

## Ocean currents structuring the mesozooplankton in the Gulf of Mannar and the Palk Bay, southeast coast of India

Jagadeesan, L<sup>1</sup>., Jyothibabu, R<sup>1\*</sup>., Anjusha, A<sup>1</sup>., Arya P. Mohan<sup>1</sup>.,  
Madhu, N.V., Muraleedharan, K. R<sup>1</sup>., Sudheesh, K<sup>2</sup>

<sup>1</sup>CSIR National Institute of Oceanography, Regional Centre, Kochi – 682018

<sup>2</sup>CSIR National Institute of Oceanography, Dona Paula, Goa – 403004

\*Corresponding author, Email: rjyothibabu@nio.org

---

### Abstract

The Gulf of Mannar and the Palk Bay, located between India and Sri Lanka, are the two least studied marine environments in the northern Indian Ocean. We hypothesize, perceptible physical barriers that exist between the deep Gulf of Mannar and shallow Palk Bay, and seasonally reversing surface circulation patterns in the region have a concerted effect on the ecology of these oceanographically important areas. In the present study, data collected from 30 locations in the Gulf of Mannar and the Palk Bay in March 2010 (Spring Intermonsoon), September 2010 (Southwest Monsoon) and January 2011 (Northeast Monsoon) were used to investigate the role of ocean currents in molding mesozooplankton community characteristics in these, geographically closer and ecologically important transitional zones. Spatial difference in salinity was evident in the area with consistently higher values in the Gulf of Mannar as compared to the Palk Bay. The surface salinity was maximal during the Southwest Monsoon followed by the Spring Intermonsoon, and the Northeast Monsoon. These variations in salinity were closely linked with the seasonally reversing ocean currents as revealed in MIKE 21 flow model results. The mesozooplankton community dominated by copepods showed significant difference in species richness between the Gulf of Mannar (81 species) and the Palk Bay (63 species). Non-metric Multidimensional Scaling (NMDS) and Agglomerative Hierarchical Cluster Analysis (AHCA) on Bray-Curtis copepod similarity clearly estranged the Gulf of Mannar and the Palk Bay waters during the Spring Intermonsoon, and the Northeast Monsoon, attributable to the truancy of durable mixing typical of these seasons. In contrast, aided by strong currents, the increased mixing resulted in a homogenous copepod population in the Gulf of Mannar and the Palk Bay during the Southwest Monsoon. Furthermore, the indicator and dominant species analysis for copepods divulged the spatial heterogeneity in species composition during the Spring Intermonsoon and the Northeast Monsoon periods. Multivariate Redundancy Analyses showed salinity as the most important variable accountable for the observed variance in copepod distribution. In general, the copepod community in the Gulf of Mannar was composed both of coastal and offshore species whereas, coastal species largely inhabited the Palk Bay. This kind of a study depicting zooplankton community organization as governed by seasonally reversing monsoon circulation patterns forms the first record from the Indian coastal waters. The findings attain absolute significance considering its ecological implications on oceanographically transitional systems like the Gulf of Mannar, and the Palk Bay.

---

Key words: zooplankton, copepods, currents, multivariate analysis, Gulf of Mannar, Palk Bay, Arabian Sea, Bay of Bengal

## 1. Introduction

The Gulf of Mannar (GoM) and the Palk Bay (PB) are located between India and Sri Lanka. The GoM opens to the Arabian Sea (AS) in the west and the PB opens to the Bay of Bengal (BoB) in the east. The GoM is separated from the PB by Pamban (Rameswaram) Island and a chain of submerged sandbars known as Ramsethu or Adams Bridge (Figure 1a). The Ramsethu acts as a subsurface physical barrier between the Rameswaram Island of India and Mannar Island of Sri Lanka. The PB waters have more characteristics of the BoB such as lower salinity and higher turbidity (Rao et al., 2008). Conversely, the GoM has a narrow shelf and steeply sloping sea floor, which cause the oceanic waters flow closer to the coastline (Kumaraguru et al., 2006). Thus the GoM waters possess intermediate characteristics of the AS and the PB (Rao et al., 2008).

In marine pelagic food web, zooplankton plays a significant role in transferring organic carbon from the phytoplankton and bacteria to higher trophic levels. Zooplankton serves as a measure of biological productivity and responds to any subtle changes in physical, chemical and biological parameters in their surroundings due to their short generation times (Anger, 2003; Beaugrand, 2004; Bonnet and Frid, 2004; Queiroga and Blanton, 2004). In recent years, there has been an upsurge of scientific interest elsewhere to understand the importance of ocean currents in structuring the mesozooplankton community (Skarðhamar et al., 2007; Heish et al., 2004; Hwang and Wong, 2005; Hwang et al., 2006; Kâ and Hwang, 2011; Chen et al., 2011; Hsiao et al., 2011). Albeit the ocean currents around the Indian subcontinent had been documented over the last several decades, their role in structuring the zooplankton community is still unknown (Jyothibabu et al., 2008).

The currents along the eastern and western coasts of India link the open ocean monsoon currents with the coastal circulation. During the Northeast Monsoon (November to February), the equator ward flowing East India Coastal Current (EICC) carries the low saline waters from the northern BoB to the south and feed the westward flowing Winter Monsoon Current (WMC) (Figure 1b). After turning around Sri Lanka, one branch of WMC carries the low saline BoB waters northward and feed the West India Coastal Current (WICC) along the west coast of India. During this time, EICC and WICC maintain continuous flow from the northern BoB to the northern AS (Shetye and Gouveia., 1998; Shetye., 1999; Shenoi, 2010). As a result, the low saline BoB waters occupy the surface waters of the southeastern AS (Shetye et al., 1993; Shankar et al., 2002), which have many biological implications (Jyothibabu et al., 2008). During the Southwest Monsoon (June to September), WICC flows southward carrying high saline AS waters and feed the eastward flowing Summer Monsoon Current (SMC), which turns around Sri Lanka and one of its branch feed northward flowing EICC along the southeast coast of India (Shetye, 1999; Vinayachandran et al., 2005). As a result, high saline waters occupy the southwest BoB during the Southwest

Monsoon (Vinayachandran et al., 1999). The Spring Intermonsoon (March - April) is a transition period from the Northeast Monsoon to the Southwest Monsoon during which the WICC along the southwest coast of India changes its direction and flows southward. During the Spring Intermonsoon, the WMC south of Sri Lanka weakens and the northward flowing EICC strengthens along the central and northeast coast of India setting up the retreating phase of the Northeast Monsoon (Shetye et al., 1993; Shankar et al, 2002).

Even though we have fairly clear understanding on the large scale circulation pattern around India and Sri Lanka, very little is known about the ocean currents in the GoM and the PB (Rao et al., 2008). Silas (1968) has described the seasonal water currents in the GoM using the surface current charts of Southwell and Kerkham, (1912). This current chart was based on the recovery of drift bottles released during different times at Cape Comorin and off Colombo. The study has shown that the direction of the currents during the onset of Southwest Monsoon is from the GoM to the PB. During the peak Southwest Monsoon, the oceanic water mass intrudes into the GoM and results in an increase in sea surface height at the head of the GoM near Ramsethu (Silas, 1968; Rao et al., 2008). During the Northeast Monsoon, the current reversal was noticed as some of the drift bottles released on the west coast of Sri Lanka were recovered from the southwest coast of India indicating northward flow of WICC carrying low saline waters from the BoB to the AS. Recently, it was found that the BoB waters intrudes into the PB during the Northeast Monsoon and flows towards the GoM (Rao et al., 2011). However, the subsurface physical barrier of Ramsethu inhibits this intruded BoB waters from making any significant influence on the hydrography of the GoM (Rao et al., 2011).

Earlier studies on zooplankton in the Indian seas with respect to the ocean physics are mostly limited to the upwelling and eddies (Madhupratap et al., 1990, 1996 & 2001; Rakhesh et al., 2006 & 2008; Fernandes and Ramaiah, 2009) and there is virtually no information available on the influence of ocean currents on the zooplankton community along the Indian coasts (Jyothibabu et al., 2010). Similarly, there is a severe lack of quantitative information on zooplankton community from the GoM and the PB. This is important when considering the amount of scientific effort placed in understanding the zooplankton community in the adjacent AS and the BoB over the years (Nair et al., 1981; Achuthankutty et al., 1980; Madhupratap and Haridas, 1990; Martin Thompson, 1990; Smith et al., 1998; Smith and Madhupratap, 2005; Rakhesh et al., 2006 & 2008; Fernandes, 2008; Fernandes and Ramaiah, 2009). The sparse information available on the zooplankton community from the GoM and the PB are largely based on qualitative historical studies, which mainly addressed taxonomy and breeding biology of different zooplankton groups (Sewell, 1914; Prasad et al., 1952; Prasad, 1954; 1956; 1958; Kartha, 1959; Ummerkutty, 1967a & b).

This paper, based on extensive seasonal sampling in the Indian sector of the GoM and the PB, provides comprehensive information on the role of seasonally changing hydrography in structuring the zooplankton community patterns. Considering the geographic location of the study area and the ocean circulation around the Indian subcontinent, we propose that there could be noticeable differences in zooplankton community in the GoM and the PB. In order to verify this hypothesis, studies were carried out in the GoM and the PB with the following objectives (a) to understand the seasonal hydrography in the GoM and the PB (b) to generate the qualitative and quantitative data on mesozooplankton community especially copepods in the GoM and the PB (c) to study the role of ocean currents in structuring the zooplankton community in the GoM and the PB.

## 2. Study area, sampling and methods

### 2.1. The GoM

The GoM under the Indian EEZ is about 15,000 km<sup>2</sup>, which extends from Tuticorin to Mandapam over a distance of 140 km along the Indian coastline (Figure 1a). The waters of GoM are transitional between the oceanic conditions of the Arabian Sea and coastal conditions of the PB (Rao et al., 2008). The Rameswaram Island of India, the submerged island chain Ramsethu (Adam's Bridge) and Mannar island of Sri Lanka act as physical barriers between the GoM and the PB (Rao et al., 2011; also see supplementary material 1). As a result, the BoB waters have more influence on the PB hydrography, while the GoM waters influences the PB to a very limited extent only (Murty and Varma, 1964). There are 21 coral islands in the GoM covering an area of about 623 ha. Fringing and patchy type coral reefs occur in the shallow sea floor of these Islands between 2 and 10 km away from the Indian coastline (Kumaraguru et al., 2006). The GoM is known for its high pelagic fishery resources and commercial fishing grounds (5,500 km<sup>2</sup>). The species diversity in the GoM include 117 species of corals, 641 species of crustaceans, 731 species of mollusks, 441 species of fin fishes, 147 species of seaweeds and 12 species of sea grasses (Rao et al., 2008). Apart from these, there are seasonally migrating whales, dolphins and porpoises. The endangered dugongs and turtles inhabit the GoM. There are large patches of mangrove vegetation along the coastline and also around the islands (Kumaraguru et al, 2006). Three minor Rivers Tamiraparani, Vembar and Vaipar empty into the GoM (Rao et al., 2008). In order to protect and conserve the rich biodiversity of the GoM, the Indian part of the GoM, covering an area of 10500 km<sup>2</sup>, has been declared as a Biosphere Reserve by the Government of India (Figure 1a).

## 2.2. The PB

The PB encompasses an area of about 12285 km<sup>2</sup> with the GoM in the south and the BoB in the north. It extends from Pamban in the south to Point Calimer in the north with a distance of 280 km (Figure 1a). It is a shallow, and more enclosed basin compared to the GoM with an average depth of 5 meters. The PB and the Palk Strait are together known as Sethusamudram, which is a wide (17000 km<sup>2</sup>) and shallow basin with an average depth of 5 meters. The PB is a large reservoir of suspended sediments brought from the BoB during the Northeast Monsoon period (Figure 2a). There are only limited stretches of coral reefs in the PB, which lies about 200 to 600 m away from the shore in the Pamban - Rameswaram area (Kumaraguru et al., 2008). The PB is known for its diverse biological resources in seagrass beds found in the tidal and sub-tidal areas (Sridhar et al., 2010; Manikandan et al., 2011; Balasubramanian et al., 2011) and also for its economically important demersal fishery resources (prawns and crabs). The seagrass meadows function as specialized ecosystem serving as feeding, breeding and nursery ground for many fishes, shrimps, and crabs. The rivers Vaigai, Vaishali and Vaiyar are the major sources of freshwater and sediment input to the PB (Rao et al., 2008). The tidal amplitude in the PB is low (0.5 to 0.8 m) (Durve and Alagarswami, 1964; Rao et al., 1987; Nayar et al., 1988). There are mangrove swamps and wild life sanctuaries in the PB, which are associated with mud flats, wet lands, brackish water and saline lagoons.

