

Ecology and trophic preference of picoplankton and nanoplankton in the Gulf of Mannar and the Palk Bay, southeast coast of India

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Abstract

The Gulf of Mannar (GoM) and the Palk Bay (PB) are two least studied marine environments located between India and Sri Lanka. The environmental and smaller plankton (0.2-20 μm) data from 30 locations in the GoM and PB during the northeast monsoon (November- February) are presented in this paper. Coastal currents during the study period was from the east to west and as a result, the PB had Bay of Bengal (BoB) waters, which was low saline (av. 28.98 ± 1.34) as compared to the GoM (av. 31.96 ± 0.58). The BoB waters caused significantly higher turbidity in the PB (av. 7.84 ± 13.59 NTU) as compared to the GoM (av. 1.76 ± 1.38 NTU). Multivariate analyses of hydrographical parameters demarcated two separate clusters in the study area clearly segregating the GoM and PB. This was mainly due to the physical barriers (Rameswaram Island, Ramsethu and Mannar Island) that inhibit the mixing of waters between the GoM and PB. The fluorescence microscopy and flow cytometry data showed high abundance of picoeukaryotes, heterotrophic bacteria and autotrophic nanoplankton in the GoM whereas, *Synechococcus* and heterotrophic nanoplankton were higher in the PB. The picoplankton and nanoplankton carbon biomass was higher in the GoM (av. 62.2 mgC m^{-3}) as compared to the PB (av. 47.6 mgC m^{-3}). The carbon biomass in the GoM and PB was mainly contributed by nanoplankton (>70%) signifying their trophic preference in the study area. The carbon contribution of different plankton components in the GoM was autotrophic nanoplankton > heterotrophic bacteria > heterotrophic nanoplankton > *Synechococcus* > picoeukaryotes. On the other hand, heterotrophic nanoplankton was the second most dominant component in the PB followed by heterotrophic bacteria, *Synechococcus* and picoeukaryotes. The Redundancy Analysis (RDA) showed that picoeukaryotes, heterotrophic bacteria and autotrophic nanoplankton are positively correlated with salinity and nitrate, whereas *Synechococcus* and heterotrophic nanoplankton are positively correlated with turbidity, phosphate and dissolved oxygen. The data presented in this paper forms the first information on the relative trophic preference of various fractions of smaller plankton in Indian coastal waters.

Key words: Plankton, multivariate analysis, flow cytometry, fluorescent microscopy, Gulf of Mannar, Palk Bay, Arabian Sea, Bay of Bengal

1. Introduction

In recent decades, studies based on fluorescent microscopy and flow cytometry provided enough evidences to believe that smaller plankton (<20 µm) are abundant in estuarine and marine environments (Li et al., 1983, 1992, Li and Wood, 1988; Burkill et al., 1993; Veldhuis et al., 1993; Landry et al., 1996; Garrison et al., 2000; Brown et al., 2002). Various smaller plankton components function as primary producers, grazers as well as mineralizers thereby, they act as an integral part of the microbial plankton food web and biogeochemical processes (Veldhuis et al., 1993; Landry et al., 1996; Brown et al., 2002). These smaller plankton components consist of both prokaryotes and eukaryotes and are distributed from polar to tropical seas (Burkill et al 1993; Veldhuis et al., 1993; Campbell et al., 1997).

The picoautotrophs in marine environment consist of prokaryotes *Prochlorococcus*, *Synechococcus* and eukaryotic plankton (Partensky et al., 1996). The smallest autotrophic picoplankton *Prochlorococcus* (0.6 - 0.8 µm) abundantly occurs in oligotrophic open oceans (Li, 1994, 1995; Vaulot et al., 1995). The other prokaryote *Synechococcus*, larger in size (0.8 - 1.5 µm), abundantly occurs in the upper well lit layers of the coastal waters (Partensky et al., 1996; Mitbavkar and Anil, 2011). Chlorophyll *a* and *b* are the predominant photosynthetic pigments in *Prochlorococcus* whereas, phycoerythrin dominates in *Synechococcus*. Eukaryotic picophytoplankton, composed of algae *Prasinophyceae*, *Pelagophyceae* and *Bolidophyceae*, contains chlorophyll *a* and abundantly occur in the estuarine and coastal environments (Courties et al., 1994; Mitbavkar and Anil, 2011). The heterotrophic bacteria are the most abundant pico-heterotrophs in marine waters, which contribute significantly to the particulate organic carbon pool in the ocean (Ducklow, 1986; Ducklow et al., 2001). They sometimes consume even half of the marine organic production and subsequently transfer it to microzooplankton (Ducklow 1986, Cho and Azam 1988, Lugioyo et al., 2007).

Autotrophic nanoplankton contributes majority of the phytoplankton biomass and primary production in marine and estuarine environments (Detmer and Bathmann, 1997; Hickel, 1998; Tarran et al., 2001; Zhang and Zhang., 2007; Madhu et al., 2010). They are mainly composed of smaller algae and flagellates, which form the main source of dissolved organic matter (Lugioyo et al., 2007). Heterotrophic nanoflagellates are the dominant consumers of picoplankton and they play a key role in energy flow and material cycling from picoplankton to higher trophic levels (Fenchel, 1982 a & b; Sanders et al., 1992, 2000; Reckermann and Veldhuis, 1993; Tong, 1997). Heterotrophic nanoplankton consists of flagellates, small ciliates and heterotrophic dinoflagellates, which form an important component of the secondary producers in marine ecosystems (Reckermann and Veldhuis, 1997; Brown et al., 2002; Sherr and Sherr, 2007).

Studies carried out in the central and western Arabian Sea (AS), as part of the international JGOFS programme, reported high abundance of picoautotrophs (>10⁷ cells L⁻¹) in the surface mixed layer (Burkill et al., 1993; Campbell et al., 1997). Later, Roy et al., (2006) presented HPLC pigment data from the southwest coast of India giving more evidence of picoautotrophs as an ecologically important plankton component. However, as of now, there is no published data available on the abundance and relative trophic preference of smaller plankton in Indian Seas. Recent brief appraisal by Mitbavkar and Anil, (2011) has presented the natural variation of picoplankton in some selected locations along the Indian coast. Lack of information on pico

and nanoplankton is more severe in the case of the BoB and the available information from the region is limited only to the discussion shared by some researchers (Jyothibabu et al., 2008a; Naik et al., 2011; Mitbavkar and Anil, 2011). The oligotrophy caused by nutrient and light limitation is considered to be favorable for the dominance of smaller phytoplankton in the BoB (Jyothibabu et al., 2008a; Naik et al., 2011; Mitbavkar and Anil, 2011).

The AS and the BoB have contrasting hydrographic characteristics, which are mainly governed by excess evaporation over precipitation in the former region and the large freshwater flux in the latter. Though the GoM and PB are interconnected, we hypothesized that there could be noticeable differences in the distribution of picoplankton and nanoplankton in these regions. In order to evaluate this hypothesis, we quantified the picoplankton and nanoplankton community in the GoM and the PB during the northeast monsoon (January 2011) based on fluorescence microscopy and flow cytometry. The hydrographical parameters were also measured to understand the environmental setting in the GoM and the PB and its link to the distribution of smaller plankton. In this study, we mainly focused on (a) the hydrographical features relevant to the plankton distribution in the GoM and the PB and (b) distribution, abundance, carbon biomass and trophic preference of various smaller fractions of plankton in the GoM and the PB.

2. Sampling and Methods

2.1. The study area

The GoM is located between the southern tip of India and the north-west coast of Srilanka (Figure 1a). It is a large and relatively deep gulf of the AS. On the other hand, the PB is an enclosed shallow basin, which connects the Indian mainland to Mannar Island of Srilanka. The coastal currents along the Indian subcontinent have been studied by many researchers (Shetye, 1998; Shetye et al., 2000; Shankar et al., 2002; Vinayachandran et al., 2005; Rao et al., 2011). Based on these studies, a schematic representation of the coastal currents around India during the northeast monsoon is depicted in Figure 1b. There are two seasonally reversing coastal currents that exchange waters between the AS and BoB. The coastal currents along the east coast of India (East India Coastal Current-EICC) bring low saline BoB water into the AS during the northeast monsoon period. In contrast, the coastal current along the west coast of India (West India Coastal Currents-WICC) brings high saline AS waters into BoB during the summer monsoon period. The GoM and the PB having located between the AS and BoB, their overall surface current are driven by the seasonal reversal of WICC and EICC (Rao et al., 2011).

The PB is a large reservoir of suspended sediments brought from the BoB during the northeast monsoon period (Figure 2a). Sediments are also brought by Rivers such as Vaigai, Vaishali, and Valryar (Chandramohan et al., 2001). The high level of sediments under the influence of weak wave action cause deposition of sediments in the PB causing emergence of sand banks (Chandramohan et al., 2001). The gross sediment transport into the PB is estimated to be around $0.448 \times 10^6 \text{ m}^3$. The GoM receives sediments from the PB and also from rivers such as Thamiraparani, Vembar and Vaippar. However, the annual sediment flux in the PB is several orders of magnitude higher than the GoM (Sanilkumar et al., 2002; Rao et al., 2008).

The waters of the GoM are intermediate between the oceanic waters of the Arabian Sea and coastal conditions of the PB (Rao et al., 2008). The Rameswaram (Pamban) island, submerged island chain Ramsethu (Adam's Bridge) and Mannar Island act as physical barriers between the GoM and PB (Figure 2b). As a result, the BoB waters significantly influence the hydrography of the PB and AS waters influences the GoM (Murty and Varma, 1964). The resultant ecological regimes in the GoM and PB are expected to have noticeable influence on the distribution of biological variables. The GoM is commonly known as the 'Paradise of Marine Biologists', which is a legally protected Marine Biosphere Reserve (Rao et al., 2008).

In recent decades, the GoM and PB were extensively studied for their economically important and vulnerable biological resources (Alagarswami et al., 1987; Paragasam and Dev, 1987; Kaliaperumal and Kalimuthu, 1993; Kaliaperumal et al., 1992, 1998; Rao et al., 2008 and references therein). On the other hand, it is surprising to note that as of now there is no comprehensive data available on various plankton components in the GoM and the PB. The fragmented information available is from the historical qualitative methods such as net plankton and settling volume (Prasad et al., 1952; Prasad., 1954., 1956., 1958). The lack of quantitative information on the plankton community in the GoM and the PB force the contemporary researchers to depend on historical data to explain the current environmental setting in these regions (Rao et al., 2008). In this context, the present study is relevant as it provides advanced quantitative information on plankton components with respect to the unique hydrographical conditions in the GoM and PB.

The field sampling was carried out in January 2011 in 30 locations, 15 each in the GoM and the PB. The locations were distributed along 10 transects (5 each in the GoM and PB), oriented perpendicular to the Indian coastline. Each transect consist of 3 locations; coastal, middle and inshore located with an approximate distance of 20 km. In each location, water samples were collected from the surface and bottom waters using 5 L Niskin samplers. Due to difference in bathymetry of the study area, there has been difference in bottom sampling depths in various locations (Table 1). This difference in bottom sampling depths can introduce certain level of error in interpretations when bottom parameters are compared between the GoM and PB. In order to minimize this error factor, comparison of bottom parameters between the GoM and PB locations is avoided throughout this paper. However, it is important to note that the surface and bottom sampling depths in both GoM and PB are actually represent within the surface mixed layer (with in upper 15m). Therefore, most of the hydrographical parameters except turbidity and dissolved oxygen show only slight differences between the surface and bottom waters (Table 2).

