

## **Trichodesmium blooms and warm-core oceansurface features in the Arabian Sea and the Bay of Bengal**

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### **Abstarct**

*Trichodesmium* is a bloom-forming, diazotrophic, non-heterocystous cyanobacteria widely distributed in the warmer oceans, and their bloom is considered a 'biological indication' of stratification and nitrogen limitation in the ocean surface layer. In the first part of this paper, based on the retrospective analyses of the ocean surface mesoscale features associated with 59 *Trichodesmium* bloom incidences recorded in the past, 32 from the Arabian Sea and the Bay of Bengal, and 27 from the rest of the world, we have showed that warm-core features have an inducing effect on bloom formation. In the second part of this paper, we have considered the environmental preferences of *Trichodesmium* bloom based on laboratory and field studies across the globe, and proposed a view about how warm-core features could provide an inducing pre-requisite condition for the bloom formation in the Arabian Sea and the Bay of Bengal. Proposed that the subsurface waters of warm-core features maintain more likely chances for the conducive nutrient and light conditions required for the triggering of the blooms.

## 1. INTRODUCTION

The marine cyanobacteria, *Trichodesmium*, are well-known for their sporadic and abrupt blooms in the surface waters of warm oceans during conducive conditions and their thick, yellowish-brown, mat-like bloom biomass that floats on the sea surface is referred to as 'Sea Sawdust' (Qasim, 1972; Capone et al., 1997; Jyothibabu et al., 2003). These blooms are expected to channel large amounts of molecular nitrogen into the photic zone of the ocean through new production and, therefore, believed to play a substantial role in ocean nitrogen cycle (Carpenter and Capone, 1992; Capone et al., 1997; Gandhi et al., 2011; Parab and Matondkar, 2012). Also, it has been believed since the last few decades that *Trichodesmium* blooms represent biological indications of prolonged ocean surface layer stratification and nitrogen limitation (Carpenter and Roenneberg, 1995; Matondkar et al., 2006). Although the formation mechanism of *Trichodesmium* blooms continues to be an enigma across the globe, several concerted field surveys and laboratory experiments in the recent decades world over have helped in significantly improving our understanding on the environmental preferences for the *Trichodesmium* bloom formation (Ohki and Fujita, 1986, 1988; Carpenter and Capone, 1992; Capone et al., 1998; Chen et al., 1996; Subramaniam et al., 1999, 2001; Jyothibabu et al., 2003; Bell et al., 2005; Matondkar et al., 2006; Parab and Matondkar., 2012). It is also pertinent to remember that ocean colour satellite remote sensing has contributed significantly in synoptically tracking thick blooms of *Trichodesmium* in ocean surface layers (Subramaniam et al., 2001; Hegde et al., 2008; Gower et al., 2014; McKinna, 2015 and references therein).

The bloom formation of *Trichodesmium* (both *Trichodesmium erythraeum* and *T. thiebautii*) in the northern Indian Ocean and their possible linkages to the ocean surface mesoscale processes are the focus points of this study. To make the evaluation in the northern Indian Ocean more reliable, certain bloom incidences from other parts of the world were also considered in this paper. Literature confirms that *Trichodesmium* population inhabits the Arabian Sea and the Bay of Bengal throughout the year, albeit their contribution to the native phytoplankton community remains insignificant except at conducive times when they proliferate (Ramamurthy, 1972; Jyothibabu et al., 2003; Hegde et al., 2008; Ashadevi et al., 2010; Mohanty et al., 2010; Parab and Matondkar., 2012). The predominant conducive season of *Trichodesmium* blooms in the northern Indian Ocean is the pre-southwest monsoon (March - May), when the region is exposed to the seasonal highest solar heating and has thermally stratified and nitrogen limited ocean surface waters (Qasim., 1972, Devassy, 1978, Capone et al., 1997; Subramaniam et al., 1999; Jyothibabu et al., 2003, Matondkar et al., 2006; D'Silva et al., 2012 and references

therein). However, it is a reality that the usual *Trichodesmium* blooms that occur in the Arabian Sea and the Bay of Bengal have only sporadic appearance with much lesser geographical extent and duration compared to the ocean surface layer stratification and nitrogen limitation, which are actually basin-scale seasonal features during the pre-southwest monsoon period. In other words, even during the stratified and nitrogen-limited pre-southwest monsoon ocean surface conditions that prevail in the entire northern Indian Ocean, *Trichodesmium* surface blooms occur sporadically and abruptly, and mostly on a micro-scale (a few km) to meso-scale (10s to 100s of km) spatial extent.

The scientific reasoning presented above and our field experience in the seas around India during the last two decades have motivated us to investigate the role of ocean mesoscale features in facilitating the optimum conducive conditions for *Trichodesmium* blooms. The other motivation behind this paper is the interesting research paper published by Davis and McGillicuddy Jr., (2006), who showed that waters in the north Atlantic with warm core (anti-cyclonic) mesoscale features harbour high abundance of *Trichodesmium* filaments. This observation was based on Video Plankton Recorder (VPR) tows across the north Atlantic during the spring season. More recently, another study from the same geographical area showed that cold core (cyclonic) eddies also harbour abundant *Trichodesmium* filaments, but during the fall season (Olson et al., 2015). The common message in these studies is the potential of the mesoscale features (both anti-cyclonic and cyclonic) to provide conducive condition for the prevalence of *Trichodesmium* populations. Nevertheless, it is relevant to recall here that the above studies from the north Atlantic neither dealt with *Trichodesmium* bloom incidences nor the possible mechanism that favour the bloom formation in the region.

Earlier studies on *Trichodesmium* blooms from the northern Indian Ocean have mainly dealt with the environmental characteristics that existed either during or just after the sighting of the surface blooms (Devassy et al., 1978; D'Silva et al., 2012 and the references therein). Therefore, they failed to capture the mechanisms that triggered/favoured the formation of the bloom, which has greatest scientific importance while considering that *Trichodesmium* population with its slow growth rate requires more than a week's time to form mat-like surface blooms (Ohki and Fujita, 1988; Chen et al., 1996; Bell et al., 2005). This indicates that the conditioning of the favourable environment that triggers *Trichodesmium* blooming begins a few weeks prior to the actual sighting of the floating bloom biomass on the ocean surface. This agrees very well with earlier observations that the floating bloom biomass on the sea surface mostly represents the collapsing/dead phase of the bloom biomass and, therefore, consists of fewer viable individuals

(Ramamurthy, 1972; Ohki and Fujita, 1988; Chen et al., 1996; Bell et al., 2005). Therefore, naturally, the environmental features recorded during the surface bloom sightings might have essentially represented the post-bloom disintegration phase rather than the actual environmental conditioning that favours the bloom formation. All the above points indicate the relevance of focussed time - series studies that begin at least a fortnight prior to the sighting of the bloom biomass on the ocean surface, to understand the environmental conditioning triggering the bloom. However, a progressive time series study to track *Trichodesmium* bloom formation in a marine environment has large uncertainties as we never know exactly when and where the bloom occurs, even when stratification and nitrogen limitation exist over an extensive geographical area. Time series data from environmental data buoys with biochemical sensors could be a promising tool in this regard, but research in this line in the northern Indian Ocean is still in the beginning phase. Therefore, in this paper we addressed the following (a) investigated the linkage between meso-scale features and the *Trichodesmium* bloom incidences in the northern Indian Ocean (b) analysed a few *Trichodesmium* bloom cases and mesoscale processes from the rest of the world ocean and (c) attempted to explain the possible mechanism behind the observed biophysical linkage.

## 2. METHODS

Although ocean-colour sensors have been used for direct synoptic-scale detection of *Trichodesmium*, a majority of such methods are non-quantitative and developed for mapping dense surface aggregations; therefore, they are unsuitable for tracking low background (cases  $< 3200$  trichomes  $L^{-1}$ ) bloom concentrations (McKinna, 2015). The approach is different in this paper, wherein, a retrospective analysis of the mesoscale ocean surface features have been carried out based on relevant satellite remote sensing data associated with *Trichodesmium* bloom incidences recorded in many literature. The geographical co-ordinates of the bloom incidences given in the literature are used to scientifically assess the proximity/linkage of these blooms with the ocean surface mesoscale processes. In these literature, the terminology 'bloom' was used for representing the sightings of thick floating biomass of *Trichodesmium* (sea saw dust) on the sea surface. The incidences of blooms analysed in the present study from the northern Indian Ocean were confined to the sampling domain of  $52^{\circ}E - 95.5^{\circ}E$  and  $5^{\circ}N - 22^{\circ}N$  (Figure 1; Table 1). The enlisted past bloom incidences showed that most of them occurred during the pre-southwest monsoon (March-May) and onset of the southwest monsoon (early June) periods. The photographs of a few *Trichodesmium* blooms encountered during our earlier cruises and the photomicrographs of the samples are presented in Figure 2. In order to have an overall

understanding of the seasonal oceanographic setting favouring the *Trichodesmium* bloom formation in the study domain, satellite remote sensing data from online databases consisting of sea surface temperature(<http://oceanwatch.pifsc.noaa.gov/>), surface wind (<http://apdrc.soest.hawaii.edu>), photosynthetically active radiation (<http://oceanwatch.pifsc.noaa.gov>), sea surface currents (OSCAR) (<http://apdrc.soest.hawaii.edu>), mean sea level anomaly (<http://las.aviso.oceanobs.com>), wave height (<http://apdrc.soest.hawaii.edu>), mixed layer depth(<http://apdrc.soest.hawaii.edu>), sea surface salinity (<http://oceanwatch.pifsc.noaa.gov>) and chlorophyll *a*(<http://oceanwatch.pifsc.noaa.gov/>) were retrieved and presented (Figure 3-6).

The time-series of the ocean surface layer mesoscale features associated with the bloom incidences recorded in the past were analysed based on satellite datasets spanning over the respective periods. The geostrophic currents for the specific periods of bloom sightings were retrieved from NOAA database (<http://aoml.noaa.gov/>) and Mean Sea Level Anomaly (MSLA) from AVISO (<http://las.aviso.oceanobs.com/>). The geographical positions of the past bloom incidences were overlaid on the merged images of the geostrophic currents and MSLA. Based on this, a retrospective weekly time-series of the mesoscale features, at least a fortnight prior to the actual sighting of the floating bloom biomass on the ocean surface were carried out. Due to the absence of relevant satellite data in most of the earlier times, bloom incidences recorded older than two decades were not attempted in the present analysis. Similarly, a few bloom sightings very close to the coastline were also omitted from the present analysis due to the large uncertainty of satellite datasets closer to the coast. Altogether **32** *Trichodesmium* incidences from the northern Indian Ocean were considered in the present study (Figure 1, Table 1). Similarly, **27** *Trichodesmium* bloom incidences from the rest of the ocean were also considered with the respective mesoscale features (Table 1). The first 9 cases of the retrospective analysis of the bloom incidences are given in the main text of this paper while the rest have been presented as supplementary material (Supplementary Materials 1-21).

As mentioned above, most of the *Trichodesmium* blooms recorded earlier from the Indian Ocean were observed during the pre-southwest monsoon, when the region receives the seasonal highest Photosynthetically Active Radiation (PAR). It is fundamental to consider the solar radiation available underwater while investigating the pre-requisite environmental conditioning for the formation of the *Trichodesmium* blooms. Many studies have showed that low PAR is conducive for *Trichodesmium* bloom formation, which is usually present in the subsurface waters in tropical oceans. Therefore, understanding underwater PAR during the bloom incidences is very relevant for defining the environmental settings favouring the *Trichodesmium* bloom

formation. To accomplish the above, MERIS, MODIS, SeaWiFS, VIIRS merged daily mean PAR and diffuse attenuation co-efficient of PAR ( $K_d$  PAR) was downloaded from online database (<http://hermes.acri.fr>). 8--days' mean downwelling PAR for typical pre-southwest monsoon conditions in the Arabian Sea and the Bay of Bengal were presented to show the overall underwater light condition in the study domain when *Trichodesmium* blooms are most frequent in the region. PAR at specific depth of the water column was derived using the formulae of Gallegos et al., (2001) and the derived PAR values in each depth were used for presenting its vertical distribution.

### 3. RESULTS AND DISCUSSION

The seasonal reversal of winds and currents during the northeast monsoon (October – February) and southwest monsoon (June - September) with a clear transition phase during the pre-southwest monsoon (March-May) are the most important seasonal climatological features of the seas around India (Figure 3). The wind in the study domain is the strongest during the southwest monsoon (south-westerly), moderated during the northeast monsoon (north-easterly) and the weakest during the pre-southwest monsoon. In the case of surface currents, strong and more organised currents are present during the southwest and northeast monsoons, whereas very weak and unorganised currents are present during the pre-southwest monsoon in major parts of the study domain with mesoscale eddy circulations. An exception to this could be the shelf regions along the southeast coast of India where East India Coastal Currents (EICC) are dominant during the pre-southwest monsoon. However, recent research shows that even EICC flows as several mesoscale eddy cells (Durand et al., 2009; Shenoi, 2010), and this feature was clearly reflected in the seasonal image presented in this paper (Figure 3). The seasonal distribution of sea surface temperature (SST) and sea surface salinity (SSS) showed the highest SST and the second highest SSS in the seas around India during the pre-southwest monsoon (Figure 4). Seasonal distribution of wave height and mixed layer depth showed the lowest values of these parameters during the pre-southwest monsoon period, indicating the calm and highly stratified sea conditions during the period (Figure 5). The PAR was the seasonal highest during the pre-southwest monsoon, followed by the southwest monsoon, and the least during the northeast monsoon period (Figure 6a-c). The seasonal surface chlorophyll *a* concentration was the highest during the southwest monsoon, followed by the northeast monsoon, and the least during the pre-southwest monsoon (Figure 6d-f). In essence, all the above show that the pre-southwest monsoon in the northern Indian Ocean

was a period with highest SST, SSS, PAR and the lowest winds, surface currents, and wave action causing thermally stratified relatively calm sea surface conditions.

As presented above, it has been documented earlier also that high SST, low or nil surface winds, and stratified and stable water column are the typical characteristics of the pre-southwest monsoon in the Northern Indian Ocean during which most of the *Trichodesmium* blooms in the past were recorded (Qasim 1970; Capone et al. 1997; Carpenter et al. 1999; Hood et al. 2001; Matondkar et al., 2006). It is logical to link the general oceanographic settings of the northern Indian Ocean during the pre-southwest monsoon with the proliferation of the *Trichodesmium* blooms. During the pre-southwest monsoon period, the mixed layer is shallow (average  $23 \pm 5$  m) and nitrate concentration in the upper euphotic column (upper 50 m) is below detectable concentration in the seas around the Indian subcontinent. The nitrate concentration gradually increases below mixed layer and the nitracline (1  $\mu$ M of nitrate) is usually found at 50-60 m depth (Madhu et al., 2006; Matondkar et al., 2006). This condition provides advantage to the slow-growing and nitrogen fixing phytoplankton community such as cyanobacteria over diatoms. Unlike diatoms, the slow growth of nitrogen fixers enables them to assimilate very low concentration of nitrate present in the water column. The marine cyanobacteria *Trichodesmium* are better advantaged during the pre-southwest monsoon as they are slow growers as well as nitrogen fixers. It was proved through experiments that *Trichodesmium* filaments multiply slowly (3-5 days), requiring more than a week to complete the exponential growth phase and form blooms (Ohki et al., 1986; Lin et al., 1998; Stihl et al., 2001; Bell et al., 2005). Also important is the fact that *Trichodesmium* blooms have much smaller geographical spread and duration compared to the ocean surface layer stratification during the pre-southwest monsoon period, suggesting that mere stratification of the ocean surface layer is not the only requirement for triggering the blooms. It is pertinent here to consider that *Trichodesmium* surface blooms in the seas around India occur sporadically and abruptly, and that, too, mostly on a micro- (<10 km) to meso- (10-500 km) scale spatial extent.

Mesoscale surface ocean features (eddies) are common in the ocean and they can play an important role in plankton distribution and patchiness as they can modify the vertical distribution of physico-chemical parameters (Mackas and Galbraith, 2002; McGillicuddy et al., 1998, 2003; Flierl and McGillicuddy, 2002; Batten and Crawford, 2005; Mackas and Coyle, 2005; Strzelecki et al., 2007; Feng et al., 2007). As evidenced in many earlier studies, eddies are common in the Bay of Bengal and the Arabian Sea and their general response on biological production shows that anti-cyclonic

(warm-core) eddies cause downwelling of surface waters and intensify oligotrophy in the ocean surface layers, whereas, cold-core eddies upwell subsurface waters and enhance biological production (Prasannakumar et al., 2007 and references therein; Jyothibabu et al., 2008, 2015; Nishino et al., 2011; Amol et al., 2014; Jineesh et al., 2015 ). Based on the above general understanding of the mesoscale features, it was rather difficult to explain how warm core eddies support high abundance of *Trichodesmium* filaments (Davis and McGillicuddy Jr., 2006). This is primarily because *Trichodesmium* is a diazotroph (nitrogen fixer) and, therefore, its preferences for the environmental parameters are different from those of the usual microphytoplankton community consisting of diatoms and dinoflagellates, which form the major portion of phytoplankton biomass during nutrient enriched environmental situations (Devassy et al., 1978).

The details of *Trichodesmium* bloom incidences analysed in the present study are shown in Table 1. Among these bloom incidences, the time series images of the satellite data of the cases from the Bay of Bengal and the Andaman Sea are presented in the main body of this paper (Figures 7-9). Images of all the remaining time series analyses of the bloom incidences are presented as supplementary materials (Supplementary Materials 1-21). The most significant features evident in the retrospective analysis with respect to each *Trichodesmium* incidence provided in the supplementary material are detailed in the respective figure captions. Interestingly, almost all earlier bloom incidences analysed in the present study showed some positive linkages/connection with warm-core features. This was true for the *Trichodesmium* incidences analysed for the northern Indian Ocean as well as the rest of the world ocean, indicating that the observed feature could have global importance. Out of 32 *Trichodesmium* incidences analysed from the northern Indian Ocean, 26 incidences (~80%) coincided with warm core mesoscale surface features. Similarly, out of 27 incidences analysed from the rest of the world, 25 incidences (~90%) coincided with warm core features. Nevertheless, it is quite intriguing to explain how warm core eddy, which usually increases the oligotrophy of the ocean surface layer, favours the *Trichodesmium* bloom formation. The above observation, in principle, corroborates the findings of Davis and McGillicuddy Jr., (2006) from the Atlantic Ocean that showed that warm-core eddy favours the proliferation of *Trichodesmium*, albeit there was neither any mention about bloom nor the mechanism that favours bloom formation. Therefore, here we propose mechanisms, which make the warm core eddies more conducive for the formation of *Trichodesmium* blooms during the pre-southwest monsoon. To



comprehend the task, it is invaluable to have a careful understanding of the relevant past studies conducted world over, dealing with the ecological and physiological aspects of *Trichodesmium* blooms.