## 2.3. Sampling and methods

The field sampling was carried out in 30 locations (15 each in the GoM and the PB) in March 2010 (spring-intermonsoon), September 2010 (Southwest Monsoon) and January 2011 (Northeast Monsoon). The locations were distributed in 10 transects (5 each in the GoM and the PB), oriented perpendicular to the coastline (Figure 1a). Each transect consisted of 3 locations; coastal, middle and inshore. In each location, water samples were collected from surface using 5 L Niskin samplers (Hydrobios-Kiel) for measuring chlorophyll *a* and dissolved oxygen. General climatic features in the GoM and the PB were inferred from (a) air temperature data from AWS installed at Mandapam (midpoint between the GoM and the PB) and (b) the mean rainfall data for the last five years (Indian Meteorological Department (IMD), Pune) for the districts of Tuticorin, Ramnathapuram and Nagapattinam (three major districts bordering the study area). The vertical salinity and temperature features were recorded using a portable Conductivity Temperature Depth profiler. The synoptic picture of the currents and estimations of exchange of waters between the GoM and the PB were obtained using model simulations. The circulation in the GoM and the PB has been simulated with MIKE 21 FM model. The model has been validated with currents measurements using RCM9 current meters deployed at selected locations in the study area (Figure 1a), which showed significant correlation between the observed and simulated features (NIO Report 2012; Sudheesh et al., 2012; also see

supplementary materials 2 a, b & c). During the Northeast Monsoon, intrusion of low saline PB waters into the GoM was investigated by deploying an ADP across the Pamban Pass (between Mandapam and Pamban Island).

The dissolved oxygen was measured from the surface waters following Winkler's method (Grasshoff et al., 1983) and chlorophyll *a* using a Turner fluorometer following standard procedure (UNESCO, 1994). Zooplankton samples were collected from waters just below the surface (~0.5m) by horizontal hauls using a standard WP net (200  $\mu$ M mesh size), attached with a calibrated digital flow meter (Hydro-bios, Germany). Onboard, the samples were filtered through a 200  $\mu$ m nylon sieve and excess water in the samples was removed using blotting papers. The biomass of the zooplankton was measured as displacement volume (Postel et al., 2000). Zooplankton samples were then preserved in 4% formalin in filtered seawater for detailed taxonomic analysis. Zooplankton sub-samples (50%) were sorted and taxonomic group level abundance was estimated (Postel et al., 2000). Among various taxonomic groups, copepods were further analyzed and identified down to the species level using standard literature (Tanaka 1956; Kasturirangan 1963; Sewell, 1999; Conway et al., 2003).

### 2.3.1. Data analysis

In order to study the spatial and seasonal variation in environmental and biological parameters in the GoM and the PB, the data collected were tested for their normality in distribution. Later, parametric ANOVA was carried out on data having normal distribution. The Tukeys HSD post hoc test was used to compare the significance of pair wise variations obtained in parametric ANOVA. On the other hand, non-parametric ANOVA was used for data having irregular distribution. Here, Dunn's post hoc test was used to analyze the significance of pair wise differences. The tests of normality, parametric and nonparametric ANOVA were carried out in XL stat pro- software package.

### 2.3.2. Segregation of locations and dominant species

Cluster analysis followed by NMDS was used to segregate locations with similar properties. Copepod species abundance data were initially log ( $X+1$ ) transformed to normalize the differences in numerical abundance (Clarke and Warwick, 2001). The Bray - Curtis similarity matrix based on group average method was used for the spatial grouping of locations in different seasonal collections. In addition to cluster analysis, similarity profile (SIMPROF) permutation test was also performed to identify significant assemblages of stations ( $p < 0.01$ ) (Clarke and Gorley, 2006).

The dominant species (common and numerically abundant species) of copepods in each group of locations was analyzed based on standard procedures (Yang et al., 1999, Lee et al., 2009, Lin et al., 2011)

$$Y_i = (N_i / N) \times f_i$$

Where,  $Y_i$  is the dominance of species  $i$ ,  $N_i$  is the number of individuals of species  $i$  in all locations,  $N$  is the number of individuals of all species in all locations, and  $f_i$  is the frequency of locations at which species  $i$  occurs. Species of copepods with a  $Y$  value of more than or equal to 0.02 were defined as dominant species (Yang et al., 1999, Lee et al., 2009, Lin et al., 2011).

### 2.3.3. Diversity and indicator species

The diversity of plankton communities were represented using three common diversity indices (i) Pielou's evenness ( $J'$  - Pielou, 1969), (ii) Simpson's dominance ( $C$  - Simpson 1949) and (iii) Shannon Wiener diversity ( $H'$  - Shannon and Wiener, 1963).

The statistical index, Indicator value (IndVal), is used to find out the most characteristic species in each group of locations (Dufrene and Legendre., 1997). IndVal explains whether the species assemblages are symmetric or dissymmetric between different groups of locations. This method takes into account combined measures of group specificity ( $A_{ij}$ ) and group fidelity ( $B_{ij}$ )

$$A_{ij} = N_{ij} / N_i \quad (1)$$

$$B_{ij} = n_j / n_{.i} \quad (2)$$

Here,  $N_{ij}$  is the mean number of individuals of species  $i$  in the samples of group  $j$ , while,  $N_i$  is the sum of the mean numbers of individuals of species  $i$  over all groups.  $n_j$  is the number of samples in group  $j$  where species  $i$  is present, while  $n_{.i}$  is the number of samples in group  $j$ .

$$\text{Subsequently, the IndVal was calculated as; } \text{IndVal} = A_{ij} * B_{ij} * 100 \quad (3)$$

The values of  $A$  and  $B$  represent independent information about species distribution, and multiplied by 100 to get the percentages. IndVal become the maximum (100%) when all the individuals of a species are found in a single group of locations, which represents the asymmetric distribution of that species between the groups. On the other hand, the IndVal become the minimum when the species is symmetrically distributed between the groups. The highest IndVal for a particular species in one cluster represent the center of distribution of that species (Hunt and Hosie, 2006, Modéran et al., 2010). According to Dufrene and Legendre, (1997), at least a minimum of 25% can be considered as the threshold level to determine IndVal species. In the present study,  $\geq 50\%$  was used as the threshold level to determining the IndVal copepods.

### 2.3.4. Redundancy analysis (RDA)

The relationships between important species of copepods (indicator and dominant species) and the environmental variables were analyzed using RDA (CANOCO 4.5). Initially, the data was analyzed using Detrended Correspondence Analysis (DCA) to select the appropriate ordination technique. The result of DCA showed axis gradient length  $< 2$ , which suggested use of linear multivariate RDA (Birks, 1998; Leps and Smilauer, 2003) analysis for the present data. The biological variables were log transformed and centered prior to the analysis. Partial RDA was also carried out to find out which parameter contributes more to the total variance of species. 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 which, the samples are displayed by points, and species and quantitative environmental variables are shown by arrows.

## 3. Results

### 3.1. Temperature, rainfall and coastal currents

The monthly mean air temperature and rainfall in the study area are presented in Figure 2b. The air temperature showed an increase from January ( $25.5\text{ }^{\circ}\text{C}$ ) to April – May ( $30.5\text{ }^{\circ}\text{C}$ ) and then a decrease towards December ( $25.9\text{ }^{\circ}\text{C}$ ). The SST was higher during the Spring Intermonsoon and the Southwest Monsoon as compared to the Northeast Monsoon (Table 1). During the Spring Intermonsoon, SST was higher in the PB (av.  $31.47 \pm 0.81\text{ }^{\circ}\text{C}$ ) as compared to the GoM (av.  $30.31 \pm 1.20\text{ }^{\circ}\text{C}$ ) whereas, the GoM had higher SST (av.  $26.55 \pm 0.49\text{ }^{\circ}\text{C}$ ) than the PB (av.  $25.45 \pm 0.61\text{ }^{\circ}\text{C}$ ) during the Northeast Monsoon. However, the difference in SST between the GoM and the PB was found to be minor during the Southwest Monsoon (av.  $29.64 \pm 1.11\text{ }^{\circ}\text{C}$  and av.  $30.29 \pm 0.64\text{ }^{\circ}\text{C}$ , respectively). The study area is characterized by very little rain in January and February (Figure 2b). The mean rainfall data clearly shows a wet period in the study area from October to December and an arid climate rest of the time (Figure 2b).

The surface currents in the GoM and the PB are closely linked with the general monsoon circulation around the Indian subcontinent (Figure 1b). It is evident from the model simulations that there is a seasonal reversal in water exchange between the GoM and the PB (Figure 3). The currents are weak except in the channels during the Northeast Monsoon and Spring Intermonsoon as compared to the Southwest Monsoon. During the Northeast Monsoon, weak currents in the PB was directed to the west and flowed towards the Pamban pass and Ramsethu. During the Southwest Monsoon, currents become strong and flow from the west to east. As a result the current along the Indian coast in the GoM flow towards the PB. The flux estimations from the model simulations clearly



showed the difference in the water volume exchange between the GoM and the PB during different time scales (Figure 4). It is very clear that the volume exchange of waters between the GoM and the PB during the Southwest Monsoon is significantly higher as compared to any other seasons.

### 3.2. Salinity

During all the seasons, sea surface salinity was higher in the GoM as compared to the PB (Table 1). A distinct seasonality in salinity distribution was evident in the study area with the highest during the Southwest Monsoon followed by the Spring Intermonsoon and the Northeast Monsoon. The spatial difference in salinity between the GoM and the PB were statistically significant during the Spring Intermonsoon and Northeast Monsoon ( $p < 0.05$ ). On the other hand, significant differences in salinity distribution could be observed within the GoM and the PB during the Southwest Monsoon compared either to the Spring Intermonsoon or the Northeast Monsoon (Table 1).

The vertical distribution of salinity in two transects on both sides of Ramsethu in the GoM and the PB shows a clear difference of  $> 2$  salinity during the Spring Intermonsoon and the Northeast Monsoon (Figure 5). However, the salinity in location 12 closest to the Pamban Pass in the GoM was low during the Northeast Monsoon. This was due to the intrusion of the low saline PB waters into the GoM through the Pamban Pass during the Northeast Monsoon, which was evident in the ADP measurements (Figure 6). In general, the difference in salinity in the GoM and the PB was prominent during the Spring Intermonsoon and the Northeast Monsoon as compared to the Southwest Monsoon. These results agree well with the surface current pattern presented in Figure 3 and the flux estimates presented in Figure 4. All these Figures clearly show that the magnitude of mixing of waters between the GoM and the PB were dissimilar during different seasons.

### 3.3. Dissolved oxygen and chlorophyll *a*

During all the seasonal observations, dissolved oxygen was in saturated levels (av.  $6.3 - 8.2 \text{ mg L}^{-1}$ ) both in the GoM and the PB (Table 1). During the Spring Intermonsoon and Southwest Monsoon, the dissolved oxygen was higher in the GoM as compared to the PB. During the Northeast Monsoon, the dissolved oxygen level was higher in the PB as compared to the GoM. The highest concentration of dissolved oxygen was recorded during the Northeast Monsoon. The dissolved oxygen values in the GoM and the PB during the Spring Intermonsoon and the Southwest Monsoon were comparable (Table 2). Throughout the study, chlorophyll *a* was fairly high ( $> 0.8 \text{ mg m}^{-3}$ ) with appreciable seasonal difference in phytoplankton standing stock between the GoM and the PB. During the Southwest Monsoon and the Northeast Monsoon, chlorophyll *a* was higher in the GoM as compared to the PB.

However, comparable concentrations of chlorophyll *a* were found in the GoM and the PB during the Spring Intermonsoon (Table 1).

