Research Article

Occurrence of Nitrogen Fixing Cyanobacterium *Trichodesmium* under Elevated $p\text{CO}_2$ Conditions in the Western Bay of Bengal

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Recent studies on the diazotrophic cyanobacterium *Trichodesmium* showed that increasing CO_2 partial pressure ($p\text{CO}_2$) enhances N_2 fixation and growth. We studied the *in situ* and satellite-derived environmental parameters within and outside a *Trichodesmium* bloom in the western coastal Bay of Bengal (BoB) during the spring intermonsoon 2009. Here we show that the single most important nitrogen fixer in today's ocean, *Trichodesmium erythraeum*, is strongly abundant in high ($\geq 300 \mu\text{atm}$) $p\text{CO}_2$ concentrations. N : P ratios almost doubled (~ 10) at high $p\text{CO}_2$ region. This could enhance the productivity of N-limited BoB and increase the biological carbon sequestration. We also report presence of an oxygen minimum zone at Thamnapatnam. Earlier studies have been carried out using lab cultures, showing the increase in growth rate of *T. erythraeum* under elevated $p\text{CO}_2$ conditions, but to our knowledge, this study is the first to report that in natural environment also *T. erythraeum* prefers blooming in high $p\text{CO}_2$ concentrations. The observed CO_2 sensitivity of *T. erythraeum* could thereby provide a strong negative feedback to rising atmospheric CO_2 but would also drive towards phosphorus limitation in a future high CO_2 world.

1. Introduction

Climate change will significantly alter the marine environment within the next century and beyond. Future scenarios predict an increase from the current ~ 380 to ~ 750 to $\sim 1,000$ ppm CO_2 in the atmosphere towards the end of this century [1, 2]. As the ocean takes up this anthropogenic CO_2 , dissolved inorganic carbon (DIC) in the surface ocean increases, while the pH decreases [3]. Rising global temperatures are likely to increase the surface ocean stratification, which may affect the light regime in the upper mixed layer as well as nutrient input from deeper waters [4]. Uncertainties remain regarding both the magnitude of the physicochemical changes and the biological responses of organisms, including species and populations of the oceanic primary producers at the base of the food web. In view of potential ecological implications and feedbacks on climate, several studies have examined the sensitivity of key phytoplankton species to $p\text{CO}_2$ [5–8]. Significant response to elevated $p\text{CO}_2$ was observed in N_2 -fixing cyanobacteria [9–13], which play a

vital role in marine ecosystems by providing a new source of biologically available nitrogen to the otherwise nitrogen-limited regions [14].

Trichodesmium, a colony-forming cyanobacterium, fixes nitrogen in an area corresponding to almost half of Earth's surface [15] and is estimated to account for more than half of the new production in parts of the oligotrophic tropical and subtropical oceans [16, 17]. Future expansion of the oligotrophic subtropical provinces to higher latitudes due to surface ocean warming and increased stratification is expected to change the spatial extent of *Trichodesmium* and hence the magnitude of global N_2 fixation by this organism [18]. Recent studies focused on the impact of different environmental factors on the *Trichodesmium* species which has high abundance and forms massive blooms in tropical and subtropical areas [16, 17]. Higher $p\text{CO}_2$ levels stimulated growth, biomass production, and N_2 fixation [10, 11, 13] and affected the inorganic carbon acquisition of the cells [13]. While elevated sea surface temperatures are predicted to shift the spatial distribution of *Trichodesmium* species toward

higher latitudes [18], the combined effects of $p\text{CO}_2$ and temperature may favour this species and increase its spatial extent even farther [10, 19]. An increase in the average light intensity, caused by the predicted shoaling of the upper mixed layer, may further stimulate photosynthesis and thus growth and N_2 fixation of *Trichodesmium* [20].