It has been recorded earlier that *Trichodesmium* can grow actively over a wide range of salinity (22-43psu), with an optimum range between 30-37psu (Fu and Bell., 2003; Bell et al., 2005; Hegde et al., 2008). Similarly, it was observed earlier that *Trichodesmium* blooms occur in a large geographical region, extending from the tropics to the temperate waters, indicating their wide range of tolerance to temperature (28-36) (Capone et al., 1997). Nonetheless, it is a very common feature in the Indian waters that low or nil wind and warmer temperatures act as a prerequisite for the formation of *Trichodesmium* blooms (Matondkar et al., 2006; Parab and Matondkar, 2012). This would mean that highly illuminated, warm and stable environmental conditions exert an inducing effect on the formation of *Trichodesmium* blooms in the northern Indian Ocean. As discussed earlier, accurate measurement of environmental factors promoting *Trichodesmium* blooms in natural environment and drawing meaningful conclusions is less effective, and a possible alternative is to adopt the results of laboratory experiments to explain the observed features in the natural environment – as attempted in a few earlier studies (Ohki et al., 1986; Lin et al., 1998; Stihl et al., 2001; Bell et al., 2005). To elucidate how warm - core eddies facilitate optimum conducive environment for the formation of *Trichodesmium* bloom in the northern Indian Ocean, we considered observations from the field and attempted to explain them logically with the results emerging from laboratory culture studies. This is very significant, considering that the environmental features that coexist during the sighting of floating bloom biomass do not reflect the actual conducive environment that triggered the bloom formation.

Fundamental to this is that optimum PAR and nutrient levels are the two most important factors for the formation of any phytoplankton blooms in the tropical region, though the optimum requirements of these two factors may vary in different phytoplankton groups. For several decades, the actual nutrient and light requirements of *Trichodesmium* to form blooms remained unclear mainly because of (a) *Trichodesmium* experimental studies were restricted earlier (b) their biomass floating on the surface, during bloom formation, is usually exposed to the highest level of solar radiation and undetectable level of nutrients, posing doubt about light and nutrient requirements, and (c) their diazotrophic (nitrogen fixing) ability introduces difficulty in distinguishing whether they are fixing their own nitrogen or absorbing it from the surroundings. Research over the last few decades made the entire scenario clearer and it is reasonably clear now that (a) *Trichodesmium* has a viable growing stock of individual filaments in the subsurface waters and a

thick mat-like floating biomass of trichomes on the sea surface, which are mostly in the declining phase (Ramamurthy, 1972; Lettier and Karl., 1998; Capone et al., 1998; Bell et al., 2005; Mohanty et al., 2010), (b) *Trichodesmium* can actively assimilate nitrate and other nitrogen compounds during their growth phase (Ohki et al., 1986; Lin et al., 1998; Stihl et al., 2001; Holl and Montoya, 2005; Martin et al., 2013), indicating their subsurface biomass build up during the initial phase of the life cycle and (c) *Trichodesmium* prefers low PAR for their proliferation and bloom formation (Ohki et al., 1986; Capone et al., 1997; Bell et al., 1999, 2005).

Studies have confirmed that *Trichodesmium* efficiently assimilates nitrate ( $\text{NO}_3$ ) from solutions even in very low concentrations, i.e.,  $<0.5 \mu\text{M}$  (Mulholland and Capone, 1999; Holl and Montoya 2005; Matondkar et al., 2006). However, availability of excess  $\text{NO}_3$  in the environment has an inhibitory effect on the nitrogen fixation of *Trichodesmium*, an initial concentration of  $0.5 \mu\text{M}$   $\text{NO}_3$  can inhibit nitrogen fixation ability by 20%,  $10 \mu\text{M}$   $\text{NO}_3$  can inhibit nitrogen fixation by 70% and beyond  $10 \mu\text{M}$  of  $\text{NO}_3$  can completely stop  $\text{N}_2$ -fixation (Holl and Montoya, 2005). It was also observed that cultures exposed to high concentration of  $\text{NO}_3$  regain their nitrogen fixing ability when  $\text{NO}_3$  concentration in the culture media deplete to the level of  $0.3 - 0.4 \mu\text{M}$ . On the other hand, *Trichodesmium* cultures maintained in high concentration continue to grow by obtaining their nitrogen requirement from  $\text{NO}_3$  sources available in the environment and not through molecular nitrogen fixation. Experimental studies have also proved that actively growing filaments of *Trichodesmium* prefer to grow in low levels of PAR ( $20-150 \mu\text{Em}^{-2}\text{s}^{-1}$ ) for their initial biomass build up, and such low light levels in the northern Indian Ocean during the pre-southwest monsoon occur only in the subsurface waters (Ohki et al., 1986; Capone et al., 1997; Bell et al., 1999, 2005; Jyothibabu et al., 2014).

All the above-mentioned points suggest that although the thick bloom biomass of *Trichodesmium* floats on the ocean surface, their initial growth and biomass built-up occur somewhere below the mixed layer where the nutrient and light conditions are conducive and stable for a longer period. It is also possible that there could be two physiologically adapted *Trichodesmium* stocks present in the water column. The first stock may occupy a niche just below the mixed layer, and assimilate the trace concentrations of  $\text{NO}_3$  available there for their initial biomass built-up; later, they may source their nitrogen requirement through fixation in the surface waters through vertical migrations. The second stock may occupy a niche deeper in the water column, utilising the available high nitrate concentration in the environment as here nitrogen fixation is prevented through feedback inhibition. The above

inference is supported by a few observations from the northern Indian Ocean, in which high abundance of phytoplankton stock has been reported below the mixed layer (20-30m depth) and also deep in the euphotic column (60-70m depth)(Matondkar et al., 2006; Parab and Matondkar, 2012). If this possibility is reasonable, then a logical explanation can be deduced regarding how warm core eddies in the northern Indian Ocean facilitate more likely chances to form a conducive environment for the formation of *Trichodesmium* blooms. This needs to be judged based on robust evidences from the north Atlantic where Davis and McGillicuddy Jr., (2006) noticed large stock of *Trichodesmium* filaments in warm core eddies during the spring whereas, Olson et al., (2015) did so in cold core eddies during the fall season. Although the common take away message in these studies is that mesoscale eddies/gyres favour high abundance of *Trichodesmium* filaments in the north Atlantic, a probable reason for the contrasting observations are yet to be evolved.

The PAR available in the Bay of Bengal and Arabian Sea surface during the pre-southwest monsoon is presented in Figure 10a and its underwater distribution in Figure 10b. It is evident that the optimum PAR favouring *Trichodesmium* proliferation as evidenced by Bell et al., (2005) is  $\sim 40 - 50 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  and occurs at a depth of  $\sim 50\text{m}$ . The mixed layer depth in the Bay of Bengal and Arabian Sea during the pre-southwest monsoon is usually around 20-25m while nitracline is around 50m (Jyothibabu et al., 2008). Considering the above, it is quite likely that the physiologically adapted *Trichodesmium* stock that usually inhabiting just below the mixed layer assimilates low nitrate concentration and performs nitrogen fixation, but is exposed to PAR in excess of the optimum level suggested by Bell et al.,(2005). This may cause a situation where optimum nitrate and PAR levels do not co-occur in the water column, which is not very conducive for triggering bloom formation. Opposite to this is the case in the deeper waters, where the *Trichodesmium* stock that survives in high nitrate level is exposed to less than the optimum PAR level suggested by Bell et al.,(2005), making that region also less conducive for triggering bloom formation. In essence, due to the mismatch in the regions of optimum PAR and nitrate levels in the water column, chances of formation of *Trichodesmium* blooms are less in the water column even during the pre-southwest monsoon. Based on the above considerations, we try here to analyse how mesoscale warm core eddies can make a difference to the above scenario and facilitate the formation of *Trichodesmium* blooms in the northern Indian Ocean.

Two typical characteristics of the warm core eddies/gyres in the northern hemisphere are the sinking of surface waters leading to the deepening of the mixed layer. Based on this fundamental understanding, here we try to explain how warm core eddies can stimulate the bloom formation, a schematic of which is presented in Figure 11. We propose here that the above-mentioned property of the warm core eddy may have a crucial role in creating optimum  $\text{NO}_3$  and PAR levels to the growing population below the mixed layer adapted to low nutrient environment and high PAR levels. As warm core eddy facilitates sinking and deepening of the mixed layer, two ways warm core eddies induce the formation of the *Trichodesmium* blooming may be (a) subsurface waters become warmer than the adjacent regions; it has been noticed that warmer waters, even during the upwelling period, can induce *Trichodesmium* bloom formation (Ramos et al., 2005) (b) low nutrient and nitrogen-fixing stocks in the subsurface waters could get more chances to stay within the optimum PAR level suggested by Bell et al., (2005) in many parts of the eddy. The down-sloping of isolines of optimum nitrate concentration may get exposed to different intensities of PAR, thereby increasing chances of optimum nitrate with PAR levels favouring the blooming of *Trichodesmium*. In other words, eddies work like a natural laboratory set-up, wherein the optimum nitrate concentration of *Trichodesmium* is exposed to different PAR levels, creating more likely chances for the co-existence of the optimum concentrations of both these parameters. As the environmental conditions in the northern Indian Ocean are relatively stable during the pre-southwest monsoon period, the optimum conducive factors provided in certain regions of the eddy may last for longer periods to induce the bloom formation in the subsurface waters. The seasonal variations in the underwater light levels could be the reason behind the observation in the north Atlantic where Davis and McGillicuddy Jr., (2006) noticed large stocks of *Trichodesmium* filaments in warm core eddies during the spring (high surface PAR), whereas Olson et al., (2015) did so in cold core eddies during the fall (low surface PAR) season. In the above cases, the only probable difference could be that the growing *Trichodesmium* population may be getting the conducive condition in relatively deep water during the spring season (anti-cyclonic) and in shallow depths during the fall season (cyclonic).

It is evident in the present study that the floating bloom biomass of *Trichodesmium* quite often occur on the boundaries of warm core eddies rather than in their centres (as in Figures 7, 8, 9; Supplementary Material 6, 11, 16, 17). There could be a few possible mechanisms favouring a situation wherein bloom biomass aggregates on the eddy boundaries. The first two possibilities are pure physical mechanisms wherein the passive biological material in the surface layers could get aggregated on the eddy boundaries, as indicated in a recent study (Samuelson, et al., 2012). The work of

Mahadevan et al., (2012) and Mahadevan (2014) showed another possibility wherein the downwelling of less dense surface waters at the centre of the warm core eddy could transport *Trichodesmium* filaments vertically downwards. These filaments may develop further and form dense blooms and later surface through eddy boundaries where the vertical suction forcing is much lesser as compared to the centre of the eddy. The third possibility could be the more likely chances of co-occurrence of optimum environmental conditions in the eddy boundaries due to the down-sloping of isolines of hydrological parameters exposed to different downwelling levels of PAR. Although this paper evidenced that *Trichodesmium* bloom events and warm core eddies have a close positive linkage, it does not argue that warm core eddies are essential to form the bloom. On the other hand, the study shows that warm core eddy provides more chances for formation of the *Trichodesmium* blooms, by providing an inducing effect, and therefore, any other environmental setting that can provide similar conducive environmental setting can also lead to the formation of the blooms. Such conducive environmental setting due to any other ocean processes might also be capable of favouring bloom formation, and this will be the reason behind cases analysed in the present study where there was no clear coincidence with the *Trichodesmium* bloom incidences and mesoscale warm-core features.

One peculiar adaptation of *Trichodesmium* is the presence of gas vacuoles, which provide buoyancy for them to position themselves in the water column (Romans et al., 1994; Capone et al., 1997; Villareal and Carpenter, 2003; White et al., 2006; Hewson et al., 2009). It is believed that *Trichodesmium* population can rise and sink in the water column using buoyancy (cell ballasting) (Capone et al., 1997; Lettier and Karl, 1998; Matondkar et al., 2006). Similarly, the high pigmentation of the bloom biomass in the surface water may provide photoprotection at high light levels on the highly illuminated surface waters (Capone et al., 1997). When sea surface is warmer and the wind stress is low for extended periods, the intrinsic buoyancy of *Trichodesmium* may help them to float upwards and form extensive mats within very short periods of time. This intriguing feature of the *Trichodesmium* bloom could have led to Dr. S.Z. Qasim, the well-known Indian biological oceanographer remarking that ‘the interesting feature (that) often puzzled both marine scientists and oceanographers is the suddenness with which the blooms of *Trichodesmium*, an organism which normally constitutes an insignificant proportion of the total biomass at sea, appear’ (Qasim, 1972). We do accept that lateral advection of surface bloom biomass can introduce uncertainty in directly linking the floating bloom biomass with surrounding environmental features (Martin et al., 2013). However, logically, this feature could be more relevant in regions with strong surface currents, whereas the typical *Trichodesmium* bloom period in the Bay of

Bengal and Arabian Sea is the pre-southwest monsoon, which is characterised by low surface currents that too dominated by mesoscale eddy circulations.

Phosphorus and iron are believed to be two critical nutrients restricting the growth and N<sub>2</sub> fixation of most of the marine nitrogen -fixers (Deutsch et al., 2001, 2007; Webb et al., 2001; Kustka et al., 2003; Shi et al., 2007; Whittaker et al., 2011) and the ways and means by which *Trichodesmium* scavenge these nutrients is reviewed in detail recently (Bergman et al., 2013). Several studies suggested that in order to overcome phosphorus limitations, *Trichodesmium* colonies migrate vertically in the water column to scavenge phosphorus and other nutrients using the buoyancy regulations through intracellular gas vacuoles present in them (Capone et al., 1997; Lettier and Karl., 1998; Matondkar et al., 2006; Bergman et al., 2013). It is believed that in the upper euphotic zone, *Trichodesmium* filaments capture and store carbon and nitrogen (Romans et al., 1994), and with this ballast, the filaments sink into deeper waters from where phosphorus is acquired (Romans et al., 1994; Villareal and Carpenter, 2003; White et al., 2006; Hewson et al., 2009). The sinking of the surface water in the core of the warm core eddies may be providing an added advantage to the *Trichodesmium* filaments sinking into the deeper waters for scavenging phosphorous and other nutrients. Similarly, iron is a pivotal co-factor in a number of cellular processes of *Trichodesmium*, such as photosynthesis, N<sub>2</sub> fixation, and oxygen scavenging (Kustka et al., 2003; Shi et al., 2007). The high iron content in *Trichodesmium* cells suggests that they are very efficient in assimilation of iron, which is otherwise a poorly soluble element in oligotrophic oceans (Kustka et al., 2003; Whittaker et al., 2010). This is well supported by a recent study showing that *Trichodesmium* employs two different iron uptake mechanisms: superoxide-mediated reduction of inorganic iron in the surrounding milieu and a superoxide-independent uptake system for ferric citrate complexes. These two iron uptake adaptation strategies may allow *Trichodesmium* to effectively scavenge iron even in oligotrophic ocean (Roe et al., 2014). Another possibility is the atmospheric transport and aerosol dust deposition, which is considered to be a crucial pathways for the input of a variety of chemical elements and nutrients into the ocean surface and stimulate the phytoplankton growth (Rubin et al., 2011). It is quite possible that *Trichodesmium* colony formation in the Indian seas may be getting particulate iron and phosphorous from eolian dust depositions as indicated in a few recent studies (Rubin et al., 2011; Srinivas and Sarin, 2012; Yadav et al., 2016 ) but, this aspect needs to be looked at more carefully based on concerted seasonal observations. Loescher et al., (2014) proposed the suitability of oxygen minimum zones (OMZ) to nurture diazotrophy of cyanobacteria, and

this may be very much important along the west coast of India where shallow OMZ zones are a typical feature during the southwest monsoon period (Karnan et al., 2017).

Singh and Ramesh (2015) hypothesized that more intense stratification in the Bay of Bengal would provide a better niche for diazotrophy as compared to the Arabian Sea. The propositions in Singh and Ramesh (2015) are quite logical when considered the intensity of stratification in the Bay of Bengal as compared to the Arabian Sea. The scientific uncertainty here then is why the Bay of Bengal does not own more *Trichodesmium* surface bloom records as compared to the Arabian Sea? First of all, here, we have to realise the lack of a systematic data to draw the above conclusion that Arabian Sea has more *Trichodesmium* bloom incidences than in the Bay of Bengal. This needs to be judged carefully with the following reasoning. The Bay of Bengal is still a less studied region as compared to the Arabian Sea. This is primarily because of (a) only less number of research programmes were undertaken in the Bay of Bengal as compared to the Arabian Sea and (b) the logistic disadvantage of the Bay of Bengal being located in the eastern side of India, whereas, most of the Indian research ships and organisations active in oceanographic research are located along the west coast of India (D'Silva et al., 2012). This essentially caused disproportionate research efforts in these two ocean basins. It is also relevant to see in this connection, that most of the earlier observations of *Trichodesmium* blooms from the Indian seas were accidental observations while attempting oceanographic expeditions intended for some other objectives (D'Silva et al., 2012 and references therein). Therefore, the disparity in research efforts in the two ocean basins in the past could be one of the reasons for the emergence of the general belief that the Arabian Sea has more *Trichodesmium* bloom incidences as compared to the Bay of Bengal.

