± 7.46	15.92	27.92	18.48	18.04	12.14	12.74	27.92	12.14	17.54 ± 5.72
SPM (mg L ⁻¹)	0.72	0.23	0.56	0.22	0.93	0.19	0.93	0.19	0.48 ± 0.31	0.13	0.17	0.15	0.14	0.10	0.13	0.17	0.10	0.14 ± 0.02
Turbidity (NTU)	7.82	3.32	3.62	3.17	0.96	1.81	7.82	0.96	3.45 ± 2.37	1.44	1.21	2.80	1.86	4.03	3.50	4.03	1.21	2.47 ± 1.15
Silicate (µM)	76.88	55.20	28.63	26.25	28.73	27.41	76.88	26.25	40.52 ± 20.94	32.21	37.34	38.28	22.54	18.99	62.88	62.88	18.99	35.37 ± 15.57
Ammonia (µM)	0.79	0.41	0.13	0.11	0.15	0.13	0.79	0.11	0.29 ± 0.27	0.17	0.14	0.14	0.12	0.12	0.13	0.17	0.12	0.14 ± 0.02
Phosphate (µM)	3.35	2.45	2.11	2.15	2.77	1.94	3.35	1.94	2.46 ± 0.52	2.17	3.11	2.80	2.46	2.20	2.27	3.11	2.17	2.50 ± 0.38
Nitrate (µM)	104.35	98.90	52.43	48.15	53.21	51.56	104.35	48.15	68.10 ± 26.08	61.92	69.55	72.42	49.68	47.85	94.63	94.63	47.85	66.01 ± 17.24
TN (µM)	2.31	1.35	0.44	0.38	0.49	0.43	2.31	0.38	0.90 ± 0.78	0.62	0.44	0.49	0.41	0.43	0.48	0.62	0.41	0.48 ± 0.08
TP (µM)	9.34	0.60	1.12	0.75	0.70	0.54	9.34	0.54	2.17 ± 3.52	0.64	0.41	0.22	0.37	0.78	0.03	0.78	0.03	0.41 ± 0.27
Chl- <i>a</i> (mg m ⁻³)																		

Note: Temp- water temperature; DO- Dissolved oxygen; TN- total nitrogen; TP- total phosphorous; Chl- chlorophyll

Table 2 — Correlation matrix (Pearson) of physicochemical and biological properties during the bloom event (Mar 2020) in the coastal waters of Kalpakkam, Southeast coast India. (TE - *Trichodesmium erythraeum*; TT - *T. thiebautii*; Total PD- total phytoplankton density; Total ZD- total zooplankton density; PS- number of phytoplankton species; ZS- number of zooplankton species)

Variables	Temp	pH	Salinity	DO	SPM	Turb.	Silicate	Ammonia	Phosphate	Nitrate	TN	TP	Chl-a	TE	TT	Total PD	Total ZD	PS	ZS	
Temp	1																			
pH	-0.595	1																		
Salinity	0.054	0.654	1																	
DO	-0.373	0.427	0.157	1																
SPM	-0.425	0.236	-0.055	-0.175	1															
Turb.	-0.262	-0.317	-0.682	-0.111	0.570	1														
Silicate	0.559	-0.628	-0.349	-0.678	-0.136	0.254	1													
Ammonia	0.238	-0.425	-0.321	-0.550	0.165	0.224	0.655	1												
Phosphate	0.233	-0.630	-0.545	-0.720	0.238	0.433	0.785	0.787	1											
Nitrate	-0.103	-0.031	-0.073	-0.669	0.820	0.423	0.323	0.533	0.602	1										
TN	0.245	-0.379	-0.246	-0.578	0.146	0.091	0.561	0.968	0.732	0.516	1									
TP	0.246	-0.641	-0.540	-0.717	0.208	0.406	0.777	0.796	0.998	0.577	0.754	1								
Chl-a	0.204	-0.528	-0.460	-0.615	0.272	0.518	0.833	0.639	0.910	0.590	0.502	0.884	1							
TE	-0.591	0.337	-0.270	0.322	0.122	0.320	-0.122	-0.048	-0.068	-0.054	-0.139	-0.092	0.027	1						
TT	-0.075	-0.264	-0.136	-0.288	0.380	0.173	0.255	0.486	0.620	0.495	0.474	0.624	0.564	-0.382	1					
Total PD	-0.469	-0.084	-0.379	-0.106	0.472	0.417	0.198	0.499	0.629	0.482	0.430	0.619	0.613	0.299	0.765	1				
Total ZD	-0.049	0.437	0.449	0.175	-0.040	-0.103	-0.192	-0.734	-0.481	-0.214	-0.730	-0.499	-0.269	0.164	-0.528	-0.465	1			
PS	-0.543	0.529	0.004	0.525	-0.035	-0.012	-0.527	-0.466	-0.577	-0.321	-0.484	-0.596	-0.500	0.806	-0.712	-0.184	0.343	1		
ZS	-0.633	0.236	-0.068	0.091	0.309	-0.046	-0.571	-0.103	-0.115	0.184	-0.060	-0.119	-0.218	0.064	0.302	0.358	-0.387	0.205	1	

Values in bold are significantly different from 0 with a significance level alpha = 0.05

Table 3 — Principal Component Analysis showing the loading of parameters on different components (TE - *Trichodesmium erythraeum*; TT - *T. thiebautii*; Total PD - total phytoplankton density; Total ZD - total zooplankton density; PS - number of phytoplankton species; ZS - number of zooplankton species)

	PC1	PC2	PC3	PC4	PC5	PC6
Variability (%)	17.189	10.461	13.597	16.372	13.141	13.520
Cumulative %	17.189	27.651	41.247	57.619	70.760	84.280
Factor loadings after Varimax rotation:						
	D1	D2	D3	D4	D5	D6
Temp	0.247	0.525	-0.530	0.145	0.031	-0.268
pH	-0.312	-0.154	0.386	-0.226	-0.691	-0.063
Salinity	-0.142	0.070	-0.163	-0.192	-0.936	-0.124
DO	-0.918	-0.013	0.265	-0.214	-0.043	0.052
SPM	0.020	-0.158	0.053	0.015	0.034	0.196
Turbidity	0.046	0.139	0.168	-0.017	0.732	0.154
Silicate	0.666	0.537	-0.120	0.278	0.250	0.200
Ammonia	0.370	0.163	-0.046	0.860	0.112	0.239
Phosphate	0.630	0.151	-0.113	0.408	0.375	0.476
Nitrate	0.514	-0.097	-0.060	0.245	-0.045	0.187
TN	0.367	0.100	-0.116	0.885	0.030	0.167
TP	0.618	0.151	-0.136	0.433	0.370	0.470
Chl-a	0.604	0.275	-0.033	0.179	0.335	0.546
TE	-0.072	0.019	0.980	-0.029	0.129	0.092
TT	0.121	-0.200	-0.459	0.272	0.039	0.779
Total PD	0.098	-0.199	0.206	0.291	0.174	0.850
Total ZD	0.036	0.345	0.186	-0.833	-0.289	-0.199
PS	-0.282	-0.197	0.841	-0.230	-0.040	-0.335
ZS	-0.096	-0.972	0.060	0.052	-0.020	0.137

phytoplankton blooming with a favourable temperature gradient. This is an important observation for the understanding of the physiological aspects of phytoplankton and in the context of seasonality and climate change aspects as well. However, this should be studied in detail with in-situ time series data on all the physicochemical parameters of the water to ascertain the exact cause of bloom formation.

