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# River plume fronts and their implications for the biological production of the Bay of Bengal, Indian Ocean

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ABSTRACT: Fronts are the physical interface between water masses of distinct hydrographic characteristics and are ubiquitous features of the Bay of Bengal (BoB). They form as a result of receiving high freshwater runoff from many large rivers, but their biological characteristics are mostly unexamined. We determined the distribution of fronts in the BoB during the fall intermonsoon period and examined the physicochemical couplings in the frontal regions and their concomitant effect on biological production. *In situ* sea surface salinity (SSS) gradients were used to delineate the fronts (threshold of 0.01 psu km<sup>-1</sup>), and 2 frontal zones with a cross-frontal SSS difference of 1–3 psu were identified. River discharge played a more significant role than direct precipitation in the frontogenesis of this ecosystem. These narrow 3-dimensional boundaries were characterized by a higher nutrient replenishment than in the contiguous non-front zones, and had a higher phytoplankton production. The highest accumulation of zooplankton biomass in water masses of intermediate salinity (31–33 psu) in the frontal regions resulted from the higher food availability and congregation by hydrodynamic convergences.

KEY WORDS: River plume fronts  $\cdot$  Bay of Bengal  $\cdot$  Chlorophyll  $a \cdot$  Primary production  $\cdot$  Zooplankton

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# **INTRODUCTION**

Fronts, the dynamic borderline between water masses of distinct hydrographic characteristics, are ubiquitous features of oceanic regions (Lentz & Limeburner 1995, Bakun 2006, Belkin et al. 2009). The driving forces behind the genesis of these narrow 3dimensional natural boundaries vary and range from current convergence, coastal upwelling, continental runoff, and differential solar heating to changes in the bathymetry (Franks 1992a, Acha et al. 2015). As a zone where laterally convergent flows induce and intensify the vertical flow, frontal regions experience nutrient replenishment of the surface waters (Owen 1981). This results in enhanced primary production, which in turn gets channeled to higher trophic levels in the pelagic food web (Laubscher et al. 1993, Lohrenz et al. 1999). Thus, the subsequent aggregation of biotic communities in frontal areas delineates them as one of the prominent pelagic foraging hotspots in the oligotrophic tropical oceanic regions (Scales et al. 2014). Comprehensive studies have been conducted on fronts and their ecological significance in the Pacific and the Atlantic Oceans (Lohrenz et al. 1999, Belkin & Cornillon 2003 and reference therein, Albaina & Irigoien 2004), but information on the occurrence, forcing mechanisms, and influence of fronts on biological production is scarce from the northern Indian Ocean. The information on fronts in that region is mostly limited to the thermal fronts of the Arabian Sea in the western half of the northern Indian Ocean (Evans & Brown 1981, Sarma et al. 2015, Vipin et al. 2015).

The Bay of Bengal (BoB) in the eastern half of the northern Indian Ocean was traditionally considered a less productive ocean basin compared to its western counterpart, the Arabian Sea, owing to the weak wind patterns and intense freshwater-influenced vertical stratification (Qasim 1977, Prasanna Kumar et al. 2002). However, in recent years, oceanographic research has indicated enhanced biological productivity in the BoB influenced by physical processes like eddies and cyclones (Madhu et al. 2002, Prasanna Kumar et al. 2004, 2007, Fernandes & Ramaiah 2013, Singh & Ramesh 2015, Singh et al. 2015) (see Table 1 for details). In contrast to the Arabian Sea, the BoB receives heavy runoff  $(1.6 \times 10^{12} \text{ m}^{-3} \text{ yr}^{-1})$ from many large perennial rivers, such as the Ganges, Brahmaputra, Irrawaddy, Godavari, Krishna, and Kaveri, and their tributaries (Subramanian 1993). These large river discharges in the north result in the formation of freshwater plumes which move equatorward against local winds because of the interaction of lighter surface water, heavier saline water, and the coast, and develop a frontal structure with an acrossfront salinity difference of 1 psu (Shetye et al. 1991). The prominent north-south gradient of sea surface salinity (SSS) in the Levitus climatology also supports this view (Fig. 1a). A mixed-layer salt budget investigation indicated that both river discharge and precipitation contribute to the SSS variability and gradient in the BoB (Chaitanya et al. 2015). Furthermore, the strength and direction of the flow of the East Indian Coastal Current (EICC) also plays a crucial role in the advection of the freshwater plume in the

BoB (Akhil et al. 2014, Chaitanya et al. 2014). The dynamics of the EICC are controlled by many forcing mechanisms like local alongshore winds, interior Ekman pumping, remote alongshore winds adjacent to the eastern boundaries of the bay, and remotely forced signals of Kelvin waves propagating from the equator (McCreary et al. 1996). Any variations in these factors influence the EICC and, in turn, generate spatiotemporal variation in the structure of the salinity front in the BoB. Hence, while investigating the salinity fronts and their influence on the biotic community in the BoB, the study of the significance of freshwater discharges, precipitation, and the EICC to frontogenesis gains importance.

There is a paucity of knowledge on the existence of fronts and their implications for the biological production of the BoB. This study therefore aimed to: (1) identify salinity fronts in the BoB; and (2) evaluate their influence on the plankton community. As a pioneering attempt addressing the influence of oceanic fronts on the plankton community of the BoB, the results will be helpful to better understand the processes modulating the biological production of this part of the northern Indian Ocean.

## MATERIALS AND METHODS

# Sampling design

There is less spatial variability in the sea surface temperature (SST) of the BoB than in its SSS, which is often pronounced in a north–south direction (Levitus 1982, Akhil et al. 2014). The SSS of the region was plotted on a monthly scale, based on the climatological data of the North Indian Ocean Atlas (www.nio. org/index/option/com\_nomenu/task/show/tid/2/sid/

Table 1. Previous major reports on the physical processes controlling biotic production in the Bay of Bengal during different sea-
sons. '+' and '-' indicate that the respective controlling factors had a positive or negative influence on the plankton community
respectively

Season	Major controlling factors	Impact	Source
Summer monsoon	Upwelling + Cold-core eddies	+	Muraleedharan et al. (2007)
Summer monsoon	Upwelling + Mini-cold pool	+	Rao et al. (2006a)
Summer monsoon	Warm gyres	_	Muraleedharan et al. (2007)
Summer monsoon	Cold-core eddies	+	Prasanna Kumar et al. (2004)
Inter monsoon	Cold-core eddies	+	Gomes et al. (2000), Prasanna Kumar et al. (2007), Fernandes (2008)
Inter monsoon	Cyclone	+	Madhu et al. (2002), Rao et al. (2006b), Smitha et al. (2006), Maneesha et al. (2011)
Winter monsoon	Upwelling + Cyclone	+	Vinayachandran & Mathew (2003), Singh et al. (2015)



Fig. 1. Sea surface salinity (SSS) in the Bay of Bengal based on (a) the Levitus climatology and (b) climatological data of the North Indian Ocean Atlas on a monthly scale, and (c) monthly variance in SSS