To test the hypothesis that *Trichodesmium* grows better in elevated $p\text{CO}_2$ conditions, we have carried out field studies within and around the *Trichodesmium* bloom in the western Bay of Bengal (BoB). In the northern Indian Ocean, studies on *Trichodesmium* bloom have been mostly in the Arabian Sea [21, 22], but N_2 fixation is a much more important source of nitrogen in BoB than in the Arabian Sea. The Bay is devoid of nutrient supply due to strong stratification, despite the nutrient supply through the rivers [23]. Satellite datasets on chlorophyll *a* (chl *a*), sea surface temperature (SST), wind stress (τ), and sea surface height anomaly (SSHA) were used to observe the spatial extent of bloom and to study the physical processes associated with it.

2. Methodology

2.1. In Situ Observations. Vertical profiles of CTD were collected from six different coastal regions along the east coast of India (Figure 1). At each region, 5 stations were collected based upon the water depth (50, 100, 200, 500, and 1000 m). Seawater samples were collected using a Rosette sampler with 5 litre Niskin bottles mounted on the CTD assembly. Salinity was measured with the help of an Autosol. Nutrients (silicate, phosphate, nitrate, and nitrite) were measured with a Skalar Autoanalyzer by standard colorimetric methods. Standards were used to calibrate the auto analyzer, and frequent baseline checks were made. The standard deviation for duplicates was $0.07 \mu\text{M}$ for silicate, $0.06 \mu\text{M}$ for nitrate, and $0.01 \mu\text{M}$ for nitrite and phosphate. Total carbon dioxide (TCO_2) content of seawater samples was determined using a coulometer (model 5014 of U.I.C. Inc., USA). The reliability of the coulometric titration was regularly checked with certified referenced materials (CRMs, Batch number 92) provided by A. Dickson (SIO, University of California). The accuracy estimated from the CRMs values was $2 \mu\text{mol}$ for TCO_2 . The pH_T and pH_f were measured at 25°C by cresol red spectrophotometry [24]. The pH_T of the samples was then corrected to the *in situ* temperature following equation of Gieskes [25]. Analytical precision was ~ 0.002 for pH. *In situ* $p\text{CO}_2$ was calculated using the dissociation constants of Dickson and Millero [26].

The CO_2 exchange flux ($\text{mmol C m}^{-2} \text{ day}^{-1}$) across the sea-air interface was calculated using equation given in Wanninkhof [27]. $F = k \times s \times \Delta p\text{CO}_2$, where k is the gas transfer velocity, s is the solubility of CO_2 gas in seawater [28], and $\Delta p\text{CO}_2$ is the difference between surface seawater and atmospheric $p\text{CO}_2$. The sea-air $p\text{CO}_2$ difference is computed using the measured surface water $p\text{CO}_2$ values and the atmospheric $p\text{CO}_2$ from the zonal mean CO_2 concentrations reported by the GLOBALVIEW- CO_2 (2009).

Water samples were collected from patches of *Trichodesmium* blooms near the coastal Thamnapatnam (in

FIGURE 1: Sampling locations (+) overlaid over the NOAA-AVHRR weekly composite sea surface temperature (SST) map during 9th–16th May 2009. Circle showing the cooling feature ($\sim 27^\circ\text{C}$ to $\sim 27.5^\circ\text{C}$) associated with the *Trichodesmium* bloom near Thamnapatnam.

Tamil Nadu, India) and then fixed in a 2% formalin solution to permit the identification and counting of phytoplankton. Samples fixed in formalin were observed through a polarising microscope for species identification.