2.2. Climate and physicochemical parameters

In order to understand the general climatic features in the study area, air temperature recorded by an AWS installed at Mandapam (midpoint between the GoM and PB) was utilized. Rainfall data (form 2004 to 2008; Indian Meteorological Department, Pune) for the districts of Tuticorin, Ramnathapuram and Nagapattinam (three major districts bordering the study area) were used to understand the seasonal rainfall pattern in the study area. The synoptic picture on the currents between the GoM and PB were obtained using MIKE 21 flow model simulations. The model results has been validated with measured currents using current meters deployed at selected locations in the study area shown in Figure 1a (NIO Report, Sudheesh et

al., 2012, please see supplemental material for reviewers1a,b&c). An Acoustic Doppler Profiler (ADP) was operated across the Pamban Pass to record the current velocity through the channel. The vertical profiles of temperature and salinity were collected using a calibrated Seabird CTD system (SEACAT SBE 19 plus V2) and the data was processed using the software SEASOFT. Water samples were collected from surface and bottom using 5 L Niskin samplers (Hydrobios-Kiel) for measuring the turbidity and nutrients. The turbidity was measured using a turbidity meter (Eutech Model TN 100) based on nephelometric principles. Water samples for dissolved oxygen were fixed onboard and estimated following Winkler's method. Dissolved inorganic nitrate (NO_3) and phosphate (PO_4) were estimated following standard colorimetric techniques (Grasshoff et al., 1983).

2.3. Biological parameters

The total chlorophyll *a* was measured by concentrating 1L of water samples on Whatman GF/F filters ($0.7 \mu\text{m}$) and subsequent extraction using 10 ml 90% acetone. The extracted chlorophyll *a* was measured using a Trilogy Turner fluorometer following standard procedure (UNESCO, 1994). The size fractionated chlorophyll *a* was estimated adopting serial filtration of water samples. Processing of samples includes filtration of 1 L of water sample in a step wise manner through $20 \mu\text{m}$ sieve (Hydrobios) and subsequently through 2 and $0.2 \mu\text{m}$ (47 mm diameter, Whatman) Glass fiber filter papers (consider Madhu et al., 2010 for the detailed procedure). The phytoplankton thus separated was estimated following the same procedure adopted for the total chlorophyll *a*. Water samples in duplicates (5ml) were collected and preserved in 1% gluteraldehyde for quantifying autotrophic pico and nanoplankton and stored in liquid nitrogen containers following the procedure of Vaulot et al., (1996). Just prior to the analysis, samples were thawed and homogenized with a laboratory shaker. The samples were then analyzed in a flow cytometer (BD FACS caliber) which facilitated the quantification of various smaller autotrophic plankton groups such as cyanobacteria and picoeukaryotes based on the forward light scatter (FLS; proxy for cell size) and cellular fluorescence from photosynthetic pigments (chlorophyll *a*, phycoerythrin and phycocyanin). In order to estimate the carbon biomass of *Synechococcus* and picoeukaryotes, the numerical conversion factors given by Garisson et al., (2000) have been used.

Fluorescence microscopy was used to quantify heterotrophic bacteria as well as autotrophic and heterotrophic nanoplankton. The heterotrophic bacteria was quantified by collecting water samples (5 ml) and preserving in 2% prefiltered formalin following the procedure of Porter and Feig (1980). 2ml of the preserved water samples were stained with DAPI (final concentration of $1 \mu\text{g ml}^{-1}$) and filtered through $0.22 \mu\text{m}$ black polycarbonate membrane filters. These filters were observed under UV excitation in an epifluorescence microscope (Olympus BX 53 equipped with progRes Capture Pro 2.6 image analyzer software). The heterotrophic bacteria, which stained bright blue, were enumerated and from each slide 25 fields were considered for counting. The abundance of heterotrophic bacteria was converted to carbon biomass based on the conversion factor of 0.01pgC per cell (Garrison et al., 2000). An aliquot of 15ml of water samples were pre-filtered through $20 \mu\text{m}$ plankton sieve for nanoplankton and from this 5ml was stained with proflavin hemisulfate with a final concentration of $1.65 \mu\text{g ml}^{-1}$ (Haas, 1982). The samples were then passed through a $0.8 \mu\text{m}$ pore size black polycarbonate filters. These filters were

analyzed under epifluorescence microscope using blue illumination for observing the nanoplankton (Bloem et al., 1986). The cytoplasm of heterotrophic nanoplankton was stained green with proflavin to distinguish them from the autotrophic forms having red autofluorescence of chlorophyll *a*. The counts of heterotrophic and autotrophic nanoplankton were taken using the image analyzer. In order to calculate the carbon biomass of both autotrophic and heterotrophic nanoplankton, dimensions of around 250 individuals of each category were randomly measured from filters using the image analyzer and their biovolume were calculated by assuming suitable geometrical shape (Garrison et al., 2000). The mean biovolume was extrapolated to the total counts at each location to obtain the total biovolume of the nanoplankton. The conversion of biovolume to organic carbon was carried out based on numerical factors given in Garrison et al., (2000).

2.4. Multivariate analyses

Multivariate statistics is useful to analyze and interpret simultaneous data on several environmental parameters. The practical application of multivariate statistics to a particular set of data may require several kinds of univariate and multivariate analysis so as to understand the relationships between the variables and their relevance to the actual problem being studied. In the present study, we used the multivariate statistical methods such as (a) cluster analysis: to assign objects into groups (clusters) so that the objects from the same cluster are more similar to each other than objects from different clusters. The Euclidian distance based hierarchical clustering was used in the present study. In the resultant cluster plots, the objects placed within the cluster represents homogeneity and between the clusters exhibit heterogeneity, (b) multidimensional scaling (MDS): comprises various algorithms to determine a set of synthetic variables that best represent pair wise distances/differences between samples. Non Metric Multidimensional Scaling (NMDS) was performed on standardized and square root transformed data sets of physicochemical variables (sea surface salinity, turbidity, dissolved oxygen, nitrate and phosphate) in 30 sampling sites to make spatial grouping of stations, and (c) Redundancy Analysis (RDA) that finds linear relationships among two sets of variables following bivariate correlation. The advantage of RDA is that it allows the user to derive a specified number of synthetic variables from one set of (independent) variables that explain as much variance as possible in another (dependent) set.

In order to carry out the RDA, de-trended correspondence analysis (DCA) was carried out initially to select the most appropriate ordination techniques for the present data. The results of DCA showed the axis gradient lengths of < 2 and therefore, linear multivariate method of RDA was considered as the most suitable analysis for the present data (Birks, 1998; Leps and Smilauer, 2003), which presents parameters correlation and scaling ordination scores. Biological variables were log transformed and centered prior to the analysis. The ordination significance was tested with Monte Carlo permutation tests (499 unrestricted permutations) ($p < 0.05$). The results of the RDA are presented in the form of Triplots. In a triplot, samples are displayed by points, and quantitative biological as well as environmental variables are shown by arrows. The direction of the parameter arrows indicates the direction of increases of that variable (Leps and Smilauer, 2003). The detailed information on the interpretation of triplot is given in section 3.2.5.

3. Results

3.1. Rainfall, temperature and water currents

The monthly mean air temperature data at Mandapam and rainfall data in three major districts of Tamilnadu adjacent to the study area are presented in Figure 3a. The air temperature in the study area peaked during April-May (pre-monsoon) and then gradually declined towards December-January (northeast monsoon). This trend was almost opposite to the rainfall pattern, which showed a prominent increase during the northeast monsoon as compared to pre-monsoon. Due to cold and dry northeast monsoon winds, the atmospheric temperature in the study area was the seasonal lowest during the study period. The surface water temperature was relatively high in the GoM (av. $26.00 \pm 0.49^\circ \text{C}$), as compared to the PB (av. $25.45 \pm 0.61^\circ \text{C}$). This spatial distribution pattern in sea surface temperature is very evident in satellite image (Figure 3b), which shows cooler surface waters in the PB as compared to the GoM. The figure also shows that this cooler water in the PB is intruded from the western BoB.

The synoptic picture of the current pattern simulated using MIKE 21 flow model is shown in figure 4a. Similarly, the current velocity through the Pamban Pass measured using an ADP is presented in figure 4b. These figures clearly show the current pattern in the study area during the northeast monsoon period, which was in well agreement with the overall coastal circulation along the Indian subcontinent. The figures evidenced the flow of BoB waters into the PB and then to the GoM during the northeast monsoon period (Figure 4a & b). The PB waters enter into the GoM through the Pamban Pass and Ram Sethu. Figure 4a also shows that the major part of the water intrusion from the PB to GoM occurs through the Ramsethu region. The currents through the Pamban pass presented in figure 4c clearly show that the water flow through the channel was directed towards southwest. This current through the Pamban Pass resulted in the decline of salinity in location 12 in the GoM (Figure 5). In general, weak currents were found in the study area but, increased velocity ($>0.55 \text{ m/s}$) was evident in the Pamban Pass, Ramsethu and also closer to the Indian coastline in the GoM.

3.1.2. Salinity and turbidity

The surface salinity distribution showed fairly high saline waters in the GoM (av. 32 ± 0.58) and low saline waters in the PB (av. 28.98 ± 1.34). The bottom salinity was clearly higher than the surface but, the trend in spatial distribution was the same as the surface waters with prominently higher values in the GoM (av. 32.89 ± 1.40) than in the PB (av. 29.74 ± 1.33). In order to understand the influence of currents in mixing the GoM and PB waters, vertical profiles of salinity along two transects on both sides of Rameswaram-Ramsethu barrier is presented in figure 5. It is very clear in this figure that there was a noticeable difference in salinity (>2) on both sides of the barrier. An exception to this was location 12 in the GoM which showed relatively low salinity due to the intrusion of the PB waters through the Pamban Pass (Figure 5). The satellite imagery of reflectance at 550 nm (an indirect measure of turbidity) shows that the suspended inorganic particles were several orders higher in the PB as compared to the GoM (Figure 6a). The suspended inorganic particles significantly interfere with the satellite chlorophyll *a* measurements, which was evident in figure 6b. The field measurements of turbidity strongly supported

the spatial distribution pattern presented in figure 6a. The surface turbidity was found to be several orders higher in the PB (av. 7.84 ± 13.59 NTU) as compared to the GoM (av. 1.76 ± 1.38 NTU). The highest surface turbidity in the GoM was in locations 1 and 12 with a turbidity range of 2 - 4 NTU. On the other hand, most of the locations in the PB showed turbidity >4 NTU. The highest surface turbidity in the entire study area was found at location 28 (56.4 NTU) followed by location 25 (8.09) in the PB and the lowest at location 9 (0.62 NTU) followed by location 5 (0.73 NTU) in the GoM. Turbidity in the bottom waters was significantly higher than the surface waters with the same spatial distribution pattern (Table 2).

