

## **Organic nutrients support high primary production in the Bay of Bengal**

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### **Abstract**

The Bay of Bengal (BoB) is known to experience low productivity but high sinking carbon fluxes to the bottom and this paradox is attributed to mineral ballast of organic matter. We found for the first time that primary production in the BoB is higher and it is supported by dissolved organic nitrogen (DON) and phosphorus (DOP) transported from the shelf regions through eddies. Both DON and DOP contribute up to 70-99% to the total dissolved nutrients in the waters above the thermocline. DON and DOP displayed positive relationship with primary production in the upper 25m of water column suggesting that organic nutrients significantly support primary producers. Primary production and export production in the BoB is comparable to that in the Arabian Sea, in contrast to the earlier belief that it has low production due to lack of inorganic nutrients caused by strong salinity stratification.

**Key words:** dissolved organic nutrients, primary production, sinking carbon, eddies, Bay of Bengal

## 1. Introduction

Perennial occurrence of oligotrophic conditions is observed in the upper 30-50 m of water column in the Bay of Bengal (BoB; northeastern Indian Ocean) with  $<0.1 \mu\text{M}$  of dissolved inorganic nitrogen (DIN) due to strong salinity stratification [Madhupratap *et al.*, 2003; Prasanna Kumar *et al.*, 2002; 2007]. As a result, low primary production has been observed throughout the year in the BoB, based on a limited coverage, compared to the adjacent basin, the Arabian Sea (AS) [Gauns *et al.*, 2005]. Gauns *et al.* [2005] recorded a primary production in the range of 184 to 512 (mean:  $344 \pm 164$ )  $\text{mgC m}^{-2} \text{d}^{-1}$ , which is lower than that found in recent studies [Anand *et al.*, 2018; 182-1261 (mean:  $936 \pm 350$ )  $\text{mgC m}^{-2} \text{d}^{-1}$ ]. The latter results are on par with that primary production in the AS [ $1032 \pm 260$   $\text{mgC m}^{-2} \text{d}^{-1}$ ; Barber *et al.*, 2001;  $924 \pm 296$   $\text{mgC m}^{-2} \text{d}^{-1}$ ; Dickson *et al.*, 2001; and  $1752 \pm 726$   $\text{mgC m}^{-2} \text{d}^{-1}$ ; Anand *et al.*, 2018]. Though DIN inputs from the rivers were reported to be low as most of them are utilized within estuaries and coastal regions [Sarma *et al.*, 2013a,b; Krishna *et al.*, 2016], the cyclonic eddies and other mixing processes seem to supply required nutrients to the primary producers [Vidya and Prasanna Kumar, 2013; Narvekar and Prasanna Kumar, 2014; Martin and Shaji, 2015]. In contrast, the sinking organic carbon flux to bottom ( $\sim 3000$  m) in the BoB [Ittekkot *et al.*, 1991] is more than that in highly productive AS [Nair *et al.*, 1989; Honjo *et al.*, 1996]. Recently it was observed that sinking organic carbon fluxes at 100 m was higher in the AS [median: 39.0 (range: 22.8 to 84)  $\text{mgC m}^{-2} \text{d}^{-1}$ ; Anand *et al.*, 2018] than BoB [median: 8.4 (range: 3.6 to 92.4)  $\text{mgC m}^{-2} \text{d}^{-1}$ ; Anand *et al.*, 2017]. Such low export production in the BoB is attributed to high utilization of organic matter by heterotrophs in the upper 100 m [Anand *et al.*, 2017]. In addition to this,  $>70\%$  of the phytoplankton were contributed by picophytoplankton [Sarma *et al.*, 2016; Sherin *et al.*, 2018] in the BoB resulting in less sinking carbon due to low density. Therefore, primary production in the BoB may not be so low as noted by Gauns *et al.* [2005], which is based on only 3 observations in the open sea regions of AS and BoB, and alternative forms of nutrients, other than inorganic nutrients in-situ, may support primary production. Srinivas *et al.* [2013] estimated that atmospheric deposition of nitrogen may contribute up to  $\sim 13\%$  of the primary production in the BoB. High concentrations of dissolved organic carbon (DOC) [Fernandes *et al.*, 2012; Shah *et al.*, 2018] and dissolved organic nitrogen [DON; Letscher *et al.*, 2013] are found in the BoB and attributed to supply through river discharge. However, the fraction of DON to the total dissolved nitrogen (TDN) pool and the role of DON as an alternative source of nutrient to support primary production in the BoB is unknown. Recently it was observed that anticyclonic eddies (ACE) transport oxygen-rich waters to oxygen minimum zone (OMZ) due to convergence leading to weakening of OMZ [Sarma and Uday Bhaskar, 2018; Sarma *et al.*, 2018]. The role of eddies on transporting coastal/shelf

nutrients to the open ocean is also unknown. The objective of this work is to evaluate 1) the contribution of dissolved organic nutrients to total dissolved nutrients, 2) the role of eddies in transporting dissolved organic nutrients to the open ocean to support primary production in the BoB, and 3) the contribution of primary production to export production at the 100 m in the BoB.