### 3.4. Mesozooplankton assemblage

#### 3.4.1. Biomass and density

The zooplankton biomass in the study area ranged from 0.07 - 0.26 ml m<sup>-3</sup> (Table 1). Seasonally, zooplankton biomass distribution in the GoM followed a pattern similar to the chlorophyll *a*. No such seasonal trends could be observed in the PB (Table 1). Significant seasonal variation in zooplankton biomass was evident in the GoM and the PB ( $P < 0.05$ ). During the Southwest Monsoon and the Northeast Monsoon, zooplankton biomass was higher in the GoM as compared to the PB. Conversely, during the Spring Intermonsoon, zooplankton biomass was higher in the PB as compared to the GoM (Table 1).

The overall trend in zooplankton abundance was similar to the trend in biomass distribution (Table 2). During the Southwest Monsoon and the Northeast Monsoon, zooplankton abundance was higher in the GoM as compared to the PB. However, during the Spring Intermonsoon, zooplankton density was higher in the PB as compared to the GoM. The zooplankton density followed the biomass pattern in the GoM, which showed an increase from Spring Intermonsoon to the Northeast Monsoon. On the other hand, seasonal trend in zooplankton density in the PB showed a decline in abundance from the Spring Intermonsoon to the Southwest Monsoon and then a slight increase towards Northeast Monsoon. In the PB, the zooplankton mean abundance was prominently higher during the Spring Intermonsoon compared to the Southwest Monsoon and the Northeast Monsoon (Table 2).

#### 3.4.2. Community structure and abundance

The zooplankton community in the GoM and the PB was composed of 18 taxonomic groups. Crustaceans in general and copepods in particular dominated the zooplankton community. The major zooplankton groups were copepods, decapods and larvae, fish eggs & larvae, small gastropods and bivalves, chaetognaths and lucifers. Hydromedusae, cladocerans, mysids, amphipods and stomatopods were present less frequently and low abundance. A list of zooplankton groups found in the GoM and the PB is presented in Table 2, which shows a noticeable spatial and seasonal difference in abundance. During the Southwest Monsoon and Northeast Monsoon seasons, the abundance of copepods was higher in the GoM as compared to the PB. Conversely, during the Spring Intermonsoon, the abundance of copepods was noticeably higher in the PB as compared to the GoM. During all three seasons, the abundance of chaetognaths (major carnivore), was several orders of magnitude higher in the GoM as compared to the PB (Table 2). The other important carnivores such as hydromedusae and siphonophores

were found either in very low abundance or absent in both the GoM and the PB (Table 2). The abundance of lucifers was generally lower in both the GoM and PB during the Southwest Monsoon season (Figure 7a). Their abundance was generally higher in the GoM during the Northeast Monsoon and Spring Intermonsoon seasons when salinity was 32 to 34 (Figure 7a). On the other hand, the distribution of lucifers in the study area did not show any noticeable link with temperature. The highest abundance of gastropods and bivalves in the GoM and the PB was found during the Spring Intermonsoon. The abundance of gastropods and larvae were significantly lower in the GoM during the Southwest Monsoon and the Northeast Monsoon periods. Conversely, their abundance was higher in the PB during the Southwest Monsoon. The fish eggs and larvae showed higher abundance both in the GoM and the PB during the spring intermonsoon period (Table 2). The abundance of fish eggs and larvae did not show any noticeable relationship with salinity or temperature (Figure 7b).

The percentage contribution of major zooplankton groups showed noticeable spatial and seasonal differences, which was similar to their abundance pattern. Copepod was the predominant zooplankton in both the GoM and the PB, which typically contributed from 61 – 77% of the total abundance. But in a few cases when there was swarming of a few species of copepods or high abundance of very small species of copepods, as in the case of the GoM during the Southwest Monsoon and the PB during the Northeast Monsoon, their overall contribution increased even up to 91%. Small gastropods and bivalves also showed drastic seasonal difference in their percentage contribution. The contribution of gastropods and bivalves was high in the PB during the Spring Intermonsoon (19%) and the Southwest Monsoon (21%), but their contribution in the GoM was higher only during the Spring Intermonsoon (18%). Lucifers contributed 8% and 7% in the GoM during the Spring Intermonsoon and the Northeast Monsoon respectively but, their abundance in the PB during the respective period was very low. Chaetognaths were noticeably higher in the GoM as compared to the PB and their abundance was highest during the Southwest Monsoon.

### 3.4.3. Diversity indices of major groups

The Shannon diversity of zooplankton was generally higher in the GoM compared to the PB. The diversity index showed noticeable seasonal and spatial differences in the GoM and the PB (Table 1). The highest Shannon diversity was found during the Spring Intermonsoon followed by the Southwest Monsoon and the Northeast Monsoon. The evenness and dominance indices followed the same trend (Table 1).

### 3.4.4. Copepod composition, species diversity and dominance

#### 3.4.4.1. Density and species diversity of copepods

The density of copepods in the GoM and the PB showed spatial and temporal differences similar to the total zooplankton density. The copepod density in the GoM was the highest during the Northeast Monsoon followed by Southwest Monsoon and Spring Intermonsoon but, the density in the PB was the highest during the Spring Intermonsoon followed by the Northeast Monsoon and the Southwest Monsoon (Table 2). The seasonal pattern of copepod abundance also showed differences in the GoM and the PB. In the PB, the differences in copepod abundance of Spring Intermonsoon vs. Southwest Monsoon and Spring Intermonsoon vs. Northeast Monsoon were statistically significant but, there was only insignificant variation ( $p > 0.05$ ) between the Southwest Monsoon and Northeast Monsoon. In the GoM, the variations of copepod species abundance between the Spring Intermonsoon and the Northeast Monsoon was statistically significant ( $p < 0.05$ ), whereas the difference in copepod abundance between the Southwest Monsoon and other seasons were statistically insignificant ( $p > 0.05$ ).

A complete list of species of copepods present in the GoM and the PB is presented in Table 3. A total of 81 species of copepods were recorded from the entire study area during the three seasonal observations. During different seasons, all the 81 species were recorded from the GoM, but only 63 species were recorded from the PB. Out of these 81 species of copepods, 53 belonged to order Calanoida, 6 to Harpacticoida, 7 to Cyclopoida and 15 to Poecilostomatoida. During the Spring Intermonsoon, altogether 68 species of copepods were recorded in the GoM and the PB. Out of these species, 67 were present in the GoM, but only 41 were found in the PB. In the GoM, copepod community was composed of 43 Calanoids (64%), 6 Harpacticoids (9%), 7 Cyclopoids (10.4 %) and 11 Poecilostomatoids (16.4%). In the PB, copepod community was composed of 24 species of Calanoids (58.5 %), 5 species of Cyclopoids (12.1%), and 6 species each (14.7%) of Harpacticoids and Poecilostomatoids.

During the Southwest Monsoon, altogether 57 species of copepods were recorded from the study area. All these 57 species were present in the GoM whereas, only 55 species were present in the PB. Out of these 57 copepods species in the GoM, there were 41 Calanoids (72%), 6 Harpacticoids (10.5%), 2 Cyclopoids (3.5%) and 8 Poecilostomatoids (14%). Out of 55 species of copepods recorded in the PB, there were 41 Calanoids (74.5%), 5 Harpacticoids (9.1%), 2 Cyclopoids (3.6%) and 7 Poecilostomatoids (12.8%). During the Southwest Monsoon, swarming of the copepod *Temora turbinata* was found in many locations in the GoM and location 19, which was just north of Ramsethu, in the PB. During this period, there was an increased abundance of *Calanopia minor* and *Pseudodiaptomus serricaudatus* in the GoM whereas *Pseudodiaptomus aurivilli* occurred in high abundance in the PB. During the Northeast Monsoon period, altogether 60 species of copepods were recorded from the GoM and the

PB. All the 60 species were present in the GoM whereas only 37 species were found in the PB. Out of 60 species of copepods in the GoM, there were 39 Calanoids (65%), 5 Harpacticoids (8.3%), 4 Cyclopoids (6.7%) and 12 Poecilostomatoids (20%). In the PB, out of 37 species recorded, 25 species belonged to Calanoida (67.6%) and 4 each (10.8%) to Harpacticoida, Cyclopoida and Poecilostomatoida. During all the seasonal observations, the diversity of copepods was higher in the GoM as compared to the PB. All diversity indices in the GoM and the PB were the highest during the Spring Intermonsoon (Table 3).

#### 3.4.4.2. Biogeography of copepods

The cluster/SIMPROF and NMDS analyses of copepod species data clearly delineated the sampling locations into two distinct clusters (cluster I, GoM and cluster II, PB) during the spring intermonsoon (SIMPROF,  $p < 0.01$ ) and the Northeast Monsoon (SIMPROF,  $p < 0.01$ ) (Figure 8). However, such clear separation of locations was not evident during the Southwest Monsoon (Figure 8). During this season, the locations 4 and 6 in the GoM remained isolated from other locations due to the swarming of the calanoid copepod *Temora turbinata*, the indicator species of coastal upwelling.

#### 3.4.4.3. Dominant species of copepods

The analyses of dominant species of copepods revealed more number of dominant species of copepods in the GoM (15 species) than in the PB (13 species) (Table 4). Out of these dominant copepods, 7 species consist of *Acartia erythraea*, *A. danae*, *Acrocalanus gracilis*, *Calanopia minor*, *Corycaeus danae*, *Paracalanus parvus*, *Pseudodiaptomus serricaudatus*, *Temora turbinata* and *Undinula vulgaris* were found common in the GoM and the PB during different seasons (Table 4). The detailed information on the dominant species of copepods present in the GoM and the PB during different seasons is presented in Table 4.

The overall results of dominant species analysis of copepods showed that *Acartia spinicauda*, *Euterpina acutifrons*, *Oncaea venusta*, *Pareucalanus attenuatus*, *Temora discaudata* and *Onychocorycaeus catus* were dominant in the GoM. The abundance of these copepods was less and some of them were even absent in the PB during different seasons. On the other hand, *Pseudodiaptomus aurivilli*, *Clausocalanus arcuicornis*, *Centropages orsinii*, *C. furcatus* were dominant in the PB and their abundance was less in the GoM. The spatial difference in abundance of four most dominant species of copepods in the GoM and the PB is presented in Figure 9. The Figure shows higher abundance of typical coastal species *Acartia danae* and *A. erythraea* in the PB and high abundance of upwelling indicator species *Temora turbinata* in the GoM during the Southwest Monsoon. Similarly, *Paracalanus*

*parvus* was more abundant in the PB during the Spring Intermonsoon and the Southwest Monsoon periods but, no spatial differences were evident during the Northeast Monsoon period.

#### 3.4.4.4. Indicator species value (IndVAL) of copepods

The indicator species of copepods showed clear difference between the GoM and the PB during all the seasons. The detailed list of the Indicator species during different seasons is presented in Table 5. As with dominant species, the number of Indicator species of copepods was also higher in the GoM as compared to the PB (Table 5). There were a total of 15 indicator species in the GoM and 8 in the PB during different seasons. The species such as *Temora turbinata*, *Acartia danae*, *A. erythraea*, *Oncaea venusta* and *Corycaeus danae* were present in the GoM irrespective of seasons. Out of various indicator species present in the GoM and the PB, the abundance of species having the highest IndVal index (>75%) is presented in Figure 10. It is clear in Figure 10 that during the Spring Intermonsoon and Northeast Monsoon, there was a clear division of indicator species between the regions.

#### 3.4.4.5. Redundancy analyses of copepods and environmental factors

The major hydrographical variables such as salinity, temperature and dissolved oxygen in the GoM and the PB varied spatially and seasonally. This spatial difference in the environmental factors reflected well on the distribution of the dominant and indicator species of copepods in the study area. The RDA triplot presented in Figure 11 delineated the dominant and indicator species of copepods in the GoM and the PB during different seasons. The results of the complete RDA has shown that salinity, temperature and dissolved oxygen together explained 33.8 %, 18.7% and 34.1 % of variations in copepods during the Spring Intermonsoon, Southwest Monsoon and Northeast Monsoon respectively. The partial RDA (salinity as the environmental variable; temperature and DO as the co-variable) carried out showed that the salinity alone explained 15.2 %, 6.6% and 32.1% of the total variations in copepods during the Spring Intermonsoon, Southwest Monsoon and Northeast Monsoon periods, respectively. The ordination significance of all the axes were tested by the Monte Carlo test, which showed that all the ordination of RDA axes representing the Spring Intermonsoon, Southwest Monsoon and Northeast Monsoon (F= 4.915, 3.311 and 3.567 respectively) were significant P<0.05).