3.1.3. Dissolved oxygen, nitrate and phosphate

The dissolved oxygen in the GoM and PB was in saturated levels during the study period with higher values in the surface than in the bottom (Table 2). The dissolved oxygen concentration in the surface was noticeably higher in the PB (av. 8.27 ± 1.24 mg l⁻¹) as compared to the GoM (av. 7.92 ± 0.75 mg l⁻¹). The highest dissolved oxygen value in the entire study period was found at locations 26 (9.65 mg l⁻¹) and 24 (9.59 mg l⁻¹) in the PB. Moderate level of nitrate was found in both GoM and PB (av. 0.5 μ M) waters with slightly higher values in the bottom waters than the surface (Table 2). In general, the surface nitrate concentration in the GoM was slightly higher (av. 0.49 ± 0.31 μ M) than the PB (av. 0.45 ± 0.47 μ M). The highest concentration of nitrate in the surface waters was found in location 19 (2.03) in the PB followed by location 2 (1.1 μ M) in the GoM. The vertical distribution of phosphate also showed a marginal increase in bottom waters as compared to the surface both in the GoM (av. 0.24 ± 0.11 μ M in surface and av. 0.41 ± 0.21 μ M in bottom) and PB (av. 0.26 ± 0.13 μ M in surface and av. 0.35 ± 0.18 μ M in bottom). The phosphate levels in the surface waters of the PB (av. 0.26 ± 0.13 μ M) were comparable to that in the GoM (av. 0.24 ± 0.11 μ M).

3.1.4. Multivariate analysis of physicochemical parameters

In order to generate a conclusive pattern in distribution of major environmental factors in the GoM and the PB, cluster analysis and MDS were carried out on standardized data of physicochemical variables in surface waters (Figure 7a-c). The results show separate clusters for the GoM and PB. To further understand the influence of major physical factors salinity and turbidity on clustering of locations, these parameters were overlaid on the overall clustering of the locations (Figure 7 b & c). It is very clear in this analysis that the high saline (>31) and less turbid (<2.5 NTU) stations formed one cluster for the GoM whereas, low saline (<31) and more turbid (>2.5 NTU) locations formed another cluster representing the PB.

3.2. Biological factors

3.2.1. Size fractionated chlorophyll *a*

The surface and bottom waters of the GoM and PB showed only minor difference in chlorophyll *a* concentration (Table 2). However, a spatial difference in chlorophyll *a* was very evident with prominently higher concentration in the GoM as compared to the PB (Table 2). The nanoplankton contributed more than 80% of the total chlorophyll *a* in both GoM and PB. The microplankton and nanoplankton chlorophyll *a* was higher in the GoM as compared to the PB (Table 2). The picoplankton

chlorophyll *a* was in comparable magnitude in the GoM and PB (Table 2). In general, the picoplankton contribution to the total chlorophyll *a* in the GoM and PB was found to be the least (av. 6%) as compared to the nanoplankton (av. 80%) and microplankton (av.14%).

3.2.2. Autotrophic picoplankton and nanoplankton

The autotrophic picoplankton community was mainly composed of *Synechococcus* and picoeukaryotes. The *Prochlorococcus* was either absent or found in very low abundance (<1000 cell L⁻¹). The flow cytometry measurements showed a distinct distribution pattern of autotrophic picoplankton and nanoplankton in the study area (Figure 8). The *Synechococcus* abundance in the study area varied significantly (2 to 6 x 10⁷ L⁻¹) and their abundance was higher in the PB as compared to the GoM (Figure 8 a & b). They were more abundant in the surface waters of GoM whereas, their abundance in the PB was comparable in both surface and bottom waters. The highest abundance of *Synechococcus* was in the surface waters of location 29 (9.83 x 10⁷ L⁻¹) in the PB. On the other hand, the abundance of picoeukaryotes in the surface waters of the GoM was higher (av. 0.20 ± 0.15 x 10⁷ L⁻¹) as compared to the PB (av. 0.13 ± 0.09 x 10⁷ L⁻¹). The highest abundance of picoeukaryotes was in the surface waters of location 4 (av. 0.46 x 10⁷ L⁻¹). The fluorescence microscopy measurements showed higher abundance of autotrophic nanoplankton in the GoM (av. 0.18 ± 0.09 x 10⁷ L⁻¹) as compared to the PB (av. 0.07 ± 0.04 x 10⁷ L⁻¹). Autotrophic nanoplankton was more abundant in the surface waters of both GoM and PB (Figure 8). The highest abundance of autotrophic nanoplankton was found in the surface waters of location 14 (av. 0.38 x 10⁷ L⁻¹) and location 9 (0.32 x 10⁷ L⁻¹) in the GoM.

3.2.3. Heterotrophic bacteria and nanoplankton

The fluorescence microscopy data of heterotrophic bacteria and nanoplankton also showed a spatial distribution pattern (Figure 8 c & d). The heterotrophic bacteria were high in the GoM as compared to the PB and showed some pockets of exceptionally higher abundance. Their abundance was generally higher in the surface waters in the GoM while in the PB the abundance was comparable in the surface and bottom waters. The heterotrophic nanoplankton showed higher abundance in the PB as compared to the GoM. The highest abundance was in the bottom waters at location 27 (4.59 x 10⁶ L⁻¹) followed by the surface waters at location 29 (4.12 x 10⁶ L⁻¹) both in the PB.

3.2.4. Carbon biomass of plankton components

The total carbon biomass of picoplankton and nanoplankton components was higher in the surface waters as compared to the bottom (Figure 9). The total organic carbon in the surface waters was noticeably higher in the GoM (av. 62.20 mgC m⁻³) as compared to the PB (av. 47.65 mgC m⁻³). The carbon biomass of heterotrophic bacteria, picoeukaryotes and autotrophic nanoplankton were higher in the GoM than in the PB. On the other hand, the biomass of heterotrophic nanoplankton and *Synechococcus* was higher in the PB as compared to the GoM. The following order of carbon biomass content was evident in the GoM; autotrophic nanoplankton > heterotrophic bacteria > heterotrophic nanoplankton > *Synechococcus* > picoeukaryotes

(Figure 9). The contribution of carbon biomass content by plankton fractions was slightly different in the PB where it was autotrophic nanoplankton > heterotrophic nanoplankton > heterotrophic bacteria > *Synechococcus* > picoeukaryotes (Figure 9). The carbon biomass of autotrophic nanoplankton in the study area was the highest with a prominent increase in the GoM (av. $39.34 \pm 19.24 \text{ mgC m}^{-3}$) as compared to PB (av. $18.46 \pm 7.91 \text{ mgC m}^{-3}$). The other component which showed significant spatial difference in carbon biomass values was the heterotrophic nanoplankton, which showed more than one fold increase in the PB (av. $17.28 \pm 5.80 \text{ mgC m}^{-3}$) as compared to GoM (av. $8.14 \pm 2.88 \text{ mgC m}^{-3}$). However, the total organic carbon present in all plankton fractions was higher in the GoM as compared to the PB.

The relative contribution of each plankton component to the total organic carbon present in the pico and nanoplankton fraction was calculated. It showed that the relative carbon biomass contribution of nanoplankton (76-77% in GoM and 70-74% in the PB) was prominently higher than the picoplankton (23-24% in GoM and 26-30% in the PB). The autotrophic nanoplankton alone contributed 59-63% and 31 – 36% of the total organic carbon available in pico and nano fractions in the GoM and PB respectively. The heterotrophic bacteria was the second most significant organic carbon contributor in the GoM (7-9%) whereas it was heterotrophic nanoplankton in the PB (15-17%). The picoplankton contribution varied from 22-23% in the GoM whereas, it was 26-29% in the PB. The autotrophic picoplankton contributed only 6-8% in the GoM and 10-11% in the PB. On the other hand, heterotrophic bacteria showed almost similar percentage contribution in GoM (15-17 %) and PB (15-18%).

3.2.5. Multivariate ecological analysis

In triplot, the relative directions of the biological variable arrows approximate the linear correlation among them. Arrows pointing in the same direction correspond to variables that are predicted to have a high positive correlation, whereas variables with a high negative correlation are predicted to have arrows pointing in opposite directions. A similar approximation is used when comparing the biological and environmental variable arrows. If the arrow for an environmental variable, points in a similar direction to a biological variable, the values for that biological variable are predicted to be positively correlated with the values for that environmental variable. The sample points can also be projected perpendicularly to the arrows of environmental variables. This provides us the approximate order of the samples in the increasing value of that environmental variable (when proceeding towards the arrow tip and beyond it). The environmental and biological variables are always centered and standardized before the ordination model is fitted. Thus, similar to project the sample points on the biological variables arrows, the ordinate system origin corresponds to the average value of that particular environmental variable in that sample. The angle between the arrows of the environmental variables can be used to approximate the correlations among those variables in the scaling focused on biological correlations.

The complete RDA analysis of surface waters of the GoM and PB showed that the first two axes explained 92% of the relationships between biological and physicochemical parameters (Figure 10). The analysis showed that 24.2% of the total variance in biological parameters is explained by physicochemical parameters. In partial RDA, where salinity, turbidity and DO are considered as the major physicochemical variables, whereas, nitrate and phosphate are the covariables. It showed that

20.8% of the total variance in biological parameters is explained by salinity, turbidity and DO whereas; nitrate and phosphate explained only minor variance. The RDA triplot demarcated the GoM locations on the left side and PB locations on the right hand side (Figure 10). The GoM side (left hand side) was characterized by increasing gradient of salinity and decreasing gradient of turbidity and DO whereas, the PB side (right hand side) was characterized by decreasing gradients of salinity as well as increasing gradient of turbidity and DO. The RDA analyses showed that the nitrate was positively correlated with salinity and negatively correlated with turbidity and DO. Phosphate was positively correlated with turbidity and DO whereas; it was negatively correlated with salinity. Biological variables such as autotrophic picoeukaryotes, autotrophic nanoplankton, heterotrophic bacteria and total chlorophyll *a* were positively correlated with salinity and nitrate. The heterotrophic nanoplankton had a significant positive correlation with turbidity and DO; and a significant negative correlation with salinity. *Synechococcus* displayed a positive correlation with turbidity, dissolved oxygen and phosphate; and a negative correlation with salinity and nitrate. The total chlorophyll *a* showed a significant positive correlation with autotrophic nanoplankton and a negative correlation with *Synechococcus*. Due to the difference in bottom sampling depths of the study area, the RDA analysis has not been attempted for the bottom waters to avoid the possible error in interpretations.

4. Discussion

The cold and dry northeasterly wind, which blows over the study area during the northeast monsoon period decrease the atmospheric as well as ocean surface temperature (Rao et al., 2008). Earlier studies showed that the seasonal air temperature variation in the study area is from 24-33 °C with a maximum during April and a minimum during January (Prasad, 1956). This seasonal climatic features were well recorded in the current data also as there was a noticeable decline in air temperature from April to January and a prominent increase in rainfall during the northeast monsoon period (Figure 3). The spatial distribution of sea surface temperature showed noticeable decrease in the PB as compared to the GoM (Figure 3b), which can be attributed to the cool BoB coastal waters present in the PB due to coastal currents flowing southward during the study period.

The coastal currents around the Indian subcontinent, which exchanges water between the BoB and AS, have been studied intensively (Shetye, 1999; Shankar et al., 2000; Rao et al., 2011). The EICC in the western BoB flow equatorward during the northeast monsoon and the main flow turn around Srilanka and transports low saline waters into the AS. Associated with the flow of EICC, the BoB coastal waters, which is cool, low saline and turbid enter into the PB and flows towards the GoM (Murty and Verma 1964; Rao et al., 2011). These currents that flow from the BoB to the PB and then to the GoM are evident in the MIKE 21 flow model result presented in figure 4a. Relatively strong current was evident in the Pamban Pass and the Ramsethu as these regions are situated between the natural islets, where intensification of currents takes place due to increased flow. The local rivers such as Vaigai, Vaishali, and Valryar are expected to bring suspended sediments and fresh water into the PB (Chandramohan et al., 2001). However, in satellite imagery presented in Figure 3 and also in the present field turbidity data, increased levels of turbidity was not evident closer to the Indian coastline in the PB. Concurrently, a decline in salinity was evident in a few locations closer to the coastline in the PB, which supports the view that suspended sediments

brought by the rivers are negligible during the study period. It also provide support to the view that the sediment inputs from the western BoB forms the potential sources of high turbidity in the PB during the northeast monsoon period.