## **2. Material and methods**

### *2.1. Sampling and analyses*

A cruise was undertaken in the western BoB covering one cyclonic eddy (CE), two anticyclonic eddies – north (ACE<sub>N</sub>) and south of the transect (ACE<sub>S</sub>) and no-eddy (NE) regions during 23 March to 6 April 2018 (Fig. 1). Water column properties, such as temperature, salinity (SBE 911 plus, USA), fluorescence (Wet Labs, USA), photosynthetic active radiation (PAR) and dissolved oxygen (DO; SBE 43, USA), were measured using sensors. The measurement accuracies of sensors are:  $\pm 0.001^{\circ}\text{C}$ ,  $\pm 0.002$  psu,  $\pm 0.01$  mg m<sup>-3</sup>, 5%, and  $\pm 2$   $\mu\text{M}$  respectively. The samples were collected at standard depths (0, 5, 10, 15, 25, 50, 75, and 100 m) with the help of 10 L Niskin bottles. Salinity, DO and fluorescence data were calibrated using results from Autosal, Winkler titration [Carritt and Carpenter, 1966] and spectrofluorometric measurements [Suzuki and Ishimaru, 1990]. The concentrations of dissolved inorganic nutrients (nitrate, nitrite, ammonium, and phosphate) and total phosphate (TP) were measured using an autoanalyzer (Technicon; Taacs, Australia) [Grasshoff *et al.*, 1983]. The detection limits for nitrate, nitrite, ammonium, dissolved inorganic phosphate (DIP) and TP were  $\pm 0.02$ ,  $\pm 0.02$ ,  $\pm 0.02$ ,  $\pm 0.01$  and  $\pm 0.06$   $\mu\text{M}$ , respectively. Dissolved organic phosphate (DOP) was estimated by difference between TP and DIP.

Total Nitrogen (TN) was determined by oxidizing dissolved nitrogen to NO<sub>x</sub> using platinum catalyst at 950°C and then reducing it to N<sub>2</sub> gas using copper catalyst at 680°C using Iso TOC analyser (M/s Elementar analytical, Germany). The concentration of N<sub>2</sub> gas is measured using Non-Dispersive Infra Red (NDIR) detector. Using high purity glutamic acid, the instrument was calibrated. The precision of the TN measurements is <3%. The DON is estimated by subtracting DIN from TN.

### *2.2. In vitro Primary production incubation*

The primary production in the water column in the upper 100 was estimated at 6 light depths with 100, 80, 60, 40, 20, 1% of the incident radiation at the surface. Water samples collected in one litre light and dark bottles in triplicates and samples were spiked with 0.2 ml of 2 mM enriched sodium bicarbonate (NaH<sup>13</sup>CO<sub>3</sub>; 99%; Sigma Aldrich, USA) and incubated for 24 hours in the deck incubator. Temperature in the incubator was maintained with running surface seawater. Different light screens were used to cut the light to the required levels appropriate for the deeper samples. The

incorporation of enriched inorganic carbon into the phytoplankton biomass was measured following the procedures of *Hama et al.* [1983]. After the incubation, samples were filtered through pre-combusted GF/F filters (400°C for 12 hours) and filters were frozen until analysis. In the shore-laboratory, filters were dried overnight at 50 °C and acid-fumed (HCl) for 12 h to remove inorganic carbon, and then dried again for analyses of organic carbon content and isotopic composition using elemental analyzer coupled to an isotope ratio mass spectrometer (IRMS; Delta V Plus, Thermo Electron, Germany).

### 2.3. Satellite Data

Sea surface height anomaly (SSHA; 0.25 x 0.25°) and Geostrophic currents (0.25 x 0.25°; Merged product) obtained from Copernicus Marine Environmental Monitoring Service ([www.marine.copernicus.eu](http://www.marine.copernicus.eu)). The origin and movement of eddy was identified using the position of the eddy using daily SSHA [Fig. 1; *Sarma et al.*, 2018]. The variability in SSHA and geostrophic currents on the day of sampling of each station are given in Supplementary Figure 1. The ACE is identified as the region with >0.2 m of SSHA associated with anticyclonic circulation and <-0.2 m of SSHA and cyclonic circulation is identified as CE.

## 3. Results

### 3.1. Variations in hydrographic properties

Relatively low temperature and low saline waters were observed in the upper 100 m of water column in the north but these increased towards south (Fig. 2a,b). Low saline water occupied the upper 20 to 60 m of water column in the north associated with cyclonic eddy (CE) and partly ACE<sub>N</sub> (Fig 2a). Occurrence of divergence of water column in the CE and convergence in the ACE were observed as evidenced from the shallow depth of 20°C isotherm in the CE (55 m) and NE (60 m) than ACE<sub>N</sub> and ACE<sub>S</sub> regions (80-90 m; Fig. 2a). Similarly, ~34.0 isohaline was also observed to be deeper in the ACE<sub>N</sub> and ACE<sub>S</sub> (>100 m) than CE and NE regions (50-60 m) (Fig. 2b). The wide variations in MLD (6.5 and 34.5 m) were observed, which are shallower in the CE and NE (~15±4 m) than in ACE (32±6 m) region [*Sarma et al.*, 2018].