18/id/229). This climatological atlas encompasses data sets of the World Ocean Atlas (Antonov et al. 2010) and information generated by various research organizations of India, and is considered a reliable ocean atlas of this region (Chatterjee et al. 2012). We used the data to choose sampling dates on one cruise during the late summer monsoon to fall intermonsoon period (September–October 2006), when the north–south gradient in salinity was high because of the influence of the freshwater plume (Fig. 1b,c). Additionally, to identify whether the *in situ* salinity distribution of the present study period was representative of the fall intermonsoon salinity distribution in the BoB, the satellite-based SSS data (Aquarius) of the respective months (September and October) were critically analyzed. Because the satellite SSS data are comparatively less readily available than the SST data, according to the accessibility of the Aquarius SSS data of the respective months, a detailed evaluation of data spanning a period of 3 yr from 2012 to 2014 was incorporated into the analysis (https://oceanwatch.pifsc.noaa.gov). The analysis of the monthly river discharges into the BoB was carried out based on the information acquired from Ismail (2011), which was estimated using the Global River Discharge Database (https://nelson.wisc.edu/sage/data-and-models/riverdata/) and data from the Central Water Commission of India (http://cwc.gov.in/). The data were further cross-checked based on information from Papa et al. (2012) and Chaitanya et al.

(2014). The climatological precipitation data were prepared based on the monthly precipitation values from the Tropical Rainfall Measuring Mission (2001–2010; https://trmm.gsfc.nasa.gov/).

Sampling locations (n = 31) were fixed along 5 zonal transects from 11 to  $19^{\circ}$  N, and the stations were distributed at intervals of  $1^{\circ}$  longitude (6–7 stations at a distance of ~110 km), extending from the coast to offshore (Fig. 2a). We identified the frontal zones in the BoB and evaluated their influence on the plankton community. To understand the diurnal changes in distribution, one coastal and one offshore station were monitored along each transect. The sampling was done at 6 h intervals for 24 h. The day and night sampling periods were determined based on the local time of sunrise/sunset.

#### Abiotic components

An SBE Seabird 911 plus CTD (accuracy of conductivity 0.0003 S  $m^{-1}$ , temperature 0.001°C, and pressure 0.015%) was deployed at each station to obtain the temperature and salinity profiles of the

water column. The instrument was operated down to 5 m off the bottom at the shallow coastal stations and down to 1000 m depth at the offshore stations. The salinity values obtained from the CTD were calibrated against an Autosal (Guildline 8400) onboard to minimize the error factor in the salinity data sets. The potential density  $(\sigma_t)$  was computed from the pressure, temperature, and salinity values obtained from the CTD. Water samples were collected using a CTD rosette sampler fitted with pre-cleaned 1.8 l Teflon-coated Go-Flo bottles (General Oceanics) deployed from standard depths down to 150 m (surface, 10, 20, 30, 50, 75, 100, 150 m). The surface water was collected between 0 and 2 m. The pH was determined using a pH meter, whereas dissolved oxygen (DO) was analyzed using Winkler's method (Grasshoff 1983). Nutrients (nitrate, phosphate, and silicate) were analyzed immediately onboard following standard colorimetric techniques (Grasshoff 1983) using a Skalar Segmented Flow Auto Analyzer (Model SA-1050). The precision of the nutrient measurement was ±0.15 µmol N l<sup>-1</sup> for nitrate,  $\pm 0.04 \ \mu mol \ P \ l^{-1}$  for phosphate, and  $\pm 0.05 \ \mu mol$ Si l<sup>-1</sup> for silicate.



Fig. 2. Distribution in the (a) station location, (b) salinity (psu), (c) potential density (kg  $m^{-3}$ ), and (d) temperature (°C) at the surface layer of Bay of Bengal. The frontal zones are enclosed by white lines and also pointed out by arrows in the salinity diagram

## **Biotic components**

Samples for the phytoplankton biomass (chlorophyll a [chl a]) and primary production (PP) estimation were collected from the standard depths down to 120 m (surface, 10, 20, 50, 75, 100, and 120 m) according to the Joint Global Ocean Flux Study (JGOFS) protocols (UNESCO 1994). For chl a, 1 l water samples from each depth were filtered through GF/F filters (pore size 0.7 µm), extracted with 10 ml of 90 % acetone in the dark and analyzed using a UV/Vis, Shimadzu spectrophotometer (Strickland & Parsons 1972). MODIS-Aqua satellite ocean color data were used to get a clear picture of the surface chl a distribution of the study region (https://giovanni.gsfc.nasa. gov/giovanni/). PP was measured at one coastal station and one offshore station in each transect (the 10 diurnal stations). For the estimation of PP, water samples were collected just before sunrise and immediately passed through a 200 µm plankton net to remove large-sized zooplankton. They were then transferred into 300 ml (3 light and 2 dark) polycarbonate bottles for each depth (Nalgene–Germany). One ml of NaH<sup>14</sup>CO<sub>3</sub> (specific activity 5  $\mu$ Ci) was added to all samples. The sample bottles were incubated in situ at the respective sampling depths for 12 h with the help of a mooring system. After the in situ incubation, bottles were retrieved and the water samples were filtered through 47 mm GF/F filters (pore size 0.7 µm) under gentle suction. The filters were exposed to concentrated HCl fumes (11.3 N) to remove the excess inorganic carbon and were subsequently stored in scintillation vials. One day before the analysis, 5 ml of liquid scintillation cocktail-T were added to each vial, and the radioactivity was measured in a scintillation counter (Wallac 1409 DSA Perkin Elmer). Decays per minute values were converted into daily production rates (mg C  $m^{-3} d^{-1}$ ) following the standard methodology described in the JGOFS protocols (UNESCO 1994). The depthwise distribution of chl a and PP was integrated to obtain the phytoplankton biomass and production of the water column following Dyson et al. (1965) as:

Column chl 
$$a/PP =$$
  
[ $(d_1 - d_0)(a_0 + a_1)/2 + (d_2 - d_1)(a_1 + a_2)/2 + ...$ ] (1)

where  $d_0$ ,  $d_1$ ,  $d_2$  are the depths sampled; and  $a_0$ ,  $a_1$ ,  $a_2$  are the chl *a*/PP of the respective depths. Sampling in shallow coastal stations was possible only down to a depth of 75 m. The integrated chl *a* and PP were thus calculated only for the 75 m water column for the spatial comparison. The assimilation number, i.e. the rate of photosynthetic carbon assimilation per weight of chl *a* (ratio of PP to chl *a*), was used as a proxy for phytoplankton growth rate (Eppley 1972).