Multivariate statistics of physicochemical parameters demarcated two distinct ecological regimes of the GoM and PB. This segregation can be attributed to (a) the proximity of the GoM to the AS and PB to BoB and (b) the physical barriers (Rameswaram Island, Ramsethu and Mannar Island) that inhibit the mixing of waters between the GoM and PB. The coastal current during the sampling period was such that the BoB coastal waters intruded into the PB and flowed towards the GoM. As a result, the hydrographic conditions in the PB were significantly influenced by the BoB waters, while the GoM waters resembled more those of the AS. The major water quality features expected in the PB during the current study period are cool sea surface temperature, low salinity, high turbidity and high nitrate levels. These features are actually the characteristic of the coastal BoB during the northeast monsoon period (Varkey et al., 1996; Prasannakumar et al., 2004; Rao et al., 2011). All these expected features in the PB were well recorded during the present study. However, the high level of nitrate expected in the PB was not found in the present study, instead a low concentration (av.0.49 μM) was evident throughout the study area.

The consequence of the intrusion of BoB waters into the AS is the enhancement of coastal phytoplankton production along the southwest coast of India. This is a traditional belief that the river influx carry large amount of nitrate and fertilize the seas to a large extent. However, several recent studies overrule the above concept especially in the case of rivers along the Indian coast (Singh and Ramesh, 2011; Prasannakumar et al., 2004). The seagrass meadows present in the PB region could be another reason for the presence of only moderate nitrate concentration during the present study (Manikandan et al., 2011). The seagrasses are capable of absorbing nitrates through their roots and leaves and act as major nutrient stabilizers in shallow marine environments (McRoy and Barsdate, 1970, Moriarty et al., 1986; Roberts and Moriarty, 1987; Sridhar et al., 2010).

The oxygen content in seawater depends primarily on factors such as salinity and temperature (Manasrah et al., 2006). The primary source of dissolution of oxygen in sea water is through air-sea exchange, leading to near saturation of oxygen concentration in surface waters. However, due to many biological processes such as photosynthesis and decomposition of organic matter, deviations can occur in the dissolved oxygen concentration in marine environments. During the present study, the higher dissolved oxygen levels observed in the PB as compared to the GoM can be attributed to the relatively cold and low saline waters in the former region, which favors better dissolution of atmospheric oxygen. The phosphate concentration in the GoM and PB was much lower ($< 0.3 \mu\text{M}$) than the concentration reported earlier (Prasad, 1956). Chandramohan et al., (2001) proposed resuspension as one of the mechanisms for the increased suspended sediments in the PB. It is well accepted that during resuspension, the PO_4 values would be higher than normal condition. Therefore, the low level of PO_4 in the PB bottom waters overrules the possibility of resuspension in the region during the present sampling period.

The phytoplankton stock present in the GoM (av. 1.75 mg m^{-3}) and the PB (av. 0.7 mg m^{-3}) are significantly higher than the values reported from the adjacent AS ($< 0.3 \text{ mg m}^{-3}$ - Madhupratap et al., 1992) and BoB (0.3 mg m^{-3} – Prasannakumar et al., 2004) during the same season. Though suspended sediment was significantly high in the PB, its inhibition on the subsurface

phytoplankton was not evident in the chlorophyll data since the concentration was found high in the bottom waters also. There were almost 3 fold higher chlorophyll *a* concentrations in the GoM as compared to the PB though in both regions nitrate and phosphate concentrations were in comparable levels (Table 2). This general difference in the amount of phytoplankton stock can be attributed to the turbidity but, the present data is insufficient to resolve this problem. One important aspect in the present study is the relative dominance of nanoplankton that contributed more than 80% of the chlorophyll *a* in both GoM and PB. Rao et al., (2008) pointed out the possibility of higher amount of nanophytoplankton stock in the PB as compared to the GoM. This was based on the assumption that nanophytoplankton would be more adapted to survive in low light conditions as suggested by Shiomoto, (1997). However, the present study does not support this assumption and evidences that the relative amount of nanoplankton stock was significantly higher in the GoM as compared to the PB (Table 2).

The trophic preference of smaller plankton in pelagic food web received concerted scientific attention since the seminal papers on microbial loop had been published (Pomeroy, 1974; Azam et al., 1983). Later, smaller plankton was considered as the major part of all biological measurements under the International JGOFS programme in the central and western AS (Garrison et al., 2000). Under JGOFS, baseline information of picoplankton communities present in the northern Indian Ocean has been generated (Burkill et al., 1993; Ducklow et al., 2001; Veldhuis et al., 1993; Landry et al., 1996; Brown et al., 2002). These studies evidenced large seasonal and spatial variations in abundance of *Synechococcus* and attributed to various environmental factors like nutrients, solar radiation and temperature. The available information on picoautotrophs from Indian waters is presented in Table 3, which clearly shows that *Synechococcus* recorded during the present study ($3- 5 \times 10^7$ ind. L⁻¹) is well within the ranges recorded earlier.

Synechococcus occurs in coastal as well as open ocean waters, but they are preferably distributed in the coastal waters where nutrient levels are high (Mitbavkar and Anil, 2011). The seasonal variation in *Synechococcus* abundance in Indian coastal waters has been linked to the river influx and nutrient input (Mitbavkar and Anil, 2011). Earlier studies conducted in temperate waters showed that *Synechococcus* utilizes nitrate, nitrite, phosphate, ammonium, urea and many amino acids (Scanlan et al., 1997; Moore et al., 2002; Palenik et al., 2003). Low salinity (<36), high temperature (>28°C) and high solar radiation can significantly alter the abundance of *Synechococcus* (Moutin et al., 2002; Mitbavkar and Anil, 2011). Since the present study area (GoM and PB) is located in the hot arid tropical region, the physical environmental factors limiting the *Synechococcus* in the temperate waters may not be significant in the present study.

The two major subgroups of *Synechococcus* in Indian coastal waters are Syn-PE (phycoerythrin rich) and Syn-PC, (phycocyanin rich) (Mitbavkar and Anil, 2011). Several diverse subgroups of Syn – PE are also reported from the coastal waters of BoB whereas; Syn-PC is the common subgroup in the coastal waters of the eastern AS. Vault et al., (1996) showed that phosphate addition can shorten the growth phase in the cell cycle of *Synechococcus* enabling them to multiply faster. It is fairly understood now that *Synechococcus* cells are phosphorous limited in oligotrophic open oceans and in such conditions, an addition of as low as 20 nM phosphates can induce their faster multiplication (Vault et al., 1996). In order to analyze the possible influence of phosphate on the natural abundance of *Synechococcus*, we attempted simple linear

correlation analysis between the parameters considering the entire study area. The result showed a weak positive correlation between *Synechococcus* abundance and phosphate level ($r = 0.17$, $n = 30$, $p > 0.05$). Conversely, there was a relatively strong positive correlation between *Synechococcus* and phosphate in the PB ($r = 0.3$, $n = 15$, $p > 0.05$) whereas, the correlation was a weak negative ($r = -0.17$, $n = 15$, $p > 0.05$) in the GoM. Since the GoM is directly connected to the AS and the PB to the BoB, we assume the dominance of different subgroups of *Synechococcus* in these regions. Syn-PE dominant in the coastal BoB may be abundant in the PB and Syn-PC dominant in the coastal AS may be abundant in the GoM. Thus, the phosphate utilization in the GoM and PB by these subgroups may be different. Unfortunately, the current data is not sufficient to differentiate these subgroups of *Synechococcus* in the GoM and PB and therefore, it is our future interest to verify this concept.

The picophytoplankton has much higher nutrient affinity as a function of their size, which makes them efficient in utilizing trace level of nutrients in oligotrophic environments. This provides autotrophic picoplankton a greater competitive advantage over larger phytoplankton in oligotrophic areas (Donald et al., 1997). The small size of picophytoplankton also confers a greater efficiency to absorb incident light compared to larger autotrophs (Augusti et al., 1994). As a result, the picophytoplankton contribute the majority ($\geq 50\%$) of phytoplankton biomass and production in oligotrophic (chl $a < 0.3 \text{ mg m}^{-3}$), nutrient poor ($\text{NO}_3 + \text{NO}_2 < 1\mu\text{M}$), and warm ($>26^\circ\text{C}$) waters, but they represent only $<10\%$ of the total autotrophic biomass and production in chlorophyll rich ($>5 \text{ mg m}^{-3}$) and cold ($<3^\circ\text{C}$) waters (Agawin et al., 2000). The relative contribution of picophytoplankton to total biomass generally declines in high nutrient and productive waters due to increase of biomass production of larger phytoplankton. The increase in production of larger phytoplankton in nutrient rich waters is due to their significantly higher intrinsic growth capacity over the picophytoplankton (Banse, 1982). Although, the picophytoplankton production also increases in nutrient enriched condition together with the whole autotrophic community, their total biomass production is much slower as compared to the larger phytoplankton (Agawin et al., 2000). The microzooplankton grazing pressure also acts as a major controlling factor of picophytoplankton biomass in productive tropical waters (Landry et al., 1998; Jyothibabu et al., 2008b).

It is important to understand the trophic preference of various plankton components in terms of their organic carbon contribution to the coastal plankton food web. There is no such data available so far from the Indian coastal waters. The present study evidenced that the major part of the total organic carbon of smaller plankton ($<20\mu\text{m}$) is contributed by nanoplankton (76-77% in GoM and 70-74% in the PB) as compared to picoplankton (23-24% in GoM and 26-30% in the PB). The autotrophic nanoplankton alone contributed 59-63% and 31 – 36% of the total organic carbon in the GoM and PB respectively. The heterotrophic nanoplankton was the second most significant component in the PB (15-17%) and the third significant component in the GoM (13-16%). These observations points towards the necessity to consider nanoplankton as the major contributor of the plankton biomass in the coastal waters of India. The RDA analysis showed significant positive correlation between autotrophic nanoplankton and total chlorophyll *a*, which essentially indicates the major contribution of the nanoplankton to the total phytoplankton biomass. It was also found in RDA that the abundance of nanoplankton was

positively related with salinity, nitrate and negatively with turbidity, which basically indicate that the GoM had high concentration of nanoplankton. When compared to the carbon content of autotrophic nanoplankton in the central and western AS (av. 5.6 mgC m⁻³ – Garrison et al., 2000), the present values for the GoM (26-39 mgC m⁻³) and PB (12-16 mgC m⁻³) are higher. The carbon biomass of heterotrophic nanoplankton was also higher in the GoM (6-8 mgC m⁻³) and PB (15-17 mgC m⁻³) as compared to the values reported earlier from the western AS (4.3 mgC m⁻³ - Garrison et al., 2000). This can be attributed to the more coastal nature of the GoM and PB as compared to the western AS.