2.2. Satellite-Derived Environmental Parameters. Satellite observations were used to study the spatial extent of bloom and the physical processes associated with it. SeaWiFS (Sea-viewing Wide Field-of-view Sensor) based Level-3 global standard mapped images (SMI) of climatological chl *a* values (9 km spatial resolution) were acquired from Goddard Space Flight Centre (GSFC), for the month of May (1997–2010). Chl *a* datasets based upon SeaWiFS operational bio-optical algorithm (i.e., ocean color, OC4) developed by O'Reilly et al. [29] and later updated (OC4v6) by National Aeronautics and Space Administration (NASA) Ocean Biology Processing Group (OBPG). The previous algorithm yields a strong correlation ($r = 0.892$) with *in situ* Chl *a* on global scale that includes samples from all water types [29]. Level-3 Pathfinder SSTs dataset (4 km spatial resolution) from the Advanced Very High Resolution Radiometer (AVHRR) was obtained from NASA's Jet Propulsion Laboratory (JPL) and utilized during the bloom period. Multiple satellite altimeters (Jason-1, TOPEX/Poseidon, ERS 1/2, and GFO) merged product on sea surface height anomalies (SSHA) at a spatial resolution of $1^\circ \times 1^\circ$ were obtained from the NASA Physical Oceanography Distributed Active Archive Center (PODAAC). QuikScat-measured wind vector (scalar wind speed with corresponding u and v components) data files available at spatial resolution of 25 km were downloaded from <http://www.ssmi.com/>. The wind stress (τ) was then calculated using variable drag coefficients (C_D) given by Yelland and Taylor [30].

FIGURE 2: Cross-section of the zonal (80.15°E to 80.75°E) physicochemical parameters collected onboard ORV-Sagar Sampada during April-May 2009. The upliftment of thermocline, halocline, nutricline, elevated CO_2 , and oxygen deficient water near 14°N (off Thamnapatnam) is due to upwelling resulted from divergence of water masses.

3. Results and Discussion

3.1. Observed Variability of Physicochemical Parameters. BoB is highly influenced by monsoons and receives large volume of freshwater from both river discharge and rainfall [31, 32] which results in low sea surface salinity (SSS). All stations had salinity < 34 and temperature > 29°C except Thamnapatnam.

At Thamnapatnam surface salinity was 34.53, and the SST was 27.2°C.

Depth profiles of SST, SSS, and nutrients (NO_3 , NO_2 , PO_4 , and SiO_4) are shown in Figure 2. Surface NO_3 concentrations were <1 μM up to 75 m depth at all stations except Thamnapatnam, where it reached concentrations of 13 μM at 20 m and went on increasing with depth. SiO_4 concentrations were

FIGURE 3: Station wise distribution of $p\text{CO}_2$ and carbon dioxide flux in Bay of Bengal.

$<5 \mu\text{M}$ up to 20 m at all stations except Thamnapatnam. Phosphate concentrations also were $<0.5 \mu\text{M}$ in surface waters, except Thamnapatnam. Dissolved oxygen concentrations were high at the surface and were above 4 mL/L at all stations. Maximum concentration was found at Chennai, reaching up to 5.89 mL/L (Figure 2). Concentration decreased rapidly with depth, and an intense oxygen minimum zone (OMZ) is seen between 150 and 500 m. At Thamnapatnam the OMZ starts from 75 m. Surface pH was greater than 8.3 at all stations and decreased with depth. $p\text{CO}_2$ was less than 300 uatm at all stations except Thamnapatnam, where the maximum $p\text{CO}_2$ was 376 uatm (Figure 3). The average CO_2 flux in Bay of Bengal was $-12.8 \text{ mmol C m}^{-2} \text{ day}^{-1}$, whereas at Thamnapatnam the CO_2 flux was $-3.9 \text{ mmol C m}^{-2} \text{ day}^{-1}$ (Figure 3). The negative sign indicates that the region is a sink for atmospheric CO_2 .