Mesozooplankton sampling was carried out from 2 discrete depth zones, viz. the mixed layer depth (MLD) and the thermocline (TC). The MLD was determined as the depth where density increases 0.2 kg m<sup>-3</sup> from the surface value (Shetye et al. 1996), and the bottom of the TC was the depth where the temperature reached 15°C. Sampling was carried out by vertical hauling  $(1 \text{ m s}^{-1})$  of the multiple plankton net (Hydrobios), which works based on the principle of the opening and closing of a series of individual plankton nets in succession at the desired depths. The mesh size of the net was 200 µm, and the opening and closing of the nets (mouth area  $0.25 \text{ m}^2$ ) at the prefixed depth zones were controlled by shipboard electronic sensors. The advantage of this net is the negligible rate of contamination among the samples along the depth layers (Weikert & John 1981). Zooplankton samples were then passed through a 200 µm mesh, and the excess water was removed with absorbent paper. The displacement volume method was followed for estimation of the mesozooplankton biomass, and expressed as ml m<sup>-3</sup> (Harris et al. 2000). Different taxa of zooplankton were sorted, enumerated under a stereo-zoom microscope, and their corresponding abundance was calculated based on the volume of water filtered through the net and expressed as ind. m<sup>-3</sup>. The mesozooplankton samples were collected from 2 discrete depth layers, and the consolidated abundance of the zooplankton community from the entire sampled depth was estimated according to the methods of Kusum et al. (2014a) as

$$X_{\text{consolidated}} = \sum_{i=1}^{n} \frac{Z_i X_i}{Z_i}$$
(2)

where  $X_i$  = biomass / abundance of zooplankton at a particular stratum in a sampling location, and  $Z_i$  = depth of the particular stratum in a sampling location.

### **Data analyses**

# Correlation analysis

The CTD-based *in situ* SSS value was correlated with the climatological data of the North Indian Ocean Atlas to assess its representability for the study area. Because the study was conducted during the months of September and October, the climatological data of the mean SSS of these 2 months were used for the analysis. Riverine influxes and precipitation are considered to play a significant role in the variability of SSS. Hence, Pearson's correlation analysis was carried out based on the monthly climatological data of the respective variables to identify the interrelation existing between them and SSS using the statistical software Graphpad prism (www.graphpad.com).

#### Analysis of variance and *t*-test

A 1-way analysis of variance (ANOVA) was carried out using the SSS data sets of both the satellite-based information for 2012 to 2014 and the in situ data of the present study. Bartlett's test for equal variances was used to assess the homogeneity of variances. A D'Agostino and Pearson omnibus normality test was performed before the analysis to check for normality in the data distribution. Based on the results of these statistical tests, either a parametric or non-parametric (Kruskal-Wallis test) ANOVA was performed for the variables with 2-tailed p-values and 95% confidence intervals. A *t*-test was carried out (2-tailed p-values and 95% confidence intervals) between the frontal and non-frontal data of phytoplankton biomass, zooplankton biomass, and abundance to assess the significance in variation. For t-tests, we also selected parametric or nonparametric (Mann-Whitney test) analyses based on the normality test. The ANOVAs and *t*-tests were performed using Graphpad Prism. For all tests, we used a significance value of  $\alpha = 0.05$ .

### Canonical analysis of principal coordinates (CAP)

A constrained CAP was performed (Anderson & Willis 2003) to understand the distinctness of the zooplankton community in the frontal zones from other locations. This analysis was done based on the Bray-Curtis similarity index (Clifford & Stephensen 1975) and applied to log-transformed data of the abundance of zooplankton taxa using PRIMER (Clarke & Warwick 2001).

# Multivariate dispersion (MVDISP) analysis and analysis of similarities

The MVDISP algorithm was used to assess variability in the zooplankton community structure of the frontal and non-frontal locations and to calculate the index of multivariate dispersion (IMD). Analysis of similarity (1-way ANOSIM) was used to describe dissimilarities in the zooplankton communities between the frontal and non-frontal regions. Both analyses were performed using PRIMER (Clarke & Warwick 2001).

# **Bio-Env** analysis

The Bio-Env analysis was carried out using PRIMER to identify the abiotic variables that best explain the assemblage of biotic variables (chl *a* and zooplankton community). This analysis is based on the unconstrained choice of resemblance matrix appropriate to the data type and uses only the rank values of the among-sample resemblances (Clarke et al. 2008).

# **Regression analysis**

Salinity is considered to have a prominent role in structuring various water masses in the BoB, and hence a regression analysis using Microsoft Excel 2016 was carried out between salinity and the abundances of the different zooplankton taxa in order to understand their affinity towards particular water masses.

## RESULTS

# Abiotic variables

The monthly climatological data of the SSS in the BoB exhibited heterogeneity in the spatial and temporal distribution (Fig. 1b). Irrespective of the months, the northern basin was less saline compared to the saltier southern part, and the variance in the SSS was most prominent during August to October (Fig. 1c).

The SSS gradient was used to identify the existence of salinity fronts, and a threshold gradient of 0.01 psu km<sup>-1</sup> was considered for the frontal detection. Two frontal zones were identified in the northern part of the BoB, formed as an interface of highand low-salinity waters (Fig. 2b). Stations (Stns) 1, 2, 10, and 11 were observed inside the first frontal zone, whereas Stns 7, 15, and 16 were in the second frontal zone (Fig. 2b). The SSS gradient across the front varied between 0.01 and 0.033 psu km<sup>-1</sup>. The crossfrontal difference in SSS was found to range between 1 and 3.6 psu (Fig. 2b). In general, the SSS exhibited a pronounced spatial variation, and ranged between 29.2 and 34.4 psu, with lower values in the northern bay compared to the southern part (Fig. 2c). The in situ SSS exhibited a significant positive correlation with that of the climatological data of the North Indian Ocean Atlas (p < 0.001). Except for the slight spatial displacement in their position with the years,

the SSS data acquired through Aquarius for 2012–2014 confirmed the existence of frontal structures in the BoB during the months of September and October (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m597p079\_supp.pdf). In the BoB, during September–October, the high freshwater discharges from the major rivers result in a prominent low-salinity region in the northern bay, followed by an intermediate saline frontal zone and a saltier region towards the south (Fig. S1). The variation among the SSS values of September–October during 2012–2014, and also the *in situ* data of this study, did not show any significant variation (1-way ANOVA,  $F_{3.243} = 2.053$ , p = 0.091).

Sea surface density exhibited a pronounced spatial variation, ranging between 17.8 and 21.6 kg  $m^{-3}$ , and was low in most of the sampling locations in the

northern bay compared to the southern part (Fig. 2c). The sampling locations in the frontal regions identified through the salinity distribution had an intermediate density between the distinct high- and low-density environments, thus delineating the role of salinity in governing the density gradient across the front. The cross-frontal difference in sea surface density varied between 0.8 and 2.8 kg m<sup>-3</sup>.

The *in situ* SST did not exhibit prominent spatial variation ( $28.4-29.8^{\circ}$ C). Unlike the SSS distribution, the gradient in the SST was quite low (< $0.01^{\circ}$ C km<sup>-1</sup>), and the cross-frontal difference was only 0.02 to 0.3°C (Fig. 2d).