Another important aspect deserving attention in the present case is if eddies are able to trigger blooms then why the Bay of Bengal does not witness more *Trichodesmium* blooms as compared to the Arabian Sea, as the former seems to have more eddy incidences compared to the latter?. The fact of the matter is that irrespective of the seasons, eddies are common in the Arabian Sea and the Bay of Bengal but, concerted studies on these are lacking from the former (Prasannakumar et al., 2007; Jyothibabu et al., 2008, 2015; Amol et al., 2014; Jineesh et al., 2015). This is also evident in many figures presented in this paper depicting that both the Arabian Sea and the Bay of Bengal harbour warm core mesoscale features. As discussed earlier in this manuscript, pre-southwest monsoon is the most conducive season for the formation of the *Trichodesmium* blooms in Indian Seas. Certainly, the warm

core mesoscale features during the pre-southwest monsoon could augment the conducive conditions for the formation of the *Trichodesmium* blooms. Even with all these conducive conditions, the formation of the thick surface blooms happens only during extended periods of high solar radiation, low/nil wind, leading to very clam/ glassy water column conditions. In the Bay of Bengal, due to the sporadic tropical cyclones and frequent depressions during the pre-southwest monsoon period, extended periods of very calm sea conditions, which is a pre-requisite for the *Trichodesmium* bloom formation, are lesser as compared to the Arabian Sea. This situation may also cause less chances for the formation of thick surface blooms of *Trichodesmium* in the Bay of Bengal, even though their filaments are abundant in the water column during the period.

Convincing evidences in the present study, especially from the oceanic regions, clearly show that warm-core features in the Arabian Sea and the Bay of Bengal have an inducing effect on the *Trichodesmium* bloom formation, which could be a robust feature applicable elsewhere as well since many of the bloom incidences considered from the rest of the world ocean also showed similar results. However, it is also true that the present study could not answer questions such as (a) do all the warm core surface features in the Arabian Sea and the Bay of Bengal cause *Trichodesmium* blooms? (b) Could the warm core that occurs in all seasons lead to *Trichodesmium* blooms? (c) What is the time period required for a warm core to lead to the formation *Trichodesmium* blooms? (d) What are the other ocean processes involved in the formation of the blooms? (e) What are the other nutrient requirements for the formation of *Trichodesmium* blooms? Obviously, answering these questions is beyond the reach of the present study as it is purely based on a retrospective study combining some applications of the satellite remote sensing and in-situ observations of the *Trichodesmium* blooms. As suggested recently by McKinna (2015), planned next-generation sensors with higher spectral resolutions, in both low earth and geostationary orbits, may help us to remotely-sense global *Trichodesmium* abundance even at low concentrations. Considering the intricacies involved in the formation of the *Trichodesmium* blooms, as detailed in many places in this manuscript, any single approach alone is not sufficient for unravelling the actual mechanisms involved in the formation of the blooms and probably, a comprehensive study combining satellite remote sensing and environmental buoy observations assisted with micro and mesocosm experiments could be more appropriate by which the refinement/validation of the idea presented in the paper could be achieved. Certainly, our future efforts will be targeted toward testing the hypotheses proposed in this paper based on satellite imagery, in-situ measurements and laboratory experiments.



#### 4. CONCLUSION

Based on a retrospective analysis of 59 *Trichodesmium* bloom incidences in the past, this study showed that warm core eddies have an inducing effect in the formation of *Trichodesmium* blooms in the Arabian Sea and the Bay of Bengal. The present observation not only corroborates the study of Davis and McGillicuddy Jr., (2006) in the north Atlantic, which reported that high abundance of *Trichodesmium* filaments occurs in warm core eddies, but advances one step further and shows that warm core features exert an inducing effect upon the formation of the *Trichodesmium* blooms in the Arabian Sea and the Bay of Bengal. Also, this study proposes how warm core eddies could possibly induce such bloom formation in a nitrogen-limited ocean surface layer, based on the evidences and observations in literature and from our own field studies. We have showed here that due to the sinking (convergence) of surface waters in warm core features, *Trichodesmium* stock in the subsurface waters get more exposed to optimum levels of temperature, nitrate and PAR. Hence, with greater chances of meeting the optimum conditions in the subsurface waters of warm-core eddies, proliferation of *Trichodesmium* filaments occurs deep in the water column. *Trichodesmium* subsequently aggregates and migrates (scavenges) vertically using buoyancy for assimilation of other nutrients such as phosphate from the depth, and finally floats abruptly on the sea surface, forming patches, bands or mats depending upon the calmness of the sea.

#### ACKNOWLEDGEMENTS

The authors thank the Director, CSIR- National Institute of Oceanography (CSIR-NIO), India for facilities and encouragement. The scientific idea presented in this paper is an outcome of the experience gained from participation in so many cruises in the Arabian Sea and the Bay of Bengal and also the discussions with several colleagues in CSIR-NIO and we thank all those well-wishers and mentors for their motivation and encouragement all these years. The first author thankfully remember Prof. Trever Platt and Dr. Subha Sathyendranath who have taught him the fundamentals of remote sensing applications to understand marine ecosystem functioning. This is CSIR-NIO contribution.....

#### REFERENCES

Amol, P., Shankar, D., Fernando, V., Mukherjee, A., Aparna, S.G., et al., 2014. Observed intraseasonal and seasonal variability of the West India Coastal Current on the continental slope. *Journal of Earth System Science* 123, 1045-1074.

- Ashadevi, C.A., Jyothibabu, R., Sabu, P., Jacob, J., Habeebrehman, H., Prabhakaran, M.P., Jayalakshmi, K.J. and Achuthankutty, C.T., 2010. Seasonal variations and trophic ecology of microzooplankton in the south-eastern Arabian Sea. *Continental Shelf Research* 30, 1070-1084.
- Batten, S.D. and Crawford, W.R., 2005. The influence of coastal origin eddies on oceanic plankton distributions in the eastern Gulf of Alaska. *Deep Sea Research II* 52, 991-1009.
- Bell, P.R., Uwins, P.J., Elmetri, I., Phillips, J.A., Fu, F.X. and Yago, A.J., 2005. Laboratory culture studies of *Trichodesmium* isolated from the Great Barrier Reef Lagoon, Australia. *Hydrobiologia* 532, 9-21.
- Bell, P.R.F., Elmetri, I. and Uwins, P., 1999. Nitrogen fixation by *Trichodesmium* spp. in the Central and Northern Great Barrier Reef Lagoon: relative importance of the fixed-nitrogen load. *Marine Ecology Progress Series* 186, 119-126.
- Bergman, B., Sandh, G., Lin, S., Larsson, J., Carpenter, E. J., 2013. *Trichodesmium* - a widespread marine cyanobacterium with unusual nitrogen fixation properties *FEMS Microbiology Review* 37, 286-302.
- Capone, D.G., Burns, J.A., Montoya, J.P., Subramaniam, A., Mahaffey, C., Gunderson, T., Michaels, A.F., Carpenter, E.J., 2005. Nitrogen fixation by *Trichodesmium* spp.: An important source of new nitrogen to the tropical and subtropical North Atlantic Ocean. *Global Biogeochemical Cycles*, 19, doi: 10.1029/2004GB002331.
- Capone, D.G., Subramaniam, A., Montoya, J.P., Voss, M., Hamborg, C., Johansen, A.M., Siefert, R.L., Carpenter, E.J., 1998. An extensive bloom of *Trichodesmium erythraeum* in the Central Arabian Sea. *Marine ecology Progress Series* 172, 281- 292.
- Capone, D.G., Zehr, J.P., Paerl, H.W., Bergman, B., Carpenter, E.J., 1997. *Trichodesmium*, a globally significant marine Cyanobacterium. *Science* 276, 1221 – 1229.
- Carpenter, E.J. and Capone, D.G., 1992. Nitrogen fixation in *Trichodesmium* blooms. In *Marine pelagic cyanobacteria: Trichodesmium and other diazotrophs*, Springer Netherlands. 211-217.
- Carpenter, E.J., Roenneberg, T., 1995. The marine planktonic cyanobacteria *Trichodesmium* spp.: photosynthetic rate measurements in the SW Atlantic Ocean. *Oceanographic Literature Review* 10, 868.
- Carpenter, E.J., Montoya, J.P., Burns, J., Mulholland, M.R., Subramaniam, A., Capone, D.G., 1999. Extensive bloom of a N<sub>2</sub>-fixing diatom/cyanobacterial association in the tropical Atlantic Ocean, *Marine Ecology Progress Series* 185, 273-283.

- Chen, Y.B., Zehr, J.P. and Mellon, M., 1996. Growth and nitrogen fixation of the diazotrophic filamentous non-heterocystous cyanobacterium *Trichodesmium* sp. IMS 101 in defined media: evidence for a circadian rhythm. *Journal of Phycology* 32, 916-923.
- D'Silva, M.S., Anil, A.C., Naik, R.K., D'costa, P.M., 2012. Algal blooms: a perspective from the coasts of India. *Natural Hazards* 63, 1225-1253.
- Davis, C.S., McGillicuddy Jr. D.J., 2006. Transatlantic Abundance of the N<sub>2</sub> – Fixing Colonial Cyanobacterium *Trichodesmium*. *Science* 312, 1517.
- Devassy, V.P., Bhattathiri, P.M.A., Qasim, S.Z., 1978. *Trichodesmium* phenomenon. *Indian Journal of Marine Sciences* 7, 168-186.
- Durand, F., Shankar, D., Birol, F. and Shenoi, S.S.C., 2009. Spatiotemporal structure of the East India Coastal Current from satellite altimetry. *Journal of Geophysical Research: Oceans*, 114 (C2).
- Feng, M., Majewski, L.J., Fandry, C.B. and Waite, A.M., 2007. Characteristics of two counter-rotating eddies in the Leeuwin Current system off the Western Australian coast. *Deep Sea Research II* 54, 961-980.
- Fernandez, A., Mourino-Carballido, B., Bode, A., Varela, M., Maranon, E., 2010. Latitudinal distribution of *Trichodesmium* spp. and N<sub>2</sub> fixation in the Atlantic Ocean. *Biogeosciences* 7, 3167-3176.
- Flierl, G. and McGillicuddy, D.J., 2002. Mesoscale and submesoscale physical-biological interactions. *The sea* 12, 113-185.
- Fu, F., Bell, P.R.F., 2003. Effect of salinity on growth, pigmentation, N<sub>2</sub> fixation and alkaline phosphatase activity of cultured *Trichodesmium* sp. *Marine ecology Progress Series* 257, 69-76.
- Gallegos, C.L., 2001. Calculating optical water quality targets to restore and protect submersed aquatic vegetation: overcoming problems in partitioning the diffuse attenuation coefficient for photosynthetically active radiation. *Estuaries* 24, 381-397.
- Gandhi, N., A. Singh, S. Prakash, R. Ramesh, M. Raman, M. S. Sheshshayee, and S. Shetye (2011), First direct measurements of N<sub>2</sub> fixation during a *Trichodesmium* bloom in the eastern Arabian Sea, *Global Biogeochemical Cycles* 25, GB4014, doi: 10.1029/2010GB003970.
- Gower, J., King, S., Young, E., 2014. Global remote sensing of *Trichodesmium*. *International Journal of Remote Sensing* 35:14, 5459-5466, DOI: 10.1080/01431161.2014.926422
- Hegde, S., Anil, A.C., Patil, J.S., Mitbavkar, S., Krishnamurthy, V., Gopalakrishna, V.V., 2008. Influence of environmental settings on the prevalence of *Trichodesmium* spp. in the Bay of Bengal. *Marine Ecology Progress Series* 356, 93-101.

- Hewson, I., Poretsky R.S., Dyhrman, S.T., Zielinski, B., White, A.E., Tripp, H.J., Montoya, J.P., Zehr J.P., 2009. Microbial community gene expression within colonies of the diazotroph, *Trichodesmium*, from the Southwest Pacific Ocean. *International Society for Microbial Ecology Journal* 3, 1286-1300.
- Holl, C.M. and Montoya, J.P., 2005. Interactions between nitrate uptake and nitrogen fixation in continuous cultures of the marine diazotroph *Trichodesmium* (cyanobacteria) 1. *Journal of Phycology* 41, 1178-1183.
- Hood, R.R., Subramaniam, A., May, L.R., Carpenter, E.J. and Capone, D.G., 2001. Remote estimation of nitrogen fixation by *Trichodesmium*. *Deep Sea Research II* 49, 123-147.
- Jabir, T., Dhanya, V., Jesmi, Y., Prabhakaran, M.P., Saravanane, N., Gupta, G.V.M., Hatha, A.A.M., 2013. Occurrence and Distribution of a Diatom-Diazotrophic Cyanobacteria Association during a *Trichodesmium* bloom in the South-eastern Arabian Sea. *International Journal of Oceanography* 2013, Article ID 350594, 6 pages, doi:10.1155/2013/350594.
- Jineesh, V.K., Muraleedharan, K.R., Lix, J.K., Revichandran, C., Hareeshkumar, P.V., NaveenKumar, K.R., 2015. Mesoscale process-induced variation of the West India coastal current during the winter monsoon. *Environmental Monitoring and Assessment* 187, No. 508, doi. 10.1007/s10661-015-4701-5.
- Jyothibabu, R., Madhu, N.V., Maheswaran, P.A., Jayalakshmy, K.V., Nair, K.K.C. and Achuthankutty, C.T., 2008. Seasonal variation of microzooplankton (20–200µm) and its possible implications on the vertical carbon flux in the western Bay of Bengal. *Continental Shelf Research* 28, 737-755.
- Jyothibabu, R., Madhu, N.V., Murukesh, N., Haridas, P., Nair, K.K.C., Venugopal, P., 2003. Intense blooms of *Trichodesmium erythraeum* (Cyanophyta) in the open waters along east coast of India. *Indian Journal of Marine Sciences* 32, 165-167.
- Jyothibabu, R., Vinayachandran, P.N., Madhu, N.V., Robin, R.S., Karnan, C., Jagadeesan, L. and Anjusha, A., 2015. Phytoplankton size structure in the southern Bay of Bengal modified by the Summer Monsoon Current and associated eddies: Implications on the vertical biogenic flux. *Journal of Marine Systems* 143, 98-119.
- Jyothibabu, R., Win, N.N., Shenoy, D.M., Swe, U.T., Pratik, M., Thwin, S., Jagadeesan, L., 2014. Interplay of diverse environmental settings and their influence on the plankton community off Myanmar during the Spring Intermonsoon. *Journal of Marine Systems* 139, 446-459.

- Karnan, C., Jyothibabu, R., Arunpandi, N., Jagadeesan, L., Muraleedharan, K.R., Pratihary, A.K., Balachandran, K.K., Naqvi, S.W.A., 2017. Discriminating the biophysical impacts of coastal upwelling and mud banks along the southwest coast of India. *Journal of Marine Systems* 172, 24-42.
- Krishnan, A.A., Krishnakumar, P.K., Rajagopalan, M., 2007. *Trichodesmium erythraeum* (Ehrenberg) bloom along the southwest coast of India (Arabian Sea) and its impact on trace metal concentrations in seawater. *Estuarine, Coastal and Shelf Science* 71, 641-646.
- Kustka, A.B., Sanudo-Wilhelmy, S.A., Carpenter, E.J., Capone, D., Burns, J., Sunda, W.G., 2003. Iron requirements for dinitrogen - and ammonium-supported growth in cultures of *Trichodesmium* (IMS 101): comparison with nitrogen fixation rates and iron: carbon ratios of field populations. *Limnology and Oceanography* 48, 1869-1884.
- Letelier, R.M., Karl, D.M., 1998. *Trichodesmium* spp. Physiology and nutrient fluxes in the north Pacific subtropical gyre. *Aquatic microbial Ecology* 15, 265-276.
- Lin, S., Henze, S., Lundgren, P., Bergman, B. and Carpenter, E.J., 1998. Whole-Cell Immunolocalization of Nitrogenase in Marine Diazotrophic Cyanobacteria, *Trichodesmium* spp. *Applied and Environmental Microbiology* 64, 3052-3058.
- Loescher, C.R., Großkopf, T., Desai, F.D., Gill, D., Schunck, H. et al., 2014. Facets of diazotrophy in the oxygen minimum zone waters off Peru, *The ISME Journal* 8, 2180-2192.
- Mackas, D.L. and Coyle, K.O., 2005. Shelf-offshore exchange processes, and their effects on mesozooplankton biomass and community composition patterns in the northeast Pacific. *Deep Sea Research II* 52, 707-725.
- Madhu, N.V., Jyothibabu, R., Maheswaran, P.A., Gerson, V.J., Gopalakrishnan, T.C. and Nair, K.K.C., 2006. Lack of seasonality in phytoplankton standing stock (chlorophyll a) and production in the western Bay of Bengal. *Continental Shelf Research* 26, 1868-1883.
- Mahadevan, A., 2014. Eddy effects on biogeochemistry, *Nature* 506 (7487), 168.
- Mahadevan, A., D'Asaro, E., Lee, C., Perry, M.J., 2012. Eddy-driven stratification initiates North Atlantic spring phytoplankton blooms, *Science* 337(6090), 54-58.
- Martin, G.D., Jyothibabu, R., Madhu, N.V., Balachandran, K.K., Nair, M., Muraleedharan, K.R., Arun, P.K., Haridevi, C.K., Revichandran, C., 2013. Impact of eutrophication on the occurrence of *Trichodesmium* in the Cochin backwaters, the largest estuary along the west coast of India. *Environmental monitoring and assessment* 185, 1237-1253.