3.2. Physical Forcing. The shoaling of thermocline, halocline, nutricline, and elevated CO_2 and oxygen deficient water (Figure 2) near 14°N (off Thamnapatnam) is due to shoaling and resulted from divergence of water masses. The shoaling-induced cooling feature is well captured by NOAA AVHRR derived SST during May 12, 2009 (Figure 4(a)) and also reflecting in weekly composite product (9–16th May 2009) signifying persistency of the feature (Figure 1). Satellite observations indicated lower SST ($\sim 27^\circ\text{C}$ to $\sim 27.5^\circ\text{C}$) and associated negative SSHA ranging from -0.1m to -0.2m near the bloom region off Thamnapatnam (Figures 4(a) and 4(b)). These features represent an upwelling area where cold, high nutrient, and dense waters are pushed to the

surface (Figure 2), leading to phytoplankton bloom. The alongshore wind stress is favourable off Thamnapatnam to induce coastal upwelling finally resulting in a phytoplankton bloom (Figure 4(c)).

3.3. Distribution of *Trichodesmium erythraeum*. Colonies of the cyanobacterium (1–2 mm size bundles of trichomes) could be seen with the naked eye in the surface water at all stations along Thamnapatnam. At Thamnapatnam stations, surface water was blooming with this cyanobacterium, possibly the dominant primary producer during this period. Analysis of the surface plankton collections revealed the presence of *Trichodesmium erythraeum* in the sample. It appeared that *T. erythraeum* was concentrated in the upper 3 meters of the water column due to its positive buoyancy [33–35] and the surface water attained a brownish color. Around 4500 filaments of *T. erythraeum* per litre seawater were observed. A colony of *T. erythraeum* collected from the Thamnapatnam consisted of $\sim 3.1 \times 10^5$ cells. *T. erythraeum* comprised 100% of total cell count and showed complete dominance over other phytoplankton.

The *T. erythraeum* bloom reported here assumes considerable importance as the BoB is believed to be a region of relatively low productivity compared to the Arabian Sea. Stratification caused by freshwater influx is thought to restrict upwelling of nutrients. Stratification in the southern BoB is weaker than in the north [36, 37].

During spring intermonsoon, eddies and recirculation zones from the coastal regions of BoB due to the western BoB current (WBC) were found to enhance phytoplankton growth [38, 39]. Since the chl *a* in the upper layer of BoB is

FIGURE 4: Satellite observations during May 12, 2009 illustrating (a) NOAA-AVHRR sea surface temperature in °C, (b) satellite altimetry-based sea surface height anomaly (SSHA) in meter, and (c) QuikSCAT-measured wind stress vectors (Pa).

limited by the availability of nutrients, such oceanic processes that can bring nutrients into the euphotic zone are of prime importance. Nutrients are brought to surface waters by coastal upwelling driven by alongshore winds (Figure 4(c)). In order to identify the physical process that could cause the high chl *a* blooms described previously, we have examined the relevant physicochemical oceanographic data, and the results corresponding to May 12, 2009 are shown in Figure 2. The winds have a large alongshore component (Figure 4(c)) and strong offshore component, thus resulting in coastal upwelling.

Since the surface water temperature was $>26^{\circ}\text{C}$, it would have favored the *Trichodesmium* bloom as marine cyanobacteria exhibit temperature optima somewhere in the range of $25\text{--}35^{\circ}\text{C}$ [40]. Studies by Suvapepun [41] and Sellner [42] have reported that cyanobacteria require higher temperature optima for growth than other phytoplankton and that the

temperature has been the most important factor contributing to cyanobacterial dominance. Buoyancy regulation by cyanobacteria plays a key role in this phenomenon, as soon as the wind abates; cyanobacteria float rapidly towards the surface due to their positive buoyancy [42]. The surface accumulations are quickly dispersed over the water column by wind-induced mixing at wind speeds over $6\text{--}8\text{ m s}^{-1}$ [43].