The vertical profiles of salinity and potential density exhibited a gradual increase with depth along all transects (Fig. 3a,b). However, the variation was more prominent in the northern than the southern



Fig. 3. Vertical distribution of (a) salinity (psu), (b) potential density (kg m<sup>-3</sup>), and (c) temperature (°C) in the upper 150 m of the study area. Station locations are indicated by the arrows. The frontal regions are indicated by red arrows

transects. In both frontal zones, an inclined interface region of distinct salinity characteristics was evident in the upper 50 m (Fig. 3a). In contrast to the salinity and density distribution, the vertical profile of temperature exhibited a gradual decrease with depth (Fig. 3c).

The monthly climatological data of direct precipitation in the BoB in 2001–2010 exhibited a pronounced spatio-temporal variation, and experienced higher rainfall (>200 mm mo<sup>-1</sup>) from May to October influenced by the southwest monsoon (Fig. 4a). The Pearson correlation analysis of the monthly climatological data (precipitation and SSS) suggested a negative relation, although the correlation coefficient was very low (r = 0.06) and insignificant (p = 0.852).

Similarly, the monthly climatological data of the river discharges into the BoB exhibited a prominent temporal variation, with higher values (>40 000 m<sup>3</sup> s<sup>-1</sup>) from July to October (Fig. 4b). The Pearson correlation analysis performed to identify the interrelation of SSS with river discharge revealed a negative relation, and the correlation coefficient, though insignificant (p = 0.398), was higher (r = 0.27) than that observed with precipitation and salinity.

The pH of surface waters varied between 8.15 and 8.38, with a mean of  $8.33 \pm 0.05$  (SD). In general, the pH gradually decreased with depth along all latitudinal transects. However, along 19°, 17°, and 15° N, we observed up-sloping of the pH isolines along the frontal locations (Fig. 5a). The surface DO ranged between 3.8 and 4.9 ml l<sup>-1</sup>, with a mean of 4.4 ± 0.2 ml l<sup>-1</sup>. Along the frontal (4.4 ± 0.3 ml l<sup>-1</sup>) and non-frontal regions (4.4 ± 0.1 ml l<sup>-1</sup>), the surface DO val-

ues were mostly the same. Although little spatial variation in the surface DO was evident, a sharp gradient was observed in the vertical profiles, which were more prominent towards the north (Fig. 5b). Similar to the pH distribution, an uplifting of the isolines of DO was observed along the frontal zones of 15°, 17°, and 19° N (Fig. 5b).

The MLD varied from 7 to 47 m. A clear variation in the MLD was observed between the locations in the frontal and the non-frontal regions (Fig. S2a). The average MLD was relatively shallower in the frontal zones (13 ± 8 m) than the non-frontal regions (22 ± 12 m). The bottom of the thermocline (BT) varied between 133 and 188 m depth (Fig. S2b). Similar to the MLD, the depth of the BT was also shallower in the frontal zones (161 ± 19 m) compared to the nonfrontal regions (167 ± 16 m).

# Nutrients

In general, nitrate, phosphate, and silicate values were relatively lower in the surface waters than in the deeper waters (Fig. 6). The surface nitrate ranged between 0.4 and 3.68  $\mu$ M, with an average of 2.01 ± 0.88  $\mu$ M, whereas phosphate varied between 0.05 and 0.92  $\mu$ M (mean 0.5 ± 0.22  $\mu$ M). The surface silicate value ranged between 2.42 and 10.71  $\mu$ M (mean 5.7 ± 2.04  $\mu$ M) (Fig. 6c). Inclined isolines of nutrients (nitrate, phosphate, and silicate) were observed along the sampling locations at the frontal zones, i.e. along 19° N (Stns 1, 2), 17° N (Stns 7, 10, 11), and 15° N (Stns 15 and 16).



Fig. 4. Monthly climatological data of (a) direct precipitation and (b) river discharge in to the Bay of Bengal, and (c) annual discharge of the major rivers into the Bay of Bengal (excluding the Irrawadi River)



Fig. 5. Vertical distribution of (a) pH and (b) dissolved oxygen (ml  $l^{-1}$ ) in the upper 150 m of the study area. Station locations are indicated by the arrows. The frontal regions are indicated by red arrows

# **Biotic components**

# Chl a

The in situ surface chl a was observed to vary between 0.07 and 0.51 mg  $m^{-3}$  during the study, with a maximum concentration at Stn 2 located in the frontal zone at 19°N (Fig. 7c). Most of the locations in the frontal zones exhibited relatively high surface chl a (mean 0.3  $\pm$  0.1 mg m<sup>-3</sup>, n = 7) compared to the nonfrontal locations (0.2  $\pm$  0.1 mg m<sup>-3</sup>, n = 24) (Fig. 7a). The difference in surface chl a concentration between the frontal and non-frontal regions was significant (Mann-Whitney test, p = 0.025). Satellite observations indicated that surface chl *a* was relatively high in the frontal zones along 15°, 17°, and 19° N latitude, and quite low in the non-frontal regions at 11° and 13° N latitudes (Fig. S3). Considering the vertical profile of chl a, the concentration was relatively higher in the upper 50 m compared to the deeper waters in both the frontal and non-frontal locations with a maximum at 10 m depth (Fig. 7a). Although the average chl a concentration at each depth was higher in the frontal locations than in the non-frontal regions, the disparity in pigment concentration between these 2 regions

was more prominent in the upper water column (up to 20 m) than in the deeper water (>20–120 m). Integrated column chl *a* (75 m) varied between 4.4 and 28.9 mg m<sup>-2</sup>, with a maximum value in the frontal location at Stn 2 (Fig. 7d). Although average column chl *a* concentration appeared higher in the frontal locations ( $17.9 \pm 6.7 \text{ mg m}^{-2}$ , n = 7) than in the non-frontal locations ( $13.9 \pm 6.8 \text{ mg m}^{-2}$ , n = 24), the difference was insignificant (Mann-Whitney test: p = 0.163).

### Primary production

PP was determined only at 1 coastal and 1 offshore station along each transect. Surface production was found to vary between 0.07 and 10.25 mg C m<sup>-3</sup> d<sup>-1</sup>, with a mean of  $3.06 \pm 2.94$  mg C m<sup>-3</sup> d<sup>-1</sup> (Fig. 7e). PP was monitored at 2 sampling locations in the frontal zones and was remarkably higher (7.14 ± 4.4 mg C m<sup>-3</sup> d<sup>-1</sup>, n = 2) compared to the non-frontal region (2 ± 1.5 mg C m<sup>-3</sup> d<sup>-1</sup>, n = 8). The vertical profile of PP exhibited a sharp decline below 10 m, and average PP was highest at the surface in frontal locations and at 10 m depth in non-frontal locations (Fig. 7b). Although PP at each depth was higher in frontal loca-



Fig. 6. Vertical distribution of (a) nitrate (μM), (b) phosphate (μM), and (c) silicate (μM) in the upper 150 m of the study area. The station locations are indicated by the arrows. The frontal regions are indicated by red arrows

tions compared to non-frontal regions, the variation between them was more prominent in the upper 10 m (Fig. 7b). The integrated column PP (0–75 m) varied between 19 and 211 mg C m<sup>-2</sup> d<sup>-1</sup> during the study period (Fig. 7f). The column PP in the frontal locations (195  $\pm$  23 mg C m<sup>-2</sup> d<sup>-1</sup>, n = 2) was characterized by higher values (1.7 times) compared to the non-frontal locations (114  $\pm$  83 mg C m<sup>-2</sup> d<sup>-1</sup>, n = 8).