The heterotrophic nanoplankton and ciliates mainly feed on heterotrophic picoplankton, *Synechococcus* and picoeukaryotes (Caron et al., 1991; Almeida et al. 2001, Ichinotsuka et al. 2006). However, they do not show grazing preference either for heterotrophic bacteria or *Synechococcus* and the grazing is based only on prey standing stocks (Christaki et al., 2001). Similar conclusions by Christaki et al., (2002) suggesting that the Ingestion rates of heterotrophic nanoplankton on picoplankton is primarily based on the prey abundance. During the present study, heterotrophic bacteria abundance was lower in the PB as compared to GoM whereas, the *Synechococcus* abundance was vice versa. The heterotrophic nanoplankton was found in higher abundance in the PB as compared to GoM. Therefore, the high grazing pressure exerted by the heterotrophic nanoplankton could be the major reason for the observed drop in heterotrophic bacteria in the PB. On the other hand, the *Synechococcus* stock in the PB was not affected by the grazing pressure of heterotrophic nanoplankton due to their high division rates. The high division rates of *Synechococcus* are higher as compared to heterotrophic bacteria, which usually grow more slowly with a generation time even up to several days (Vaulot et al., 1995; Kirchman et al., 1995). The high multiplication rate probably enables the *Synechococcus* in the PB to maintain their abundance unaffected even when there was a high grazing by heterotrophic nanoflagellates. The heterotrophic bacteria present along the coastal waters of BoB are physiologically inactive having low production rates (Fernandes et al., 2008; Ramaiah et al., 2009, 2010). A major part of these bacteria are actually brought through the rivers, which when exposed beyond certain salinity levels become dormant and physiologically inactive causing low production rates (Ramaiah et al., 2009, 2010).

The paper provides information on the relative trophic preference of smaller sizes classes of plankton in the GoM and PB, two least studied marine environments along the east coast of India. The scientific relevance of this paper lies on the paucity of information on various smaller plankton components in Indian coastal waters. The study points towards the role of nanoplankton as a significant organic carbon contributor in the lower plankton food web in the coastal waters of India. The physiological rate measurements of smaller plankton components are still absent from Indian coastal waters and therefore needs attention in future studies.

5. Conclusion

The influence of hydrography on the composition and spatial distribution of smaller plankton components (<20 µm) in the GoM and the PB are presented in this paper. The coastal current in the east –west direction during the study period brought cold, low saline and turbid BoB waters into the PB. There was a noticeable spatial difference in physicochemical parameters in

the GoM and the PB, which caused differences in the spatial distribution of biological parameters. The total chlorophyll *a* was higher in the GoM as compared to the PB with a clear dominance of nanoplankton (>80%). The fluorescence microscopy and flow cytometry data showed higher abundance of picoeukaryotes, heterotrophic bacteria, and autotrophic nanoplankton in the GoM whereas; *Synechococcus* and heterotrophic nanoplankton were more abundant in the PB. The total carbon biomass of pico and nanoplankton fractions was higher in the GoM (av.61.5mgC m⁻³) as compared to the PB (av. 45.6mgC m⁻³). The multivariate redundancy analysis evidenced positive correlation of picoeukaryotes, heterotrophic bacteria and autotrophic nanoplankton with salinity and nitrate. On the other hand, *Synechococcus* and heterotrophic nanoplankton were positively linked with turbidity, phosphate and dissolved oxygen. The present study clearly showed that nanoplankton forms the major organic carbon contributor (>70%) of the lower plankton food web in the GoM and the PB.

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Figure captions

Figure 1a - Station locations. Locations 1-15 and 16-30 represent the Gulf of Mannar and the Palk Bay respectively. Locations of current meter deployment and Automatic Weather Station installation is also shown

Figure 1b- Coastal currents around the Indian subcontinent during the northeast monsoons. WICC- West India coastal Current, LH- Lakshadweep High, WMC – Winter Monsoon Current, EICC – East India Coastal Currents

Figure 2 – (a) MODIS -Terra satellite imagery showing extensive sediment plumes in the Palk Bay in January (www.visibleearth.nasa.gov). The movement of sediment plumes from the PB to the GoM through Pamban Pass and Ramsethu is evident (b) diagrammatic representation of the sea bed from Mandapam (India) to Mannar Island (Srilanka) based on ADP measurements in Pamban Pass (square I) and hydrography chart No. 358 in the Ramsethu Region (square II). Also see in Sivalingam (2005).

Figure 3 – (a) Monthly mean rainfall (mm) and air temperature (°C) and (b) MODIS monthly mean 4km SST (°C) for January 2011. The monthly mean air temperature data is from the AWS installed at Mandapam for one year (study period) and the rainfall data represent 5 year mean (2005-2010) representing three major districts (Tuticorin, Ramnathapuram and Nagapattinam) bordering the study area. The Rainfall data is from IMD data sets available online in which a noticeable decline in air temperature and rainfall was noticeable in January. The intrusion of cool BoB waters into the PB is evident in SST distribution presented in 3b.

Figure 4 – (a) The MIKE 21 simulated pattern of currents in the study area (b) current velocity and (c) current direction in the Pamban Pass during January 2011. Currents flow from the PB to the GoM through the Pamban Pass and Ramsethu. The main flow is through the Ramsethu as evident in the first figure. The current flow through the Pamban Pass was maximum towards the northwest causing low salinity in location 12 in the GoM.

Figure 5 – Vertical distribution of salinity in (a) two transects on both sides of the Ramsethu considered for vertical salinity structure during the northeast monsoon. The locations in blue and red color represent the GoM and the PB respectively. The marked difference in salinity levels between the GoM and the PB was clear during the study period. However, the salinity in location 12 in the GoM had comparable salinity as that of the PB as evident in the vertical profiles in right panel (the blue line clustered with the red lines). This is due to the intrusion of the PB waters into the GoM through the Pamban pass as evident in figure 4.

Figure 6 - MODIS satellite weekly imagery (17-28 Jan. 2011) showing (a) reflectance at 555 nm (10^{-2} sr^{-1}) and (b) chlorophyll *a* (mg m^{-3}). The high suspended inorganic particles in the PB evident in figure 6a caused overestimation of chlorophyll *a* as evident in figure 6b. The actual chlorophyll *a* (*in-situ*) and nephelometric turbidity presented in table 2 strongly support the features mentioned above.

Figure 7 - (a) Dendrogram of hierarchical cluster using group-average linkage of Euclidian distance based on standardized square root transformed data sets of physicochemical variables in 30 sampling sites in the GoM and the PB; cluster I represents the GoM locations and cluster II represents PB locations, (b) salinity and (c) salinity and turbidity over laid non-metric multidimensional scaling (MDS) ordination plot visualizing difference in salinity and turbidity on spatially assembled data. Slices and contour lines show the level of resemblances in distances, symbols show the salinity and turbidity and numbers represents the stations. The locations 19 and 28 are placed away from the cluster due to exceptionally higher concentration of nitrate and turbidity respectively.

Figure 8 - Abundance of autotrophic pico and nanoplankton in (a) surface waters (b) bottom waters (c) abundance of heterotrophic bacteria and (d) abundance of heterotrophic nanoplankton in the GoM and the PB. Abbreviations: SYN- Synechococcus, APE- Autotrophic picoeukaryotes, ANP- Autotrophic nanoplankton, HB – Heterotrophic bacteria, HNP- Heterotrophic nanoplankton