pH values during the study did not show any significant fluctuation in CNW (avg. 8.26±0.05) and COW (avg. 8.31±0.01) regions. In general, fluctuations in seawater pH cause a decrease in algae biomass. On the other hand, acidification contributes to decreasing the pH level in the ocean which harms phytoplankton growth and dinitrogen fixation⁵³. However, stable marine conditions as found in the present study, are linked with phytoplankton proliferation. Salinity is an important factor that controls the distribution of *Trichodesmium* and other phytoplankton species. During the study, salinity variations were found to be negligible in both transects; however, the average variation in salinity between CNW and COW was about 1 PSU. The registered average salinity was 33.20±0.23 PSU and 34.01±0.04 PSU at CNW and COW, respectively. The salinity range between 33 to 37 PSU has been reported to support the *Trichodesmium* proliferation⁵⁴ and their distribution in marine ecosystems appears to be influenced by salinity⁶. DO concentrations ranged from 4.14 to 5.82 mg L⁻¹ in CNW and 4.73 to 5.82 mg L⁻¹ in COW. Marginally high DO content was observed in the COW region compared to the CNW region. Similarly, the DO level was lower in the southern part of the Kalpakkam coast, where bloom biomass was less than in the northern region. A similar pattern of DO content during *Trichodesmium* bloom has also been reported earlier^{6,48}. During the study period, the turbidity and SPM concentrations exhibited an erratic trend of variation in both transects. Turbidity values registered an average of 0.48±0.31 NUT at CNW and 0.14±0.02 NUT at COW. COW showed marginally higher SPM content (avg. 17.54±5.72 mg L⁻¹) than the CNW (avg. 16.79±7.46 mg L⁻¹).

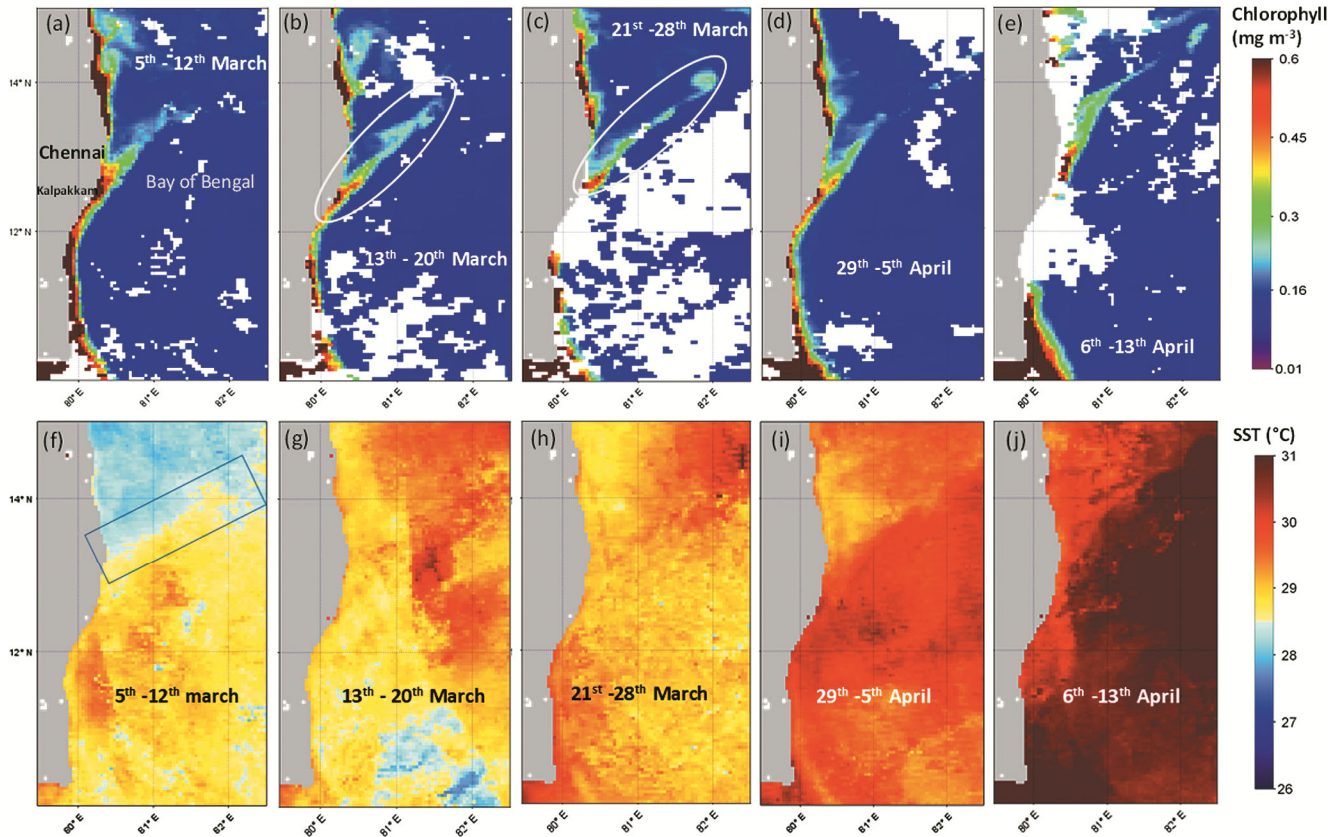


Fig. 3 — (a – e) MODIS Aqua derived 8-days composite chlorophyll concentration images, and (f – j) SST images along the Tamil Nadu coastal and offshore water depicting the phytoplankton bloom dynamics and temperature based water mass characteristics during March – April 2020

Nutrient dynamics

In general, nutrients are essential components for algal growth. Nutrient replenishment in the marine environment occurs either through in-situ regeneration or ex-situ input through rivers and runoffs⁵⁵. In this present study, nutrient concentrations in the sampled regions followed similar patterns, with peak bloom regions having significantly higher concentrations than the lower bloom regions. The average nitrate concentrations at CNW (avg. $2.46 \pm 0.52 \mu\text{M}$) and COW (avg. $2.50 \pm 0.38 \mu\text{M}$) were almost same. The obtained nitrate values did not show any direct significance with *Trichodesmium* bloom. However, the present nitrate values are almost two times higher than the values reported for the same period during the previous year ($1.4 \pm 0.22 \mu\text{M}$)³⁶. The overall increase in nitrate concentration during the bloom could be due to the biological oxidation of ammonia which is synthesized by *Trichodesmium*⁵⁶. Ammonia and TN concentrations were much higher than the usual level (non-blooming concentrations during 2019 post-monsoon period: ammonia - $12.21 \pm 11.19 \mu\text{M}$;