## Specific growth rate

The specific growth rate of the phytoplankton was measured at the stations (n = 10) where both PP and chl *a* were estimated, and varied between 0.5 and 30.1 (Fig. S4). It was higher in the frontal locations

 $(20.7 \pm 13.4 \text{ mg C} (\text{mg chl } a)^{-1} \text{ d}^{-1}, \text{ n} = 2)$  compared to the non-frontal locations  $(9.1 \pm 5.8 \text{ mg C} (\text{mg chl } a^{-1}) \text{ d}^{-1}, \text{ n} = 8)$ .

### Mesozooplankton biomass and abundance

Integrated mesozooplankton biomass of the upper 2 layers (MLD and TC) varied between 0.03 and 0.53 ml m<sup>-3</sup>, with an average of 0.18  $\pm$  0.11 ml m<sup>-3</sup> (n = 31, Fig. 7g). The biomass was evidently higher in the frontal zones (0.3  $\pm$  0.12 ml m<sup>-3</sup>, n = 7) compared to the non-frontal regions (0.1  $\pm$  0.1 ml m<sup>-3</sup>, n = 24). The variation in the biomass between the fronts and the non-frontal locations was significant (Mann-Whitney test: p = 0.002) (Table S1 in the Supplement).



Fig. 7. Vertical profile of the mean values of (a) chlorophyll (chl)  $a (mg m^{-3})$  and (b) primary production (PP; mg C m<sup>-3</sup> d<sup>-1</sup>) in the frontal and non-frontal region, and distribution of (c) surface chl  $a (mg m^{-3})$ , (d) integrated column chl  $a (mg m^{-2})$ , (e) surface PP (mg C m<sup>-3</sup> d<sup>-1</sup>), (f) integrated column PP (mg C m<sup>-2</sup> d<sup>-1</sup>), (g) integrated mesozooplankton biomass (ml m<sup>-3</sup>), and (h) integrated mesozooplankton abundance (ind. m<sup>-3</sup>) of the mixed layer depth and thermocline in the Bay of Bengal. The frontal regions are indicated by red dots

For abundance, the minimum value was observed at Stn 27 (50 ind. m<sup>-3</sup>) in the non-frontal region, and the maximum at Stn 16 (1143 ind. m<sup>-3</sup>) in the frontal zone (Fig. 7h). In general, the abundance was higher in the frontal zones (506 ± 305 ind. m<sup>-3</sup>, n = 7) compared to the non-frontal regions (244 ± 171 ind. m<sup>-3</sup>, n = 24), and this variation was significant (Mann-Whitney test: p = 0.011).

## Mesozooplankton composition

In total, 24 zooplankton taxa were observed, among which Copepoda dominated at all sampling locations, contributing 58 to 97% of the total zooplankton population (Table 2). Chaetognatha, ostracods, euphausiids, and Copelata were the other abundant taxa compirising >1% of the total zooplankton population. In the frontal zone, of the 22 groups of zooplankton taxa observed in total, copepods contributed 92.5% of the total population (Table 2). Among the non-copepod taxa, Chaetognatha formed the only group comprising >1% of the total population. In the non-frontal regions, 24 zooplankton taxa were observed in total. Although copepods also dominated in the non-frontal region, their contribution to the total population (86.8%) was comparatively lower than in the frontal zone. The other abundant zooplankton taxa (>1%) in the non-frontal regions were Chaetognatha, Ostracoda, euphausiids, and Copelata. In the frontal zones, the abundance of copepods (468  $\pm$  318 ind. m<sup>-3</sup>, n = 7) was 2.2 times higher than in the non-frontal regions  $(212 \pm 147 \text{ ind.})$  $m^{-3}$ , n = 24), and this difference was significant (p = 0.005) (Table 2). Except ostracods, foraminiferans, gastropod larvae, and stomatopods, all other zoo-

Table 2. Mean  $\pm$  SD abundance (ind. m<sup>-3</sup>; integrated value for mixed layer depth and thermocline) of zooplankton taxa in the frontal (n = 7) and non-frontal zones (n = 24) of the Bay of Bengal. The p-values indicate the results of a *t*-test on the abundance of zooplankton taxa between the frontal and non-frontal locations. Asterisks indicate significant values ( $\alpha = 0.05$ )

Fronts	р	Fronts	Non-fronts	Front: non-front ratio
Copepoda	0.0049*	$468 \pm 318$	$212 \pm 147$	2.21
Foraminifera	0.5	$0.75 \pm 1.3$	$1.72 \pm 3.7$	0.44
Medusa	0.152	$1.03 \pm 1.9$	$0.37 \pm 0.6$	2.78
Siphonophora	0.002*	$2.2 \pm 1.2$	$0.86 \pm 0.8$	2.56
Anthozoa		0	< 0.01	0
Ctenophora		0	$0.01\pm0.02$	0
Polychaete larvae	< 0.001*	$1.7 \pm 1.1$	$0.51 \pm 0.5$	3.33
Pteropoda	< 0.001*	$0.9 \pm 0.6$	$0.21 \pm 0.2$	4.29
Heteropoda	0.3184	$0.15 \pm 0.2$	$0.06 \pm 0.08$	2.5
Gastropod larvae	0.5774	$0.34 \pm 0.4$	$0.53 \pm 0.9$	0.64
Cephalopoda	0.024*	$0.1 \pm 0.1$	$0.03 \pm 0.05$	3.33
Ostracoda	0.555	$2 \pm 1.7$	$11 \pm 39$	0.18
Amphipoda	0.093	$0.87 \pm 0.5$	$0.64 \pm 1.1$	1.36
Euphausiids	0.0076*	$4.14 \pm 2.6$	$2.79 \pm 8.1$	1.48
Decapod larvae	0.0316*	$2.5 \pm 1.6$	$1.13 \pm 1.6$	2.21
Stomatopoda	0.7064	$0.01\pm0.02$	$0.01 \pm 0.02$	1
Chaetognatha	0.0355*	$13.3 \pm 6.6$	$7.29 \pm 4.5$	1.82
Copelata	0.7156	$3.93 \pm 5.2$	$3.28 \pm 3.8$	1.2
Pyrosoma		0	$0.34 \pm 1.5$	0
Salpa	0.887	$0.35 \pm 0.4$	$0.32 \pm 0.5$	1.09
Doliolida	0.011*	$1.15 \pm 1.5$	$0.25 \pm 0.4$	4.6
Fish eggs	0.533	$0.13 \pm 0.1$	$0.34 \pm 0.9$	0.38
Fish larvae	0.002*	$0.5 \pm 0.3$	$0.15 \pm 0.2$	3.33
Mysida	0.031*	$0.71 \pm 1.4$	$0.05 \pm 0.1$	14.2
Amphioxus	0.007*	$1.14 \pm 1.2$	$0.33 \pm 0.4$	3.45

plankton taxa which were observed in both regions exhibited relatively higher abundance in the frontal zones compared to the non-frontal regions (Table 2).