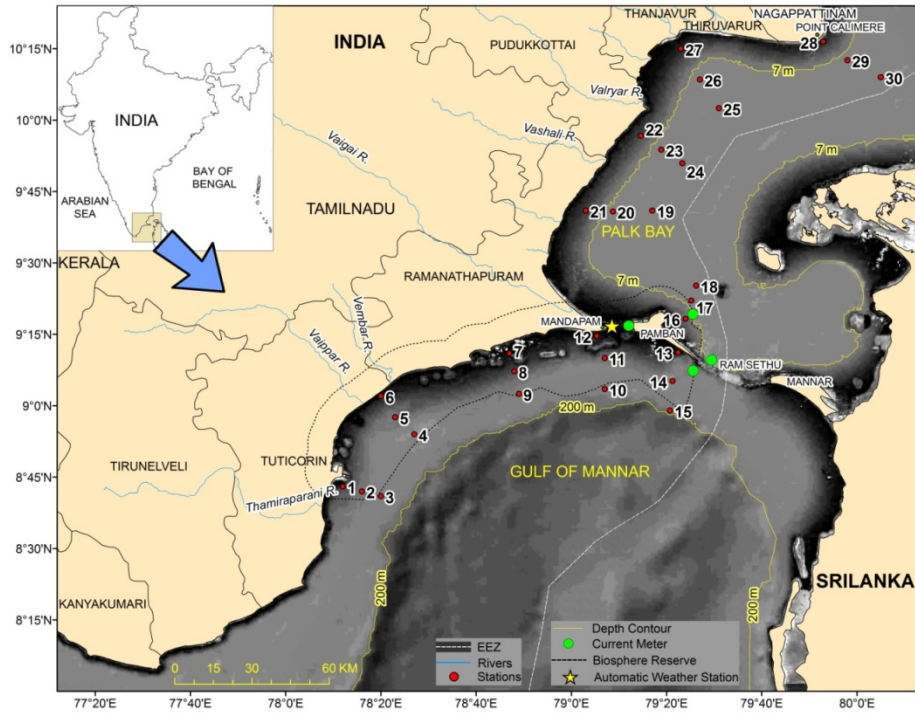


Figure 1a

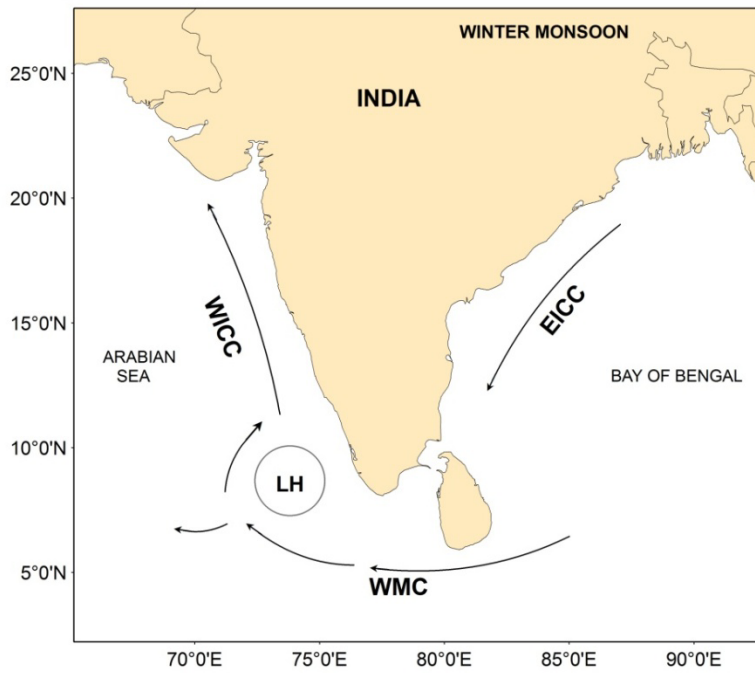


Figure 1b

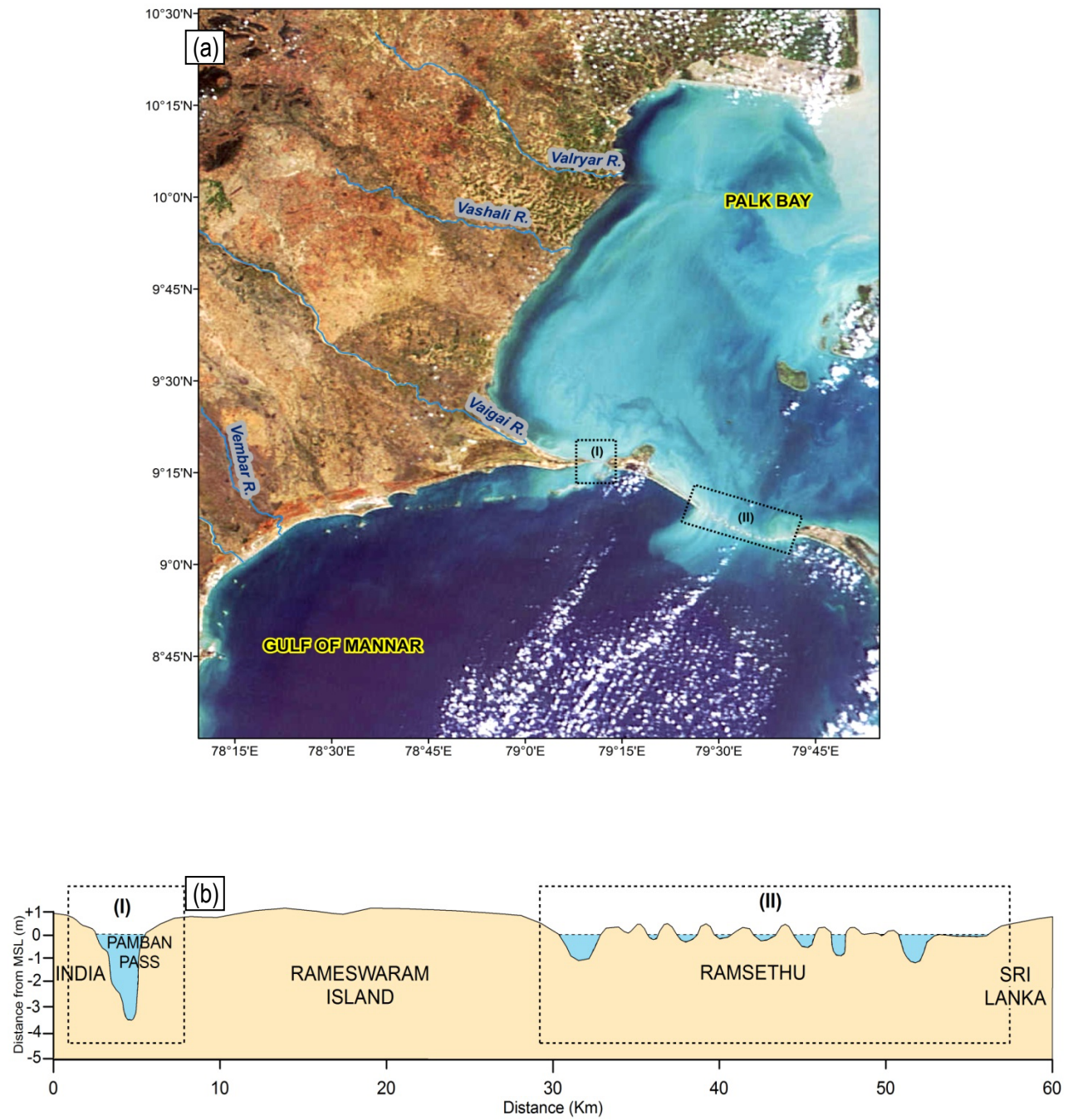


Figure 2

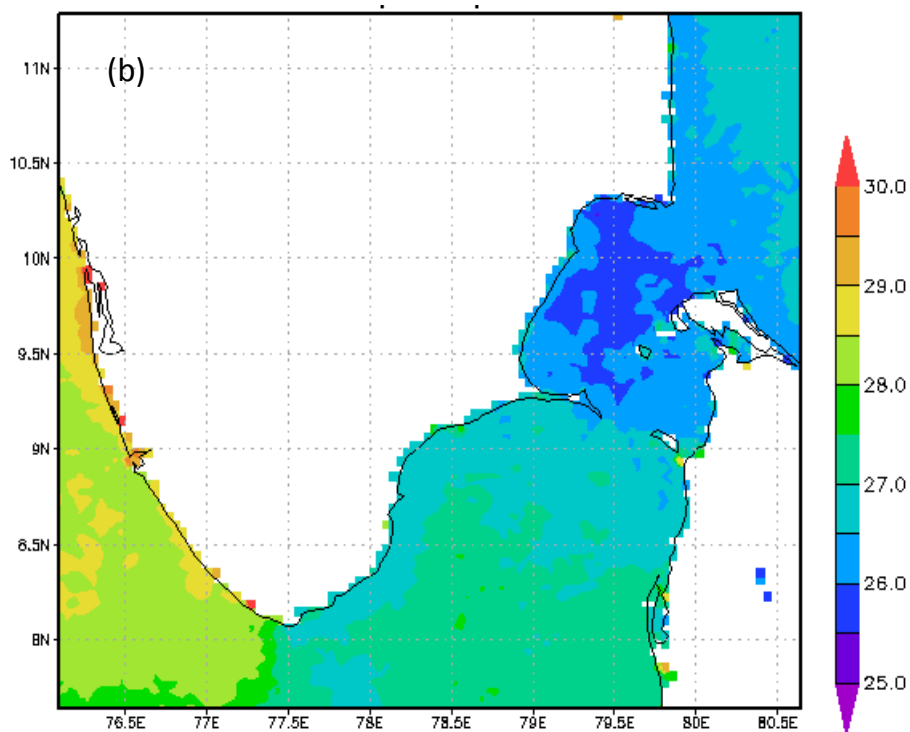
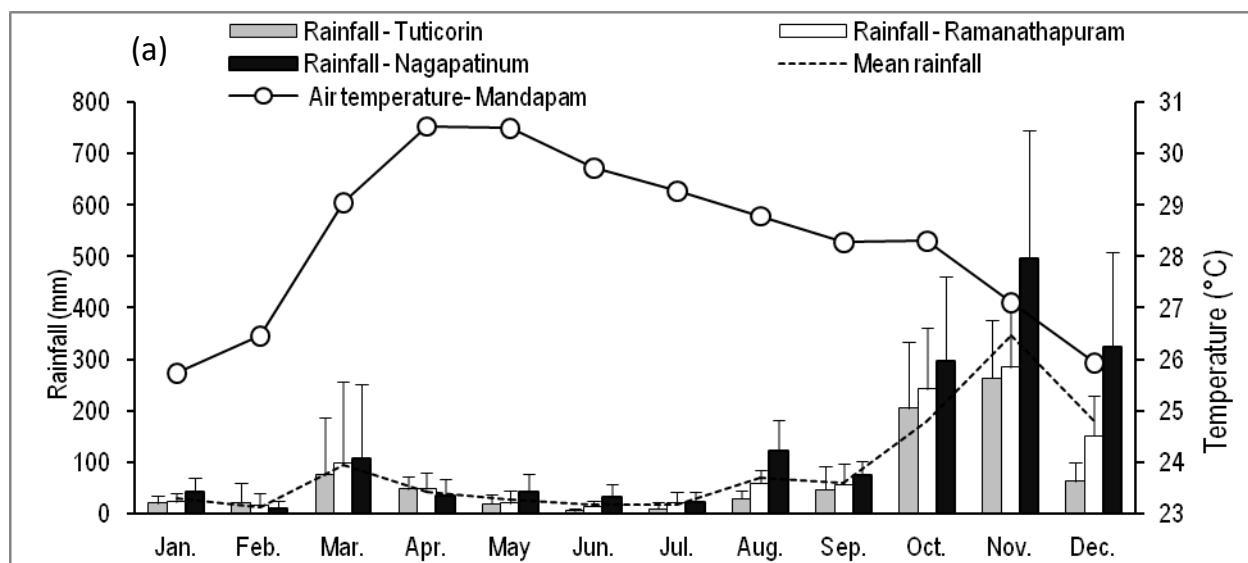


Figure 3

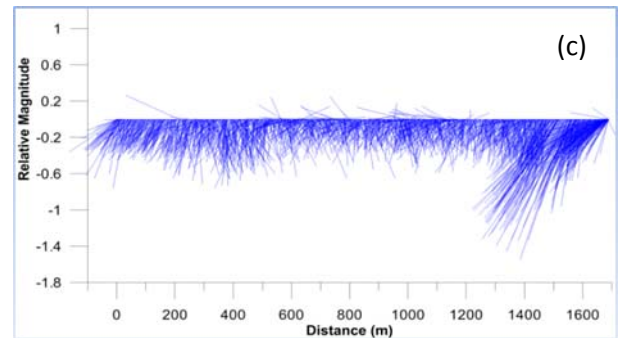
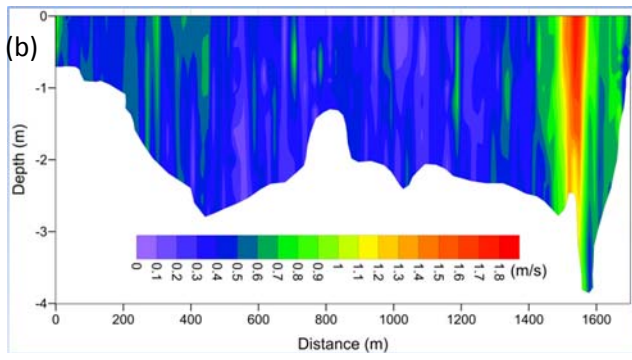
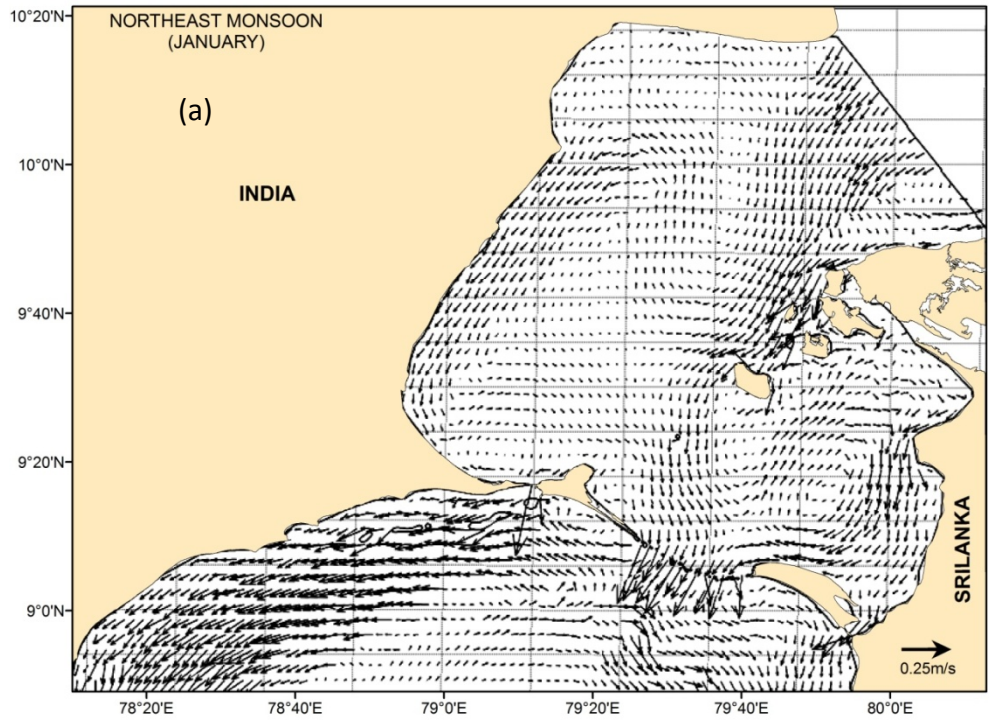