TN - $37.7 \pm 1.7 \mu\text{M}$)³⁶. The maximum and minimum concentration for ammonia and TN were recorded in the CNW (Avg. ammonia: $40.52 \pm 20.94 \mu\text{M}$; avg. TN: $68.10 \pm 26.08 \mu\text{M}$) and COW (Avg. ammonia: $35.37 \pm 15.57 \mu\text{M}$; avg. TN: $66.01 \pm 17.24 \mu\text{M}$) regions, respectively. At present, we recorded an extreme amount of ammonia concentration in the entire study region, which might be attributed to *Trichodesmium*'s diazotrophic nature, which exhibits the capability to produce ammonium from dinitrogen through the nitrogen fixation process⁵⁷. Similarly, TN concentrations during the study were significantly high as compared to non-blooming periods of the same season⁵⁵. Since N_2 fixed by *Trichodesmium* can be excreted as only dissolved organic nitrogen (50 %), and amino acids (50 – 100 %), an increase in TN content is expected. The increased values of ammonia and TN during this study indicate a direct impact of bloom on water quality.. Many researchers have also documented an unusual increase of both ammonia and TN levels during the *Trichodesmium* bloom^{5-6,22,28,30} claiming that the bloom is generally ungrazed and decomposes, resulting in higher nitrogenous levels.

Phosphate in the aquatic ecosystems promotes growth for organisms and acts as a limiting factor in phytoplankton production in tropical coastal marine ecosystems⁵⁸. During the bloom appearance, Orthophosphate (OP) and Total Phosphorus (TP) concentration showed similar spatial patterns between both transects. The mean concentration of OP was $0.29 \pm 0.27 \mu\text{M}$ at CNW and $0.14 \pm 0.02 \mu\text{M}$ at COW. Similarly, the average concentration of TP was $0.90 \pm 0.78 \mu\text{M}$ at CNW, and $0.48 \pm 0.08 \mu\text{M}$ at COW. Non-blooming concentrations of OP and TP from the same locality were $0.44 \pm 0.08 \mu\text{M}$ and $1.82 \pm 1.10 \mu\text{M}$ ^(ref. 36). Comparatively high concentration of OP and TP were recorded at CNWs than the COWs, which could be attributed to various processes most likely decomposition of algal (*Trichodesmium*) biomass, desorption of phosphate and buffering action of sediments as well as the microbial activity⁵⁹⁻⁶⁰. Both OP and TP showed positive correlation with *T. thiebautii*, which could be due to the dominance of *T. thiebautii* over *T. erythraeum* at certain locations with relatively high OP and TP concentrations; for example, CN1 and CN2. The above observation was further supported by PC6 (Table 3) where *T. thiebautii* was found positively loaded with OP and TP. It has been reported that phosphate plays an important role in the growth and development of the *Trichodesmium* filament and ultimately control the biomass⁶¹. The lower concentration of OP and TP was found at COWs that most probably due to utilization by microalgae and the process of phosphate solubilization through particular bacterial communities in the surface waters⁵⁸. It is worth noting that the Bay of Bengal has a higher level of organic phosphate in the surface waters when compared to inorganic phosphate⁶². Interestingly, *Trichodesmium* can meet the majority of its phosphorus requirements from phosphoesters, a major fraction (75 %) of the organic phosphorus⁶³. Mulholland *et al.*⁶⁴ reported that organic phosphate alleviated P limitation and promoted P uptake and growth of phytoplankton. The dominance of the *Trichodesmium* in the Bay of Bengal and the reported low concentration of PO_4 indicate the potential importance of the mechanisms such as phosphorus mining⁶⁵. In this context, the TP concentration in the Arabian sea has been reported to be relatively higher ($0.44 - 8.2 \mu\text{M}$)⁶⁶ than Bay of Bengal ($0.5 - 3.2 \mu\text{M}$)⁶⁷.

Silicate is an important factor that supports the phytoplankton growth, and their fluctuation in the

coastal environment depending on environmental conditions with favourable seasons. In the present study, the higher concentrations were observed in CNW ($3.45 \pm 2.37 \mu\text{M}$); whereas, COW showed the lower concentrations ($2.47 \pm 1.15 \mu\text{M}$). The maximum concentration of silicate ($7.82 \mu\text{M}$) was recorded at CNW1, which could be due to the influx of silicate-rich freshwater from the nearby backwaters. The highest algal biomass and chlorophyll-*a* concentration was also recorded from the same region. The silicate values documented in this present study corroborated with prior investigations in the same coastal location^{5-6,29}. Unlike in diatom blooms, where silicate plays a significant role in bloom propagation, its role in cyanobacteria blooms development has not been clearly known.

Chlorophyll-*a*

The photosynthetic pigment Chl-*a* was much higher (9.34 mg m^{-3}) at one location in the CNW region (CN1) during the bloom event. Mean Chl-*a* was relatively high ($2.17 \pm 3.52 \text{ mg m}^{-3}$) at the CNW region compared to the COW region ($0.41 \pm 0.27 \text{ mg m}^{-3}$). Out of the 12 stations sampled, ten stations showed lower concentrations ($< 1 \text{ mg m}^{-3}$) of Chl-*a*, except station CN1 and station CN3 (1.12 mg m^{-3}). The highest Chl-*a* concentration coincided with the highest phytoplankton density observed from the same location. Various researchers have reported similar observations of wide variations in pigment concentrations during *Trichodesmium* bloom around the Indian coast^{5-6,27,68-69}.

The bloom feature and its dynamics have been observed in the five-week images derived from the MODIS Aqua satellite (Fig. 3a – e). The 8-days composite chlorophyll concentration images corroborated with the in-situ observation of the bloom. It depicted the high concentration of Chl-*a*, typical to algal bloom ($> 0.50 \text{ mg m}^{-3}$) and an elongated dense feature movement towards offshore water. The 3rd week (21st to 28th March 2020) chlorophyll image showed the lengthiest straight line-like pattern and at its offshore end, the feature observed of circular shape. The chlorophyll concentration within the bloom feature near the coastal water was observed in the range of 1.0 to 1.6 mg m^{-3} . In far coastal and offshore water, the concentration is reduced and appeared in a uniform range ($0.2 - 0.3 \text{ mg m}^{-3}$). The bloom feature continued for about a month time (Fig. 3a – e).