The mean Chlorophyll-a (Chl-a) in the upper 50 m of water column was higher in the CE region (0.35±0.08 mg m<sup>-3</sup>) than NE (0.22±0.06 mg m<sup>-3</sup>), ACE<sub>N</sub> (0.11±0.06 mg m<sup>-3</sup>) and ACE<sub>S</sub> regions (0.10±0.03 mg m<sup>-3</sup>; Fig. 2c). High depth integrated Chl-a in the upper 100 m was observed in CE (34.6±4 mg m<sup>-2</sup>) than in NE (26.4±4 mg m<sup>-2</sup>), ACE<sub>N</sub> (23.6±3 mg m<sup>-2</sup>) and ACE<sub>S</sub> (22.2±3 mg m<sup>-2</sup>). The subsurface Chl-a maximum was found between 20 and 30 m in the study region with low

maximal values below  $ACE_N$  and  $ACE_S$  compared to CE and NE regions (Fig. 2c). The distribution of DO followed that of temperature and salinity and upward pumping of low DO waters to 30 m was observed in the CE and high DO concentrations were found in the  $ACE_N$  and  $ACE_S$  regions in the upper 100 m (Fig. 2d).

### 3.2. Variations in DIN and DIP in the water column

Upsloping of 1  $\mu\text{M}$  of DIN isolines from subsurface was noticed in the CE whereas downsloping was observed in the  $ACE_N$  and  $ACE_S$  regions (Fig. 2e). The concentration of DIN was  $<0.1 \mu\text{M}$  (undetectable to  $<0.1 \mu\text{M}$ ) in the upper 20 m to 40 m of water column in the ACE whereas  $<0.2 \mu\text{M}$  in the CE and NE regions (Fig. 2e). Increase in concentration of DIN was observed below 25 m depth in the CE and NE regions due to upward mixing of nutrient-rich waters and such increase was observed below 75 m in the ACE regions (Fig. 2e). The mean concentrations of DIN in the upper 50 m was 1.98 and 1.58  $\mu\text{M}$  in the CE and NE regions, respectively, and it was 0.02 and 0.12  $\mu\text{M}$  in the  $ACE_N$  and  $ACE_S$ , respectively. Similar to DIN, the concentration of DIP was relatively higher in the CE and NE than that in  $ACE_N$  and  $ACE_S$  (Fig. 2f). However, concentrations of DIP in the upper 40 m in the CE and NE and 80 m in the ACEs were above limiting levels ( $>0.1 \mu\text{M}$ ) than DIN ( $<0.1 \mu\text{M}$ ). Below 40 m significant increase in DIP concentration ( $>0.75 \mu\text{M}$ ) was observed in the CE and NE regions (Fig. 2f).

### 3.3. Spatial variations in DON and DOP

The concentrations of DON ranged between 1.5 and 12  $\mu\text{M}$  in the study region with relatively higher concentrations ( $>6 \mu\text{M}$ ) in the upper 40 m than below in the CE and NE regions (Fig 2g). The concentration of DON in the CE region was relatively higher in the upper 25 m (5-9  $\mu\text{M}$ ) of water column but decreased to  $<2 \mu\text{M}$  below 50 m whereas higher concentrations (6-12  $\mu\text{M}$ ) were observed in the upper 100 m in the  $ACE_N$  and  $ACE_S$  regions (Fig. 2g). The concentration of DON followed the depth of 20° C isotherm (Fig. 2a). DON showed negative relationship with salinity ( $r^2=0.39$ ;  $p<0.001$ ) and positive relation with temperature ( $r^2=0.42$ ;  $p<0.001$ ) and DO ( $r^2=0.52$ ;  $p<0.001$ ) in the upper 100 m. DON displayed significant negative relationship with DIN ( $r^2=0.52$ ;  $p<0.001$ ) and DIP ( $r^2=0.48$ ;  $p<0.001$ ) in the study region. The concentration of DON contributed up to 70-99 % of the total dissolved nitrogen (TDN) in the upper 30 m in CE and upper 80 m in the  $ACE_N$  and  $ACE_S$  regions. The DOP varied between 0.5 and 3.2  $\mu\text{M}$  and higher concentration was observed in the upper 20-30 m in the CE but entire upper 100 m of water column in the  $ACE_N$  and  $ACE_S$  regions (Fig. 2h). Lower DON and DOP was observed in the CE region than  $ACE_S$  and  $ACE_N$  in association with higher Chl-a in the former than latter region (Fig. 2c, g,h). The DOP contributed

to 70 to 90% to the total dissolved phosphate (TDP) in the upper 35m in the CE and 80m in the ACE regions. DOP displayed weak negative relationship with salinity ( $r^2=0.26$ ;  $p<0.05$ ) and weak positive relation with temperature ( $r^2=0.12$ ;  $p<0.1$ ) and DO ( $r^2=0.21$ ;  $p<0.05$ ) in the upper 100 m. DOP displayed weak positive relationship with DIP ( $r^2=0.20$ ;  $p<0.05$ ) and DIN ( $r^2=0.19$ ;  $p<0.05$ ) in the study region. The DON:DOP ratio varied between 1.1 and 16.6 with mean of  $5.8\pm 3$ . The mean DON:DOP ratio was  $5.2\pm 1$  in the CE and it was higher in the ACE<sub>N</sub> ( $6.8\pm 1$ ) and ACE<sub>S</sub> ( $6.1\pm 2$ ) regions.