The RDA of the Spring Intermonsoon data demarcated the locations in the GoM (1-15) on the left hand side and the PB (16-30) on the right hand side of the Triplots (Figure 11). The GoM locations were characterized by high salinity, high DO and low temperature whereas; the PB locations were characterized by low salinity, low DO and high SST. The DO was positively related with salinity, and negatively related with SST. The chlorophyll *a* and copepods indicator species *Farranula gibbula*, *Metis jousseaumei*, *Corycaeus danae*, *Tortanus barbatus*,

*Subeucalanus crassus*, *Pareucalanus attenuatus*, *Metacalanus aurivilli*, *Oncaea venusta*, *Temora discaudata*, *Temora turbinata*, *Calanopia minor* and *Onychocorycaeus catus* were positively related with the salinity and were characteristic of the GoM. On the other hand, *Centropages orsinii*, *Clausocalanus arcuicornis*, *Acartia erythraea*, *Acrocalanus gracilis*, *Centropages furcatus*, and *Acartia danae* were placed in the PB side indicating their affinity with the PB region.

The RDA for the Northeast Monsoon showed high salinity and temperature in the GoM. The typical PB characteristics of low salinity formed the opposite side. The dominant and indicator species of copepods, *Oncaea venusta*, *Undinula vulgaris*, *Pareucalanus attenuatus*, *Temora turbinata*, *Paracandacia simplex*, *Corycaeus danae*, *Candacia discaudata*, *Candacia pachydactyla* were represented in the GoM due to their preference to high salinity and temperature. The copepod *Acartia erythrae*, *Clausocalanus arcuicornis*, *Acrocalanus gracilis* and *Paracalanus parvus* were placed, along the direction of negative gradient of salinity and positive gradient of dissolved oxygen indicating their preference to the PB region.

Due to increased homogeneity of environmental conditions and similarity of copepod community in the GoM and the PB, RDA could not explain the biotic - abiotic interactions during the Southwest Monsoon. The environmental variables salinity and dissolved oxygen together with chlorophyll a showed increasing gradients towards the GoM. The abundance of dominant copepods in the GoM and the PB differed significantly, which was also evident in the Triplot. The indicator species *Corycaeus danae*, *Macrosetella gracilis*, *Pseudodiaptomus serricaudatus*, *Oncaea venusta*, *Onychocorycaeus catus*, *Oithona similis*, *Labidocera acuta*, and *Temora turbinata* were more abundant in the GoM side. Similarly, indicator species *Acartia erythraea*, *Calanopia minor*, *Pseudodiaptomus aurivilli* were more abundant in the PB side.

## 4. Discussions

### 4.1. Seasonal environmental characteristics of the GoM and the PB

During most part of the year, the Indian landmass surrounding the GoM and PB is warm and arid. This climatic feature was well reflected in the air temperature and sea surface temperature presented in Figure 2b. The air temperature varied from 25.5 – 30.5°C with the lowest during the Northeast Monsoon when cold northeasterly wind blown over the region. The seasonal SST varied from 25.5 – 31.5°C with the lowest during the Northeast Monsoon. The rainfall in the study region peaks during the early Northeast Monsoon, which then drastically declines by the late Northeast Monsoon (Figure 2b). During the peak Northeast Monsoon, the rivers that empty into the GoM and the PB bring turbid flood water (Chandramohan et al., 2001). However, in the present study, there was no

indication of high suspended sediment inputs from the rivers into the GoM and the PB during the Northeast Monsoon, which could be due to the sampling in January (late Northeast Monsoon). As indicated in Figure 2b, the rainfall and freshwater influx into the GoM and the PB are very low during the late Northeast Monsoon.

The seasonal pattern of salinity distribution in the GoM and the PB was in general agreement with the ocean circulation around the Indian subcontinent. During the Northeast Monsoon period, the southward EICC enter into the PB and flow towards the GoM (Rao et al., 2011). Due to weak currents and subsurface barrier effect of Ramsethu, the intruded BoB water fails to make substantial impact on the hydrography of GoM (Rao et al., 2011). This was well reflected in the salinity distributions in both sides of the Ramsethu. The surface salinity data for the Northeast Monsoon period clearly shows significantly higher values in the GoM (av. 31.7) than in the PB (av. 28.5). This was also evident in the vertical profiles of salinity showing a noticeable difference (2 psu) between both sides of Ramsethu. The SST data also showed clear differences in both sides of the Ramsethu with noticeably higher values in the GoM (av. 26.69°C) than in the PB (av. 25.71°C). The estimates of water exchange between the GoM and the PB also showed that the flux from the PB to the GoM during the Northeast Monsoon is significantly lower than the flux from the GoM to the PB during the Southwest Monsoon. All these support the view that compared to the Southwest Monsoon; there is only less amount of water being exchanged between the PB and the GoM during the Northeast Monsoon period. This observation is in general agreement with Rao et al., (2011), who used satellite data to show that the BoB waters intruding into the PB during the Northeast Monsoon are not effective enough to alter the hydrography of the GoM significantly.

The Spring Intermonsoon is the transition phase between the Northeast Monsoon and Southwest Monsoon. The northeasterly winds prevalent in the GoM and the PB during the Northeast Monsoon period weaken during the Spring Intermonsoon, which eventually change its course to southwesterly during the Southwest Monsoon (Shankar et al., 2002). These weak winds in the GoM and the PB during the Spring Intermonsoon translate into weak surface currents (Figure 3 & 4), which are inhibited by Ramsethu causing only less exchange of water between the PB and the GoM. This was well reflected in the salinity distribution in both sides of the Ramsethu showing clear segregation of the GoM (av.33.6) and the PB (av.28.5). This was further supported by the flux estimates from the model result which showed that the exchange of water between the GoM and the PB was very minimal during the Spring Intermonsoon period (Figure 4). Due to high solar heating, air temperature and SST was the seasonal highest during the Spring Intermonsoon (Table 1). However, the distribution of SST on both sides of the Ramsethu presented relatively low values in the GoM (30.29°C) as compared to the southern PB (31.36°C). This difference also indicates that the GoM and PB waters have very limited mixing during the Spring Intermonsoon.



During the Southwest Monsoon, the equatorward flowing WICC carries coastal AS waters and feed the SMC that flows towards the east, south of Sri Lanka. In this course of circulation, high saline AS waters enter into the GoM and flows towards the PB through Ramsethu and Pamban pass (Rao et al., 2008). These currents are much stronger compared to other seasons, and result in well mixing of waters in the GoM and the PB. This was well reflected in the present study as there were only weak gradients in surface salinity on both sides of Ramsethu in the GoM (35.3) and the PB (35.1). The vertical salinity profiles also showed same level of salinity on both sides of the Ramsethu. The flux estimates between the GoM and the PB also showed significantly higher exchange during the Southwest Monsoon as compared to other periods (Figure 4). All these evidences suggest that there was effective mixing of the GoM and the PB waters during the Southwest Monsoon.

## 4.2. Zooplankton spatial and temporal distribution

Seasonally, zooplankton biomass in the GoM and the PB varied from 0.1 - 0.3 ml m<sup>-3</sup> (av. 0.2 ml m<sup>-3</sup>) and 0.01 - 0.2 ml m<sup>-3</sup> (av. 0.1 ml m<sup>-3</sup>), respectively. The mean biomass values in the GoM was found to be higher than the earlier reported values from the southwest and southeast coast of India (Madhupratap et al., 1990 & 1992), which indicates high zooplankton standing stock in the GoM as compared to the adjacent areas. The zooplankton biomass and abundance in the GoM was the lowest during the Spring Intermonsoon, moderate during the Southwest Monsoon and the highest during the Northeast Monsoon period. This seasonal pattern of zooplankton biomass and abundance in the GoM was in close agreement with the seasonal pattern of zooplankton along the southeast coast of India (Panikkar., 1968; Jyothibabu et al., 2008). The Northeast Monsoon induces enhancement in phytoplankton biomass along the Indian east coast, which eventually translates into high zooplankton stock (Madhu et al., 2006; Rakesh et al., 2006; 2008). Similarly, during the Southwest Monsoon period, the biologically productive waters from the southwest coast of India brought by the WICC support high zooplankton stock in the GoM. The Spring Intermonsoon is a low productive season with low zooplankton stock along the southeast coast of India (Jyothibabu et al., 2008). It is important to see that the zooplankton seasonal trend in the GoM has a close coupling with phytoplankton, which was well reflected in the RDA triplot (Figure 11). The significant enhancement in zooplankton biomass associated with the enhancement of phytoplankton biomass has been reported earlier from the Indian coast (Ashadevi et al., 2009; Jyothibabu et al., 2008 and references therein). Earlier studies also showed that the salinity differences can influence the overall composition and community structure of zooplankton in coastal waters (Gaudy et al., 2000; Blanco-Bercial et al., 2006; Berasategui et al., 2006). The optimum salinity level for *Lucifer hanseni* and *L. typus* (dominant species in the present study area- Prasad et al., 1952; Prasad, 1954) is

from 32 to 34 psu (Xu, 2010). This optimum salinity range was prevailing in the GoM during the Northeast Monsoon period, which probably helped the lucifers to increase their abundance during the period.

The seasonal trend of zooplankton distribution was found to be different in the PB and the GoM. The zooplankton biomass in the PB was the lowest during the Southwest Monsoon period, moderate during the Spring Intermonsoon and the highest during the Northeast Monsoon. On the other hand, the zooplankton density was the highest during the Spring Intermonsoon and moderate during the northeast and Southwest Monsoon periods. This kind of seasonal mismatch of zooplankton biomass and density was recorded earlier in the eastern Arabian Sea (Padmavati and Goswami, 1996). This mismatch is due to the seasonal difference in abundance of larger organisms such as siphonophores, mysids, lucifers and cladocerans in zooplankton samples (Padmavati and Goswami, 1996). During the Spring Intermonsoon, copepods in the PB were composed of smaller species such as *Acrocalanus gracilis*, *Clausocalanus arcuicornis*, *Paracalanus parvus*, *Acartia erythraea* and *Corycaeus danae*, which are efficient grazers of the microbial food web components (Turner, 2004).

It is important to note that the seasonal pattern of zooplankton in the PB was not matching with the seasonal trend in phytoplankton. There was a lack of seasonality in the surface chlorophyll *a* concentration as well. On the other hand, the observed seasonal difference in zooplankton biomass could be attributed to the seasonal shift in the alternative nutritional pathway of zooplankton (microbial loop) in the study area. In the western AS, the total organic carbon (TOC) concentrations in the upper mixed layer are at their annual maximum during the SIM (Hansell and Peltzer, 1998). During the period, biomass of heterotrophic bacteria and nanoplankton are also higher in the region as compared to other seasons (Ducklow et al., 2001; Garrison et al., 2000). This food web setting support an active microbial loop, which sustain high zooplankton biomass during the SIM when phytoplankton biomass is generally low in the western Arabian Sea (Smith and Madhuratap., 2005). The abundance of heterotrophic bacteria, heterotrophic nanoflagellates and microzooplankton was significantly higher in the PB as compared to the GoM (Anjusha et al., 2012). The microbial food web dominated the classical one during the Spring Intermonsoon, which could be reason for the enhanced zooplankton stock in the PB during this period. In seas around India, the microbial loop is most dominant during the Spring Intermonsoon season when water column is thermally stratified (Madhuratap et al., 1996; Jyothibabu et al., 2008). The same seasonal trend was found both in the GoM and the PB but, the enhancement of microbial food web was many folds higher in the PB as compared to the GoM, which might have supported the high zooplankton stock during the Spring Intermonsoon (Anjusha et al., 2012).