Phytoplankton community structure

Two species of *Trichodesmium* viz. *T. erythraeum* and *T. thiebautii* mainly constituted the bloom. The average population density of *T. erythraeum* and *T. thiebautii* were $4.8 \pm 1.3 \times 10^5$ cells L^{-1} and $3.9 \pm 1.9 \times 10^5$ cells L^{-1} , respectively. These two species together contributed almost 97.8 % (55.2 % - *T. erythraeum* and 42.6 % - *T. thiebautii*) to the total phytoplankton community (Fig. 4a). Available literature related to bloom formation by the *Trichodesmium* spp. are well documented in the Indian coastal regions^{5-6,24,27,29,31}, though the mixed bloom of *T. erythraeum* and *T. thiebautii* is rarely reported from the Indian waters⁶⁹⁻⁷⁰. Bloom samples showed bundles of *Trichodesmium* filaments and colonies, which seems like fusiform or tuft colonies and radial or puff colonies. The collected

samples particularly from the northern zone of the sampling regions remained pink after the settlement of the plankton. Such a pink discoloration could be due to the discharge of a water-soluble accessory pigment (*e.g.*, phycoerythrin) through extracellular leachate from *Trichodesmium*, which signifies the beginning of decay phase of *Trichodesmium* cells¹⁹.

During the survey, the phytoplankton community comprised 69 species, of which a maximum number of species (35) were recorded in the COW region, whereas the minimum numbers (21 species) were registered at CNW regions (Table 4). The total phytoplankton density ranged from $6.01 - 12.57 \times 10^5$ cells L^{-1} (Fig. 5). The phytoplankton species were categorized broadly into to 3 groups represented by diatoms, dinoflagellates, and Cyanophyceae (blue-green algae). The group Cyanophyceae, consisted of *T. erythraeum*, *T. thiebautii* and *Richelia intracellularis* which together contributed about 97.9 % of the phytoplankton population density. The percentage contributions of diatoms, dinoflagellates were 1.5 % and 0.6 %, respectively (Fig. 4a). The

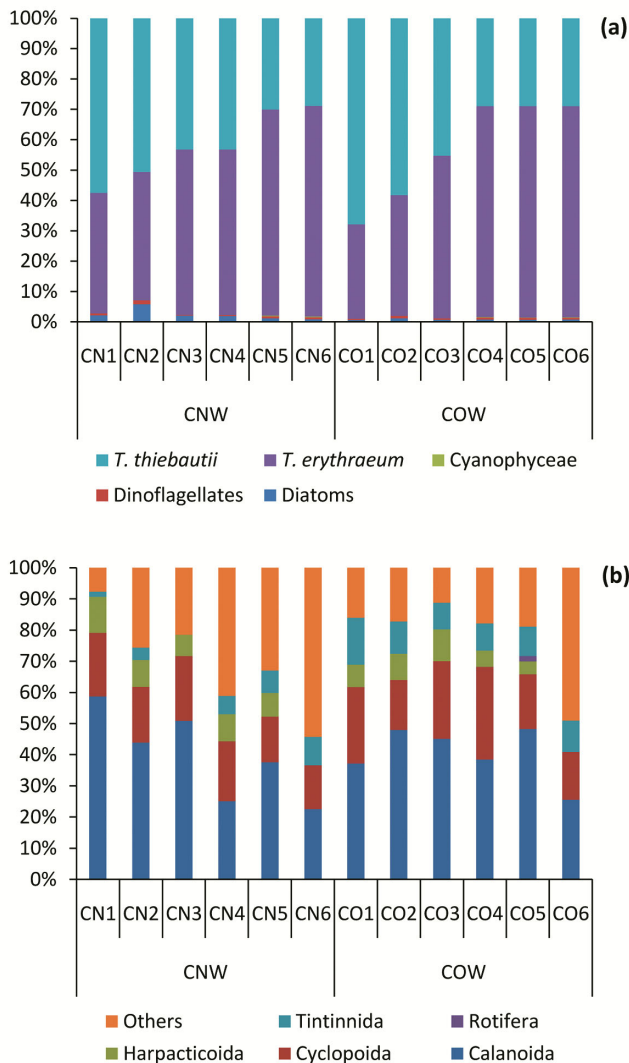


Fig. 4 — Percentage contribution of (a) phytoplankton and (b) zooplankton groups during the bloom event

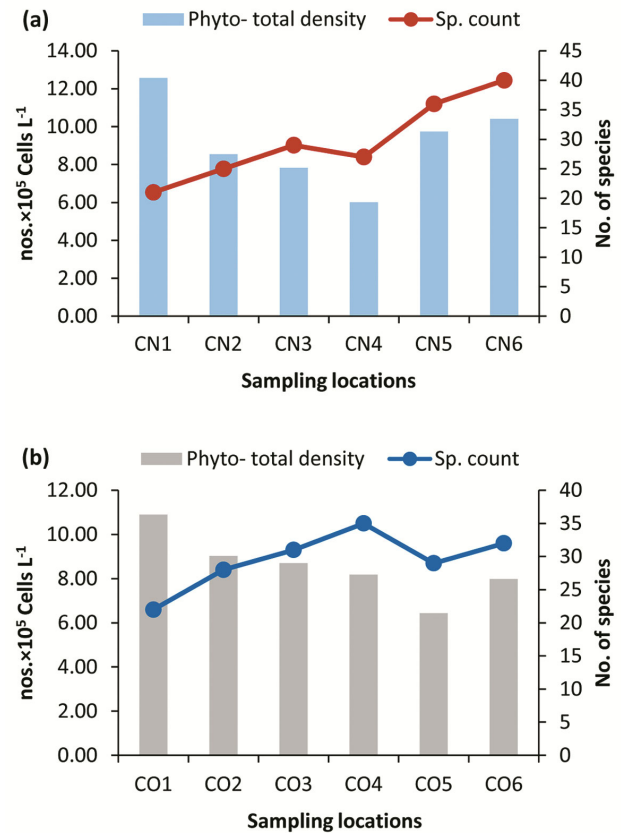


Fig. 5 — Spatial (a - CNW and b - COW) variation of total phytoplankton abundance and species richness during the bloom (March 2020) event at Kalpakkam coast

Table 4 — List of identified phytoplankton species and their abundance (cells L⁻¹) in March 2020 in Kalpakkam coastal waters, Southeast coast of India (*Blooming species; – denote absent)