# Diurnal variability

We observed that in the diurnal locations of both frontal zones (Stn 1 and Stn 7 in the first and the second frontal zones, respectively), the biomass was relatively higher during the day compared to night, whereas in the non-frontal locations (8 stations) it was higher during the night (Fig. 8). Zooplankton abundance had a similar pattern of distribution in the frontal and non-frontal regions (Fig. 8). Among the zooplankton taxa, copepods, siphonophores, ostracods, amphipods, and pteropods exhibited higher daytime abundance in the frontal region, whereas in the non-frontal region, they exhibited an opposite trend in their distribution (Fig. 8). Chaetognatha, Copelata, salps, and Doliolida had a higher abundance at night in both the frontal and non-frontal regions, with a relatively higher night:day ratio in the frontal region (Fig. 8).

#### **Data analyses**

Sampling locations of the frontal and nonfrontal regions exhibited a difference in their position along the CAP axis based on the abundance of zooplankton taxa (Fig. 9). The squared canonical correlation of the axis ( $\delta^2$ ) was 0.57. The variability observed in the zooplankton community structure during the study was further investigated using the MVDISP algorithm. The variability was higher at the sampling locations in the non-frontal region (dispersion factor value = 1.024), compared to the locations in the frontal zone (dispersion factor value = 0.678). However, the IMDs exhibited a negative value (-0.347) in the pairwise comparisons among frontal and non-frontal locations, indicating that in the case of the zooplankton community structure, similarities in station locations within each group (frontal and non-frontal) were greater than the similarities present between these 2 groups. In the 1-way ANOSIM, the zooplankton community in the frontal zone was significantly distinguishable from the com-



Fig. 8. Diurnal ratio (night:day) in the abundance of the zooplankton taxa in the (a) frontal and (b) non-frontal regions. Only the taxa which were present in both day and night periods in both frontal and non-frontal regions are plotted



Fig. 9. Canonical analysis of principal coordinates (CAP) based on the abundance of different zooplankton taxa

munity in the non-frontal region (global R = 0.178, p = 0.047).

A quadratic regression analysis was performed to assess the preferred water mass of the various zooplankton taxa. The resultant binomial curvilinear regression line was dome shaped for most of the zooplankton taxa (Fig. 10).

The result of the Bio-Env analysis indicated that the combination of nitrate, DO, and potential density were the most important factors that best explained the variability in the abundance and distribution of the biotic variables (Table 3).



Fig. 10. Result of the quadratic regression analysis between salinity and abundance of various zooplankton taxa. Only taxa which were present in >50% of the sampling locations and contributed >0.01% of the total zooplankton population were selected for the analysis (SIP: Siphonophora, MED: Medusa, CHA: Chaetognatha, DEC: Decapod larvae, COP: Copepoda, AMP: Amphipoda, EUP: Euphausiids, MYS: Mysida, OST: Ostracoda, FOR: Foraminifera, SAL: Salpa, DOL: Doliolida, PTE: Pteropoda, HTE: Heteropoda, GAS: Gastropod larvae, POL: Polychaete larvae, FE: Fish eggs, FL: Fish larvae, COPL: Copelata, AMPH: Amphioxus). Significant correlation coefficient (r) values are marked with an asterisk

Table 3. Results of the Bio-Env analysis indicating the factors that best explained the variability in the abundance and distribution of biotic variables in the Bay of Bengal. DO: dissolved oxygen

No. variables	Correlation	Factors
3	0.25	DO (ml $l^{-1}$ ), nitrate ( $\mu$ M), potential density (kg m <sup>-3</sup> )
3	0.24	DO (ml l <sup>-1</sup> ), nitrate (µM), salinity
2	0.24	DO (ml l <sup>-1</sup> ), nitrate (µM)

# DISCUSSION

The hydrodynamics associated with mesoscale physical processes provide the auxilliary energy for augmenting PP, leading to rich resources for superior growth conditions of apex trophic levels in the pelagic food web (Bakun 2006). Marine fronts, regions where auxiliary energy generated by hydrodynamic convergences concentrates in disproportionate quantities in small areas, have gained significance in ecological process studies in the global ocean (Acha et al. 2015). Two river plume fronts identified through the SSS gradient were observed in the northern BoB (Fig. 2). These frontal zones were found at the interface of 2 distinct salinity water masses with a sharp horizontal gradient (0.01 and 0.033 psu km<sup>-1</sup>). Considering the 6 types of fronts of large marine ecosystems, the inclusion of BoB as a river plume front is significant (Tables 1 & 5 in Belkin et al. 2009). The cross-frontal difference of 1-3.6 psu in SSS is in accordance with an earlier record in the northern BoB (Shetye et al. 1991). Although the cross-frontal difference in SSS can be as large as 2-3 psu, the typical difference in the large frontal system is usually observed to be between 0.3 and 1.0 psu (Belkin et al. 2009), and thus the evident cross-frontal difference in the BoB clearly delineates their status as salinity fronts. The sea surface density, displaying sharp gradients in the frontal zones in agreement with the SSS, indicates the role of salinity in the frontogenesis in the BoB.

The vertical profile of salinity and water density in the upper 50 m established the frontal zone as a region separating water masses of different hydrographic characteristics. The vertical profile of pH and DO also affirmed the existence of the narrow 3-dimensional frontal zones in the study region (Fig. 6). However, the low variation in SST ( $28.4-29.8^{\circ}$ C) and low SST gradient (< $0.01^{\circ}$ C km<sup>-1</sup>) in comparison to the SST gradient observed in the frontal region of the Arabian Sea ( $0.04-0.08^{\circ}$ C km<sup>-1</sup>) (Vipin et al. 2015), the western counterpart of BoB, point towards the weak influence of temperature in the frontogenetic process.