### 4.3. Zooplankton composition

The percentage contribution of copepods to the total zooplankton abundance in the GoM and the PB showed marked differences during different seasons. The copepods generally contributed 61-77% of the total zooplankton community which was in agreement with earlier records from the GoM and the PB (Prasad, 1954; Kartha, 1959), coastal waters of the AS (Madhupratap et al., 1990; 1992 ) and the BoB (Rakhesh et al., 2006 & 2008; Fernandes et al., 2008). Density and contribution of gastropods and bivalves larvae to the total zooplankton density showed two seasonal peaks in the PB, one during the Spring Intermonsoon and the other during the Southwest Monsoon. Prasad (1954) also found bimodal peaks in mollusks larval density in the PB. But uni-model seasonal peak was noticed in the GoM, which was during the Spring Intermonsoon period and this was associated with their breeding season (Sirajmeetan and Marichamy, 1986; Natarajan, 1957; Marichamy et al., 1985).

During all the seasons, the abundance of sergistsids (lucifers) was high in the GoM as compared to the PB. They are found throughout the year in the GoM but they flourish and form swarms during the Northeast Monsoon and Spring Intermonsoon (Prasad, 1954). This was due to the prevalence of optimal salinity for sergistsids in the GoM (32 – 34) during the Spring Intermonsoon. During all the seasons, the abundance of chaetognaths was higher in the GoM as compared to the PB. The literature suggests that the abundance of chaetognaths is mainly controlled by salinity and availability of food preferably copepods (Ohman, 1986; Madhupratap, 1987; Giesecke and Gonza'lez, 2008). The present observation is in general agreement with the above understanding and the highest abundance of chaetognaths in the study area was found during the Southwest Monsoon period when the salinity was the highest and the copepods were abundant. Conversely, the density of chaetognaths in the GoM declined during low saline conditions of the Northeast Monsoon when copepods were still abundant there.

The group diversity of zooplankton community depends on the density and proportionate contribution of each group to the total community abundance. The abundance of major zooplankton groups showed significant temporal and spatial variations within and between the GoM and the PB. Irrespective of seasons, zooplankton diversity was found to be higher in the GoM than in the PB. The relatively low percentage contribution of copepods and significant contribution of Lucifers and meroplankton larvae were the major reasons for the highest zooplankton community diversity observed in the GoM during the Spring Intermonsoon period. The literature suggest the Spring Intermonsoon period as the breeding season of mollusks (Sirajmeetan and Marichamy, 1986; Natarajan, 1957, Marichamy et al., 1985) and fishes (Marichamy et al., 1985; Prasad, 1954) in the study area, which may be due to high availability of smaller plankton fractions during the period (Anjusha et al., 2012). Furthermore, the stable

environmental conditions that prevail during the Spring Intermonsoon season are conducive for diversification of the plankton community.

The biological signatures of upwelling along the southwest coast of India are mostly evident from June to September (Madhuratap et al., 1990 & 1992; Banse, 1996). During the peak upwelling period (July - August), extensive phytoplankton blooms are evident along the southwest coast of India (Nair et al., 1992; Jyothibabu et al., 2008). The physical process of upwelling and enrichment of nutrients in the surface waters weakens by September, but the response of biological production remains even up to October (Madhuratap et al., 1992; Jyothibabu et al., 2008; MLR Plankton Atlas, 2011). This is primarily due to the time lag between nutrient enrichment, phytoplankton proliferation and zooplankton swarms (Madhuratap et al., 1990). Swarms of copepods and high abundance of larger carnivores such as chaetognaths, siphonophores and hydromedusae are common along the southwest coast of India during the Southwest Monsoon (Madhuratap and Haridas, 1986; Madhuratap et al., 1990). Equatorward flow of WICC during the Southwest Monsoon carries this upwelled water and feeds the eastward flowing SMC south of Sri Lanka (Shetye and Gouveia 1998; Vinayachandran et al., 2004 & 2005). On the course of this circulation, part of the upwelled waters enter into the GoM and flow towards the PB through the Ramsethu and Pamban Pass (Figure 3). During the Southwest Monsoon period, the typical upwelling zooplankton community consisting of abundant chaetognaths, siphonophores and hydromedusae along with swarming of upwelling indicator species of copepods *Temora turbinata* was found in the GoM. This zooplankton community structure in the GoM provides biological evidence to consider that the upwelled Arabian Sea coastal waters have influence on the hydrography of the GoM during the Southwest Monsoon season. The predominance of copepods and the presence of less abundant groups such as siphonophores, ctenophores and thaliaceans were the reasons for the low zooplankton group diversity during the Southwest Monsoon.

The chaetognaths, hydromedusae, siphonophores and ctenophores are the major planktonic carnivores in marine environments (Reeve, 1980; Feigenbaum and Maris 1984; Mills, 1995). Their predation on other plankton groups significantly influence the overall structure and magnitude of the zooplankton community (Huntley and Hobson, 1978; Matsakis and Conover, 1991; Hansson et al., 2005). Many of the coastal copepods are capable of rapid increase in their populations when conditions are conducive and therefore a decline of predatory pressure of carnivorous plankton favors increase in copepod abundance. During the Northeast Monsoon period, a few species of copepods contributed the majority of the zooplankton in the study area. This situation considerably decreases the diversity of zooplankton as reported earlier from the west and east coast of India (Madhuratap et al., 1990; Rakesh et al., 2006). During the Northeast Monsoon, the high abundance of copepods and low abundance of other zooplankton groups reduced the diversity and evenness of zooplankton in the PB.

#### 4.4. Copepod density and species in the GoM and the PB

Altogether, 81 species of copepods were recorded from the GoM and the PB during the three seasonal observations. The spatial and temporal difference in copepod density during different seasons was analyzed using ACHA clustering/ SIMPER, revealed a noticeable community difference between the GoM and the PB during the Spring Intermonsoon and Northeast Monsoon periods; whereas, the species difference was less prominent during the Southwest Monsoon. During all the seasons, copepod *Paracalanus parvus* was found both in the GoM and the PB with higher abundance in the latter region. Earlier studies of Prasad (1954) and Kartha (1959) presented similar results showing widespread occurrence of *Paracalanus parvus* in the GoM and the PB. Similarly, *Acrocalanus gracilis*, *Centropages orsinii*, *C. furcatus*, *Acartia danae*, *A. erythraea* were also abundant in the PB, where they contributed ~60 % of the total community. These species are low saline and abundantly occur in the lower reaches of estuaries and inshore waters along the east and west coasts of India (Madhupratap et al., 1992; Dalal and Gowsami, 2001; Achuthankutty et al., 1997; Padmavati and Gowsami, 1996; Rakesh et al., 2006). Their salinity preference was well reflected in their percentage contribution showing a noticeable decrease in the GoM (~16%) as compared to the PB (~60 %). On the other hand, copepods preferring high saline coastal waters (*Temora turbinata*, *T. discaudata*, *Calanopia minor*), shelf waters (*Oncaea venusta*, *Onychocorycaeus catus*) were found abundant in the GoM. The offshore species of copepods such as *Undinula vulgaris*, *Pareucalanus attenuates* and *Sapphrina* sp., were also found in low abundance in the GoM.

The seasonal difference in copepod composition during the Spring Intermonsoon and Southwest Monsoon was evident in the results. The low saline copepods *Acrocalanus gracilis*, *Centropages orsinii*, *C. furcatus*, *Acartia danae* and *A. erythraea* were abundant during the Spring Intermonsoon period, which was replaced by high saline species *Temora turbinata*, *Pareucalanus attenuatus*, *Pseudodiaptomus serricaudatus* and *Undinula vulgaris* during the Southwest Monsoon. *Tortanus* sp. was also found in relatively high abundance during the Southwest Monsoon period. The copepod *Temora turbinata*, which is an indicator species of coastal upwelling, was also found abundant during the Southwest Monsoon period. They are opportunistic species capable of exploiting upwelling induced high phytoplankton stock prevailing along the west coast of India during the Southwest Monsoon (Stephen, 1978; Haridas et al., 1980; Madhupratap et al., 1990 & 1992; Goswami and Padmavati, 1996). The predominance of opportunistic species of copepods, exploiting their favorable nutritional conditions has been reported earlier from many other regions such as east coast of India (Rakesh et al., 2008), off Rio de Janeiro (Lopez et al., 1999), northern Taiwan (Lo et al., 2004) and north eastern China Sea (Tseng et al., 2008).

During the Southwest Monsoon, there was a decline in diversity and evenness of zooplankton especially in the GoM, which can be attributed to the proliferation of a few opportunistic species. Similar situations were reported earlier from the upwelling regions along the west and east coasts of India (Madhupratap et al., 1990; Rakhesh et al., 2008). Earlier studies reported the swarming of *Temora turbinata* and the dominance of hyper-saline species of the genera *Tortanus*, *Undinula*, *Oncaea*, *Eucalanus* and *Pareucalanus* along the west coast of India during the Southwest Monsoon (Madhupratap et al., 1990; Nair et al., 1992; Madhupratap et al., 1992; Stephen, 1978). These swarming copepods were abundant in the GoM during the Southwest Monsoon indicating the relatedness of water masses of the coastal Arabian Sea and the GoM during this period. This continuity between the coastal Arabian Sea and the GoM is mainly governed by the basin scale Southwest Monsoon circulation discussed earlier in section 2.4. The strong eastward flowing currents in the GoM during the Southwest Monsoon, causes effective mixing of the GoM and the PB waters in the Ramsethu region. During this time, the salinity was the seasonal highest in the PB, favoring an increase in the abundance of high saline species of copepods. However, it is important to note that the overall abundance of all copepods, except *Pseudodiaptomus aurivilli*, was lower in the PB as compared to the GoM.

The present study showed the active role of ocean currents in structuring the copepod community in the GoM and the PB. During the Northeast Monsoon, copepods *Paracalanus parvus*, *Acartia erythraea*, *Acrocalanus gracilis*, *Clausocalanus arcuicornis* were dominant in the PB, which contributed ~70% of the total abundance. The dominance of these species in the inshore and estuarine environments along the southeast and west coast of India has been well established (Table 6). Therefore the high abundance of low saline species in the PB during the northeast east monsoon season can directly be linked with the ocean currents, which bring low saline BoB waters into the PB. Since the intruded BoB waters cause less influence on the hydrography of the GoM due to the obstruction from the Ramsethu, the high saline species of copepods (*Farranula gibbula*, *Oncaea venusta*, *Candacia sp.*, *Sapphirina*, *Copila mirabilis*, *Pareucalanus attenuatus*) occur abundantly in the GoM. Similarly, the absence of shelf and offshore species of copepods in the PB can be explained by the seasonal salinity levels and the ocean current there. As the ocean currents bring low saline BoB waters into the PB during the northeast and Spring Intermonsoon periods, the hydrography of the PB behaves like a continuation of the coastal BoB. This causes the absence of high saline copepod species in the PB except during the Southwest Monsoon period when the high saline GoM water intrudes into the PB. On the other hand, the GoM is permanently open to the neighboring AS, which facilitate the frequent occurrence of high saline species in the region.

#### 4.5. Biogeography of copepods with respect to the hydrography

The salinity superimposed on biotic assemblage patterns clearly showed the influence of salinity on copepods assemblage in the GoM and the PB during the Spring Intermonsoon and Northeast Monsoon, which in turn was governed by the ocean currents (Figure 4 & 8). The partial RDA showed that salinity alone is responsible for 15.2 %, 6.6% and 32.1% of the total variance of copepods during the Spring Intermonsoon, Southwest Monsoon and Northeast Monsoon respectively. Altogether 81 species of copepods were recorded from the GoM and the PB during different seasons. All the 81 species were present in the GoM but, only 63 species were present in the PB. 18 species of copepods, which normally occurs in the continental shelf and offshore waters (*Rhincalanus cornutus*, *Rhincalanus nasutus*, *Candacia discaudata*, *Candacia bradyi*, *Candacia pachydactyla*, *Paracandacia simplex*, *Calanopia aurivilli*, *Pontella spinipes*, *Pontellopsis armata*, *Pontellina plumata*, *Mettis jousseaumei*, *Oithona simplex*, *Oncaea conifera*, *Copilia vitrea*, *Copilia mirabilis*, *Sapphirina ovatolanceolata*, *Sapphirina auronitens*, *Sapphirina nigromaculata*) were found only in the GoM. Also the list of dominant and Indicator species of copepods revealed noticeable difference in copepod composition between the GoM and the PB (Table 4 & 5). Earlier records of these species from other parts of the Indian seas is presented in Table 6, which provides clear evidences to infer that the copepod community in the GoM is composed of coastal, shelf and offshore species whereas, the copepods in the PB is composed of coastal/ inshore species.