While effects of CO_2 -related seawater acidification have been demonstrated for a variety of marine microalgae and cyanobacteria [44], mainly focusing on carbon acquisition and concentrating mechanisms [45], little is known about its impact on marine diazotrophs. Earlier studies by Hutchins et al. [10], Ramos et al. [9], Levitan et al. [11], and Kranz et al. [13] reported from lab experiments that *T. erythraeum* prefers high CO_2 conditions. This trend is predominantly attributed to changes in cell division [10, 11] but also altered elemental ratios of carbon to nitrogen [11] or nitrogen to

FIGURE 5: SeaWiFS observed climatological chl *a* concentration (1997–2010) for the month of May at the *Trichodesmium* bloom location in western Bay of Bengal.

phosphorus [9]. A first step toward a mechanistic understanding of responses in *T. erythraeum* has been taken by Levitan et al. [11], focusing on $p\text{CO}_2$ dependency of nitrogenase activity and photosynthesis. We tried to investigate the same hypothesis in natural environment, and we found *T. erythraeum* blooms at Thamnapatnam station which had the highest $p\text{CO}_2$ concentrations. At Thamnapatnam all the 5 stations had $p\text{CO}_2$ concentrations $\geq 300 \mu\text{atm}$. In *T. erythraeum*, photosynthetically generated energy (ATP and NADPH) is primarily used for the fixation of CO_2 in the Calvin-Benson cycle. Cyanobacterial Rubisco possesses one of the lowest CO_2 affinities among phytoplankton [46], their Rubisco is confined to multiple capsid-like carboxysomes and helps to minimize CO_2 leakage [47] thus giving them advantage over other phytoplankton groups.

Nitrogen fixation by *Trichodesmium* also alters the N:P ratio and could drive towards phosphate limitation. N:P ratio was 10 at Thamnapatnam, whereas in Chennai it was 5.3, clearly indicating phosphorus limitation in *Trichodesmium* blooms. The average N/P ratio upto 200 m at all stations was less than 10, indicating large deviations from the standard Redfield's N/P ratio of 16. Analysis of climatological SeaWiFS chlorophyll *a* image for the month of May off Thamnapatnam (Figure 5) indicated elevated chl *a* concentration up to $\sim 3 \text{ mg/m}^3$. Jyotibabu et al. [48] have reported primary productivity as high as $2160 \text{ mg C m}^{-2} \text{ d}^{-1}$ within the bloom in BoB.

Upwelling brought high $p\text{CO}_2$ water and nutrients from subsurface to surface and led to blooming of *Trichodesmium* at surface. The underlying processes responsible for the strong CO_2 sensitivity in this important diazotroph are currently unknown. Our results clearly indicate that with rise in CO_2 in future, the abundance of *Trichodesmium* sp. and N_2 fixation could have potential biogeochemical implications, as it may stimulate productivity in N-limited oligotrophic regions and thus provide a negative feedback on rising atmospheric CO_2 levels.

4. Conclusion

This study has been carried out by conjunctive analysis of *in situ* and satellite observations within and outside a

Trichodesmium bloom in the western Bay of Bengal during the spring intermonsoon 2009. Oceanic environmental parameters such as SST, chl *a*, wind, and SSHA measured from remote sensing satellites are useful to study the bloom due to its synoptic, high spatial resolution, and repetitive characteristics. In this study we show that *Trichodesmium* is strongly abundant in high $p\text{CO}_2$ ($>300 \mu\text{atm}$) concentrations. N:P ratios almost doubled (~ 10) at this high CO_2 region. We also report presence of an oxygen minimum zone in the Bay of Bengal. Earlier studies have been carried out using lab cultures, showing the increase in growth rate of *Trichodesmium* in high $p\text{CO}_2$ conditions, but our study proves for the first time that in natural environment also *Trichodesmium* bloom in high $p\text{CO}_2$ waters. The observed CO_2 sensitivity of *Trichodesmium* could thereby provide a strong negative feedback to rising atmospheric CO_2 but could also lead towards phosphate limitation. Our study also proves that Thamnapatnam is a site for coastal upwelling, OMZ, and *Trichodesmium* bloom formation. However, metabolic processes must be studied in detail to understand the responses of *Trichodesmium* to changes in environmental conditions.

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