- Matondkar, S.G.P., Parab, S.G., Desa, E., Dwivedi, R.M., 2006. Basin scale distribution of *Trichodesmium* spp. In the Arabian Sea using Ocean sat I/OCM. Remote sensing of the Marine Environment (Eds. Kawamura et al.) Proceedings of SPIE 6406, 64060V, 1-10.
- McGillicuddy, D.J., Anderson, L.A., Doney, S.C. and Maltrud, M.E., 2003. Eddy-driven sources and sinks of nutrients in the upper ocean: Results from a 0.1 resolution model of the North Atlantic. *Global Biogeochemical Cycles* 17(2).
- McGillicuddy, D.J., Robinson, A.R., Siegel, D.A., Jannasch, H.W., Johnson, R., Dickey, T.D., McNeil, J., Michaels, A.F. and Knap, A.H., 1998. Influence of mesoscale eddies on new production in the Sargasso Sea. *Nature* 394, 263-266.
- McKinna, L.I., 2015. Three decades of ocean-color remote-sensing *Trichodesmium* spp. in the World's oceans: A review. *Progress in Oceanography* 131, 177-199.
- Mohanty, A.K., Satpathy, K.K., Sahu, G., Hussain, K.J., Prasad, M.V.R. and Sarkar, S.K., 2010. Bloom of *Trichodesmium erythraeum* (Ehr.) and its impact on water quality and plankton community structure in the coastal waters of southeast coast of India. *Indian Journal of Marine Sciences* 39, 323.
- Mulholland, M.R., Capone, D.G., 1999. Nitrogen fixation, uptake and metabolism in natural and cultured populations of *Trichodesmium* spp. *Marine ecology Progress Series* 188, 33-49.
- Nishino, S., Itoh, M., Kawaguchi, Y., Kikuchi, T. and Aoyama, M., 2011. Impact of an unusually large warm-core eddy on distributions of nutrients and phytoplankton in the south-western Canada Basin during late summer/early fall 2010. *Geophysical Research Letters* 38 (16).
- Ohki, K. and Fujita, Y., 1988. Aerobic nitrogenase activity measured as acetylene reduction in the marine non-heterocystous cyanobacterium *Trichodesmium* spp. grown under artificial conditions. *Marine Biology* 98, 111-114.
- Ohki, K., J. G. Rueter and Y. Fujita, 1986. Cultures of the pelagic cyanophytes *Trichodesmium erythraeum* and *T. thiebautii* in synthetic medium. *Marine Biology* 91, 9-13.
- Olson, E.M., McGillicuddy Jr. D.J., Flierl, G.R., Davis, C.S., Dyrhman, S.T., Waterbury, J.B., 2015. Mesoscale eddies and *Trichodesmium* sp. Distributions in the south-western North Atlantic. *Journal of Geophysical Research: Oceans* 120, 4129-4149.
- Padmakumar, K.B., Smitha, B.R., Thomas, L.C., Fanimol, C.L., Sreeranjima, G., Menon, N.R., Sanjeevan, V.N., 2010. Blooms of *Trichodesmium erythraeum* in the South Eastern Arabian Sea during the onset of 2009 Summer Monsoon. *Ocean Science Journal* 45, 151-157

- Parab S.G., Matondkar, S.G.P., 2012. Primary productivity and nitrogen fixation by *Trichodesmium* spp. In the Arabian Sea. *Journal of Marine Systems* 105, 82-95.
- Prasannakumar, S.P., Nuncio, M., Ramaiah, N., Sardesai, S., Narvekar, J., Fernandes, V. and Paul, J.T., 2007. Eddy-mediated biological productivity in the Bay of Bengal during fall and spring Intermonsoon. *Deep Sea Research* 54, 1619-1640.
- Qasim, S.Z., 1970. Some characteristics of a *Trichodesmium* bloom in the Laccadives. In *Deep Sea Research and Oceanographic Abstracts*, Elsevier 17, 655-660.
- Qasim, S.Z., 1972. Some observations on *Trichodesmium* blooms. In *International Symposium on Taxonomy and Biology of Bluegreen Algae*, 1st, Madras, 1970. Papers.
- Ramamurthy, V.D., 1972. Procedure adopted for the laboratory cultivation of *Trichodesmium erythraeum*. *Marine Biology* 14, 232 -234.
- Ramos, A.G., Martel, A., Codd, G.A., Soler, E., Coca, J., Redondo, A., Morrison, L.F., Metcalf, J.S., Ojeda, A., Suárez, S. and Petit, M., 2005. Bloom of the marine diazotrophic cyanobacterium *Trichodesmium erythraeum* in the Northwest African Upwelling. *Marine Ecology Progress Series* 301, 303-305.
- Roe, K.L., Barbeau, K.A., 2014. Uptake mechanisms for inorganic iron and ferric citrate in *Trichodesmium erythraeum* IMS101. *Metallomics* 6, 2042-2051.
- Romans, K.M., Carpenter, E.J., Bergman, B., 1994. Buoyancy regulation in the colonial diazotrophic cyanobacterium *Trichodesmium* Tenue - ultrastructure and storage of carbohydrate, polyphosphate, and nitrogen. *Journal of Phycology* 30,935-942.
- Rubin, M., Berman-Frank, I., Shaked, Y., 2011. Dust- and mineral-iron utilization by the marine dinitrogen-fixer *Trichodesmium*. *Nature Geosciences* 4, 529-534.
- Samuelson, A., Hjøllø, S. S., Johannessen, J. A., Patel, R.,2012., Particle aggregation at the edges of anticyclonic eddies and implications for distribution of biomass. *Ocean Science* 8, 389– 400.
- Shenoi, S.S.C., 2010. Intra-seasonal variability of the coastal currents around India: A review of the evidences from new observations. *Indian Journal of Marine Sciences* 39, 489-496.

- Shi, T., Sun, Y., Falkowski, P.G., 2007. Effects of iron limitation on the expression of metabolic genes in the marine cyanobacterium *Trichodesmium erythraeum* IMS101. *Environmental Microbiology* 9, 2945-2956
- Singh, A., Ramesh, R., 2015. Environmental controls on new and primary production in the northern Indian Ocean, *Progress in Oceanography* 131, 138-145.
- Srinivas, B., Sarin, M.M., 2012. Atmospheric pathways of phosphorous to the Bay of Bengal: contribution from anthropogenic sources and mineral dust. *Tellus B* 64, 17174.
- Stihl, A., Sommer, U. and Post, A.F., 2001. Alkaline phosphatase activities among populations of the colony-forming diazotrophic cyanobacterium *Trichodesmium* spp. (cyanobacteria) in the Red Sea. *Journal of Phycology*, 37, 310-317.
- Strzelecki, J., Koslow, J.A. and Waite, A., 2007. Comparison of mesozooplankton communities from a pair of warm-and cold-core eddies off the coast of Western Australia. *Deep Sea Research II* 54, 1103-1112.
- Subramaniam, A., Carpenter, E.J., Karentz, D. and Falkowski, P.G., 1999. Bio-optical properties of the marine diazotrophic cyanobacteria *Trichodesmium* spp. I. Absorption and photosynthetic action spectra. *Limnology and Oceanography* 44, 608-617.
- Subramaniam, A., Brown, C. W., Hood, R. R., Carpenter, E. J., Capone, D. G., 2001. Detecting *Trichodesmium* blooms in SeaWiFS imagery. *Deep-Sea Research II* 49, 107-121.
- Villareal, T.A., Carpenter, E.J., 2003. Buoyancy regulation and the potential for vertical migration in the oceanic cyanobacterium *Trichodesmium*. *Microbial Ecology* 45, 1-10.
- Webb, E.A., Moffett, J.W., Waterbury, J.B., 2001. Iron Stress in Open-Ocean Cyanobacteria (*Synechococcus*, *Trichodesmium*, and *Crocospaera* spp.): Identification of the IdiA Protein. *Applied Environmental Microbiology* 67, 5444-5452
- White, A.E., Spitz, Y.H., Letelier, R.M., 2006. Modelling carbohydrate ballasting by *Trichodesmium* spp. *Marine Ecology Progress Series* 323, 35-45.
- Whittaker, S., Bidle, K.D., Kustka, A.B., Falkowski, P.G., 2011. Quantification of nitrogenase in *Trichodesmium* IMS 101: implications for iron limitation of nitrogen fixation in the ocean. *Environmental Microbiology Reports* 3, 54-58.
- Yadav, K., Sarma, V.V.S.S., Rao, D.B., Dileepkumar, M., 2016. Influence of atmospheric dry deposition of inorganic nutrients on phytoplankton biomass in the coastal Bay of Bengal. *Marine Chemistry* 187, 25-34.



## Figure Captions

**Figure 1-** Past incidences of *Trichodesmium* (red and green filled circles) in the northern Indian Ocean analysed in the present study. A total of 32 incidences from the northern Indian Ocean are presented in which 9 are from Bay of Bengal and 23 from the Arabian Sea. The bloom incidences considered from the rest of the world (other than the Indian Ocean) are not represented here. Red filled circles represent sighting of the surface blooms whereas, green filled circles indicate the presence of high abundance of *Trichodesmium*. Serial numbers of the bloom incidences here are the same in Table 1, wherein, more details of each bloom incidence are given.

**Figure 2** - Floating surface bloom biomass (sea sawdust) of *Trichodesmium* observed in the Bay of Bengal. Panels represent the bloom incidences (a) April 2001 in the South-western Bay of Bengal - Jyothibabu et al., (2003), (b) April 2002 in the northern Andaman Sea - Jyothibabu et al., (2014) and (c) May 2014 in the central western Bay of Bengal - Jyothibabu et al., (unpublished). All these were sighted as floating bloom biomass on the sea surface, indicating their declining phase. The morphological and structural details of a *Trichodesmium* bundle (trichome) in different magnification under a fluorescent microscope are presented in panels (d) trichome intact, (e) and (f) trichome gently pressed under a cover slip to differentiate individual filaments.

**Figure 3** - Seasonal distribution of (a-c) wind ( $\text{m s}^{-1}$ ) and (d-f) ocean surface currents ( $\text{m s}^{-1}$ ) in the northern Indian Ocean. Overall, winds and currents were the weakest during the pre-southwest monsoon/ spring inter monsoon (SIM) indicating the monsoonal transition phase. The red arrows in panels (d-f) indicate more organised surface currents during the southwest and northeast monsoons compared to the pre-southwest monsoon. Weak currents with mesoscale eddy circulations were very common during the pre-southwest monsoon. Even the better organised East Indian Coastal Currents (EICC), along the Southeast coast of India during the pre-southwest monsoon period, encompasses mesoscale eddy cells, which is highlighted in red arrows in panel (e).

**Figure 4** - Seasonal distribution of (a-c) sea surface temperature ( $^{\circ}\text{C}$ ) and (d-f) sea surface salinity in the northern Indian Ocean. The seasonal highest SST and high salinity prevails in the northern Indian Ocean during the pre-southwest monsoon period.

**Figure 5-** Seasonal distribution of (a-c) significant wave height (cm) and (d-f) mixed layer depth (MLD) in the northern Indian Ocean. The seasonal lowest wave height and the shallowest mixed layer depth was found during the pre-southwest monsoon period.

**Figure 6-** Seasonal distribution of (a-c) Photosynthetically Active Radiation (PAR) and (d-f) chlorophyll *a* in the northern Indian Ocean. Overall, PAR was the highest and the chlorophyll *a* was the lowest during the pre-southwest monsoon period.

**Figure 7** - (A) *Trichodesmium* bloom sighted in the northern Andaman Sea in April 2002 (Jyothibabu et al., 2014) and (B) *Trichodesmium* bloom sighted in the south-western Bay of Bengal in April, 2001 (Jyothibabu et al., 2003). In all panels, the time-series of mean sea level anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale ocean surface features prevailed in the region. In all panels, the region of the floating bloom biomass sighted is indicated by a blue discontinuous circles. The blue arrows indicate the period of sighting the blooms. The right hand side panels represent the environmental setting that prevailed in the region one week prior to the bloom sighting on the sea surface. The analyses showed that the floating bloom biomass in both incidences coincided with a persistent warm core features in the region.

**Figure 8** - (A) *Trichodesmium* bloom observed in May, 2014 in the central western Bay of Bengal and the bloom region is marked in blue dashed circles (Jyothibabu et al., unpublished) and (B) *Trichodesmium* bloom observed in April, 2014 in the central western Bay of Bengal and the bloom region. In all panels, the time-series of mean sea level anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale ocean surface features prevailed in the region. In all panels, the region of the floating bloom biomass sighted is indicated by a blue discontinuous circles. The blue arrows indicate the period of sighting the blooms. The right hand side panels represent the environmental setting that prevailed in the region one week prior to the bloom sighting on the sea surface. The analyses showed that the floating bloom biomass in both incidences were linked to persistent warm core features in the region.

**Figure 9** - (A) *Trichodesmium* bloom biomass sighted floating on the sea surface of north-western Bay of Bengal in April, 2001 (Jyothibabu et al., 2003). The mean sea level anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. The region of the floating bloom biomass sighted is indicated by a blue discontinuous circles and the blue arrows indicate the period of sighting the bloom. The right hand side panel represent the environmental setting that prevailed in the region one week prior to the bloom sighting on the sea surface. (B) *Trichodesmium* filaments noticed in the surface waters in different regions across the Bay of Bengal in October 2000 and August 2002 (Hegde et al., 2008). The surface sampling in every  $1^\circ$  distance was carried out along a ship route from Chennai to Singapore. The regions where *Trichodesmium* filaments were recognised are indicated with a blue discontinuous circle, all of them coincided with warm core mesoscale features.

**Figure 10-** (a) Spatial distribution of the PAR in the Arabian Sea and the Bay of Bengal during the pre-southwest monsoon. The vertical distribution of PAR in the study region considering two equal spaces (white rectangles in the above panel) in the Arabian Sea and the Bay of Bengal are presented in panels (b). Optimum PAR levels of  $40\text{-}50 \mu\text{E m}^{-2}\text{Sec}^{-1}$  was found at the depth of 42 - 46m in Arabian Sea and 43 - 46 m in the Bay of Bengal, which means that the most conducive PAR levels for triggering the formation of the *Trichodesmium* bloom in the region is located somewhere deep in the sub-surface waters.

**Figure 11** - Diagrammatic representation of the warm- core and cold - core mesoscale features. The blue dotted lines indicate the down-sloping/up-sloping of isolines of nitrate and white dotted arrows represent the downwelling PAR. It is clear that the environmental setting in the mesoscale features is such that same isolines of nutrient are exposed to different PAR levels facilitating more likely chances of coinciding optimum light and nutrient conditions, thereby facilitating the most conducive micro-environment for triggering the bloom.

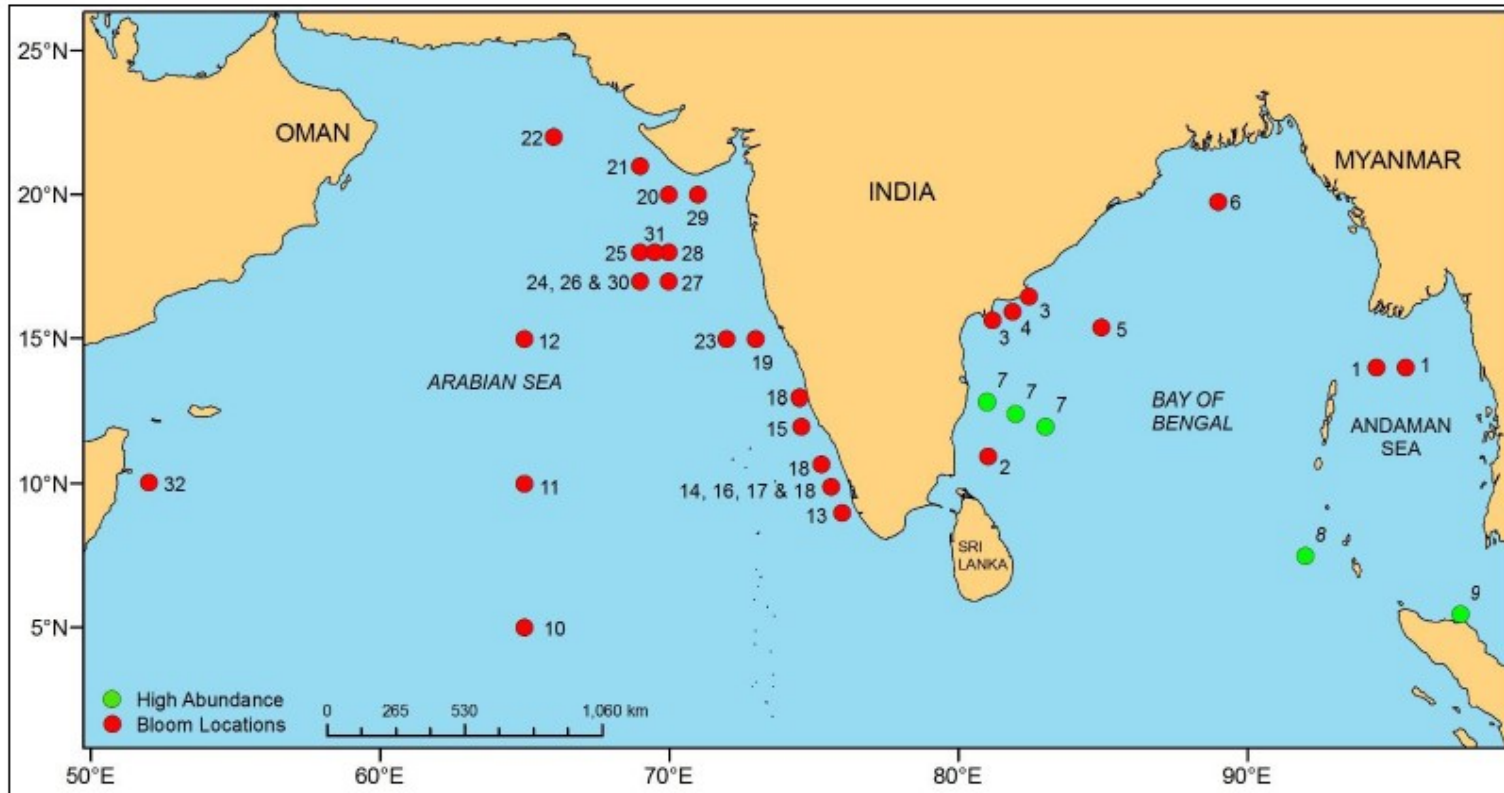
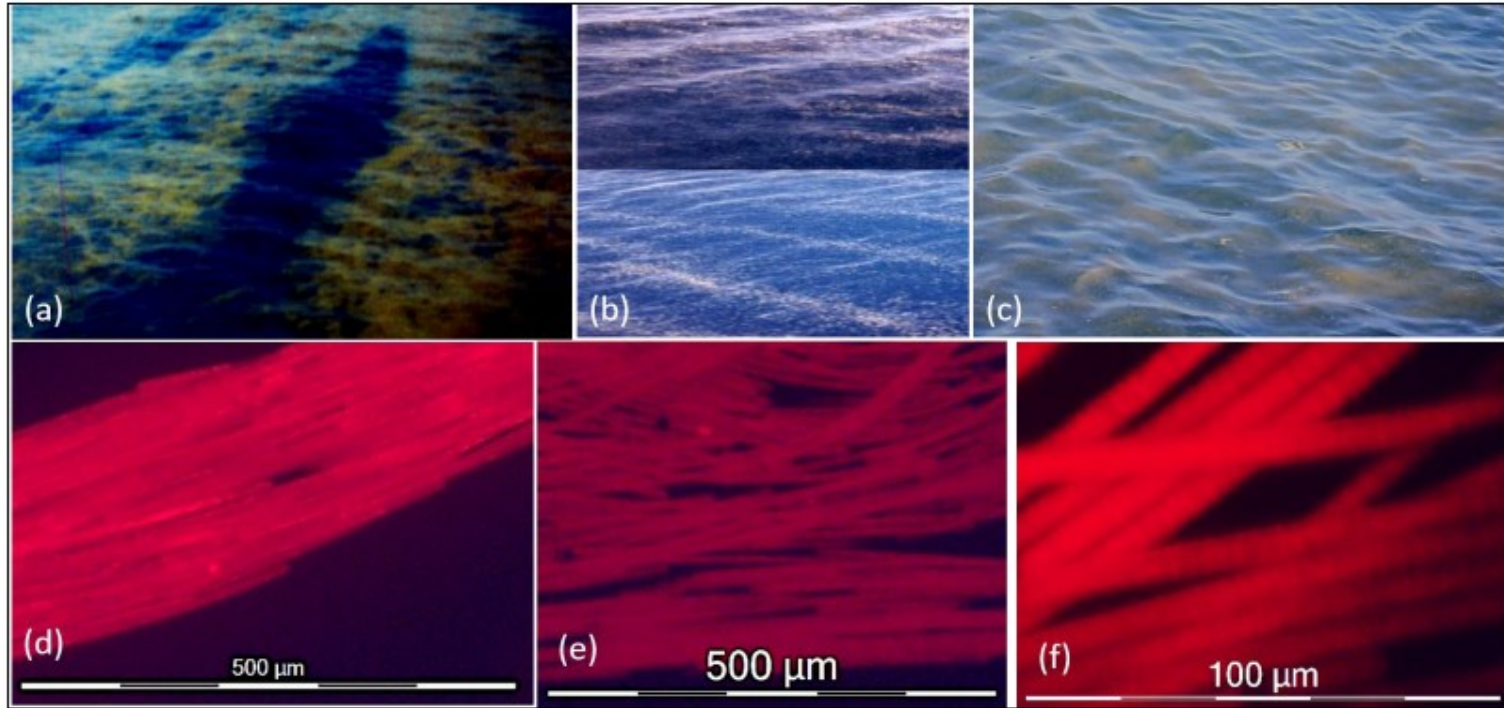