#### 5. Conclusion

The hydrography of the GoM and the PB exhibited clear seasonal pattern in response to the seasonally reversing ocean currents in the region. During the Northeast Monsoon, low saline BoB waters intrude into the PB, which eventually decreases the salinity and supports the low saline coastal species of copepods (*Paracalanus parvus*, *Acrocalanus spp.* etc). During the Southwest Monsoon, the intrusion of the upwelled AS waters changes the zooplankton community structure in the GoM. The swarming proportions of the upwelling indicator copepod *Temora turbinata*, and increased abundance of high saline copepods points to the region's biogeographic continuity with the southwest coast of India during this season. During the Spring Intermonsoon season, the monsoon currents weaken and reverse its direction in the GoM and the PB. The stable environmental condition during this period favored the diversification of copepods with the dominance of *Clausocalanus arcuicornis*, *Acartia danae*, *Centropages orsinii*, *Paracalanus parvus*, *Acrocalanus gracilis* and *Acartia erythraea*. In summary, the study evidenced a noticeable difference in copepod composition in the GoM and the PB during the Spring Intermonsoon and Northeast Monsoon. This was due to the lack of strong mixing of GoM and the PB waters during these periods, which was primarily linked with relatively weak ocean currents and subsurface barrier effect of Ramsethu. On the

other hand, increased mixing of waters during the Southwest Monsoon resulted in a homogenous copepod community in the study area. The overall results clearly show that the copepod community in the GoM was composed of coastal and offshore species whereas, the community in the PB was consisted mostly of coastal species.

## Acknowledgements

The authors thank Dr. S. R. Shetye, Director, CSIR- National Institute of Oceanography (CSIR-NIO), India for facilities and encouragement. We thankfully acknowledge all our colleges in National Institute of Oceanography, India who helped in carrying out the seasonal field work in the GoM and the PB. We express our sincere thanks to Prof. P. N. Vinayachandran, IISc, Bangalore, India and Dr. K.K. Balachandran, CSIR-NIO Regional Center, Kochi, India for their valuable suggestions on an earlier version of this manuscript. We also thank Dr. Antony Joseph, NIO Goa for providing AWS data. The authors thank the Ministry of Shipping for the financial support. This is NIO contribution XXXX.

## References

Achuthankutty, C.T., Madhupratap, M., Nair, V.R., Nair, S.R.S., Rao, T.S.S., 1980. Zooplankton biomass and composition in the western Bay of Bengal during the late summer monsoon. *Indian Journal of Marine Sciences* 9, 201–206.

Achuthankutty, C.T., Ramaiah, N., Padmavati, G., 1997. Zooplankton variability and copepod assemblage in the coastal and estuarine waters of Goa along the central west coast of India. Intergovernmental Oceanographic Commission, 1 workshop report no. 142 (eds.) Pierrot-Bults A. C. and Vander Spoel S., UNESCO, Paris, 1–11.

Anjusha, A., Jyothibabu, R., Jagadeesan, L., Arya P. Mohan, Sudheesh, K., Kiran Krishna., Ullas, N., Deepak, M.P. 2012. Plankton food web structure and carbon biomass in the Gulf of Mannar and Palk Bay, southeast coast of India (Under review in *Journal of Marine Systems*)

Ashadevi, C.R., Jyothibabu, R., Sabu, P., Josia Jacob., Habeebrehman, H., Prabhakaran, P., Jayalakshmi K.J., Achuthankutty C.T., 2010. Seasonal variation and trophic ecology of microzooplankton (20 – 200µm) in the southeastern Arabian Sea. *Continental Shelf Research* 30 (9), 1070-1084.

Anger, K., 2003. Salinity as a key parameter in the larval biology of decapod crustaceans. *Invertebrate Reproduction and Development* 43, 29–45.

Balasubramanian, T., Anantharaman, P., Thangaradjou, T., 2011. Seagrass productivity and mapping in the Gulf of Mannar Biosphere Reserve. In. *Compendium of Research Findings on Biodiversity Conservation and Sustainable*



Use in the Gulf of Mannar Biosphere Reserve, Gulf of Mannar Biosphere Reserve Trust, Ramnathapuram, India, Science Outreach Series No. 1, 18-40.

Banase, K., Sumitra Vijayaraghavan, Madhupratap, M., 1996. On the possible causes of the seasonal phytoplankton blooms along the southwest coast of India. *Indian Journal of Marine Sciences* 25, 283 – 289.

Beaugrand, G., 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. *Progress in Oceanography* 60, 245–262.

Berasategui, A.D., Menu Marque, S., Gomez-Erache, M., Ramirez, F.C., Mianzan, H.W., Acha, E.M., 2006. Copepod assemblages in a highly complex hydrographic region. *Estuarine Coastal Shelf Sciences* 66, 483–492.

Birks, H.J.B., 1998. Numerical tools in palaeolimnology -Progress, potentialities and problems. *Journal of Paleolimnology* 20, 307 - 332.

Blanco-Bercial, L., Alvarez-Marques, F., Cabal, J.A., 2006. Changes in the mesozooplankton community associated with the hydrography off the northwestern Iberian Peninsula. *ICES Journal of Marine Sciences* 63, 799–810.

Bonnet, D., Frid, C.L.J., 2004. Seven copepod species considered as indicators of water-mass influence and changes: results from a Northumberland coastal station. *ICES Journal of Marine Sciences* 61, 485 –491.

Chandramohan, P., Jena, B.K., Sanilkumar, V., 2001. Littoral drift sources and sinks along the Indian coast. *Current science* 81 (3), 292-297.

Chen, H., Qi, Y., Liu, G., 2011. Spatial and temporal variations of macro- and mesozooplankton community in the Huanghai Sea (Yellow Sea) and East China Sea in summer and winter. *Acta Oceanologica Sinica* 30, 84-95.

Clarke, K.R., Warwick, R.M., 2001. *Changes in marine communities: An approach to statistical analysis and interpretation* 2<sup>nd</sup> editions PRIMER- E LTD, Plymouth Marine Laboratory, United Kingdom.

Clarke, K.R., Gorley, R.N., 2006. *PRIMER V6 User Manual / tutorial*, PRIMER- E LTD, Plymouth Marine Laboratory, United Kingdom, pp.190

Conway, D., White, R., Hugues-Dit-Ciles, J., Gallienne, C., Robins, D., 2003. *Guide to the coastal and surface zooplankton of the south western Indian Ocean*. Occasional Publication No. 15, Marine Biological Association of the United Kingdom, 354.

Dalal, S.G., Goswami, S.C., 2001. Temporal and ephemeral variations in copepod community in the estuaries of Mandovi and Zuari - west coast of India. *Journal of Plankton Research* 23(1), 19-26.

Ducklow, H.W., Smith, D.C., Campbell, L., Landry, M.R., Quinby, H.L., Steward, G.F., Azam, F., 2001. Heterotrophic bacterioplankton in the Arabian Sea: Basinwide response to year-round high primary productivity. *Deep-Sea Research II* 48, 1303–1324.

- Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67, 345–366.
- Durve V.S., Alagarwami, K., 1964. An incidence of fish mortality in Athankarai estuary near Mandapam. *Marine Biological Association of India* 6, 147-151.
- Feigenbaum, J.D.L., Maris, R.C., 1984. Feeding in the Chaetognatha. *Annual Review of Oceanography and Marine Biology* 22, 343-392.
- Fernandes, V., 2008. The effect of semi-permanent eddies on the distribution of mesozooplankton in the central Bay of Bengal. *Journal of Marine Research* 66, 465-488.
- Fernandes, V., Ramaiah, N., 2009. Mesozooplankton community in the Bay of Bengal (India): spatial variability during the summer monsoon. *Aquatic Ecology* 43, 951–963.
- Gaonkar C.A., Krishnamurthy, V., Anil, A.C., 2010. Changes in the abundance and composition of zooplankton from the ports of Mumbai, India. *Environmental Monitoring and Assessment* 168, 179-194.
- Garrison, D.L., Gowing, M.M., Hughes, M.P., Campbell, L., Caron, D.A., Dennett, M.R., et al., 2000. Microbial food web structure in the Arabian Sea: A US JGOFS study. *Deep-Sea Research II* 47, 1387–1422.
- Gaudy, R., Cervetto, G., Pagano, M., 2000. Comparison of the metabolism of *Acartia clausi* and *A. tonsa*: influence of temperature and salinity. *Journal of Experimental Marine Biology and Ecology* 247, 51-65.
- Giesecke, R., and Gonzalez, H.E., 2008. Reproduction and feeding of *Sagitta enflata* in the Humboldt Current system off Chile. *ICES Journal of Marine Sciences* 65, 361–370.
- Goswami, S.C., Padmavati, G., 1996. Zooplankton production, composition and diversity in the coastal waters of Goa. *Indian Journal of Marine Sciences* 25, 91-97.
- Grasshoff, K., Ehrhardt, M., Kremling, K., 1983. *Methods of Seawater Analysis*, (eds.) Grasshoff, K., Ehrhardt, M., Kremling, K. (Verlag Chemie, Weinheim), 89 – 224.
- Hansell, D.A., Peltzer, E.T., 1998. Spatial and temporal variations of total organic carbon in the Arabian Sea. *Deep-Sea Research II* 45, 2171–2194.
- Hansson, L.J., Moeslund, O., Kiørboe, T., Riisgård, H.U., 2005. Clearance rates of jellyfish and their potential predation impact on zooplankton and fish larvae in a neritic ecosystem (Limfjorden, Denmark). *Marine Ecology Progress Series* 304, 117–131.
- Haridas, P., Menon, P.G., Madhupratap, M., 1980. Annual variations in zooplankton from a polluted coastal environment. *Mahasagar – Bulletin of National Institute of Oceanography, India* 13, 239 - 248.

Hsiao, S.H., Ka, S., Fang T.H., Hwang, J.S., 2011. Zooplankton assemblages as indicators of seasonal changes in water masses in the boundary waters between the East China Sea and the Taiwan Strait *Hydrobiologia* 666, 317–330.

Heish, C.H., Chiu, T.S., Shih, C.T., 2004. Copepod diversity and composition as indicators of intrusion of the Kuroshio Branch Current into the Northern Taiwan Strait in Spring 2000. *Zoological Studies* 43, 393 – 403.

Hunt, B.P.V., Hosie, G.W., 2006. The seasonal succession of zooplankton in the Southern Ocean south of Australia, part I: The seasonal ice zone. *Deep-Sea Research I* 53, 1182–1202.

Huntley, M.E., Hobson, L.A., 1978. Medusa predation and plankton dynamics in a temperate fjord, British Columbia. *Journal of Fisheries Research Board of Canada* 35, 257–261.

Hwang, J.S., Wong, C.K., 2005. The China Coastal Current as a driving force for transporting *Calanus sinicus* (Copepoda Calanoida) from its population centers to waters of Taiwan and Hong Kong during the N.E monsoon period in winter. *Journal of Plankton Research* 27, 205-210.

Hwang, J.S., Souissi, S., Tseng, L.C., Seuront, L., Schmitt, F.G., Fang, L.S., Peng, S.H., Wu, C.H., Hsiao, S.H., Twan, W.H., Wei, T.P., Kumar, R., Fang, T.H., Chen, Q.C., Wong, C.K., 2006. A 5-year study of the influence of the northeast and Southwest Monsoons on copepod assemblages in the boundary coastal waters between the East China Sea and the Taiwan Strait. *Journal of Plankton Research* 28, 943 – 958.

Jyothibabu, R., Madhu, N.V., Maheswaran, P.A., Jayalakshmy, K.V., Nair, K.K.C., Achuthankutty, C.T., 2008. Seasonal variation of microzooplankton (20 – 200µm) and its possible implications on the vertical carbon flux in the western Bay of Bengal. *Continental Shelf Research* 28, 737-755.

Jyothibabu, R., Madhu, N.V., 2007. Zooplankton in the Mandovi and Zuari estuary, In: *Mandovi and Zuari estuaries*. (eds.) S.R. Shyete., M. Dileep Kumar., D. Shankar, 83 - 90.