Figure 4

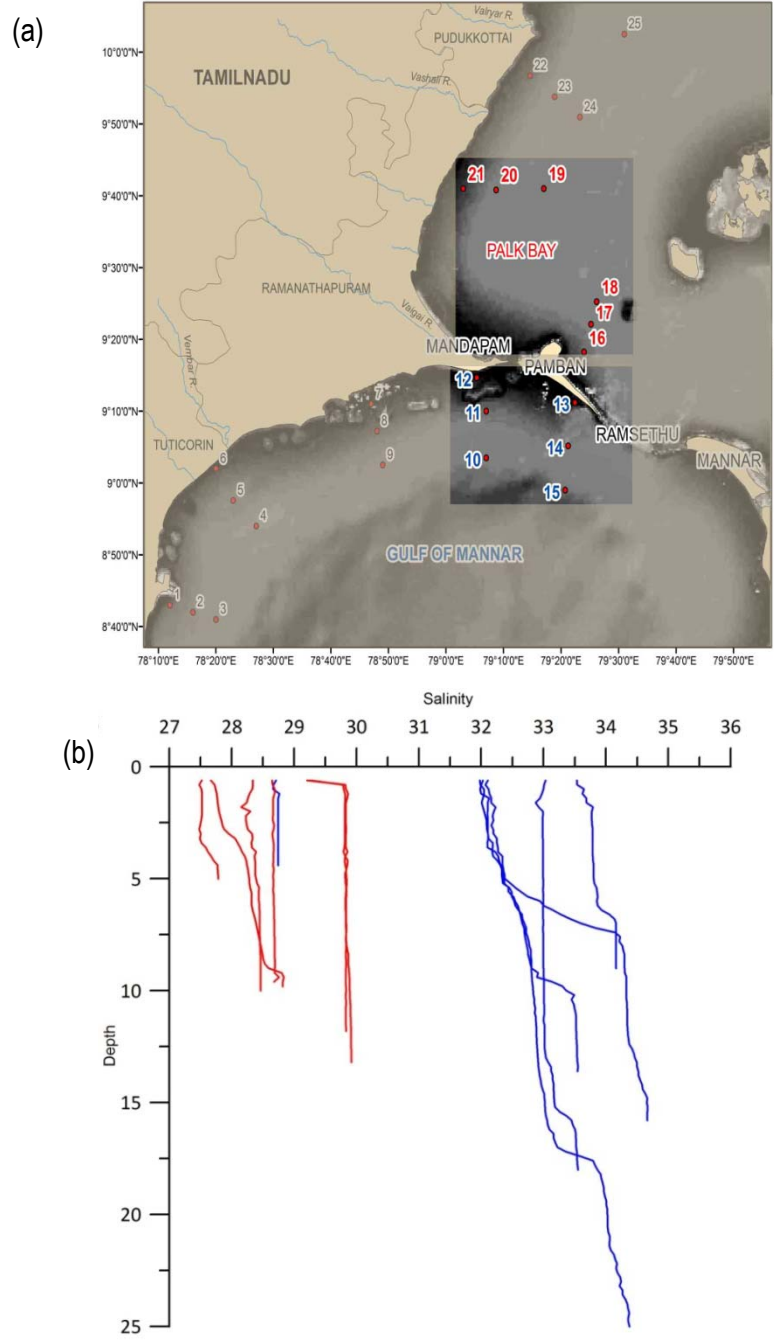


Figure 5

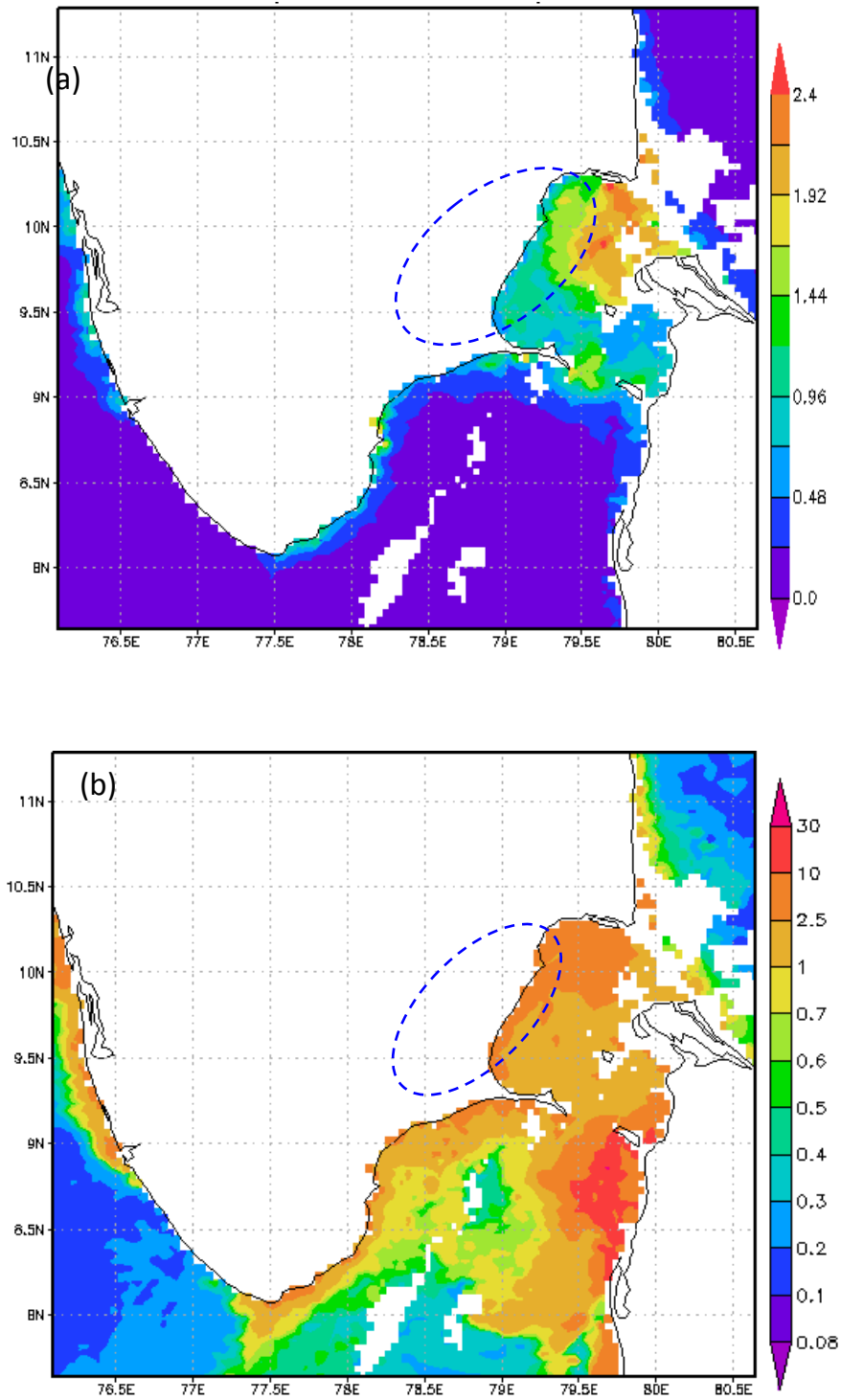


Figure 6

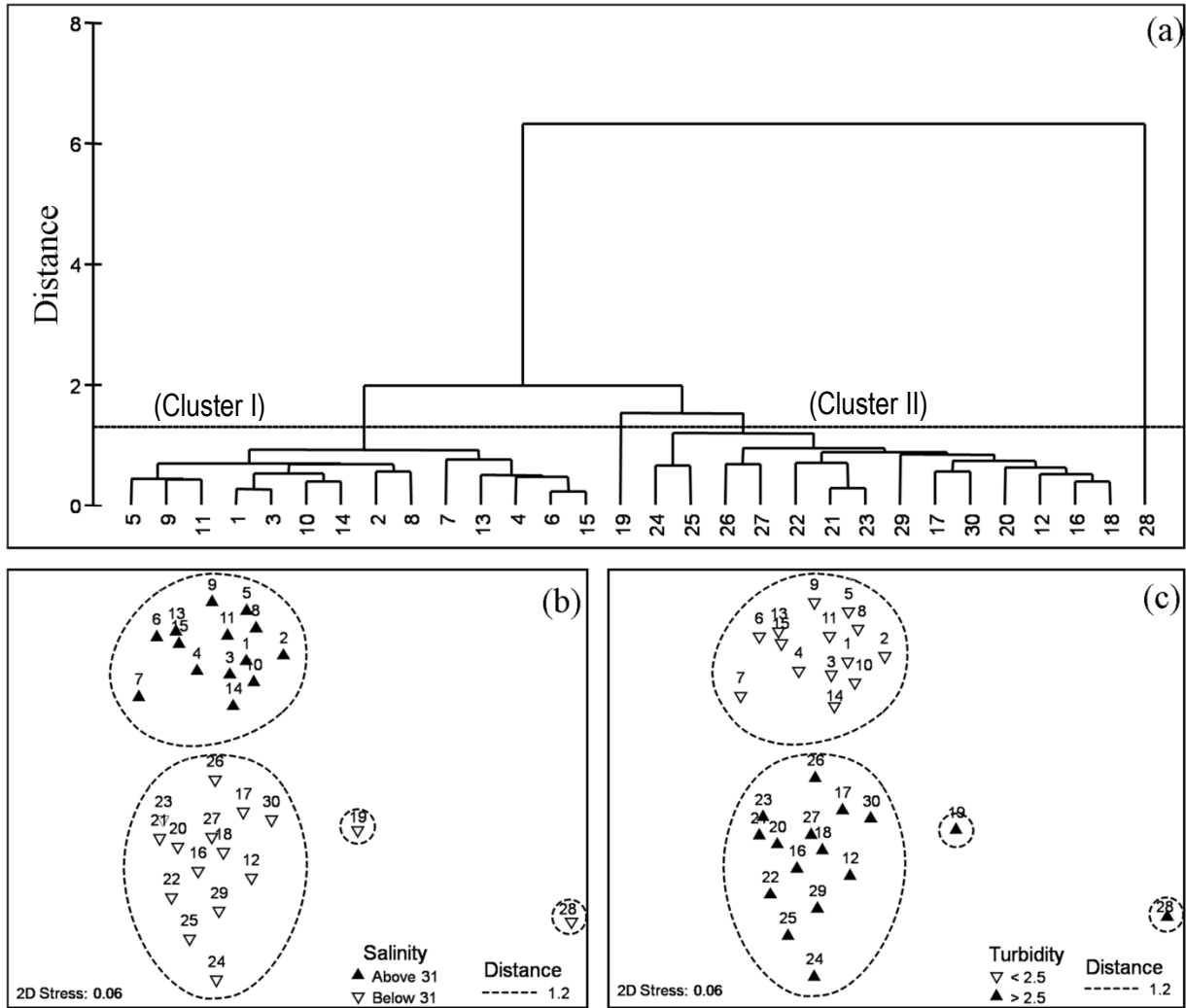


Figure 7

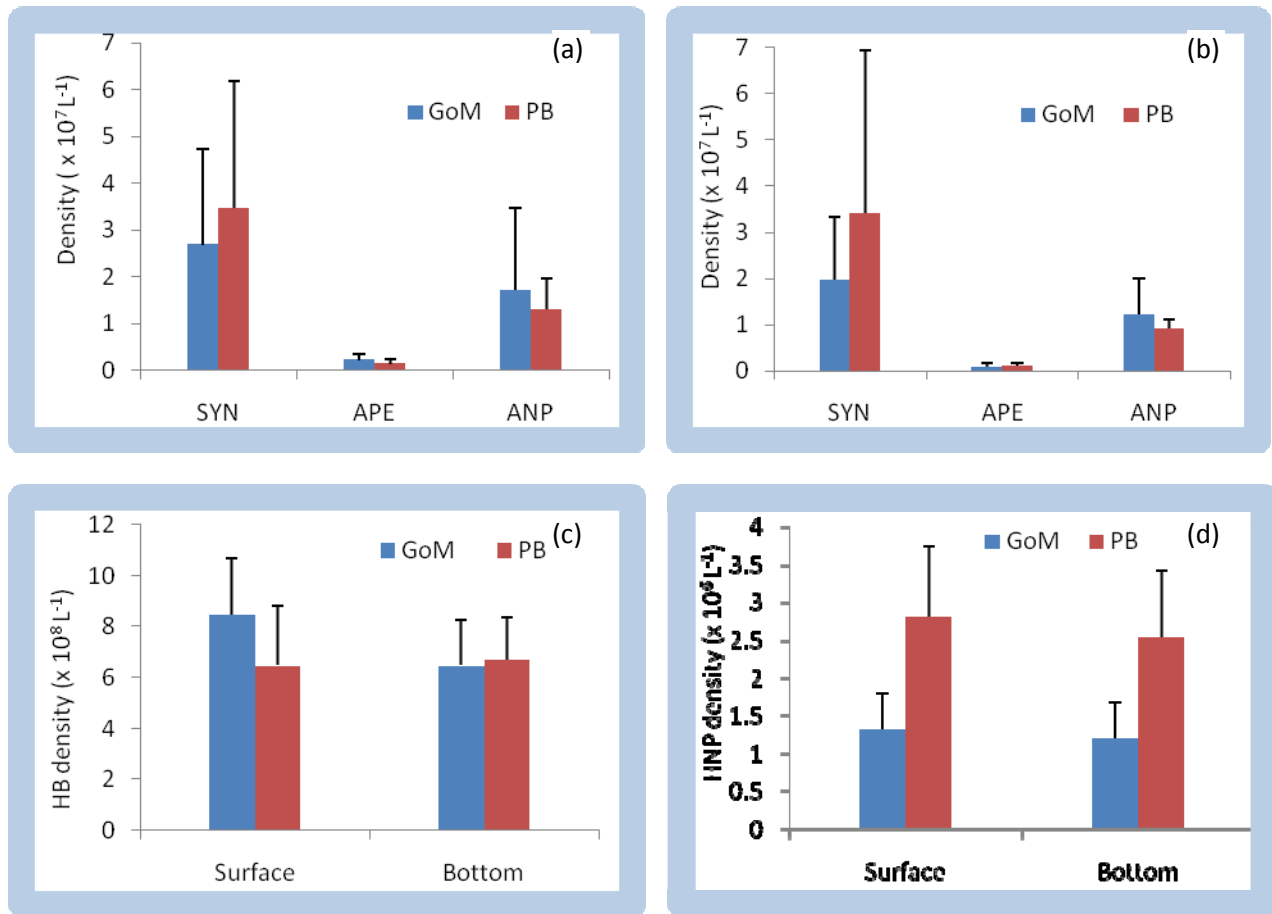


Figure 8

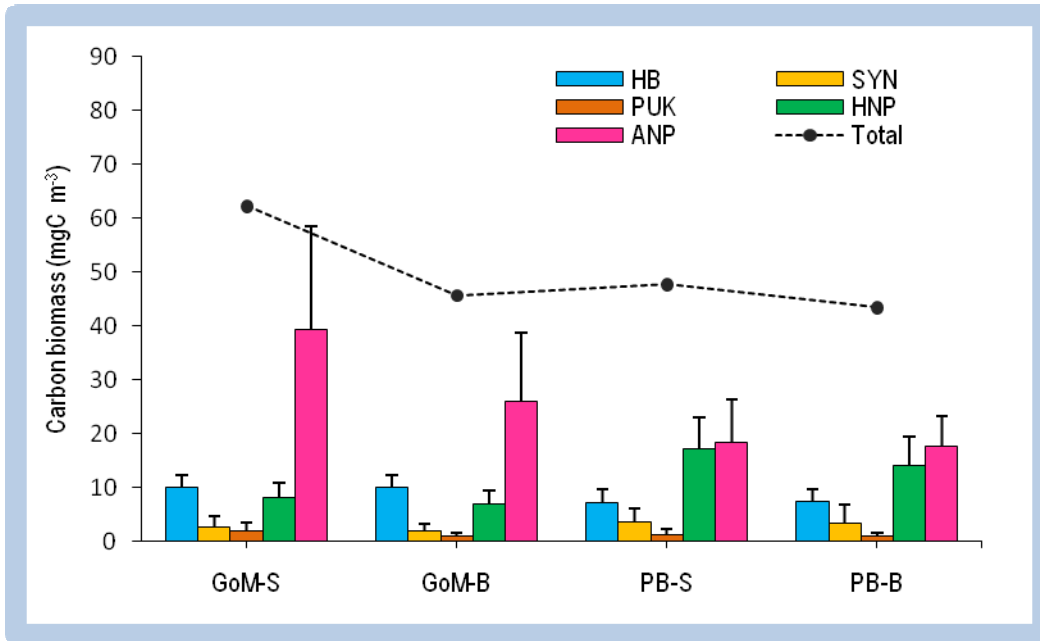
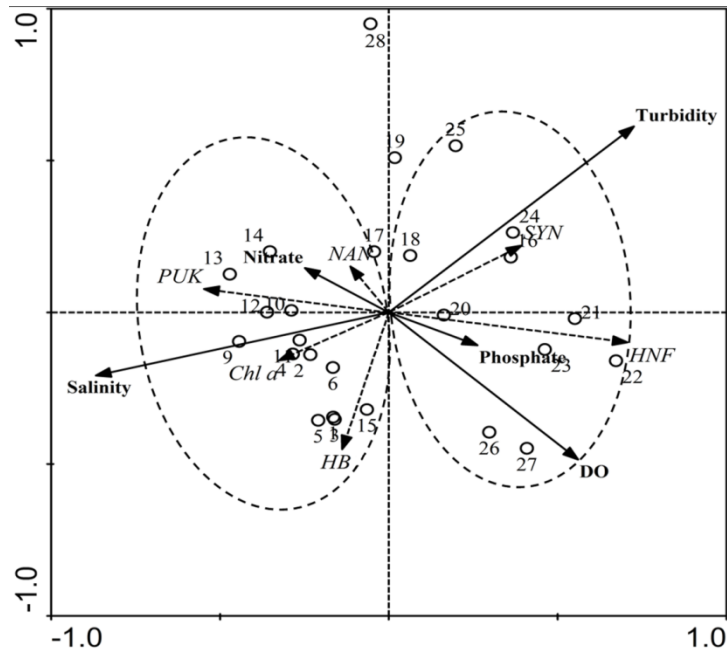


Figure 9



Analysis	Axes				
	1	2	3	4	Total variance
Complete RDA^a					
Eigen values	0.183	0.039	0.012	0.007	1.000
Species-environment correlations	0.759	0.381	0.273	0.197	
Cumulative percentage variance of species data	18.3	22.3	23.5	24.2	
Cumulative percentage variance of species-environment relation	75.8	92.0	97.0	100.0	
Sum of all canonical Eigen values					0.242
Partial RDA^b					
Eigen values	0.161	0.038	0.009	0.338	1.000
Species-environment correlations	0.740	0.385	0.364	0.000	
Cumulative percentage variance of species data	16.7	20.6	21.5	56.5	
Cumulative percentage variance of species-environment relation	77.5	95.8	100.0	0.0	
The sum of all eigen values is after fitting covariables					0.966
Sum of all canonical eigen values after fitting covariables					0.208

^a Complete RDA considering all environmental variables, ^b Partial RDA considering salinity, turbidity and DO as the environmental variables; phosphate and nitrate as the co-variables

Figure 10

Locations	Latitude (°N)	Longitude (°E)	Depth (m)
1	8.72	78.20	4
2	8.70	78.27	15.2
3	8.68	78.33	25.6
4	8.90	78.45	18.6
5	8.96	78.38	11.4
6	9.03	78.33	3.6
7	9.18	78.78	6.8
8	9.12	78.80	11.8
9	9.04	78.82	18.8
10	9.06	79.12	18.2