#### 3.4. Spatial variations in primary production

The primary production in the upper 100 m of water column ranged from 0.3 to 18.4 mgC m<sup>-3</sup> d<sup>-1</sup> and lower production was observed in the north than southern BoB (Supplementary Figure S1). The primary production integrated in the upper 100 m of water column ranged between 411 and 920 ( $758\pm 220$ ) mgC m<sup>-2</sup> d<sup>-1</sup>. The depth integrated primary production to 25 m of water column contributed to 40 to 70% of the production in the 100 m. The primary production in the upper 25 m of water column, where DIN concentration was  $<0.1\ \mu\text{M}$ , showed significant linear correlation with DON ( $r^2=0.45$ ;  $p<0.001$ ) in the study region. Similarly, significant relationship between primary production and DOP was observed in the CE and ACE<sub>N</sub> regions ( $r^2=0.40$ ;  $p<0.01$ ) where DIP was  $<0.1\ \mu\text{M}$  but it is insignificant in other regions where DIP is  $>0.2\ \mu\text{M}$  (Fig. 3).

### 4. Discussion

#### 4.1. Spatial variations in DON and DOP concentrations in the western BoB

The higher values of DON ( $>4\ \mu\text{M}$ ) were confined to the upper 40 m that decreased with depth in the CE and NE regions whereas higher values ( $>6\ \mu\text{M}$ ) were observed up to 100 m or more in the ACE regions in association with the deepened thermocline (Fig. 2g). Relatively higher DON values were observed to be related with low salinity in the upper 25 m suggesting that river water may be a significant source of DON to the BoB. The range of DON is consistent with the other regions; for instance, Bronk [2002] compiled the DON concentrations from different regions and found that  $9.9\pm 8.1\ \mu\text{M}$  for coastal and continental shelf regions with which our results agree of these values. Letscher *et al.* [2009] found that 4.4 to 6.8  $\mu\text{M}$  in the surface waters of the BoB. Duursma [1961] reported 5.8 to 12.4  $\mu\text{M}$  of DON in the coastal region near Texel. Butler *et al.* [1979] found DON values between 4.5 and 10  $\mu\text{M}$  in the English Channel.

Similar to DON, the concentrations of DOP were higher in the upper 25 m compared to depth below. Higher DOP concentrations in the upper 100 m of water column were observed within ACE<sub>N</sub> and

ACE<sub>S</sub> and it was lower in the CE and NE regions (Fig. 2h). The enhanced concentration of DON and DOP in the ACE region may be due to convergence of high DON and DOP waters under ACE and also advection of shelf waters as ACE<sub>N</sub> seems originated in the north eastern shelf region whereas ACE<sub>S</sub> was originated in the eastern BoB and advected to the study region (Fig. 1). It has been reported that convergence of oxygen-rich waters in ACE regions led to weakening of oxygen minimum zone (OMZ) in the BoB [Sarma and Uday Bhaskar, 2018; Sarma et al., 2018]. DON and DOP contributed to 80-99% to the TDN and TDP pools in the waters above thermocline suggesting ACE bring organic nutrients from the coastal region that may support primary production in the open sea region where inorganic nutrients are very low (<0.1  $\mu\text{M}$ ) (Fig. 2e).

The distribution patterns of DON and DOP appear to be different, perhaps reflecting differences in the availability of DIN and DIP or differences in bioavailability of DON and DOP. The concentrations of DIN in the upper 20-30 m in the CE and upper 50 m in the ACE regions are very low (undetectable to 0.1  $\mu\text{M}$ ) suggesting that DIN is severely limiting the phytoplankton production. On the other hand, the concentrations of DIP were ~0.1 to 0.28  $\mu\text{M}$  in the upper 40 m in the CE and 80 m in the ACE regions suggesting that significant availability of DIP for phytoplankton production. Since DIN concentrations are low, phytoplankton may utilize DON as an alternative source of nitrogen in the BoB. The DON:DOP ratio varied between 1.1 and 16.6 with a mean of  $5.2 \pm 3$ , which is lower than Redfield ratio of 16, suggesting that biological removal of DON could be the reason.

#### 4.2. Source of DON and DOP in the BoB

DON and DOP enters the marine systems through physical transport and coastal systems are characterised by significant terrestrial DON and DOP inputs. Riverine DON and DOP are first used in the estuary or in the adjacent coastal zone, depending on the water residence time in the estuary [Seitzinger and Sanders, 1997]. Upon entering into marine waters, the bioavailability of DON to bacteria sometimes increases [Stepanauskas et al., 1999]. The reactivity of riverine DON is so high that the terrestrial signature almost vanishes before it crosses the continental shelf [Hedges et al., 1997]. However, the concentration of DON in the continental shelf and its possible advection to the open sea region depends on the quality of DON and bacterial activity. Since phytoplankton biomass is higher in the coastal/shelf regions, higher production of DON is expected [Sarma et al., 2013a,b]. Prasad [2014] found higher DON concentrations (10-15  $\mu\text{M}$ ) in the coastal BoB during peak discharge period (July-August). In addition to this, DON is produced in-situ through biological processes. For instance, Collos et al. [1992] reported that DON releases from diatom cells and its