Figure 1



**Figure 2**

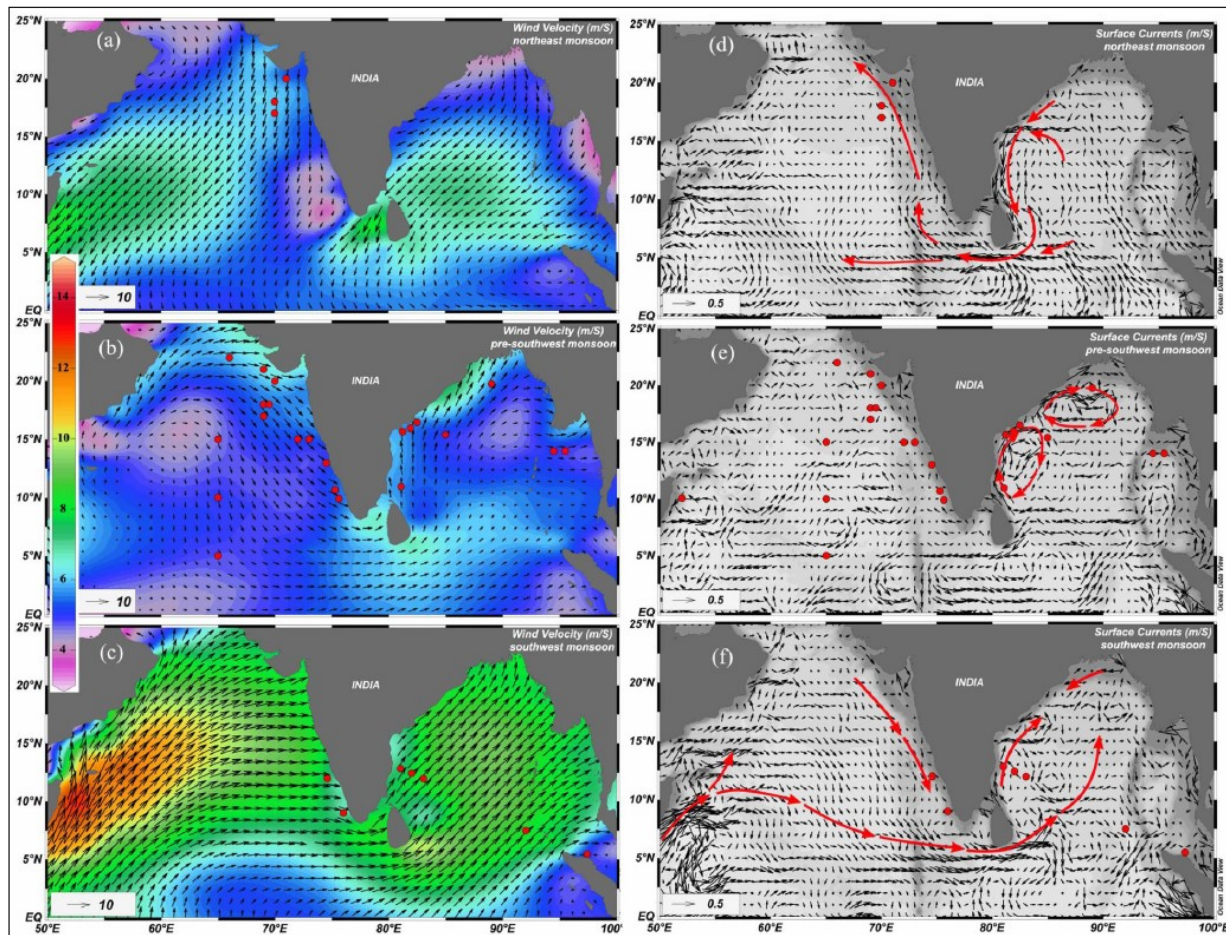


Figure 3

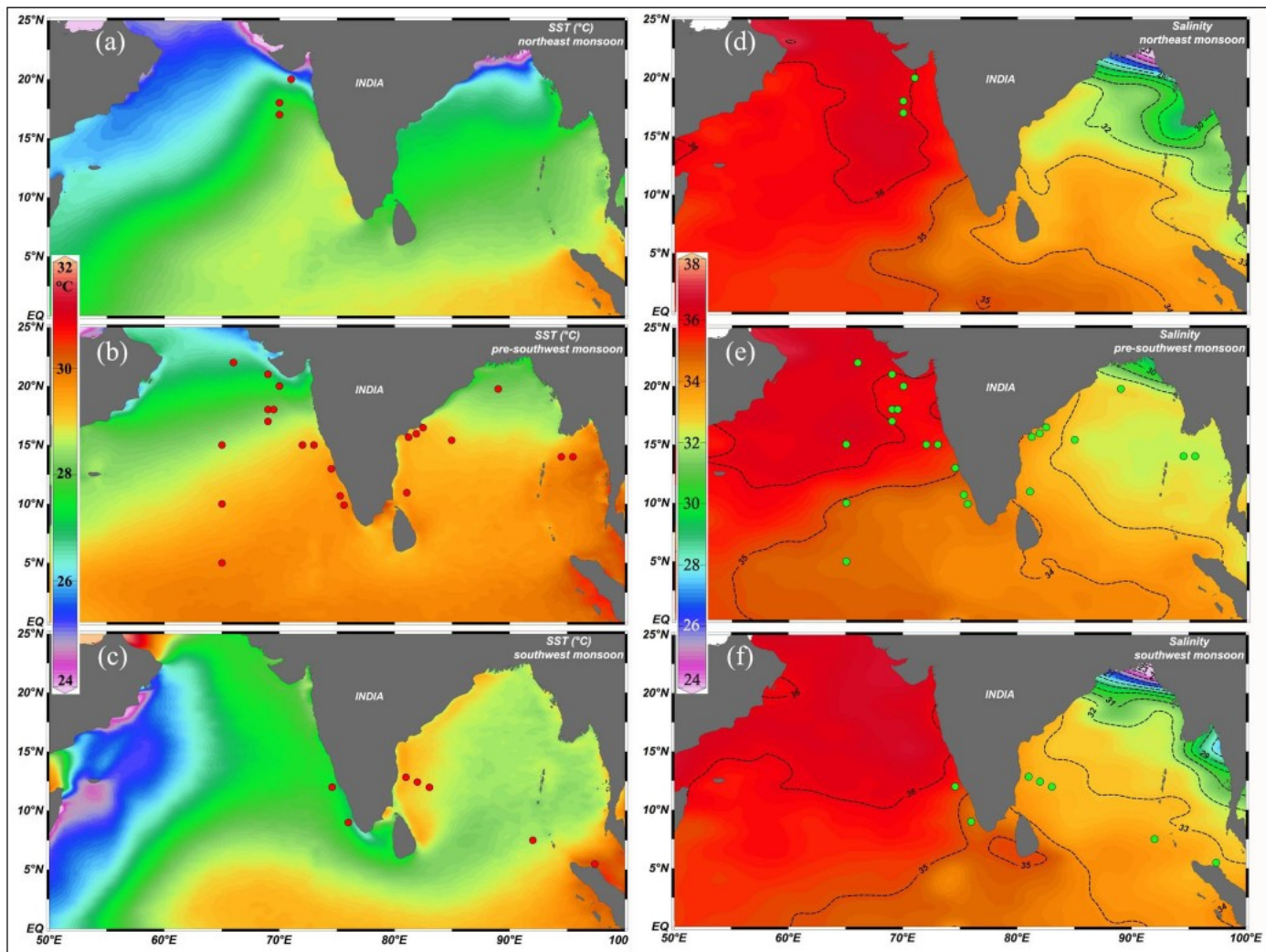


Figure 4

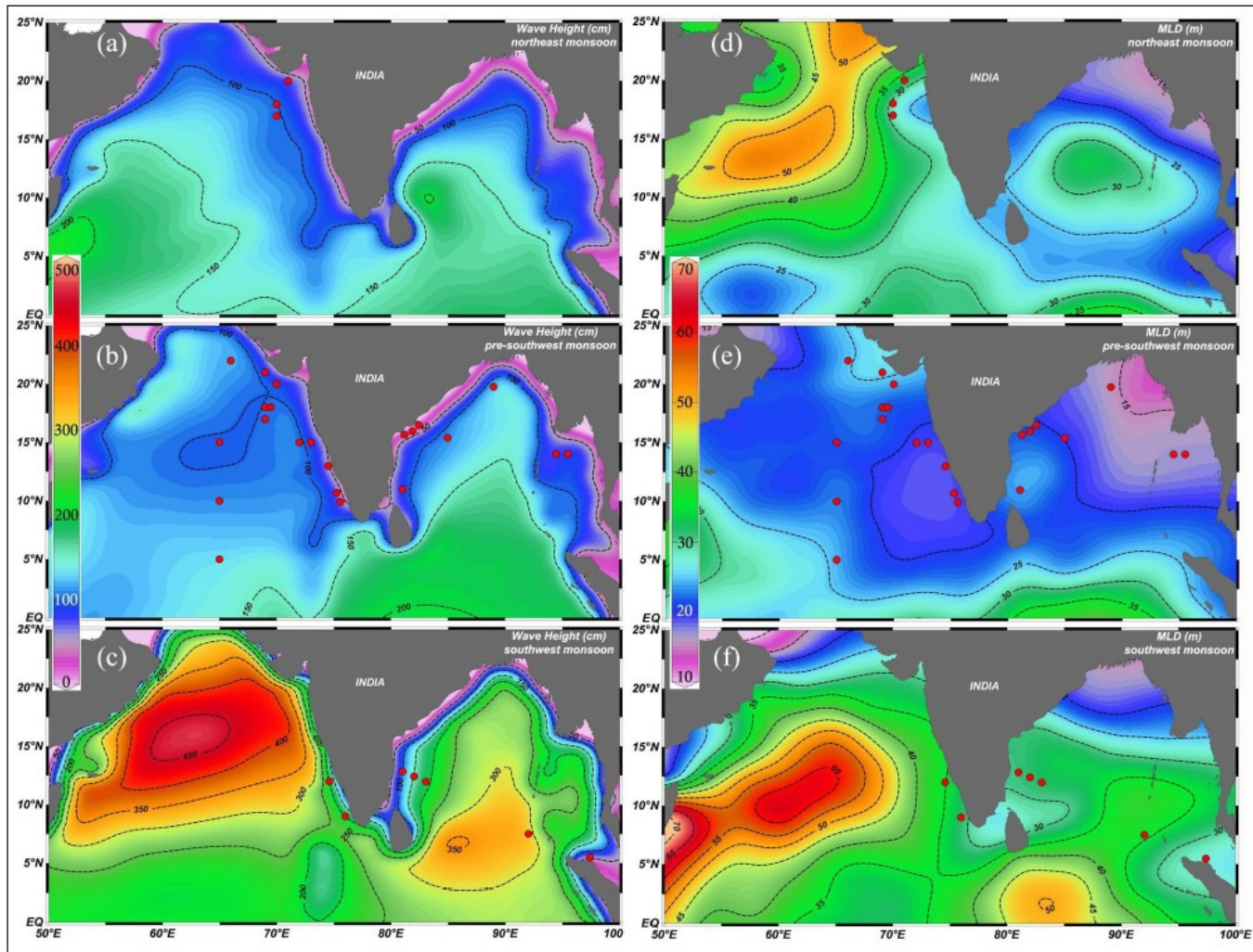


Figure 5

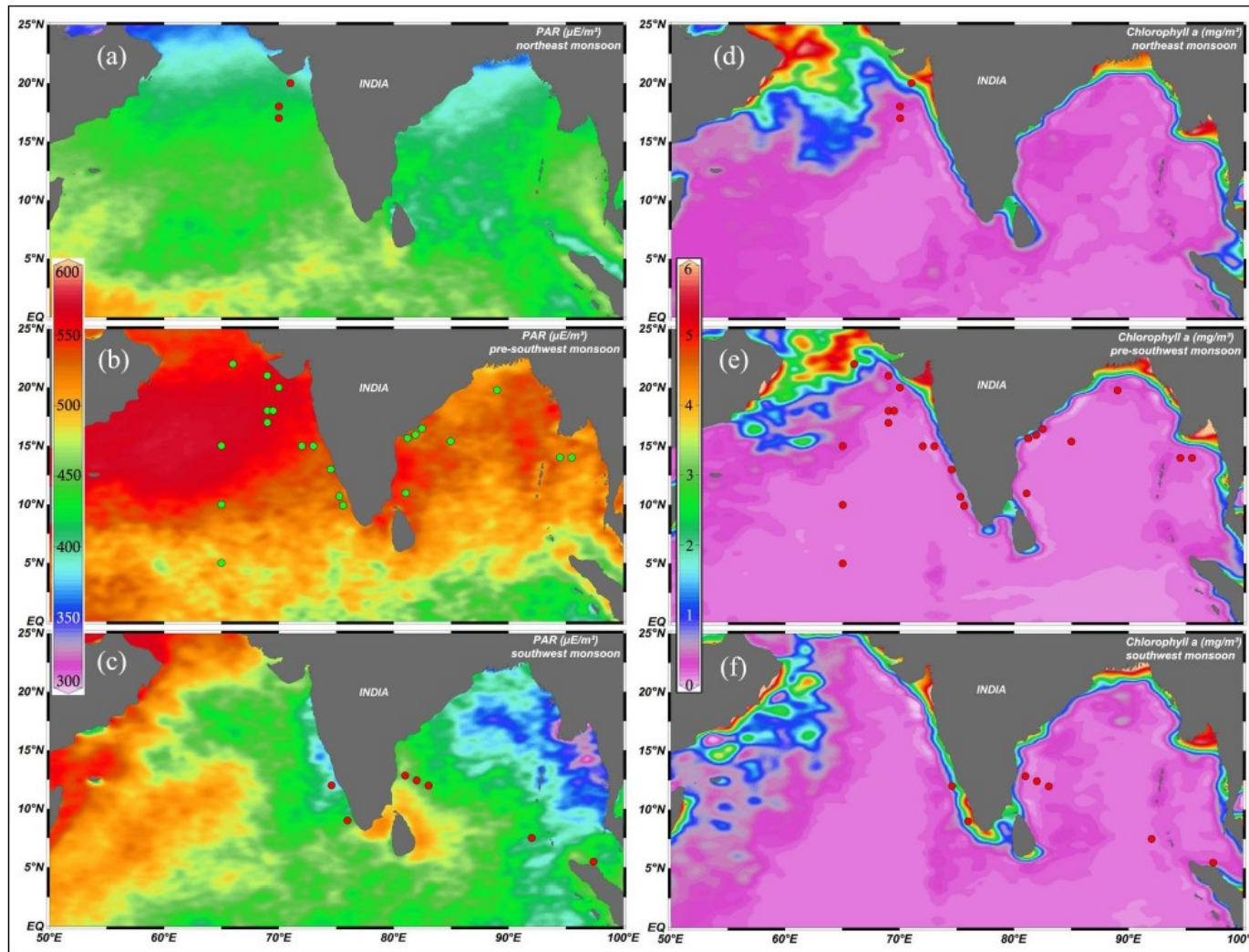


Figure 6



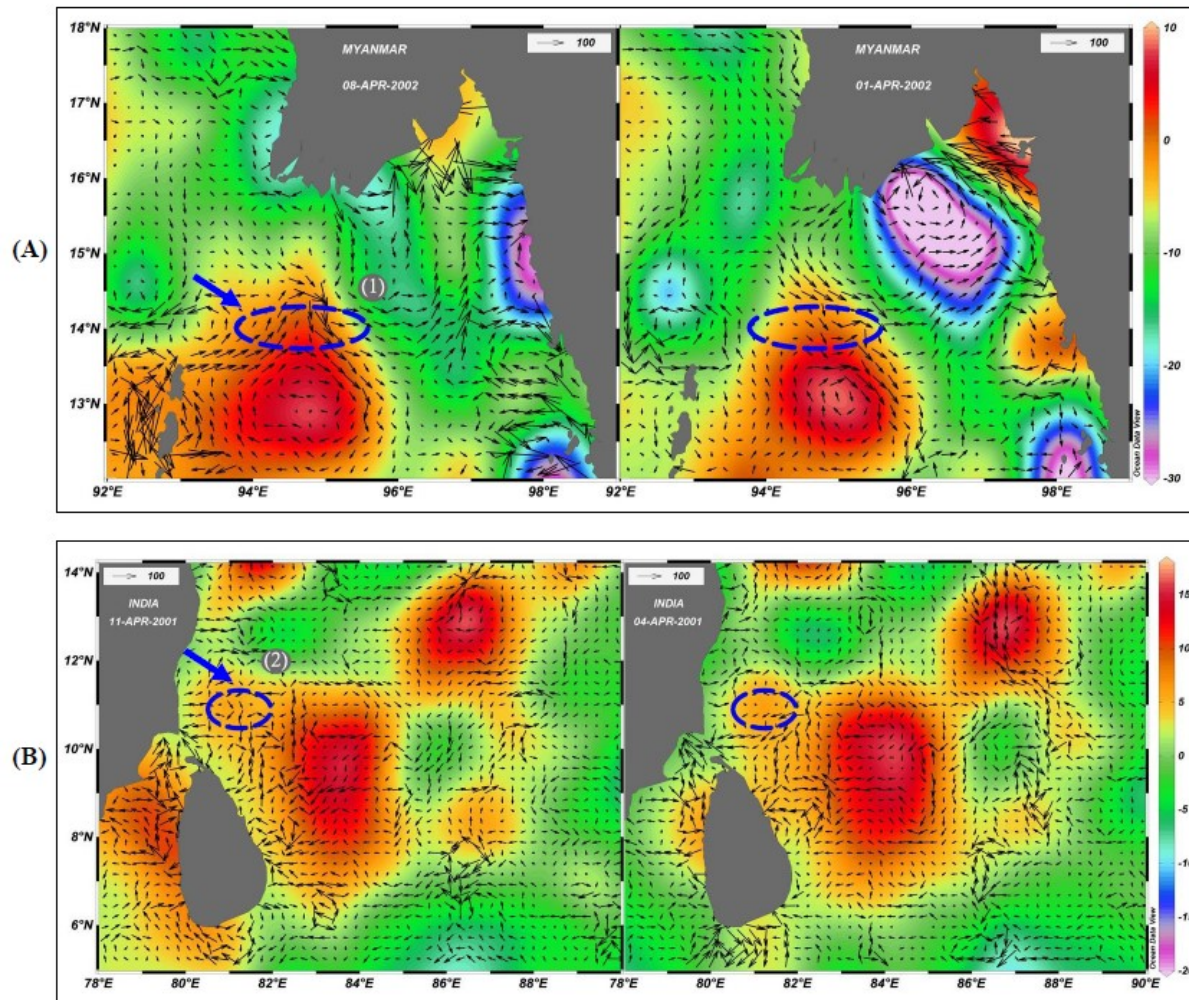


Figure 7

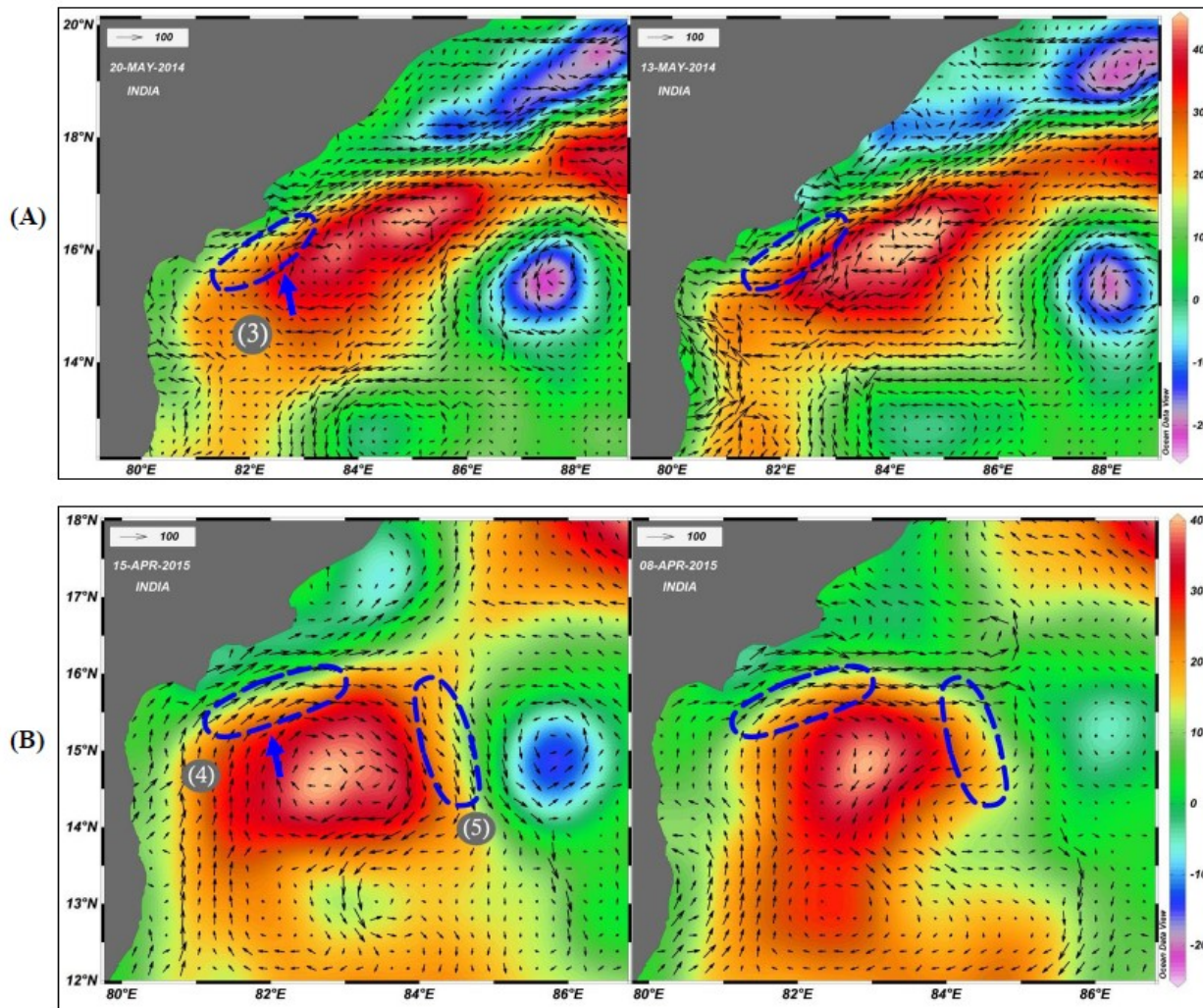


Figure 8

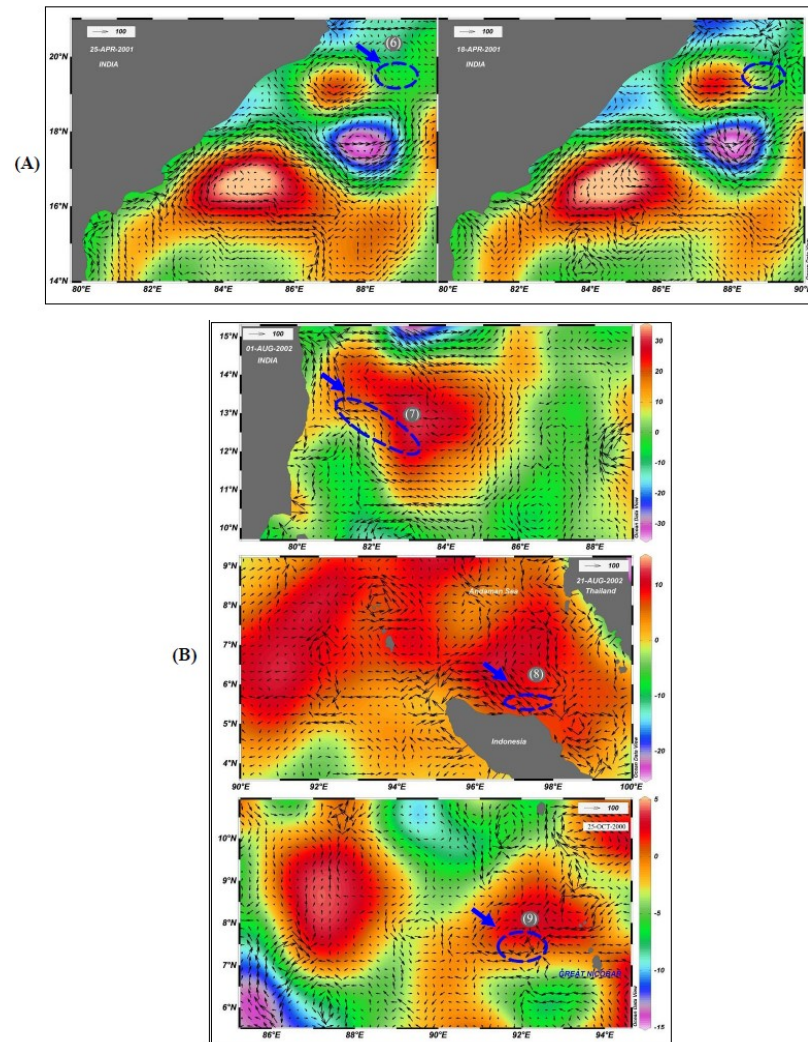


Figure 9

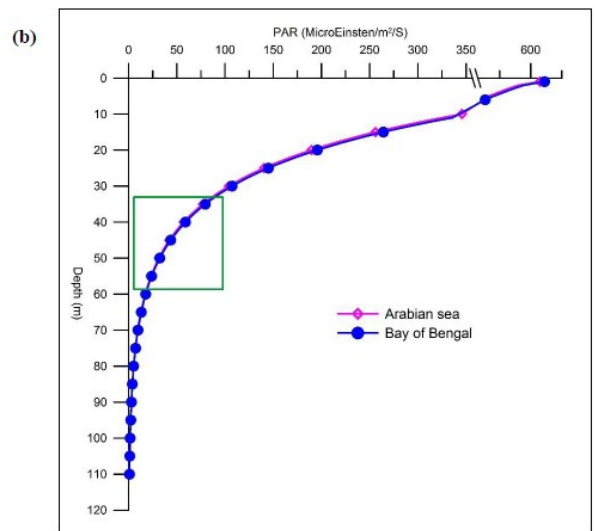
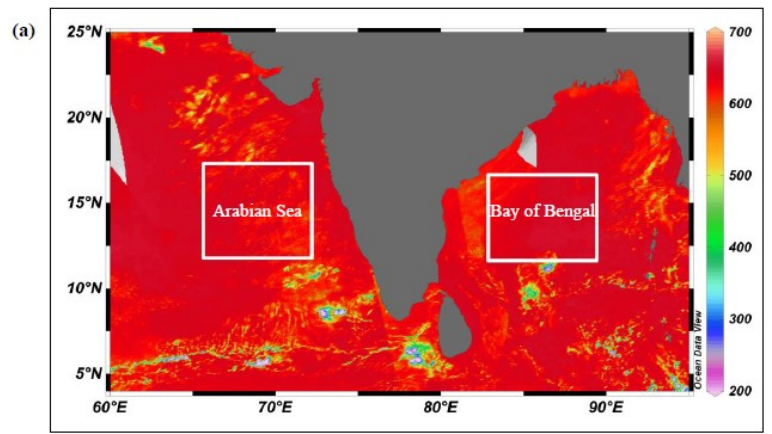
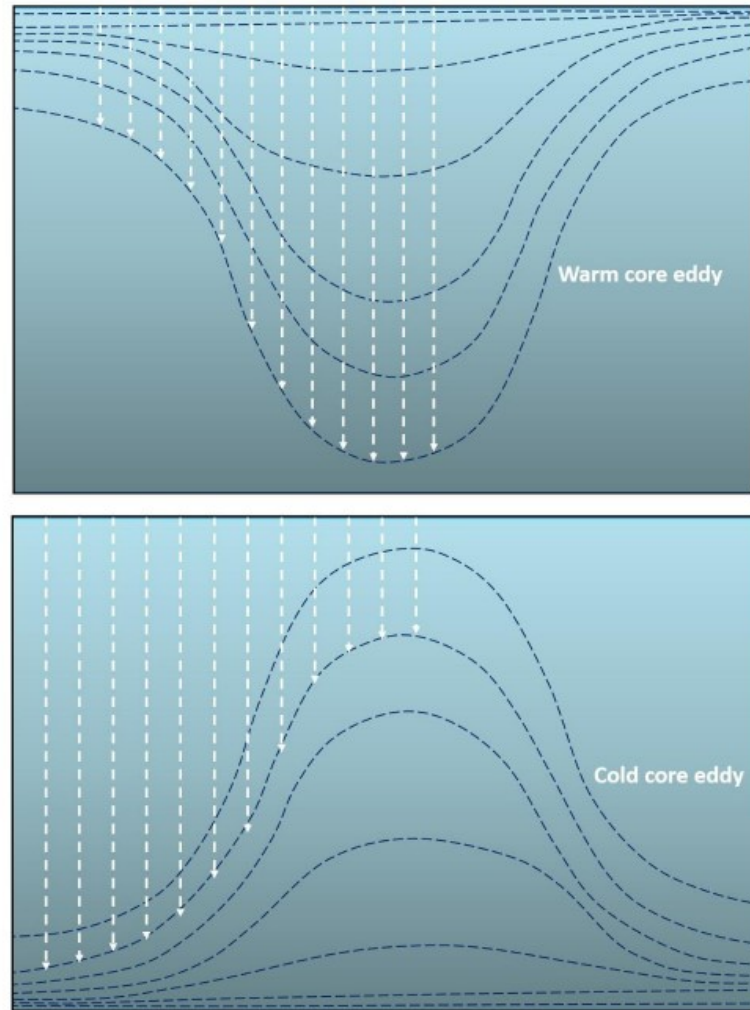
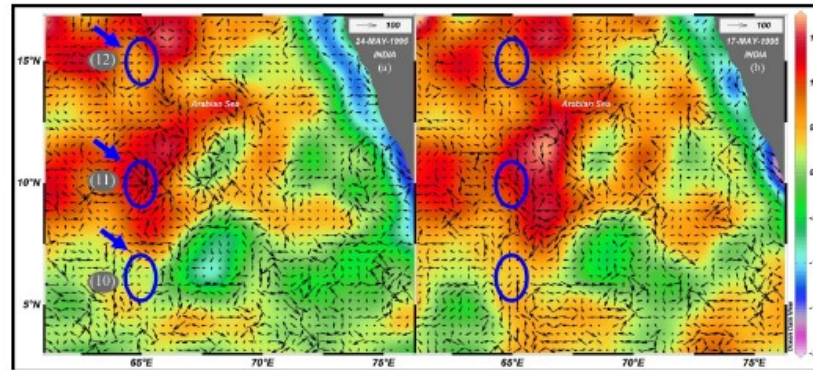


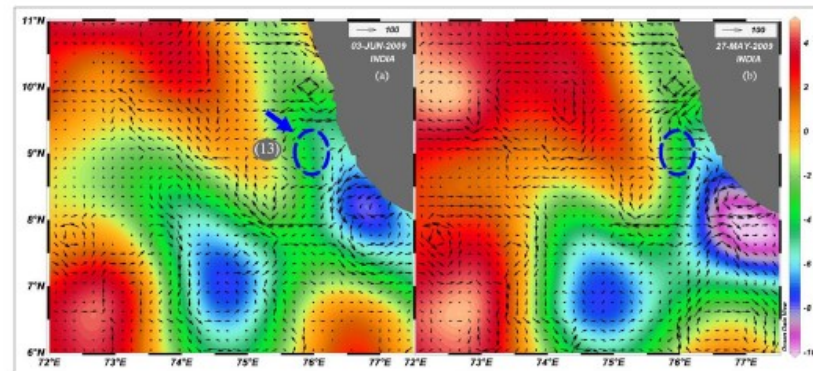