The enormous freshwater input from the major perennial rivers (Ganges, Brahmaputra, Irrawaddy, and Mahanadi), contributing ~75% of the total river runoff to the head of the BoB (frontal zone 1), and the Godavari to the central BoB (frontal zone 2), contributed to diluting the salinity of the bay, resulting in a

sharp horizontal gradient in salinity (Chaitanya et al. 2014). The plume of low-salinity coastal waters extending offshore led to isopycnal mixing with highsalinity offshore water across the boundary of the interface and resulted into distinct frontal zones in the northern BoB. The influence of freshwater plumes in the frontogenetic processes along the tropical Atlantic and Pacific Oceans by major rivers like the Mississippi, Amazon, and Yangtze (Tian et al. 1993, Lentz & Limeburner 1995, Lohrenz et al. 1999), substantiates observations about the role of salinity in the genesis of oceanic fronts. The negative interrelation between the monthly climatological data of river discharge and SSS is expected because of the prominent influence of fresh water in lowering salinity. However, the insignificant correlation coefficient between river discharge and SSS might be because of the lag in the river influx and corresponding decrease in salinity (Fig. 4).

Both river discharge and precipitation play a role in the salinity distribution of the BoB (Akhil et al. 2014, Chaitanya et al. 2015), but the expected negative interrelation between the SSS and precipitation was not very strong (r = -0.06, p = 0.852). The lag between the peak in precipitation and the consequent drop in SSS can be attributed to this weak negative relation. The disparity between the influence of river discharge and the direct precipitation in the frontogenesis of the BoB happens because the locations of river discharges do not change temporally, and the continuous freshwater influx during the monsoon contributes to the maintenance of the frontal structure. In contrast, the influence of precipitation on the spatial variation of salinity depends on the duration and spatial cover of precipitation, with changes happening only for a short period producing only a local effect on the lowering of SSS. Hence, compared to the river influxes, direct precipitation was less significant in the frontogenesis of BoB.

Although the river plume fronts were evident in the BoB during September and October, it was a prerequisite to identify how the scenario resembles the general pattern of freshwater plumes and salinity distribution in this region. The significant positive correlation (p < 0.001) between the *in situ* and the monthly atlas data validates the present SSS as a representative of salinity distribution for this period in the BoB. The insignificant variation in the SSS retrieved from Aquarius (2012 to 2014) and the present data (p =0.091) in the BoB further supported the present SSS as a typical surface salinity distribution for this period. The existence of low-salinity water in the vicinity of the major rivers in the northern part, the small patch of the low-salinty tongue along the Indian coast between 15° and 19° N, and the intermediate-salinity water with a higher gradient in SSS during 2012 to 2014 indicated the general nature of the river plume fronts in the BoB. However, there was little temporal variability in the spatial structure of the SSS (Fig. S1).

Of the multiple factors governing the spatial distribution of SSS from the vicinity of the river mouth to the offshore region, the influence of coastal currents, wind patterns, and the amount of river discharges are the primary ones (Lentz & Limeburner 1995, Grimes & Kingsford 1996). In the western BoB, the EICC flows northward from February to September with a strong peak in March-April. Interior Ekman pumping, remote alongshore wind, and equatorial forcing all contribute to the March-April peak, whereas the local alongshore wind forms the only primary driving force in the remaining course of the northward flow (McCreary et al. 1996). The southward flow of the EICC during October to January is mostly governed by the local alongshore wind and interior Ekman pumping. The propagation of the freshwater plume along the western BoB is consistent with alongshore advection of the EICC (Chaitanya et al. 2014). Hence, depending on the strength of the local and remote alongshore winds and Ekman pumping, the dynamics of the EICC influence the spatial distribution of the freshwater plume as evidenced in the Aquarius dataset. The annual variability in freshwater discharge from the major rivers is also evident in the BoB (Gates et al. 2000). All of these factors contribute to the spatial variation in salinity resulting in the spatial displacement of the intermediate saline frontal zones documented. The climatological monthly SSS of the BoB helped to understand the persistence of the frontal structures along a temporal scale. Although the north-south gradient in SSS was observed every month, the variance was more prominent during August-October (Fig. 1) when the freshwater influx from the major rivers is high (Jian et al. 2009). Hence, it can be postulated that, although frontogenesis can happen at a smaller scale throughout the year, it becomes obvious during August–October when freshwater discharges are high.

Fronts are designated as vertically inclined interfaces between water masses of distinct hydrographic properties where the intense mixing of nutrient-rich subsurface waters forms a conducive environment supporting high biotic production (Lohrenz et al. 1999). The presence of inclined interfaces in the vertical profiles of nutrients (nitrate, phosphate, and silicate) in the frontal zones (Fig. 6) confirms that fronts are important zones of nutrient pumping and replenishment in the surface waters (Franks & Chen 1996). Hence, a comprehensive understanding of the implications of this dynamic frontal system on the biotic community gains relevance (Corredor et al. 2003, Powell & Ohman 2015).

The observed high chl a and enhanced PP (both surface and column) in the frontal zones compared to the non-frontal locations validate the frontal zone as a region promoting higher growth and proliferation of the phytoplankton community in the BoB. Earlier observations of higher chl a in the Mississippi River plume front by Lohrenz et al. (1999) also support the productive nature of frontal regions. Nutrient replenishment of surface waters occurring in concurrence with isopycnal mixing during frontogenesis favors higher primary production. The mixing between 2 adjacent water masses of discrete hydrographic properties provides the optimum conditions (nutrients, warmth) for increased preponderances of the phytoplankton community that neither water masses might contain alone (Quartly & Srokosz 2003). Hence, fronts are best defined as 'typically the site of enhanced phytoplankton biomass' (Franks 1992a, p 121). However, riverine nutrients may have a linear relationship to biotic productivity from coast to offshore (Singh & Ramesh 2011). Hence it was important to separate the role of fronts from the direct influence of nutrients of the riverine inputs. We observed higher productivity in frontal zones of intermediate salinity than in lowand high-salinity regions. This productivity pattern supports the influence of fronts on the phytoplankton community.

Zooplankton biomass and abundance were also higher in the frontal zones, and the significant variation in biomass (p = 0.002) and abundance (p = 0.011) among 2 groups (front and non-front) clearly indicates the positive influence of fronts on the zooplankton biomass and abundance. This is in contrast to the observations of Jasmine et al. (2009) where the microbial loop regulated zooplankton abundance and showed less variation among frontal and other locations during austral summer in the Southern Ocean region. The discrete existence of frontal locations in the CAP plots (based on zooplankton abundance) affirms the distinctness of frontal regions in the BoB. Higher zooplankton abundance in the frontal zones could be the outcome of either new recruits of organisms, a consequence of differential growth and mortality, or aggregation due to physical forces. Although zooplankton mortality or growth rate was not estimated, food availability in terms of higher phytoplankton biomass in the frontal regions might have supported the zooplankton community aggregated by hydrodynamic convergences. The relatively high zooplankton abundance (2.1 times) compared to that of phytoplankton biomass (1.5 times) in the frontal regions substantiates the influence of food availability on the congregated zooplankton. Higher biomass and abundance of the zooplankton community in the Mississippi River plume front in the Atlantic Ocean (Grimes & Finucane 1991) further validates the positive influence of fronts on the zooplankton community. The higher abundance of zooplankton in the frontal region helped to elucidate the vertical profile of chl a and PP. Surface zooplankton (epiplankton) has been observed to display subsurface maxima in its vertical distribution (Longhurst 1976, Rezai et al. 2011). This subsurface inhabitance and subsequent utilization of the phytoplankton resulted in less variation in chl *a* and PP in the subsurface water column compared to surface waters (0-10 m). Hence, it can be anticipated that frontal zones play a crucial role in the energy transfer in the BoB.