subsequent uptake by dividing cells of the same species during the night, which could provide a competitive advantage over co-occurring primary producers that would not be able to take up these compounds. This does suggest an active excretion. Passive loss of DON from intact primary producers is probably due to osmotic gradients that are sustained by bacteria [Bjornsen, 1988]. Another source of terrestrial DON and DOP is submarine ground water discharge (SGD). Ground water is generally enriched in nitrogen and phosphorus due to both natural processes (eg. Weathering, leaching of soils) and anthropogenic inputs (use of fertilizers, seepage of sewage). Rengarajan and Sarma [2015] found that up to 35% of the coastal inorganic nutrients was supported by SGD. Debnath and Mukherjee [2016] suggested that SGD should significantly contribute to the nutrient budget of the BoB and needs evaluation.

The significant relation of salinity with DON and weak relation with DOP suggests that DON and DOP are transported into the interior of the BoB through lateral transfer by meso-scale eddies, i.e., ACEs. This path way is more clearly revealed in this study with higher concentrations of DON and DOP in the ACE which were formed in the northeastern and eastern coastal regions, therefore source from the river waters or coastal waters is possible (Fig. 2g). Advection of DON and DOP from shelf to offshore region by eddies was observed in the North Atlantic [Roussenov *et al.*, 2006]. In contrast, low DIN concentrations were observed in the ACE in the study region suggests that occurrence of low DIN concentrations in the regions where ACEs are formed. Sarma *et al.* [2013a,b] found that sharp decrease in DIN concentrations from close to coast to 10 km offshore was observed in the western coastal BoB suggesting that DIN was utilized within shelf itself. This study suggest that ACEs bring organic nutrients from the coastal waters to the oligotrophic regions and support primary production in the BoB. However, the utilization of organic nutrients by phytoplankton is depended on the quality of DON and DOP and their nature (labile versus refractile). The composition of neither DON nor DOP is known in the BoB.

#### 4.3. DON and DOP as nutrients source to primary production in the BoB

Phytoplankton utilization of DON as alternative source of nitrogen has long been recognized [see. Antia *et al.*, 1975; Admiraal *et al.*, 1987; Bronk, 2002; and Bronk *et al.* 2007 for an over view]. Both bacteria and phytoplankton are known to use DON as nitrogen source [Bronk and Gilbert, 1993; Bronk *et al.*, 2007; Veuger *et al.*, 2004]. Dominance of DON over DIN is observed in oligotrophic and mesotrophic systems [Bronk, 2002; Torres-Valdes *et al.*, 2009]. In coastal ecosystems DON contributes up to 50% of the total dissolved nitrogen (TDN) [De Galan *et al.*, 2004] while it is up to 90% in the oligotrophic open ocean regions [eg: Abell *et al.*, 2000; Mahaffey *et al.*, 2004; Torres-Valdes *et al.*, 2009].



The primary production in the upper 100 m of water column ranged from 0.2 to 14 mgC m<sup>-3</sup> d<sup>-1</sup> in the study region and about 45 to 70% of the production in the upper 100 m observed in the upper 25 m of water column alone where DIN was <0.1 μM and DON was >6 μM. The primary production in the upper 25 m of water column displayed significant linear relation with DON ( $r^2=0.45$ ;  $p<0.001$ ) in the entire study region. On the other hand, DOP displayed significant relation with primary production in the CE and northern part of ACE<sub>N</sub> (up to a distance of 600 km) where DIP was low (<0.1 μM; Fig. 2f) suggesting that DOP is supporting primary production in the north and its role is insignificant in the south where phosphate was >0.2 μM (Fig. 2f). This study suggests that organic nutrients are significantly supporting primary production in the BoB where inorganic nutrients are low that differs from the earlier contention that unavailability of inorganic nutrients [Gauns *et al.*, 2005] in the upper ocean, due to weak vertical mixing, inhibits primary production.