Jyothibabu, R., Madhu, N.V., Habeebrehman, H., Jayalakshmi, K.V., Nair, K.K.C., Achuthankutty, C.T., 2010. Re-evaluation of paradox of mesozooplankton in the eastern Arabian Sea based on ship and satellite observations. *Journal of Marine Systems* 81, 235-251.

Ka, S., Hwang, J. S., 2011. Mesozooplankton Distribution and Composition on the Northeastern Coast of Taiwan during Autumn: Effects of the Kuroshio Current and Hydrothermal Vents. *Zoological Studies* 50, 155-163.

Kartha, 1959. A study of the copepods on the inshore waters of Palk bay and Gulf of Mannar. *Indian Journal of Fisheries* 6, 256 - 267.

Kasturirangan, L.R, 1963. A key for the identification of the more common planktonic Copepoda of the Indian coastal waters, Publication No.2. Indian National Committee on Oceanic Research, 1- 87.

Krishnamurthy, K., 1967. Seasonal variation in the plankton of Porto. Novo Waters (India). *Hydrobiologia* 29, 226-238.

Kumaraguru, A.K., Edwin Joseph, V., Marimuthu, N., Jerald Wilson, J., 2006. Scientific information on Gulf of Mannar - A Bibliography. Centre for Marine and Coastal Studies, Madurai Kamaraj University, Madurai, India. pp. 656.

Kumaraguru, A.K., Edwin Joseph, V., Rajee, M., Blasubramanian, T., 2008. Palk Bay - Information and Bibliography, CAS in Marine Biology, Annamalai University, Parangipettai and Centre for Marine and Coastal Studies, Madurai Kamaraj University, India, pp. 227.

Lee, C.Y., Liu, D.C., Su, W.C., 2009. Seasonal and Spatial Variations in the Planktonic Copepod Community of Ilan Bay and Adjacent Kuroshio Waters off Northeastern Taiwan. *Zoological Studies* 48, 151-161.

Leps, J., Smilauer, P.S., 2003. Multivariate analysis of ecological data using CANOCA. Cambridge University Press, Cambridge, United Kingdom, pp.269

Lin, D., Li, X.Q., Fang, H.D., Dong, Y.H., Huang, Z.X., Chen, J.H., 2011. Calanoid copepods assemblages in Pearl River Estuary of China in summer: Relationships between species distribution and environmental variables. *Estuarine Coastal and Shelf Science* 93, 259-267.

Lo, W.T., Hwang, J.S., Chen, Q.C., 2004. Spatial variations of copepods in the surface waters of southeastern Taiwan Strait. *Zoological Studies* 43, 218–228.

Lopez, R.M., Brandini, F.P., Gaeta, S.A., 1999. Distribution pattern of epipelagic copepods off Rio de Janeiro (SE Brasil) in summer 1991/1992 and winter 1992. *Hydrobiologia* 411, 161 - 174.

Madhu, N.V., Jyothibabu, R., Balachandran, K., Honey, U., Martin, G., Vijay, J., Shiyas, C., Gupta, G., Achuthankutty, C., 2007. Monsoonal impact on planktonic standing stock and abundance in a tropical estuary (Cochin backwaters - India). *Estuarine Coastal and Shelf Science* 73, 54-64.

Madhu, N.V., Jyothibabu, R., Maheswaran, P.A., Vijay John Gerson, Gopalakrishnan, T.C., Nair, K.K.C., 2006. Lack of seasonality of phytoplankton standing stock (chlorophyll *a*) and production in the western Bay of Bengal. *Continental Shelf Research* 26, 1868–1883.

Madhupratap, M., 1987. Status and strategy zooplankton of tropical Indian estuaries: a review. *Bulletin of Plankton Society of Japan*, 65-81.

Madhupratap, M., Gopalakrishnan, T.C., Haridas, P., Nair, K.K.C., Aravindakshan, P.N., Padmavati, G., Paul, S., 1996. Lack of seasonal and geographic variation in mesozooplankton biomass in the Arabian Sea and its structure in the mixed layer. *Current Science* 71, 863–868.

Madhupratap, M., Haridas, P., Ramaiah, N., Achuthankutty, C.T., 1992. Zooplankton of the southwest coast of India: abundance, composition, temporal and spatial variability in 1987. In: Desai BN (ed) Oceanography of the Indian Ocean. Oxford & IBH, New Delhi, 99-112.

Madhupratap, M., Nair, S. R. S., Haridas, P., Padmavati, G., 1990. Response of zooplankton to physical changes in the environment: coastal upwelling along the central west coast of India. *Journal of Coastal Research* 6, 413–426.

Madhupratap, M., Gopalakrishnan, T.C., Haridas, P., Nair, K.K.C., 2001. Mesozooplankton biomass, composition and distribution in the Arabian Sea during the Fall Intermonsoon: implications of oxygen gradients. *Deep-Sea Research II* 48, 1345 -1368.

Madhupratap, M., Haridas, P., 1986. Epipelagic calanoid copepods of the northern Indian Ocean. *Oceanologica Acta* 9, 105 -117.

Madhupratap, M., Haridas, P., 1990. Zooplankton, especially calanoid copepods, in the upper 1000 m of the south east Arabian Sea. *Journal of Plankton Research* 12, 305–321.

Manikandan, S., Ganesapandian, S., Parthipan, K., 2011. Distribution and zonation of seagrass in the Palk Bay, Southeastern India. *Journal of Fisheries and Aquatic Science* 6 (2), 178-185.

Marichamy, R., Gopinathan, C.P., Siraimetan, P., 1985. Studies on primary and secondary production in relation to hydrography in the inshore waters of Tuticorin. *Journal of Marine Biology Association of India* 27 129-137.

Martin Thompson, P., 1990. Ecology of the neritic and oceanic cyclopoid copepods along the south-west coast of Indian and the Laccadive Sea. *Journal of Marine Biological Association of India* 32, 38-65.

Matsakis, S., Conover, R.J., 1991. Abundance and feeding of medusae and their potential impact as predators on other zooplankton in Bedford Basin (Nova Scotia, Canada) during spring. *Canadian Journal Fisheries and Aquatic Sciences* 48, 1419–1430.

Mills, C.E., 1995. Medusae, siphonophores and ctenophores as planktivorous predators in changing global ecosystems. *ICES Journal of Marine Sciences* 52, 575 - 581.

Modéran, J., Bouvais , P., David, V., Noc, S.L., Bouhet, B.S., Niquil, N., Miramand, P., Fichet, D., 2010. Zooplankton community structure in a highly turbid environment (Charente estuary, France): Spatio-temporal patterns and environmental control. *Estuarine Coastal and Shelf Science* 88, 219 - 232.

MLR Plankton Atlas., 2011. Atlas on environmental parameters and productivity of the Indian EEZ and adjoining seas. (Eds). Nair, K.K.C. Centre for Marine Living Resources and Ecology, Ministry of Earth Sciences, New Delhi, pp.294.

Murty, A.V.S., Varma, U.P., 1964. The hydrographical features of the waters of Palk Bay during March, 1963. *Journal of Marine Biological Association of India* 6, 207 - 216.

Nair, S.R.S., Devassy, V.P., Madhupratap, M., 1992. Blooms of phytoplankton along the west coast of India associated with nutrient enrichment and the response of mesozooplankton. *Science of the Total Environment, Supplement*, Elsevier Science Publishers B.V., Amsterdam, 819 – 828.

Nair, S.R., Nair, V.R., Achuthankutty, C.T., Madhupratap, M., 1981. Zooplankton composition and diversity in the western Bay of Bengal. *Journal of Plankton Research* 3, 493-508.

Natarajan, A.V., 1957. Studies on the egg masses and larval development of some prosobranchs from the Gulf of Mannar and the Palk Bay. *Proceedings of the Indian Academy of Sciences* 46, 170-228.

Nayar, K.N., Mahadevan, S., Rao, K.S., Sivalingam, D., Nayar, K.R., 1988. Exploitation of molluscan shell deposits in Vaigai estuary at Athankarai. *Central Marine Fisheries Research Institute, India, Bulletin* 42, 35-39.

NIO Report., 2012. Environmental impact assessment of the 4A alignment of the Sethusamudram Ship Channel Project. Ministry of Shipping, New Delhi, pp. 210.

Ohman, M.D., 1986. Predator-limited population growth of the copepod *Pseudocalanus* sp. *Journal of Plankton Research* 8, 673 - 713.

Padmavati, G., Goswami, S.C., 1996. Zooplankton ecology in the Mandovi Zuary estuarine system of Goa, west coast of India. *Indian Journal of Marine Sciences* 25, 268-273.

Padmavati, G., Goswami, S.C., Vidya, P.S., 1997. Diurnal variation in zooplankton in the Zuari Estuary, west coast of India. *Journal of the Marine Biological Association of India* 39, 166-171.

Panikkar, N.K., 1968. International Indian Ocean Expedition, Plankton Atlas, Vol.1, Fasc.1, Maps on total MSP biomass in the Arabian Sea and Bay of Bengal, CSIR, New Delhi, pp. 22.

Perumal, N.V., Rajkumar, M., Perumal, P., Rajasekar, K.T., 2009. Seasonal variations of plankton diversity in the Kaduviyar estuary, Nagapattinam, southeast coast of India. *Journal of Environmental Biology* 30, 1035-1046

Pielou, E., 1969. *Introduction to mathematical ecology*, Wiley Interscience, pp. 286.

Postel, L., Fock, H., Hagen W., 2000. Biomass and abundance, ICES Zooplankton Methodology manual. (ed.) Harris R.P., Wiebe. P.H., Leiz. J., Skjoldal et al., Academic Press, 193 – 213.

Prasad, R.R., 1954. The characteristics of plankton at an inshore station in the Gulf of Mannar near Mandapam. *Indian Journal of Fisheries* 1, 1-36.

Prasad, R.R., 1956. Further studies on the plankton of the inshore waters off Mandapam. *Indian Journal of Fisheries* 3, 1-42.

Prasad, R.R., 1958. Plankton calendars of the inshore waters at Mandapam with note on the productivity of the area. *Indian Journal of Fisheries* 5, 170-188.

Prasad, R.R., Bapat, S.V., Tampi, P.R.S., 1952. Observations on the distribution of plankton at six inshore stations in the Gulf of Mannar. *Journal of Zoological Society of India* 4, 141-151.

Queiroga, H., Blanton, J., 2004. Interactions between behaviour and physical forcing in the control of horizontal transport of decapod crustaceans larvae. *Advances in Marine Biology* 47, 107–204.

Rakshesh, M., Raman, A.V., Sudarsan, D., 2006. Discriminating zooplankton assemblages in neritic and oceanic waters: a case for the northeast coast of India, Bay of Bengal. *Marine Environmental Research* 63, 93 – 109.

Rakesh, M., Raman, A.V., Kalavati, C., Subramanian, B.R., Sharma, V.S., Sunitha Babu, E., Sateesh, N., 2008. Zooplankton community structure across an eddy- generated upwelling band close to a tropical bay-mangrove ecosystem. *Marine Biology* 154, 953-972.

Rao K.S , Sivalingam, D., Nair, P.N.R., Unnithan, K.A., 1987. Oyster resources of Athankarai estuary, southeast coast of India. *Central Marine Fisheries Research Insitute, India, Bulletin* 38, 17-29.

Rao, R.R., Girishkumar, M.S., Ravichandran, M., Gopalakrishna, V.V., Pankajakshan, T., 2011. Do cold, low salinity waters pass through the Indo-Sri Lanka Channel during winter?. *International Journal of Remote Sensing* 32 (22), 7383-7398.

Rao, S. D.V., Rao, S.K., Iyer, C.S.P., Chittibabu, P., 2008. Possible ecological consequences from the Sethu Samudram Canal Project, India. *Marine Pollution Bulletin* 56, 170–186.

Reeve, M. R., 1980. The biology of chaetognatha. 1. Quantitative aspects of growth and egg production in *Sagitta hispida*. In: Steele JH (ed.) *Marine Food Chains*. University of California Press, Berkeley, 168-189.