Sampling location	Coastal near-shore						Coastal offshore					
	CN1	CN2	CN3	CN4	CN5	CN6	CO1	CO2	CO3	CO4	CO5	CO6
Phytoplankton species												
Diatoms												
<i>Asterionella</i> sp.	2010	629	–	–	–	–	–	–	–	–	–	–
<i>Bacillaria paradoxa</i>	–	–	567	436	–	–	–	–	–	–	–	–
<i>Bacteriastrium camosum</i>	–	–	521	400	1756	1139	980	1447	735	897	710	880
<i>Bacteriastrium furcatum</i>	–	–	–	–	390	194	165	248	126	153	145	180
<i>Bacteriastrium hyalinum</i>	–	–	–	–	756	639	534	815	414	503	395	490
<i>Bellerochea malleus</i>	–	6105	326	250	439	167	–	–	–	–	–	129
<i>Bellerochea</i> sp.	2501	194	–	–	–	–	–	–	–	–	–	–
<i>Biddulphia</i> sp.	–	1952	–	–	–	–	–	–	–	–	–	–
<i>Biddulphia tridens</i>	–	–	474	364	–	–	–	–	–	–	–	–
<i>Chaetoceros affinis</i>	–	–	1841	1416	–	–	–	–	–	–	–	–
<i>Chaetoceros concavicornis</i>	–	–	–	–	439	250	–	319	162	197	156	194
<i>Chaetoceros decipiens</i>	–	–	–	–	293	333	–	–	376	262	207	257
<i>Chaetoceros diversus</i>	–	–	–	–	805	917	990	1483	753	722	571	708
<i>Chaetoceros eibenii</i>	–	1859	–	–	268	306	270	394	200	241	190	235
<i>Chaetoceros peruvianus</i>	–	–	–	–	244	250	–	317	161	197	–	–
<i>Chaetoceros tortissimus</i>	–	–	–	–	366	417	368	531	270	328	265	328
<i>Climacodium frauenfeldianum</i>	–	–	623	479	–	–	–	–	–	–	–	–
<i>Corethron hystrix</i>	–	–	–	–	–	167	–	–	–	131	–	–
<i>Coscinodiscus gigas</i>	434	–	–	–	–	–	–	–	–	–	–	–
<i>Coscinodiscus granii</i>	–	–	297	228	–	–	–	–	–	–	–	–
<i>Coscinodiscus radiatus</i>	–	–	725	557	–	–	–	–	–	–	–	–
<i>Ditylum brightwellii</i>	983	–	–	–	–	–	–	–	–	–	–	–
<i>Ditylum sol</i>	1236	629	753	579	–	–	–	–	–	–	–	–
<i>Eucampia zoodiacus</i>	–	–	–	–	366	333	287	429	218	262	244	302
<i>Guinardia cylindrus</i>	–	–	–	–	–	139	–	405	206	109	–	–
<i>Guinardia flaccida</i>	–	–	–	–	220	167	–	–	–	–	–	–
<i>Lauderia borealis</i>	1300	9250	–	–	–	–	–	–	–	–	–	–
<i>Leptocylindrus danicus</i>	–	3608	–	–	–	–	–	–	–	–	–	–
<i>Leptocylindrus</i> sp.	4240	–	–	–	–	–	–	–	–	–	–	–
<i>Navicula</i> sp.	–	629	–	–	–	–	–	–	–	–	–	–
<i>Nitzschia closterium</i>	4098	3423	539	414	73	–	–	–	–	–	–	–
<i>Nitzschia longissima</i>	1346	–	–	–	–	–	–	–	–	–	–	–
<i>Nitzschia seriata</i>	–	–	167	–	–	–	–	–	–	–	–	–
<i>Odontella mobiliensis</i>	–	–	335	–	146	167	710	1069	543	131	104	129
<i>Odontella sinensis</i>	–	–	1507	1159	–	139	–	216	110	109	–	–
<i>Planktoniella sol</i>	–	–	655	580	–	–	–	–	–	–	–	–
<i>Pleurosigma directum</i>	–	–	1144	880	–	–	–	–	–	–	–	–
<i>Pleurosigma elongatum</i>	–	2868	605	465	–	–	–	–	–	–	–	–
<i>Pleurosigma normanii</i>	–	–	–	–	146	–	–	–	–	–	–	–
<i>Pleurosigma</i> sp.	–	–	–	–	–	83	–	–	–	–	–	–
<i>Pseudo-nitzschia australis</i>	763	1127	–	–	707	417	350	527	268	328	258	320
<i>Pseudo-nitzschia pungens</i>	1073	1794	1195	919	927	500	424	636	323	394	315	390
<i>Pseudosolenia calcar-avis</i>	–	–	–	–	512	111	–	–	–	–	–	115
<i>Rhizosolenia alata</i>	102	4810	730	330	–	–	–	–	–	–	–	–
<i>Rhizosolenia costracanei</i>	–	–	–	–	–	56	–	–	–	–	–	68
<i>Rhizosolenia crassispina</i>	–	–	484	372	463	306	260	390	198	241	202	250
<i>Rhizosolenia hebetata</i>	–	–	–	–	537	306	–	–	205	241	–	–
<i>Skeletonema costatum</i>	678	1739	1288	760	–	–	–	–	–	–	–	–
<i>Stephanopyxis palmeriana</i>	534	–	391	300	–	–	–	–	–	–	–	–
<i>Thalassionema nitzschioides</i>	3498	1665	195	150	1000	1028	890	1306	663	809	641	795
<i>Thalassiothrix frauenfeldii</i>	1706	6845	316	234	341	–	–	–	–	–	–	–
Dinoflagellates												
<i>Ceratium breve</i>	–	–	–	–	220	250	–	–	–	198	160	198
<i>Ceratium furca</i>	1473	1739	567	436	1049	944	800	1201	610	744	618	766

(Contd.)

Table 4 — List of identified phytoplankton species and their abundance (cells L⁻¹) in March 2020 in Kalpakkam coastal waters, Southeast coast of India (*Blooming species; – denote absent) — (Contd.)

Sampling location	Coastal near-shore						Coastal offshore					
	CN1	CN2	CN3	CN4	CN5	CN6	CO1	CO2	CO3	CO4	CO5	CO6
Phytoplankton species												
<i>Ceratium fusus</i>	–	–	–	–	756	861	658	900	574	678	532	660
<i>Ceratium inflatum</i>	–	–	–	–	854	611	–	782	397	481	379	470
<i>Ceratium macroceros</i>	5512	4810	772	593	–	378	521	541	275	290	240	297
<i>Ceratium trichoceros</i>	–	642	–	–	561	639	337	447	227	503	395	490
<i>Ceratium tripos</i>	–	983	381	293	390	444	441	551	280	350	279	346
<i>Dinophysis caudata</i>	859	1739	–	–	–	–	–	–	–	–	–	–
<i>Diplopsalis</i> sp.	–	–	–	–	659	750	–	–	490	592	–	–
<i>Protoperdinium obovatum</i>	–	–	–	–	–	167	268	382	194	131	104	129
<i>Protoperdinium pellucidum</i>	–	–	–	–	634	722	600	906	460	569	444	550
<i>Protoperdinium remotum</i>	–	–	567	436	439	500	420	634	322	393	310	385
<i>Protoperdinium</i> sp.	–	1119	–	–	–	–	–	–	–	–	–	–
<i>Pyrophacus horologium</i>	–	–	–	–	195	222	–	–	–	175	140	174
<i>Pyrophacus steinii</i>	–	–	–	–	293	333	–	413	210	262	206	256
Cyanophyceae												
<i>Richelia intracellularis</i>	–	–	–	–	2317	2639	–	–	–	990	934	1158
<i>Trichodesmium erythraeum</i> *	500166	362073	426740	328261	662073	722888	339414	359121	466559	569203	448441	556067
<i>Trichodesmium thiebautii</i> *	722888	432609	338007	260005	292609	300166	740432	525648	393730	236351	186206	230896
Total Density	1257400	854840	782712	601296	974243	1041043	1090119	902058	870259	818165	643791	798612