#### 4.4. Possible underestimation of Primary production in the BoB

The primary production in the BoB is believed to be lower than adjacent basin AS [Prasanna Kumar, 2002; 2004; Madhupratap *et al.*, 2003; Gauns *et al.*, 2005; Ramaiah *et al.*, 2010] and it was attributed to less inorganic nutrients availability caused by stratification. These authors used the same data set collected during Bay of Bengal Process Study when only 3 stations were occupied for primary production in the open sea region. Therefore, it is possible that data may be biased due to lack of spatial coverage. On the other hand, the depth integrated primary production in the upper 100 m ranged between 411 and 920 (mean of 758±220) mgC m<sup>-2</sup> d<sup>-1</sup> in this study region which is significantly higher than earlier estimates [184 to 512 (344±164) mgC m<sup>-2</sup> d<sup>-1</sup>; Gauns *et al.*, 2005] during intermonsoon period and it is even less during other periods. On the other hand, Anand *et al.* [2017] measured primary production in the range of 182 to 1261 (936±350) mgC m<sup>-2</sup> d<sup>-1</sup> during spring intermonsoon (March-April, 2014) in the BoB and it is consistent with the present estimations (758±220 mgC m<sup>-2</sup> d<sup>-1</sup>). Recent primary production results from BoB [Anand *et al.*, 2017 and this study] are comparable to that of the Arabian Sea [1032±260 mgC m<sup>-2</sup> d<sup>-1</sup>; Barber *et al.*, 2001; 924±296 mgC m<sup>-2</sup> d<sup>-1</sup>; Dickson *et al.*, 2001 and 1752±726 mgC m<sup>-2</sup> d<sup>-1</sup>; Anand *et al.*, 2018]. On the other hand, sinking organic carbon fluxes at 100 m are almost equal in the Arabian Sea [22.8 to 84 mgC m<sup>-2</sup> d<sup>-1</sup>; Anand *et al.*, 2018] and BoB [3.6 to 93.2 mgC m<sup>-2</sup> d<sup>-1</sup>; Anand *et al.*, 2017] that further suggests that the primary production in the BoB was underestimated due to lack of enough coverage as measurements were conducted only at 3 stations during each season [Gauns *et al.*, 2005]. The present study further suggests that 40 to 70% of the primary production in the BoB occurs in the upper 25 m of water column where significant amount of organic nutrients is available indicating

that organic nutrients are acting as an alternative source of nutrients, in the absence of inorganic nutrients. The almost equal sinking carbon fluxes to the bottom in the open sea region of BoB [5.6-7.2 mgC m<sup>-2</sup> d<sup>-1</sup>; *Ittekkot et al.*, 1991] and AS [3.3-8.9 mgC m<sup>-2</sup> d<sup>-1</sup>; *Nair et al.*, 1989; *Honjo et al.*, 1999] are attributed to removal of organic matter in association with river-borne mineral particles in the BoB and high primary production in the AS. In contrast, the present study suggests that higher primary production, supported by organic nutrients, is responsible for higher sinking carbon fluxes in the BoB, however, mineral ballast may be possible in the northern Bay where higher suspended load is observed [*Ittekkot et al.*, 1991; *Sarma et al.*, 2016]. Therefore, primary production in the BoB is not lower than that of AS as has been hitherto interpreted.

## 5. Summary and Conclusions

In order to examine organic nutrients as an alternative source of nutrient to the phytoplankton production, the possible role of eddies on transporting coastal nutrients to the open sea, the present study was conducted in the BoB. The concentration of DIN was significantly low (<0.1 μM) in the upper 25 m of water column in CE and 80 m in the ACE regions whereas DIP was 0.01-0.28 μM suggesting that DIN is severely limiting the primary production in the BoB. Higher concentrations of DON and DOP were observed in the upper 40 m of water column that decreased with depth in the CE and NE whereas uniformly higher concentrations were observed in the upper 100 m of water column in the ACE regions suggesting that ACEs transport coastal nutrients to the open sea regions. Both DON and DOP contributed 70-99% to the TDN and TDP in the upper 40 and 80 m of water column in the CE and ACE regions respectively. DON displayed significant positive relationship with primary production in the upper 25 m of water column whereas DOP displayed such relation only in the northern Bay where DIP was <0.1 μM suggesting that organic nutrients are significantly used by the primary producers. Though BoB is stratified due to river discharge from the major rivers and inhibits vertical DIN inputs, ACEs bring DON and DOP through convergence particularly from the continental shelf regions. Primary production in the upper 100 m in the BoB is almost equivalent to that in the Arabian Sea in contrast to that earlier belief due to lack of spatial coverage in the former basin. This study suggests that primary production in the BoB is high and supported by organic nutrients. Though this study was conducted during non-monsoon period, organic nutrients may also support during summer monsoon period when higher discharge brings in significant amount of organic nutrients from the rivers and ACEs may transport these to the open ocean regions to support production. More than 50 eddies form every year in the BoB [*Chen et al.*, 2012], the impact of these eddies on nutrient dynamics and primary production needs evaluation.

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## Legends to Figures

Figure 1: The map showing 10 days mean (25 March to 3 April 2018) sea surface height anomaly (m; color code) overlaid by geostrophic currents in the Bay of Bengal during study period. The station locations and their numbers are shown with black closed symbols. The sampled eddies were also marked for identification as cyclonic eddy (CE), north anticyclonic eddy ( $ACE_N$ ), non-eddy (NE) and south anticyclonic eddy ( $ACE_S$ ). The track of each eddy on the day of origin until the day of sampling of last station of each eddy was marked as pink (CE), red ( $ACE_N$ ) and blue ( $ACE_S$ ). The primary production experiments were conducted at stations 2, 4, 6, 10, 13,14, 18, 20 and 21.

Figure 2: Spatial variations a) temperature ( $^{\circ}C$ ), b) salinity, c) chlorophyll-a ( $mg\ m^{-3}$ ), d) dissolved oxygen ( $\mu M$ ), e) DIN ( $\mu M$ ), f) DIP ( $\mu M$ ), g) DON ( $\mu M$ ), h) DOP ( $\mu M$ ) along the transect. Station numbers are given in the upper x-axis and distance from station 1 is given in the lower x-axis. The stations covered under CE, ACE and NE are marked.