Figure 10



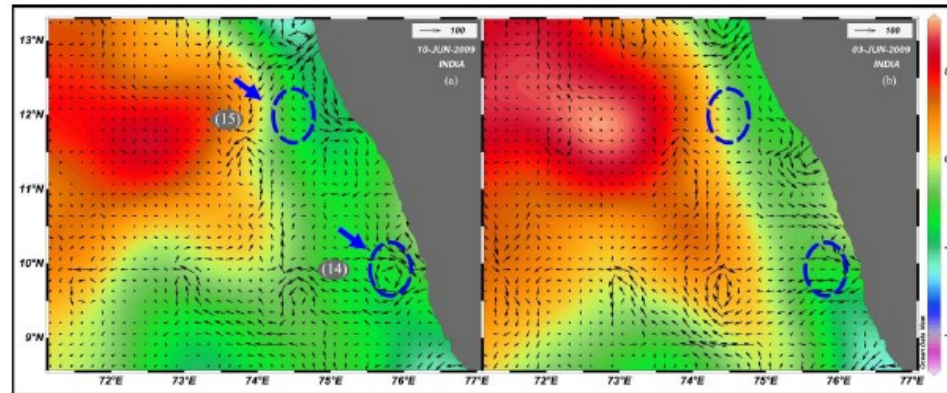
**Figure 11**



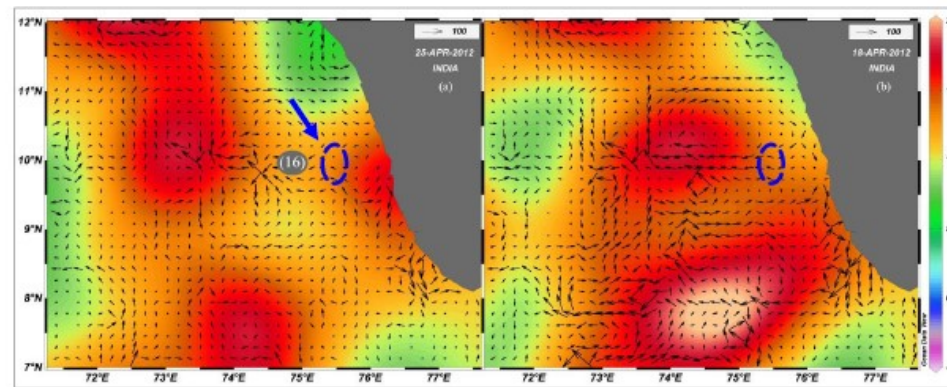
**Supplementary Material 1** - *Trichodesmium* bloom observed in May, 1995 in the Central Arabian Sea (Capone et al., 1998). Time-series of Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. In all panels, the bloom locations are indicated with blue ellipses. The mesoscale features in the region one week before surface bloom incidences are presented in panel (b), which shows that all the three bloom incidences were closely associated with long persistent warm-core features.