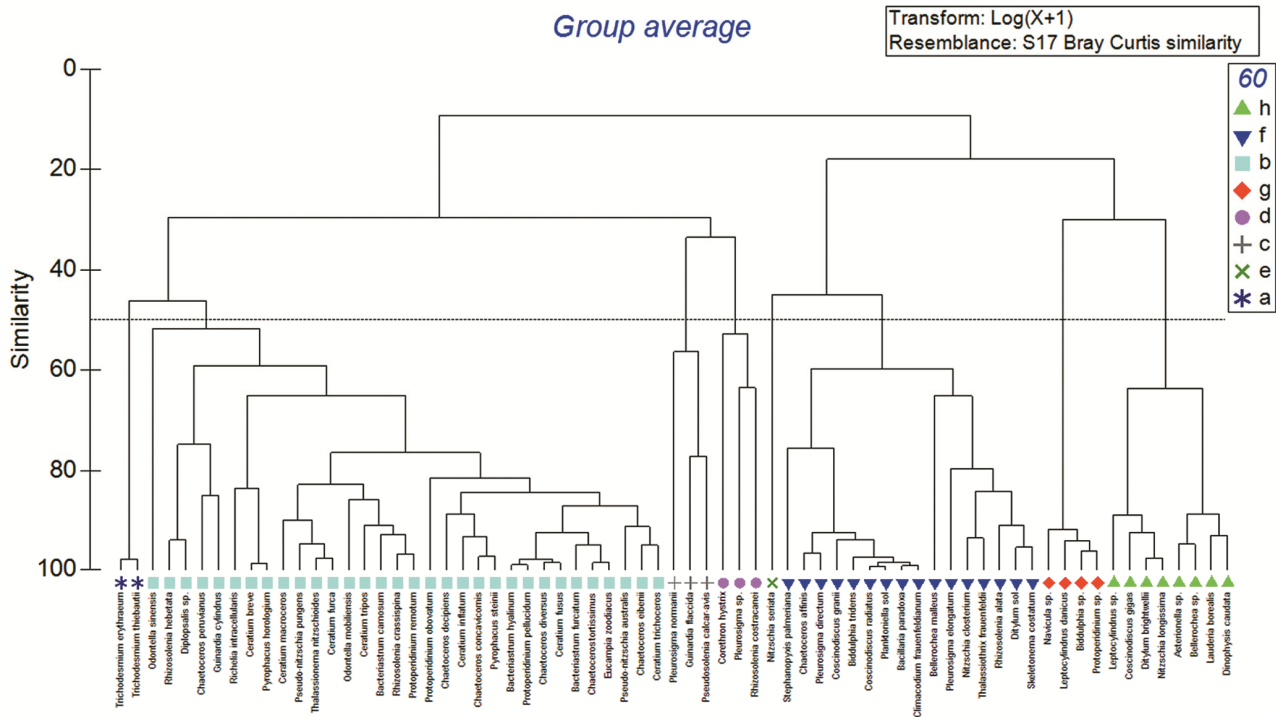


Fig. 6 — Dendrogram showing the grouping of phytoplankton species during the bloom

blooming species (*Trichodesmium*) were dominant in all the stations; however, an unusually high density of *T. thiebautii* (7.4×10^5 cells L⁻¹) was noticed in the northern region. *Trichodesmium erythraeum* dominated in the southern region (7.2×10^5 cells L⁻¹) of the Kalpakkam coastal waters. The cluster analysis (Fig. 6) indicated that various species such as

Bacteriastrum camosum, *Odontella mobiliensis*, *Pseudo-nitzschia* spp., *Rhizosolenia crassispina*, *Thalassionema nitzschioides*, *Ceratium* spp., and *Protoperdinium remotum* were more common at all these stations and their occurrences were linked to the *Trichodesmium* abundance. Species such as *Rhizosolenia costracanei*, *Pleurosigma normanii*,

Guinardia flaccid, *Pseudosolenia calcar-avis*, *Nitzschia seriata*, etc., which appeared sporadically, formed separate clusters. Interestingly, several species such as *Coscinodiscus gigas*, *Nitzschia longissima*, *Leptocylindrus danicus*, *Lauderia borealis*, *Dinophysis caudata*, etc. exclusively appeared at CN1 and CN2 locations where the bloom biomass was relatively high. In general, this coastal area is rich in phytoplankton diversity^{29,49,71}. However, in the present study, a relatively low number of species were observed which could be due to the impact of the bloom (*Trichodesmium*). Though *T. erythraeum* showed a positive correlation with phytoplankton species number, *T. thiebautii* showed a negative correlation with the same. This might be due to adverse conditions created by *T. thiebautii* for other phytoplankton species as compared to *T. erythraeum*. PCA results showed that, the two bloom forming

species were significantly loaded in two components *i.e.* PC3 and PC6 (Table 3). The positive loading of *T. erythraeum* and phytoplankton species number, and the negative loading of *T. thiebautii* in the PC3 supported the above observation. Several other studies have also reported fall in phytoplankton diversity during the bloom of *Trichodesmium* from the Indian coastal regions^{5-6,29,48,68,72}.

Zooplankton community structure

Physicochemical conditions and the ample availability of phytoplankton in the environment influence the zooplankton species production and growth. During the current investigation, significant spatial variation was detected in zooplankton abundance and species composition along the Kalpakkam coast. Totally 59 species of zooplankton were identified in the present study (Table 5). The

Table 5 — List of identified zooplankton species and its spatial abundance (nos. m⁻³) in Kalpakkam coastal waters, Southeast coast of India (– denote absent)