11	9.17	79.12	13.8
12	9.24	79.09	4.6
13	9.19	79.37	9.2
14	9.09	79.35	16
15	8.98	79.35	32.2
16	9.30	79.40	9.8
17	9.36	79.42	13.4
18	9.39	79.43	12
19	9.68	79.28	10
20	9.68	79.15	10.2
21	9.68	79.05	5.2
22	9.95	79.24	4.6
23	9.90	79.31	7.8
24	9.85	79.39	12.8
25	10.04	79.52	11
26	10.14	79.45	9.2
27	10.25	79.38	5.8
28	10.28	79.88	7.6
29	10.21	79.97	8.8
30	10.15	80.08	12.6

Table 1- Station positions and their bottom depth in the GoM (1-15) and the PB (16-30). Large variations are evident in the bottom depth in different locations.

Parameters	GoM		PB	
	Surface	Bottom	Surface	Bottom
Temperature (°C)	(26 ± 0.49)	(26.94 ± 0.22)	(25.45 ± 0.61)	(25.73 ± 0.32)
Salinity	(31.96 ± 0.58)	(32.89 ± 1.40)	(28.98 ± 1.34)	(29.74 ± 1.32)
Turbidity (NTU)	(1.76 ± 1.38)	(2.73 ± 1.87)	(7.84 ± 13.59)	(11.32 ± 18.83)
DO (mg L ⁻¹)	(7.92 ± 0.75)	(6.74 ± 1.18)	(8.27 ± 1.24)	(7.64 ± 1.11)
PO ₄ (µM)	(0.24 ± 0.11)	(0.41 ± 0.21)	(0.26 ± 0.13)	(0.35 ± 0.18)
NO ₃ (µM)	(0.49 ± 0.31)	(0.60 ± 0.43)	(0.45 ± 0.47)	(0.53 ± 0.62)
Chl. <i>a</i> (mg m ⁻³)	(1.79 ± 1.62)	(1.58 ± 1.33)	(0.76 ± 0.49)	(0.73 ± 0.44)
Microplankton - Chl. <i>a</i>	(0.24 ± 0.19)	(0.11 ± 0.09)	(0.11 ± 0.07)	(0.09 ± 0.07)
Nanoplankton - Chl. <i>a</i>	(1.49 ± 1.19)	(1.38 ± 0.91)	(0.61 ± 0.31)	(0.6 ± 0.43)
Picoplankton - Chl. <i>a</i>	(0.06 ± 0.04)	(0.09 ± 0.07)	(0.04 ± 0.02)	(0.04 ± 0.03)

Table 2- Distribution of major hydrographical parameters in the GoM and the PB. Cool, low saline and turbid Bay of Bengal waters intruded in to the PB is evident.