Copepods exhibited a markedly higher abundance and an increased contribution to the total zooplankton population in the frontal zone (Table 2). Because of their unique proficiency to remotely detect prey through hydromechanical and chemical cues along with their feeding-current feeding mode, copepods might have out-competed the other zooplankton taxa in the utilization of the food-rich environment of frontal regions (Mauchline 1998, Kiørboe 2011). Further, their smaller size, diverse feeding guilds, and short generation time makes them the most suitable to efficiently use resources of productive areas, like frontal zones or cold core eddy regions (Lopes et al. 2016). Moreover, the dome-shaped curvilinear binomial regression line obtained based on the interrelation of their abundance with salinity indicates their affinity towards intermediate-salinity frontal water masses. Although there can be species-specific variation in food preferences and tolerance towards the physical environment, our results indicate the overall

positive influence of fronts on the copepod community. Chaetognatha, a major carnivorous zooplankton taxon in both the eastern and western part of the northern Indian Ocean (Kusum et al. 2011, 2014 a,b, Nair et al. 2015), formed the second most abundant taxon in the frontal zones. The vital role of copepods as a major prey contributing to the higher abundance of chaetognath populations has been recorded from various parts of the global ocean (Stuart & Verheye 1991, Kehayias & Ntakou 2008). Hence, the increased abundance of copepods (2.3 times) in the frontal regions might have helped to sustain the higher abundance of chaetognaths (2 times).

Besides chaetognaths, the higher abundance of most of the other predominant taxa (decapod larvae, euphausiids) points towards their aggregation in the food-rich environment of frontal zones compared to non-frontal locations. The dome-shaped curvilinear binomial regression lines observed for most of the zooplankton taxa clearly support their aggregation in the intermediate-salinity frontal water mass. Reports on physical aggregations of zooplankton by surface currents contributing to higher abundances in many frontal regions support our observations (Franks 1992b, Hetland et al. 2002). However, taxa like foraminiferans, gastropods, and stomatopods had lower abundances in the frontal zone (Table 2). The foodrich environment of the frontal region might be favorable for a majority of zooplankton taxa, but the physiological challenges imposed by thermal or haline stresses characteristic of these regions might limit the abundance of some organisms (Olson 2002).

The diurnal distribution of the zooplankton community exhibited a contrasting trend in frontal and non-frontal locations. Mesozooplankton abundance is higher in surface waters at night in concurrence with diel vertical migration (Lampert 1989, Doney & Steinberg 2013), which was also evident in the present study. However, it was higher during the day in the frontal zone. In aquatic ecosystems, changes in vertical distribution along diel scales provide zooplankton with many ecological benefits, among which the metabolic advantages of feeding in warm food-rich surface waters at night and the protection from light-dependent mortality imposed by visually oriented predators, are considered the most beneficial (Lampert 1989). The contrasting trend observed in frontal regions can be the result of a strategy of optimum exploitation of food resources by the zooplankton community. In the barren tropical oceans, frontal regions are often a 'natural oasis' with a bountiful supply of food resources for the zooplankton community. The food-rich environment in surface

waters of frontal regions might have prevented the zooplankton community from migrating down to deeper waters where food resources are comparatively poor. Moreover, the relatively higher night:day ratio of the abundance of chaetognaths in the frontal regions also reinforced the higher daytime abundance of the zooplankton community in frontal zones. Being voracious carnivores, chaetognaths impose a significant effect on the abundance and distribution of the zooplankton community (Froneman & Pakhomov 1998, Pakhomov et al. 1999). Their higher nighttime abundance and increased predatory activity on the zooplankton community might have resulted in the observed disparity in the diel distribution pattern in frontal zones.

The MVDISP algorithm demonstrated variability in the zooplankton community structure of frontal zones and other locations. The higher homogeneity in zooplankton community structure in fronts resulted in a lower dispersion value compared to other locations. Frontal zones are often considered productive regions characterized by sharp gradients in environmental variables (Sournia 1994, Belkin et al. 2009). Thus, the abundance of zooplankton taxa, which were physiologically adapted to the dynamic environment of fronts and also efficient at harvesting the food resources of this productive region, contributed to reduced variability in the zooplankton community structure. This, in turn, resulted in greater dissimilarities in community structure between the frontal and non-frontal regions compared to the similarities they share (as indicated by the negative IMD value).

The dissimilar characteristics of the zooplankton community evidenced through the MVDISP algorithm in frontal zones and other sampling locations were further reflected in the 1-way ANOSIM. The significantly distinguishable community between the frontal and the non-frontal zones (Global R = 0.178, p =0.047) might be the result of variation in the auxiliary energy required for enhanced biotic production.

BIOENV analysis identified potential density, nitrate, and DO as the most prominent factors that best explained variability in the abundance and distribution of the phytoplankton and zooplankton communities. Fronts are mostly generated at the interface of water masses with different potential densities (Franks 1992a, Bakun 2006), where intense mixing and enrichment of nutrients aid in supporting higher plankton production (Lohrenz et al. 1999). Thus, the combination of these factors identified by BIOENV as governing higher production in frontal zones of the BoB is validated.

The higher abundance of fish larvae in the frontal zone compared to other regions might have been due to spatial displacement resulting from hydrodynamic convergence in the frontal zone (Grimes & Finucane 1991). In addition, fish larvae aggregate in productive oceanic regions characterized by higher prey density (Alemany et al. 2014). The higher food availability in terms of both phytoplankton and zooplankton (copepods) also contributed to their higher abundance in the frontal zone. Copepods are often considered preferred prey and the prime constituent of the diet of many pelagic fishes and fish larvae (Pepin & Penney 2000, Heath & Lough 2007). Hence, the higher abundance of copepods, contributing about 92.5% of the total zooplankton population in the frontal zones, played a significant role in making this region a better breeding and nursing ground, leading to increased larval abundance. Fishes often prefer to spawn in regions where better feeding opportunities facilitate enhanced growth and survival rates of their highly vulnerable early life stages (Swalethorp et al. 2015). The aggregation of fish larvae in the frontal zones of tropical river plumes compared to contiguous water masses in response to the availability of their preferred prey is well documented (Grimes & Finucane 1991, Govoni 1993). The incident increased abundance of higher trophic levels (herbivorous and carnivorous zooplankton and fish larvae) in frontal regions documented in this study identifies them as zones persisting for a considerable period of time and allowing for efficient transfer of energy to successive trophic levels (Olson & Backus 1985).

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