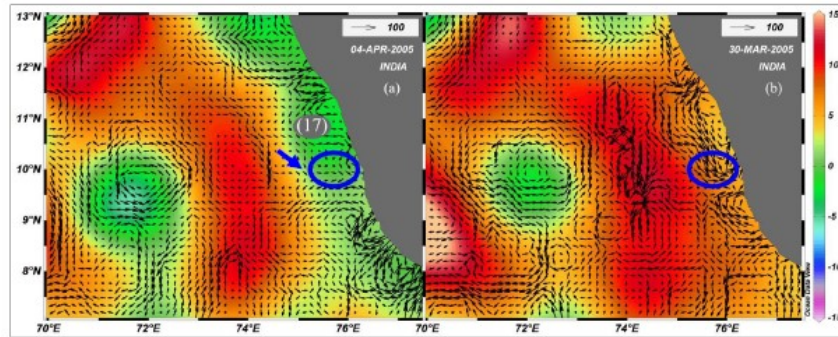
**Supplementary Material 2** - *Trichodesmium* bloom observed in the south-eastern Arabian Sea in early-June, 2009 (Padmakumar et al., 2010) indicated in blue dashed circle. Time-series of Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. The retrospective analyses of the mesoscale features in the region is presented in panels (b). It is clear that this bloom incidence was not directly linked to any warm core mesoscale processes, even though a large warm core was present in the region until late - May (pre-southwest monsoon period) as evident in panel (b).



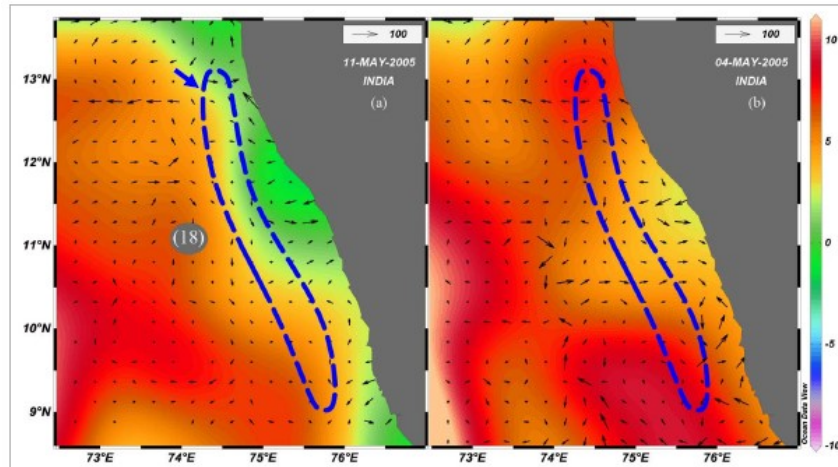
**Supplementary Material 3** - *Trichodesmium* blooms observed in the south-eastern Arabian Sea in early-June 2009 (Padmakumar et al., 2010), indicated in blue dashed circles. Time-series of Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. The retrospective analyses of the mesoscale features in the region is presented in panel (b). As in the case presented in Supplementary Material 2, these bloom incidences were also not directly attributable to any warm core mesoscale processes, even though a large warm core was present in the region until late - May (pre-southwest monsoon period) as evident in panel (b).



**Supplementary Material 4** - *Trichodesmium* bloom recorded in the south-eastern Arabian Sea during April 2012 (Jabir et al., 2013). Time-series of Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. In both panels, the bloom location is indicated with a blue dashed ellipse. The retrospective analyses of the mesoscale features in the region is presented in right side panel, which shows a close association of the bloom with the warm core feature in the region.

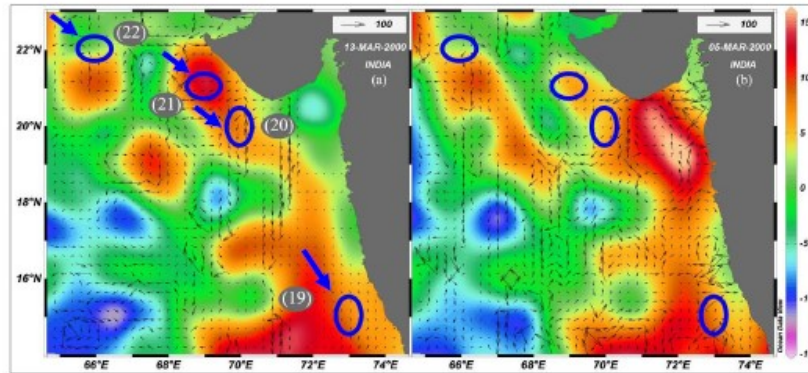


**Supplementary Material 5** - *Trichodesmium* blooms recorded along the west coast of India in April, 2005 (Martin et al., 2013). Time-series of Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. Marked in blue ellipse represents the sighting bloom biomass at surface. The retrospective analyses of the mesoscale features in the region is presented in right side panel. As evident, the bloom was situated associated with a persistent warm-core eddy.

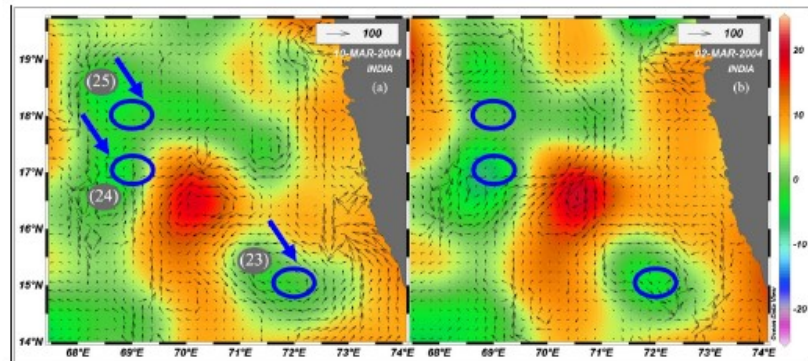


**Supplementary Material 6** - *Trichodesmium* blooms recorded along the west coast of India during May, 2005 between 9°N to 13°N (Krishnan et al., 2007). Time-series of Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. Region marked with blue band represent the patches of blooms observed along the coast. The retrospective analyses of the mesoscale features in the region is presented in panel (b), which shows that the bloom was situated on the boundary of a long persistent warm-core feature.

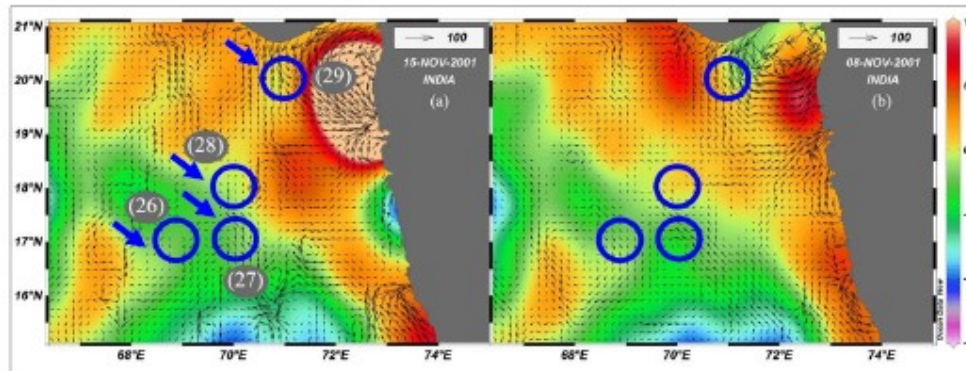




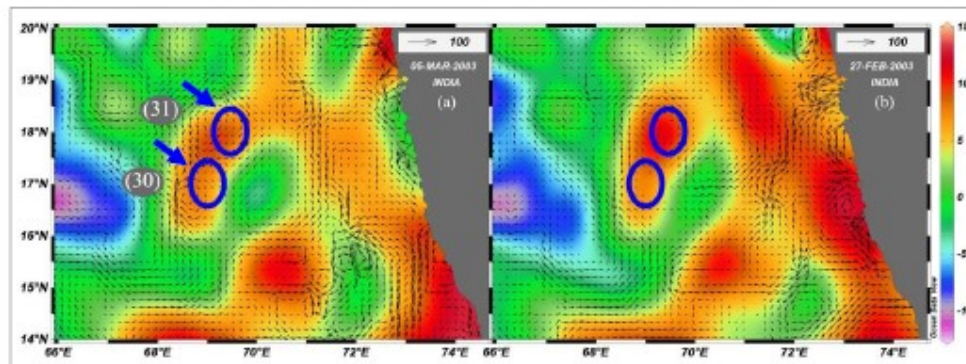
Supplementary Material 7 - The regions of the *Trichodesmium* bloom biomass noticed in the eastern Arabian Sea in March 2000 (Parab and Matondkar, 2012). Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. The blue ellipses indicate the locations in the region where blooms were observed. The retrospective analyses of the mesoscale features in the region is presented. As evident, all these blooms incidences coincided with warm-core features.



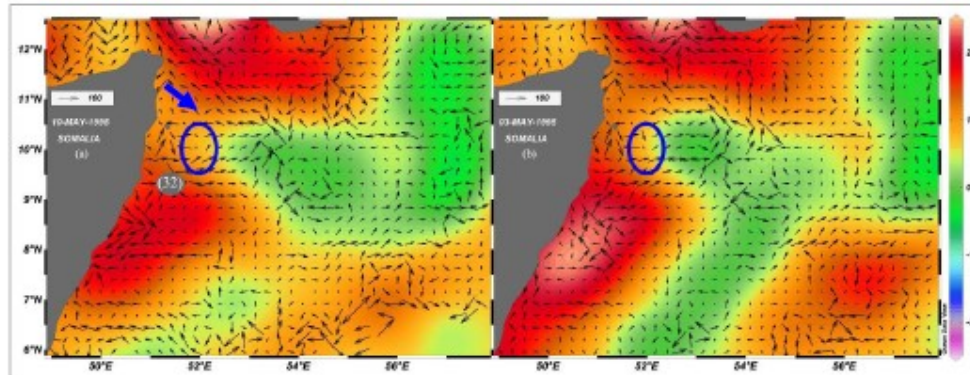
Supplementary Material 8 - The regions of the *Trichodesmium* bloom biomass noticed in the eastern Arabian Sea in March 2004 (Parab and Matondkar, 2012). The Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. The blue ellipses indicate the locations in the region where blooms were observed. The retrospective analyses of the mesoscale features in the region are presented. As evident, these blooms were not directly linked to mesoscale features even though a few have occurred very close to the boundary of long persistent warm-core features.



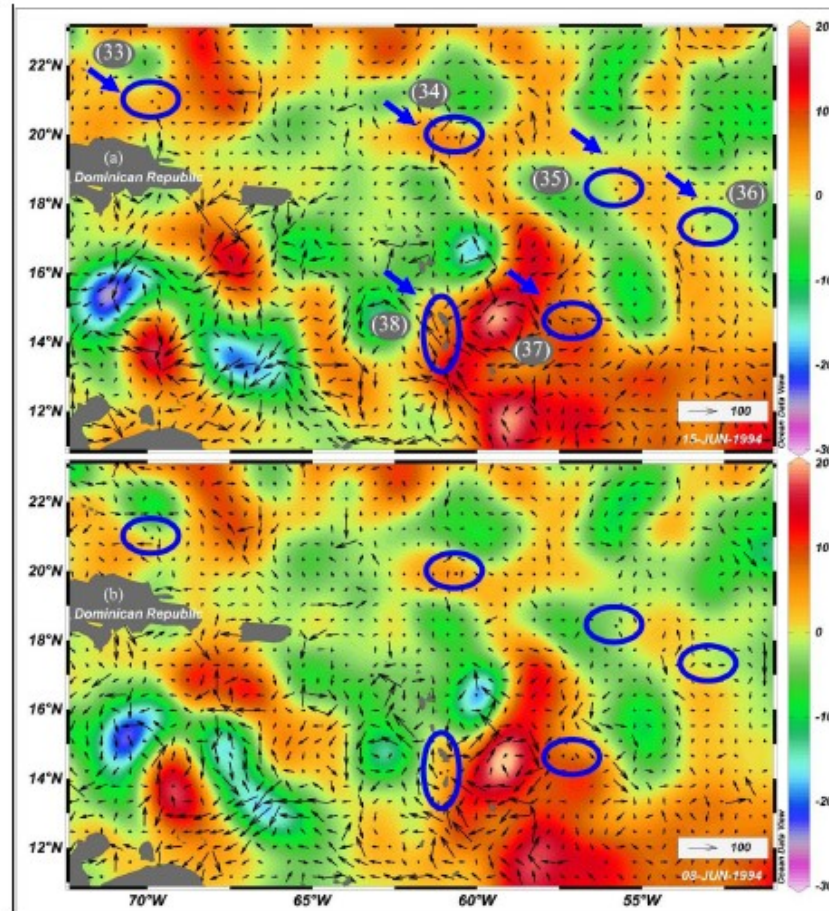
**Supplementary Material 9** - The regions of the *Trichodesmium* bloom biomass noticed in the eastern Arabian Sea in November 2001 (Parab and Matondkar, 2012). Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. The blue circles indicate the locations in the region where blooms were observed. The retrospective analyses of the mesoscale features in the region are presented. As evident, two out of four bloom incidences have coincided with persistent warm-core features in the region.



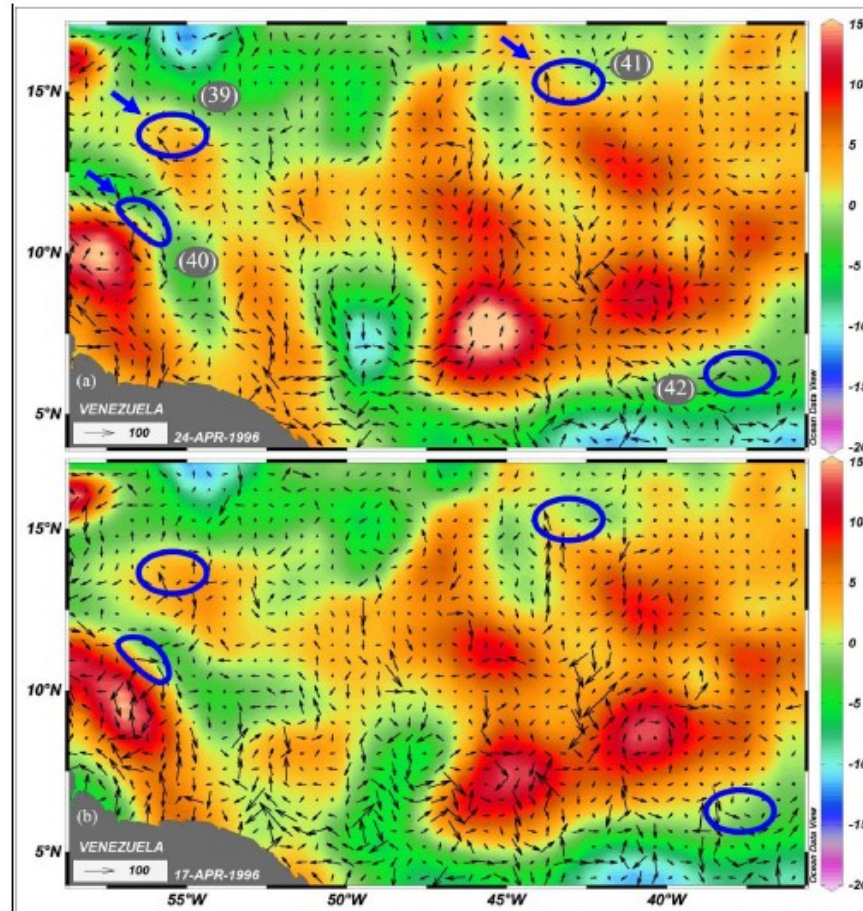
**Supplementary Material 10** - The regions of the *Trichodesmium* bloom biomass noticed in the eastern Arabian Sea in March 2003 (Parab and Matondkar, 2012). Time-series of Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. The blue ellipses indicate the locations in the region where blooms were observed. The retrospective analyses of the mesoscale features in the region are presented. As evident, the bloom incidences were linked to persistent warm-core features.



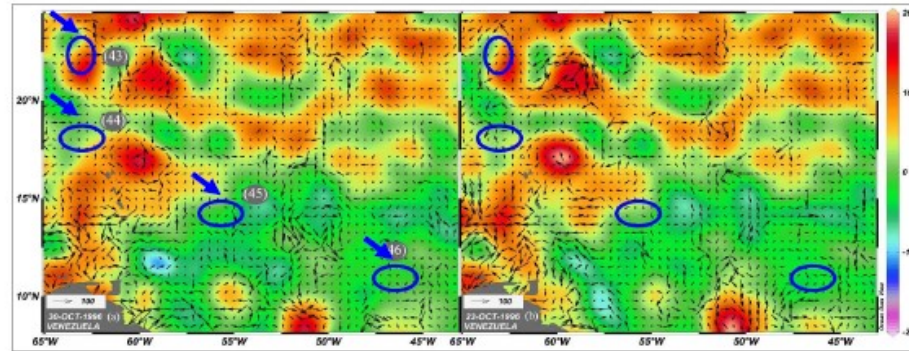
**Supplementary Material 11** - *Trichodesmium* bloom biomass sighted floating in May, 1995 in the Western Arabian Sea (Subramaniam et al., 1999). Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. In both panels, the bloom location is indicated with a blue ellipse. The retrospective analyses of the mesoscale features in the region is presented in right side panel, which shows that the bloom was situated on the boundary of a long persistent warm-core feature.