Figure 3: The relationship of primary production with a) DON and b) DOP in the upper 25m of water column. Closed circles in Figure 3b are from CE and  $ACE_N$  regions and open circles from NE and  $ACE_S$ .

Figure 1:

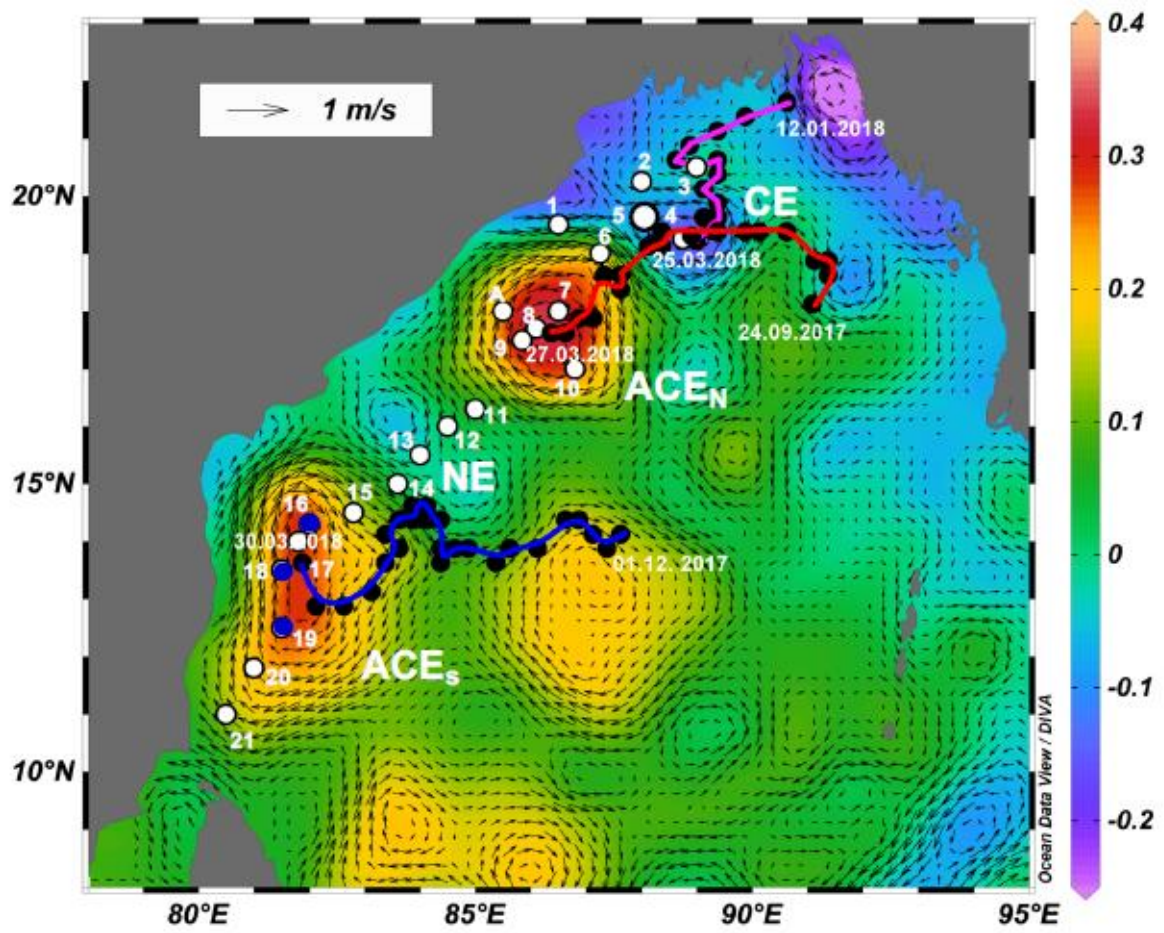




Figure 2:

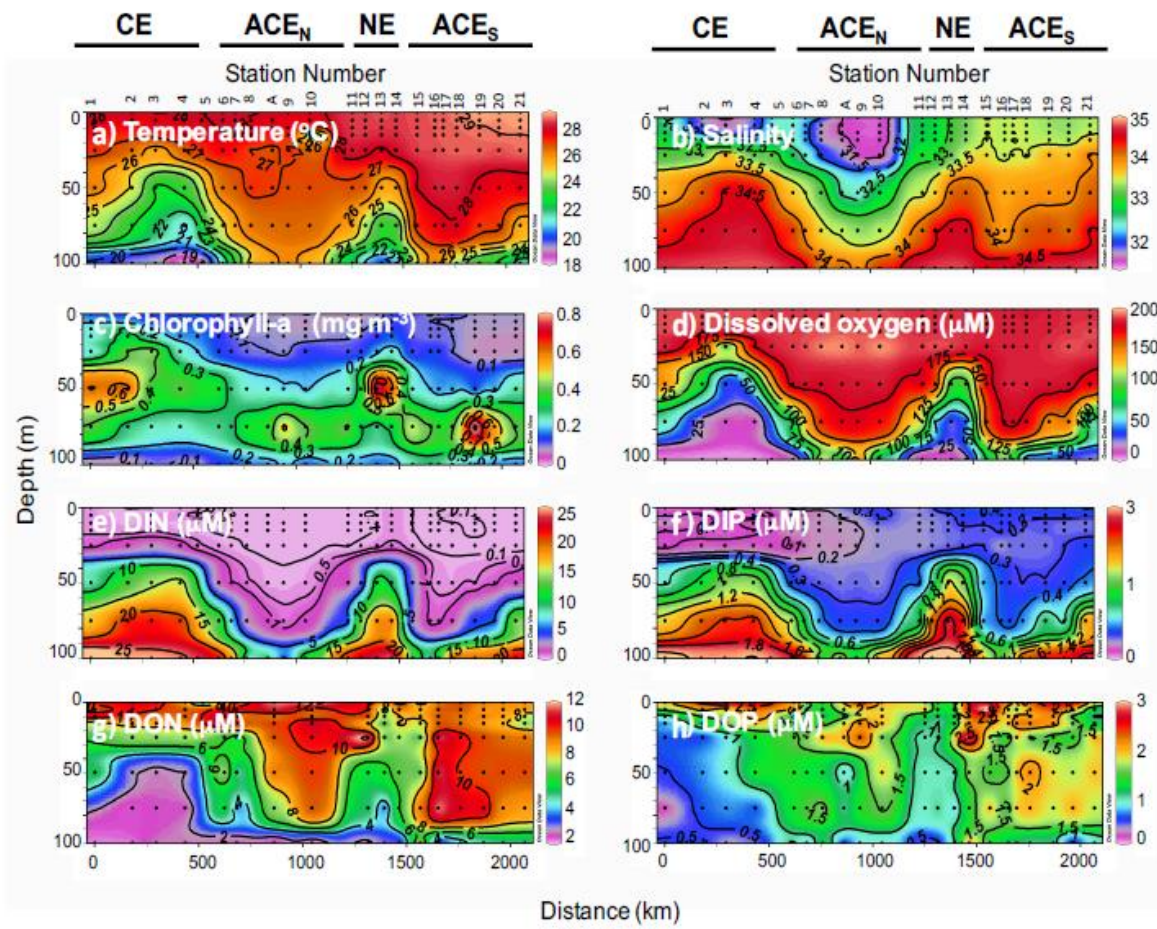
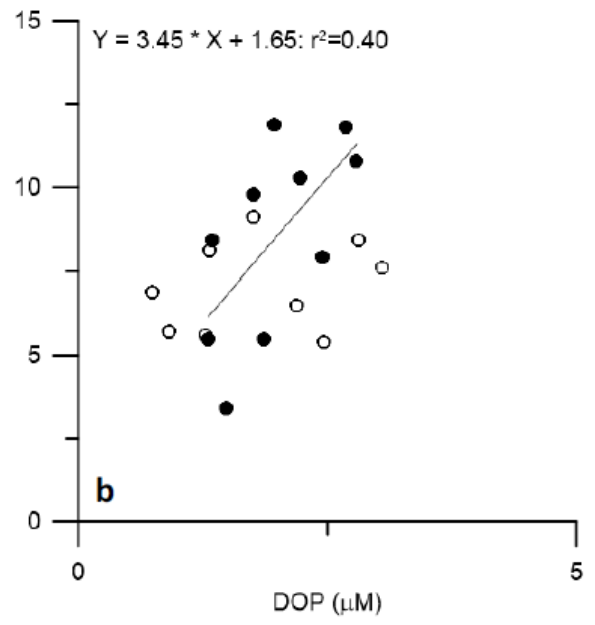
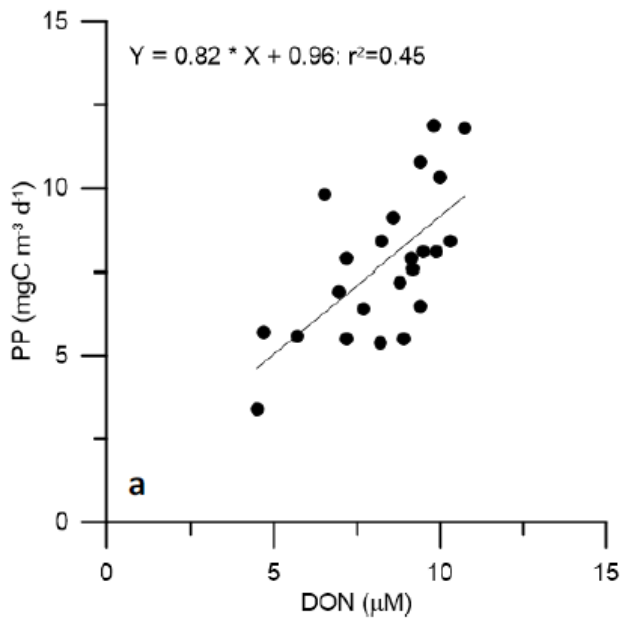


Figure 3:



Supplementary Figure S1: Spatial and vertical distribution of primary production (mgC/m<sup>3</sup>/d) along the transect. The station numbers are given on the upper x-axis.