Sampling location	Coastal near-shore						Coastal offshore					
	CN1	CN2	CN3	CN4	CN5	CN6	CO1	CO2	CO3	CO4	CO5	CO6
Calanoida												
<i>Acartia spinicauda</i>	340	325	464	468	778	479	–	798	175	856	1295	440
<i>Acrocalanus gibber</i>	460	160	425	684	302	101	512	932	879	800	1425	90
<i>Calanopia thompsoni</i>	321	130	–	–	170	–	321	–	298	562	395	–
<i>Canthocalanus pauper</i>	402	225	398	325	175	–	–	–	197	524	308	–
<i>Centropages furcatus</i>	369	230	458	310	1080	–	–	–	441	–	–	–
<i>Centropages orsinii</i>	–	–	–	–	–	–	–	–	324	–	–	–
<i>Centropages sp.</i>	–	–	–	–	–	222	–	–	–	–	–	198
<i>Centropages tenuiremis</i>	–	–	–	–	–	–	–	–	341	–	–	–
<i>Copilia sp.</i>	400	270	–	–	–	–	–	–	–	–	–	–
<i>Eucalanus elongatus</i>	510	185	–	–	302	202	541	285	–	260	395	180
<i>Eucalanus monachus</i>	–	–	–	–	–	–	–	–	–	200	235	–
<i>Euchaeta marina</i>	166	–	562	–	–	126	–	–	–	–	–	110
<i>Labidocera acuta</i>	–	–	391	156	475	303	321	375	445	815	752	270
<i>Nannocalanus minor</i>	–	120	–	–	–	–	423	–	357	380	–	–
<i>Paracalanus parvus</i>	630	352	790	206	302	278	841	959	893	–	1645	264
<i>Pontella danae</i>	–	–	530	–	–	–	–	–	–	–	260	–
<i>Pseudodiaptomus serricaudatus</i>	–	–	–	–	–	–	–	–	–	387	–	–
<i>Temora discaudata</i>	170	160	382	238	648	151	184	–	–	240	295	145
<i>Temora turbinata</i>	–	–	499	–	–	–	–	382	382	160	981	–
Cyclopoida												
<i>Corycaeus sp.</i>	179	–	–	–	–	–	–	–	–	–	–	–
<i>Corycaeus catus</i>	–	220	591	621	562	303	528	452	574	520	–	270
<i>Corycaeus danae</i>	–	–	495	499	216	328	562	279	801	409	1420	291
<i>Oithona brevicornis</i>	137	–	374	–	–	–	–	–	–	601	395	–
<i>Oithona rigida</i>	365	180	542	382	562	202	276	249	159	720	457	185
<i>Oithona similis</i>	–	–	–	325	–	–	391	270	720	527	271	–
<i>Oithona spinirostris</i>	230	160	–	–	–	–	–	–	–	824	213	–
<i>Oncaea venusta</i>	400	147	–	–	302	278	310	–	–	403	142	226
<i>Sapphirina sp.</i>	–	174	–	–	–	50	–	–	360	–	–	44

(Contd.)

Table 5 — List of identified zooplankton species and its spatial abundance (nos. m⁻³) in Kalpakkam coastal waters, Southeast coast of India (– denote absent) — (Contd.)

Sampling location	Coastal near-shore						Coastal offshore					
	CN1	CN2	CN3	CN4	CN5	CN6	CO1	CO2	CO3	CO4	CO5	CO6
Harpacticoida												
<i>Euterpina acutifrons</i>	–	–	–	468	475	–	–	654	360	–	–	–
<i>Lucifer hansenii</i>	630	125	657	359	382	–	–	–	456	502	391	–
<i>Metis</i> sp.	–	130	–	–	–	–	–	–	–	–	–	–
<i>Microsetella</i> sp.	110	170	–	–	–	–	–	–	–	–	–	–
<i>Microsetella norvegica</i>	–	–	–	–	–	–	610	–	258	200	287	–
Rotifera												
<i>Brachionus plicatilis</i>	–	–	–	–	–	–	–	–	–	–	297	–
Tintinnida												
<i>Favella brevis</i>	110	193	–	561	519	126	629	510	720	338	1080	112
<i>Favella philippinensis</i>	–	–	–	–	292	631	642	298	180	832	470	555
Others												
<i>Aurelia aurita</i>	–	–	–	–	216	50	–	–	–	–	–	46
Bivalve veliger	–	–	–	–	980	1100	–	–	140	440	620	990
<i>Cladonema californicum</i>	110	–	–	–	–	–	–	–	–	–	–	–
<i>Chlamydonon exocellatus</i>	–	–	–	312	–	–	–	–	–	–	–	–
Crab zoea	–	–	–	–	–	–	–	–	–	–	47	–
<i>Creseis</i> sp.	–	265	–	365	–	151	–	–	–	–	44	134
Crustacean nauplii	–	–	–	561	–	–	–	–	–	–	–	–
<i>Evadne tergestina</i>	–	–	–	–	270	302	–	–	–	–	–	268
Fish eggs	63	147	580	211	98	32	–	–	–	–	–	33
Fish larvae	–	–	320	310	371	17	–	–	–	–	–	22
Gastropod larvae	–	–	–	–	–	900	–	–	–	327	550	790
Isopod sp.	–	–	358	312	259	580	–	–	–	–	–	–
<i>Longipedia weberi</i>	170	–	–	340	–	–	526	274	471	580	661	–
<i>Obelia</i> sp.	–	–	–	520	–	–	–	–	–	–	–	–
<i>Oikopleura</i> sp.	–	233	287	472	691	290	–	–	–	465	741	267
Phyllosoma larvae	–	–	–	–	–	–	165	–	–	–	–	–
Protozoan zoea	–	130	–	–	–	227	–	–	–	–	–	–
Radiolarian sp.	–	147	–	–	137	50	187	–	564	280	–	–
<i>Sagitta</i> sp.	–	–	523	–	–	–	–	–	–	–	–	–
<i>Sagitta bipunctata</i>	–	165	–	156	302	202	231	417	–	–	254	180
<i>Sagitta enflata</i>	–	–	–	109	389	101	248	652	–	320	–	92
Squilla larvae	–	–	–	–	–	151	–	–	–	–	–	133
<i>Tretomphalus bulloides</i>	148	173	–	247	–	328	–	–	–	–	213	302
Total density	6420	4916	9626	9517	11255	8261	8448	7786	10495	13472	16539	6637

population density of zooplankton ranged from 4916 to 16539 nos. m⁻³ (Fig. 7). The abundance of the zooplankton was maximum in COWs (CO2) while it was minimum at CNWs (CN2). Copepods dominated the zooplankton community contributing ~65 % of the total population. The percentage contributions of dominant groups were: Calanoida (40.1 %), Cyclopoida (19.6 %), Harpacticoida (6.5 %), Rotifera (0.1 %), Tintinnida (7.5 %), and others (26.1 %) (Fig. 4b). Out of the total zooplankton reported in the current study, only some of the species such as *Acartia spinicauda*, *Acrocalanus gibber*, *Eucalanus elongates*, *Labidocera acuta*, *Paracalanus parvus*, *Temora* spp., *Corycaeus* spp., *Oithona rigida*, *Favella* spp., *Oikopleura* sp., *Sagitta* spp. were found

commonly at all the locations (Fig. 8). Some copepod species such as *Paracalanus parvus*, *Acartia spinicauda*, *Acrocalanus gibber* and *Oithona rigida* dominated at all the locations. These copepods are well documented as heavy grazers and are involved in the alternate feeding to the *Trichodesmium* instead of diatoms. On the other hand, the holoplankters such as *Evadne tergestina*, *Oikopleura* sp., and *Sagitta* spp. were also recorded in good numbers, which indicate that these organisms may have selective grazing habits, especially on *Trichodesmium*. Similar species dominance has also been reported earlier from the same study region during *Trichodesmium* bloom⁵⁰. Veliger larvae of Bivalves and Gastropods were encountered in good numbers during the study period.