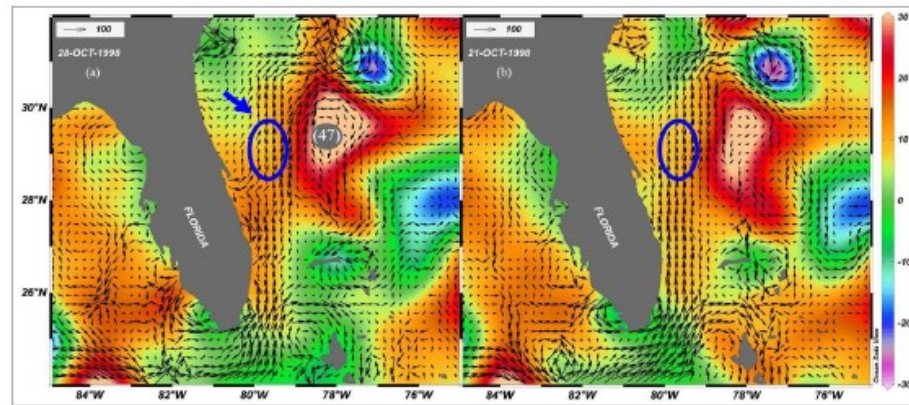
**Supplementary Material 12 - Record of *Trichodesmium* blooms at many locations in the Atlantic Ocean in period of May-June, 1994 (Capone et al., 2005). Time-series of Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. In both panels, the bloom locations are indicated with a blue ellipses. The retrospective analyses of the mesoscale features in the region is presented in the bottom panel (b), which indicate that these blooms have a close linkage to the mesoscale warm core features.**



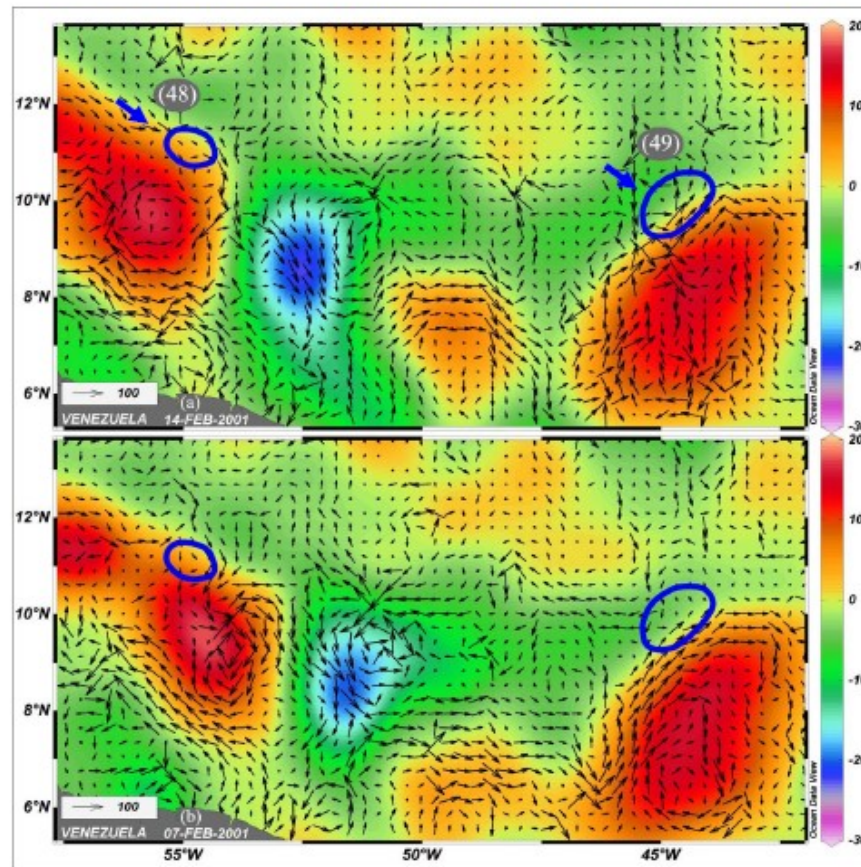
Supplementary Material 13 - Record of *Trichodesmium* at different locations of Atlantic Ocean in April, 1996 (Capone et al., 2005). Time-series of Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. In both panels, the bloom locations are indicated with a blue ellipse. The retrospective analyses of the mesoscale features in the region is presented in bottom panel (b), which indicate that these blooms were associated with mesoscale warm core eddy features.



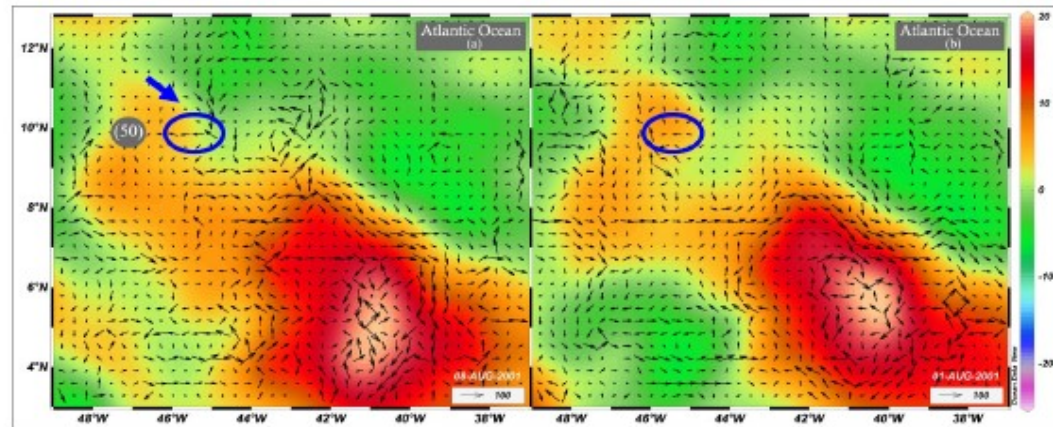
Supplementary Material 14- Record of *Trichodesmium* (from the nitrogen fixation), during October, 1996 found in North Atlantic Ocean (Capone et al., 2005). Time-series of Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. In both panels, the bloom locations are indicated with blue circles. The retrospective analyses of the mesoscale features in the region is presented in right side panel, which indicate that two out of four bloom incidences were associated with mesoscale warm core features.



Supplementary Material 15 - Record of *Trichodesmium* bloom at eastern Atlantic Ocean on October, 1998 marked presented (Subramaniam et al., 2002). Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. In both panels, the bloom location is indicated with blue circle. The retrospective analyses of the mesoscale features in the region is presented in right side panel, which indicates that the formation of the bloom was associated with mesoscale warm core feature.

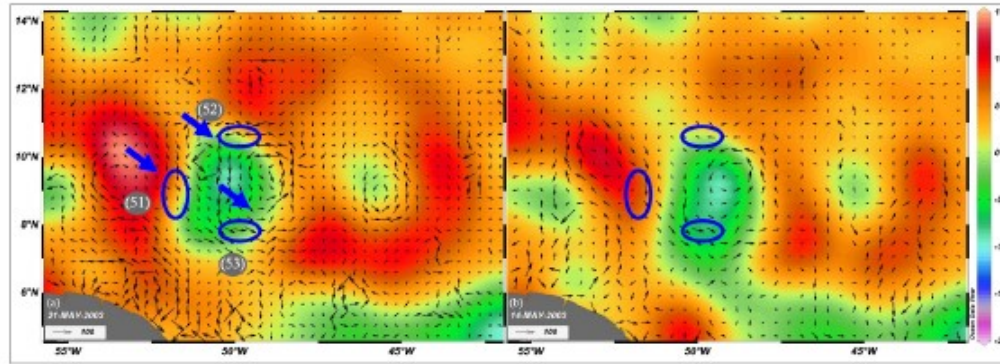


Supplementary Material 16 - Record of *Trichodesmium* (from the nitrogen fixation) at different locations of Atlantic Ocean, in February 2001 (Capone et al., 2005). Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. Both panels, the bloom locations are indicated with blue circles. The retrospective analyses of the mesoscale features in the region is presented in the bottom panel (b), which indicate that these two blooms were associated with mesoscale warm core features.

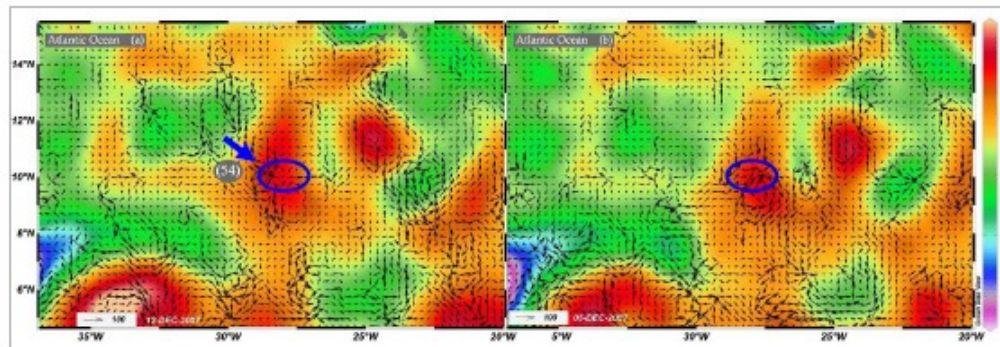


**Supplementary Material 17** - *Trichodesmium* bloom incidence marked in blue ellipse, during June -August, 2001 (Capone et al., 2005). Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. The bloom region is indicated by a blue circle. The retrospective analyses indicate that the bloom incidence was on the boundary of a mesoscale warm core eddy feature.

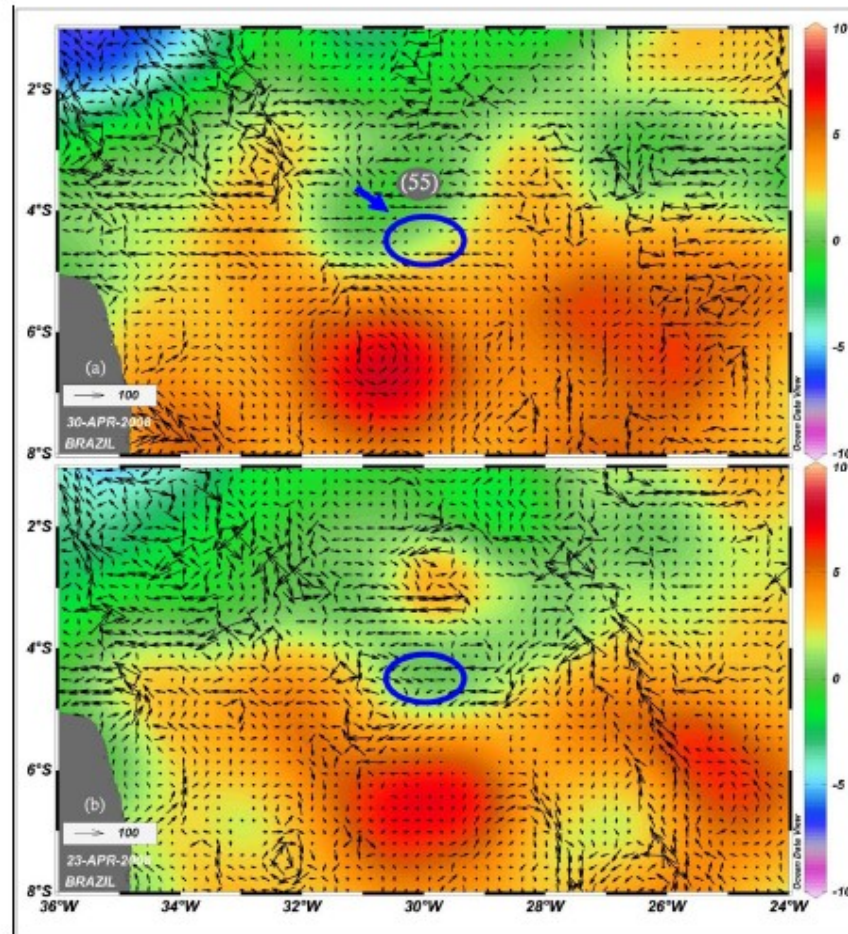




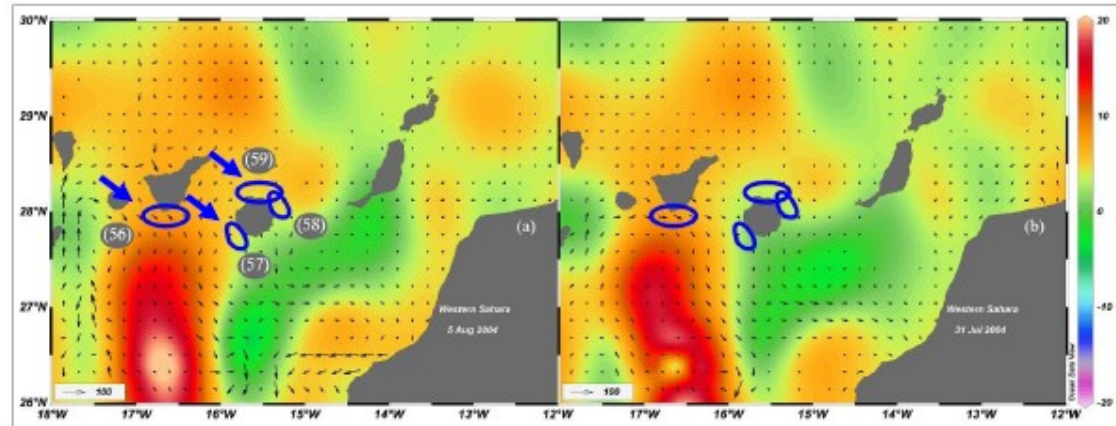
**Supplementary Material 18** - Record of *Trichodesmium* (from the nitrogen fixation), during May, 2003 presented above (Capone et al., 2005). Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. In both panels, the bloom locations are indicated with blue circles. The retrospective analyses of the mesoscale features in the region is presented in right side panel, which indicates that the bloom incidences were on the boundary of a mesoscale warm core feature.



**Supplementary Material 19** - *Trichodesmium* bloom observed in North Atlantic Ocean during December, 2007 (Fernandez et al., 2010). The Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. In both panels, the bloom location is indicated with a blue circle. The retrospective analyses of the mesoscale features in the region is presented in right side panel, which indicate that the bloom was associated with mesoscale warm core features.



Supplementary Material 20 - Record of *Trichodesmium* bloom in South Atlantic Ocean during April, 2008 (Fernandez et al., 2010). Time-series of Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. In both panels, the bloom locations are indicated with a blue circle. The retrospective analyses of the mesoscale features in the region is presented in the bottom panel, which indicates that the bloom was formed on the boundary of a mesoscale warm core feature.



Supplementary Material 21 - Record of *Trichodesmium* bloom in the north western Atlantic Ocean during August, 2004 (Ramos et al., 2008). Time-series of Mean Sea Level Anomaly (cm) and geostrophic currents ( $\text{cm s}^{-1}$ ) were merged to delineate the mesoscale features in the region. In the both panels, the bloom locations are indicated with blue circles. The retrospective analyses of the mesoscale features in the region is presented in the right side panel, which indicate that all these bloom incidences were associated with mesoscale warm core features.

SL.	FIG./SM	Geographical Region	Period	Source
<b>I Bay of Bengal</b>				
1	FIG. 7a	Andaman Sea	April, 2002	Jyothibabu et al., 2014
2	FIG. 7b	Western Bay of Bengal	April, 2001	Jyothibabu et al., 2003
3	FIG. 8a	Western Bay of Bengal	May, 2014	Jyothibabu et al., (Unpublished)
4,5	FIG. 8b	Western Bay of Bengal	April, 2015	Jyothibabu et al., (Unpublished)
6	FIG. 9a	Northern Bay of Bengal	April, 2001	Jyothibabu et al., 2003
<i>7,8,9</i>	<i>FIG. 9b</i>	<i>Southern Bay of Bengal</i>	<i>October, 2000 August, 2002</i>	<i>Hegde et al., 2008</i>
<b>II Arabian Sea</b>				
10,11,12	SM 1	Central Arabian Sea	May, 1995	Capone et al., 1998
13	SM 2	South-eastern Arabian Sea	June, 2009	Padmakumar et al., 2010
14,15	SM 3	South-eastern Arabian Sea	June, 2009 June, 2009	Padmakumar et al., 2010
16	SM 4	South-eastern Arabian Sea	April 2012	Jabir et al., 2013
17	SM 5	South-eastern Arabian Sea	April 2005	Martin et al., 2013
18	SM 6	South-eastern Arabian Sea	May, 2005	Krishnan et al., 2007
19,20,21,22	SM 7	North Eastern Arabian Sea	March 2000	Parab & Matondkar, 2012
23,24,25	SM 8	North Eastern Arabian Sea	March 2004	Parab & Matondkar, 2012
26,27,28,29	SM 9	North Eastern Arabian Sea	November 2001	Parab & Matondkar, 2012
30,31	SM 10	North Eastern Arabian Sea	March 2003	Parab & Matondkar, 2012
32	SM 11	North western Arabian Sea	May, 1995	Subramaniam & Carpenter, 1999
<b>III Other Oceans</b>				
33-38	SM 12	North Atlantic Ocean	May-June, 1994	Capone et al., 2005
39-42	SM 13	North Atlantic Ocean	April, 1996	Capone et al., 2005
43-46	SM 14	North Atlantic Ocean	October, 1996	Capone et al., 2005
47	SM 15	North western Atlantic Ocean	October, 1998	Subramaniam et al., 2002
48-49	SM 16	North Atlantic Ocean	January - February, 2001	Capone et al., 2005
50	SM 17	North Atlantic Ocean	July - August, 2001	Capone et al., 2005
51-53	SM 18	North Atlantic Ocean	April - May, 2003	Capone et al., 2005
54	SM 19	North Atlantic Ocean	November - December, 2007	Fernandez et al., 2010
55	SM 20	South Atlantic Ocean	April - May, 2008	Fernandez et al., 2010
56-59	SM 21	North West Atlantic Ocean	August, 2004	Ramos et al., 2008

**Table 1** - The location and date of the *Trichodesmium* incidences analysed in the present study. The images representing the analyses of the first six incidence is presented in the main text of the manuscript (Figures 7 to 9) and all other cases are presented as Supplementary Materials (1-21). Serial Numbers 7, 8 & 9 (italicised) represent a few incidences in the Bay of Bengal where abundance of *Trichodesmium* filaments in the surface waters were noticed during the late-southwest monsoon (Hegde et al., 2008). The serial numbers of the bloom incidences in this Table are followed in all the Figures and Supplementary Materials detailing bloom incidences in this paper. Abbreviations: FIG - Figure and SM - Supplementary Material.