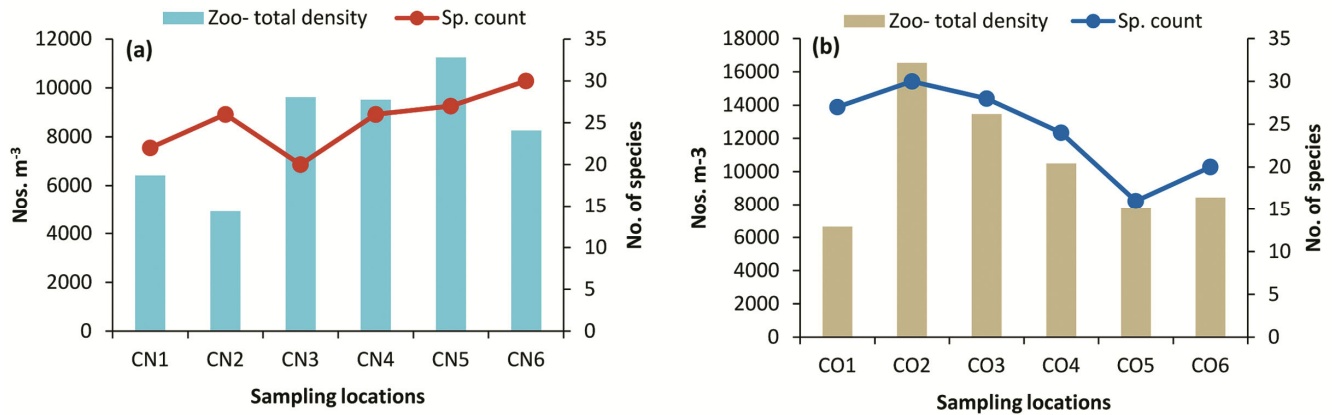


Fig. 7 — Spatial (a - CNW and b - COW) variation of zooplankton abundance and species richness during the bloom (March 2020) event at Kalpakkam coast

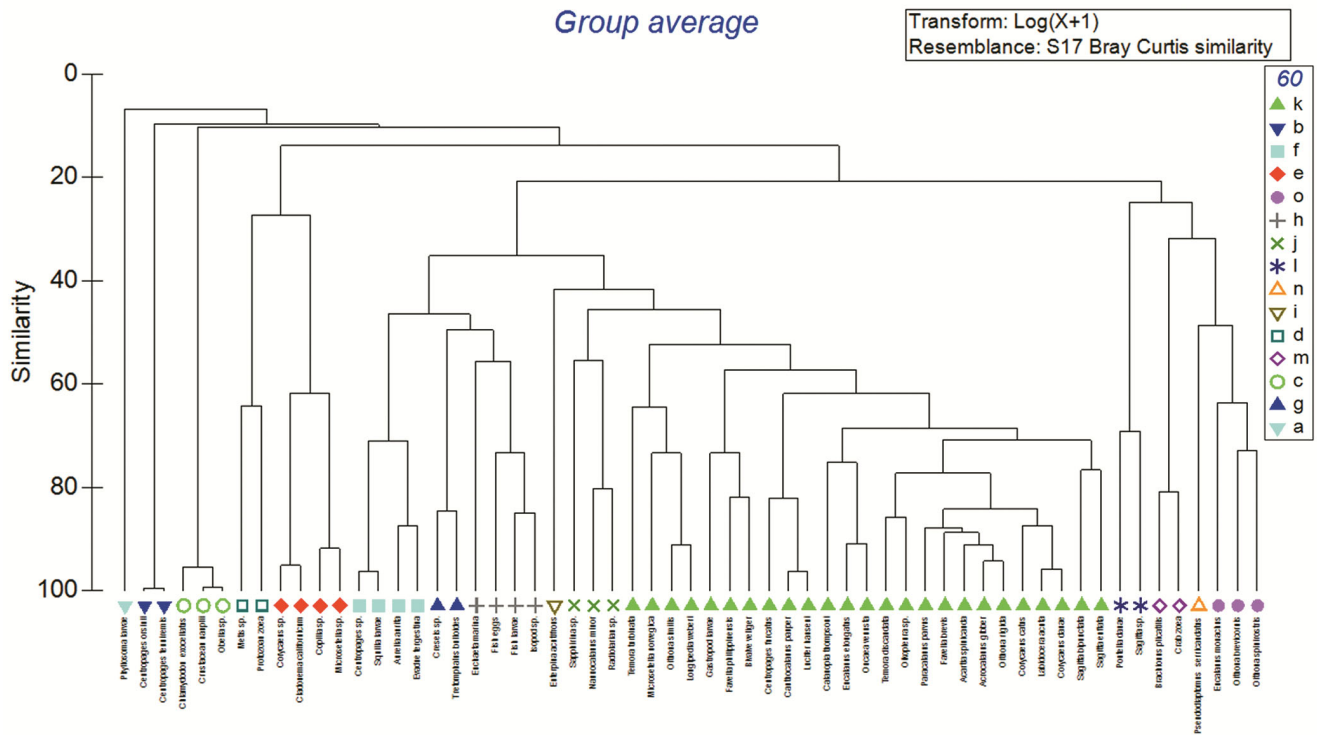


Fig. 8 — Dendrogram showing the grouping of zooplankton species during the bloom

These larval forms are widely distributed and acknowledged as powerful biofilters⁷³⁻⁷⁵. The ample food availability in the form of organic matter from bloom biomass could be the reason for their abundance⁷⁶.

Conclusion

Several studies in the Kalpakkam coastal region have attributed the monsoonal influence and backwater discharge as the prime reasons behind the ecological and environmental changes. However, in

the present study, the environmental changes, especially the change in temperature regime, due to movement of relatively warmer water mass towards north has resulted in the formation of a phytoplankton bloom. *Trichodesmium* species namely *T. erythraeum* and *T. thiebautii* formed the bloom. The MODIS Aqua satellite-derived Sea Surface Temperature (SST) and chlorophyll data further supported the in-situ observations. Nitrates and phosphates were distributed evenly in the entire study region. Concentration of ammonia and total nitrogen increased

significantly during the bloom as compared to non-bloom periods. The blooming species *T. erythraeum* and *T. thiebautii* contributed 53.98 % and 43.82 % of the phytoplankton population density. The number of phytoplankton and zooplankton species was relatively low during the study. The results indicated that the higher temperature (≥ 29 °C) and constant salinity (≥ 33 PSU) are the conducive factors for *Trichodesmium* growth and subsequent bloom.

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Conflict of Interest

Authors declare that there is no conflict of interest.

Author Contributions

GS: Investigation, formal analysis, writing original draft; RSS: Formal analysis, writing original draft; AKM: Conceptualization, software, writing- review & editing; RS: Investigation, formal analysis; KDA: Funding acquisition, supervision, writing; RKS: Writing - review & editing; VS & RV: Supervision, writing - review & editing.

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