Santhanam, P., Perumal, P., 2003. Diversity of zooplankton in Parangipettai coastal waters, southeast coast of India *Journal of the Marine Biological Association of India* 45, 145-151.

Sewell, R.B.S., 1914. Notes on the surface copepoda of the Gulf of Mannar. *Spolia Zeylanica* 9, 191- 262.

Sewell, R., 1999. The copepoda of Indian seas. *Biotech Books, Delhi, India*, pp. 407.

Shankar, D., Vinayachandran, P.N., Unnikrishnan, A.S., 2002. The monsoon currents in the north Indian Ocean. *Progress in Oceanography* 52, 63 – 120.

Shannon, C.E., Wiener, W., 1963. The mathematical theory of communication. University of Illinois press, Urbana, Illinois, pp. 117.

- Shenoi, S.S.C., 2010. Intra-seasonal variability of the coastal currents around India: A review of the evidences from new observations. *Indian Journal of Geo-Marine Sciences* 39, 489-496.
- Shetye, S.R., 1999. Dynamics of circulation of the waters around India; In: *Ocean Science: Trends and Future directions* (ed.) B.L.K Somayajulu, Indian National Science Academy, New Delhi, 1-21.
- Shetye, S.R., Gouveia, A.D., 1998. Coastal circulation in the north Indian Ocean. In: *The Global Ocean: Regional studies and syntheses*. (eds.) Robinson, A.R., Bring, K.H, John Wiley and Sons, Inc., New York, 11, 523–556.
- Shetye, S.R., Gouveia, A.D., Shenoi, S.S.C., Sundar, D., Michael, G.S., Nampoothiri, G., 1993. The Western boundary current of the seasonal subtropical gyre in the Bay of Bengal. *Journal of Geophysical Research* 98 (C1), 945 – 954.
- Silas, E.G., 1968. Tuna fishery of the Tinnevely coast, Gulf of Mannar. In: *Proceedings of the Symposium on Scombroid Fishes, Part 3*, Marine Biology Association of India, 1083 -1120.
- Simpson, E.H., 1949. Measurement of diversity. *Nature*, London 163, 688.
- Sirajmeetan, P., Marichamy, R., 1986. Seasonal abundance of bivalve and gastropod larvae in the plankton off Tuticorin coast. *Central Marine Fisheries Research Institute, India, Bulletin* 42, 225-231.
- Skarðhamar, J., Slagstad, D., Edvardsen, A., 2007. Plankton distributions related to hydrography and circulation dynamics on a narrow continental shelf off Northern Norway. *Estuarine Coastal and Shelf Science* 75, 381- 392.
- Smith, S., Roman, M., Prusova, I., Wishner, K., Gowing, M., Codispoti, L.A., Barber, R., Marra, J., Flagg, C., 1998. Seasonal response of zooplankton to monsoonal reversal in the Arabian Sea. *Deep-Sea Research II* 45, 2369 - 2403.
- Smith, S.L., Madhupradap, M., 2005. Mesozooplankton of the Arabian Sea: Patterns influenced by seasons, upwelling, and oxygen concentrations. *Progress in Oceanography* 65, 214 -239.
- Southwell, T., Kerkham, 1912. Currents on the Ceylon pearl banks superficial and deep. *Reports of Ceylon Marine Biological Laboratory* 1, 232 - 248.
- Sridhar, R., Thangaradjou, T., Kannan, L., 2010. Spatial and temporal variations in phytoplankton in coral reef and seagrass ecosystems of the Palk Bay, southeast coast of India. *Journal of Environmental Biology*. 31(5), 765 – 77.
- Stephen, R., 1978. Copepod composition along the southwest coasts of India. *Oceanography of the Indian Ocean*. In: Desai BN (ed) *Oceanography of the Indian Ocean*. Oxford & IBH, New Delhi.
- Sudheesh, K., Babu, M.T and Vethamony, P., 2012. Meandering 'S-shaped' through flow in Sethu Samudram across the Adams bridge, Gulf of Mannar and Palk bay (Unpublished)



- Tanaka, O., 1956. The pelagic copepods of the Izu region, Middle Japan, Systematic account I. Publications of the Seto Marine Biological Laboratory 5, pp.525
- Tseng, L.C., kumar, R., Dahms, H.U., Chen, C.T., Souissi, S., Chen, Q.C., Hwang, J.S., 2008. Copepod community structure over a marine outfall area in the north-eastern South China Sea. *Journal of Marine Biology Association of United Kingdom* 88, 955–966.
- Turner, J.T., 2004. The Importance of Small Planktonic Copepods and Their Roles in Pelagic Marine Food Webs. *Zoological Studies* 43, 255-266.
- Ummerkutty, A.N.P., 1967a. Studies on Indian copepods. Observations on the diurnal vertical movements of planktonic copepods in the Gulf of Mannar, *Bombay Natural History Society* 63, 332 - 343.
- Ummerkutty, 1967b. Observations on the breeding and seasonal abundance of ten species of planktonic copepods of the Gulf of Mannar. *Proceedings of the Symposium on Crustacea, Part 2, Marine Biological Association of India, 12-16 January 1965, Ernakulam, 685 - 697.*
- UNESCO, 1994. *Protocols for the Joint Global Ocean Flux Study (JGOFS). Core Measurements, IOC Manuals and Guides 29, UNESCO, Paris, pp. 170.*
- Vinayachandran, P.N., Chauhan, P., Nayak, S.R., 2004. Biological response of the sea around Sri Lanka to summer monsoon. *Geophysical Research Letters* 31, L01302, doi:10.1029/2003GL018533.
- Vinayachandran, P.N., Kagimoto, T., Masumoto, Y., Chauhan, P., Nayak, S.R., Yamagata, T., 2005. Bifurcation of the East India Coastal Current east of Sri Lanka. *Geophysical Research Letters* 32, L15606, doi:10.1029/2005GL022864.
- Vinayachandran, P.N., Masumoto, Y., Mikawa, T., Yamagata, T., 1999. Intrusion of the southwest monsoon current into the Bay of Bengal. *Journal of Geophysical Research* 104 (C5) 11, 07711085.
- XU, Z.L., 2010. Determining optimal temperature and salinity of Lucifer (Dendrobranchiata: Sergestoidea: Luciferidae) based on field data from the East China Sea. *Plankton and Benthos Research* 5, 136–143.
- Yang, G.M., He, D.H., Wang, C.S., Miao, Y.T., Yu, H.H., 1999. Study on the biological oceanography characteristics of planktonic copepods in the waters north of Taiwan, II. Community Characteristics. *Acta Oceanologica Sinica* 21, 72-80.

## Figure captions

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

Figure 1b- Seasonal reversal of ocean currents around the Indian subcontinent during the Southwest Monsoon and the Northeast Monsoon. WICC- West India coastal Current, LL- Lakshadweep Low, LH- Lakshadweep High, SMC – Summer Monsoon Current, WMC- Winter Monsoon Current, EICC – East India Coastal Currents

Figure 2a –MODIS -Terra satellite imagery showing extensive sediment plumes in the Palk Bay in January ([www.visibleearth.nasa.gov](http://www.visibleearth.nasa.gov)). The movement of sediment plumes from the PB to the GoM through the Pamban Pass and Ramsethu is evident

Figure 2b – Seasonal trend in temperature and rainfall in the study area. The monthly mean air temperature data is from the AWS installed at Mandapam during the study period and the rainfall data represent 5 year mean (2005-2010) representing three major revenue districts Tuticorin, Ramnathapuram and Nagapattinam bordering the study area. The Rainfall data is from IMD data sets available online.

Figure 3 – MIKE 21 simulated seasonal current pattern in the Gulf of Mannar (GoM) and the Palk Bay (PB) during (a) January representing the Northeast Monsoon, (b) March representing Spring Intermonsoon and (c) September representing Southwest Monsoon. The simulated pattern of currents were validated using RCM 9 current meters data collected from selected locations shown in figure 1a. The currents that flow from the PB to the GoM during the northeast monsoon and spring intermonsoon are weak when compared with the currents that flow from the GoM to the PB during the Southwest Monsoon period

Figure 4 - Flux estimates between the Gulf of Mannar (GoM) and the Palk Bay (PB) during different time scales (in  $m^3/\text{second}$ ). The data is derived from MIKE 21 flow model output. The direction of the arrow indicates the direction of the ocean currents and the size of the arrow indicates the proportionate volume transported. It is evident that the quantity of the water transported from the GoM to the PB during the Southwest Monsoon is several orders higher than other seasons.

Figure 5 – Vertical distribution of salinity in (a) two transects on both sides of the Ramsethu. The locations in blue and red color represent the Gulf of Mannar (GoM) and the Palk Bay (PB) respectively. The marked difference in salinity levels between the GoM and the PB was clear during the (b) Spring Intermonsoon and (c) Northeast Monsoon periods whereas, such gradients in salinity was not evident during the (d) Southwest Monsoon due to effective mixing of waters caused by strong currents

Figure 6 - Water velocity in the Pamban Pass during the Northeast monsoon sampling. The data was collected by using Acoustic Doppler Profiler (ADP) across the Pamban pass and it is clear in the figure that the currents were towards northwest. This direction of the current caused the intrusion of the low saline Palk Bay (PB) waters into the Gulf of Mannar (GoM) through the Pamban Pass, which was reflected in location 12. Please see figure 5 for the vertical profiles of the salinity

Figure 7 – Mean abundance of (a) lucifers and (b) fish eggs and larvae ( $\text{No. } 100 \text{ m}^{-3}$ ) plotted against temperature and salinity during different seasons. The red bubbles indicate the Gulf of Mannar (GoM) and blue bubbles indicate the Palk Bay (PB). The numbers close to the bubbles represents the abundance during a particular season. Abbreviations: NEM - Northeast Monsoon, SIM - Spring Intermonsoon and SWM - Southwest Monsoon.

Figure 8 Dendrogram of hierarchical clusters /SIMPROF using group-average linkage of Bray–Curtis similarities based on  $\log(X + 1)$  transformed copepod species in 30 sampling locations (1 -15 in GoM; 16- 30 in PB) during (a) SIM, (b) SWM and (c)

NEM. The significant differences (SIMPROF,  $P < 0.01$ ) in the abundances of copepods community between groups of locations are shown by solid black lines, whereas red dotted lines indicate lack of significant statistical difference (d-f) salinity over laid non-metric multidimensional scaling (NMDS) ordination plot of sampling locations to show the influence of salinity on spatially assembled groups during the (d) Spring Intermonsoon, (e) Southwest Monsoon and (f) Northeast Monsoon. Slices and contour lines show 50 % level of similarity and bubbles sizes corresponds to the proportionate salinity values.

Figure 9 - Bray-Curtis similarities based on group averaging of Nonmetric Multidimensional Scaling (NMDS) plot of copepod abundance based on  $\log(X+1)$  transformed data over laid with the bubble plots of major dominant species showing their densities and distribution during (A1- A4) March, (B1- B4) September and (C1- C4) January on spatially assembled groups of locations. In figures A, B and C, the numbers represents the locations (1-15 in the GoM and 16-30 in the PB). The bubble positions in Figure A1- A4, B1-B4 and C1 – C4 correspond to the stations positions in figure A, B and C respectively. Bubble size is proportional to the number of ind.m<sup>-3</sup>. Contour lines indicate the 50 % similarity level. In Figure: SIM – Spring Intermonsoon; SWM – Southwest Monsoon; NEM – Northeast Monsoon; ADA – *Acartia danae*; AER – *Acartia erythrae*; TTU – *Temora turbinata*; PPA – *Paracalanus parvus*.

Figure 10 - Bray-Curtis similarities based on group averaging of Nonmetric Multidimensional Scaling (NMDS) plot of copepod abundance based on  $\log(X+1)$  transformed data over laid with bubble plots of important Indicator species (having >75 Indval Index value during any one of the season) showing their densities and distribution during (A1- A4) Spring Intermonsoon, (B1- B4) Southwest Monsoon and (C1- C4) Northeast Monsoon on spatially assembled groups of locations. In figure A, B and C, the numbers represents the locations (1-15 in the GoM and 16-30 in the PB). The bubble positions in figures A1- A4, B1 - B4 and C1 – C4 corresponds to the stations positions in figure A, B and C respectively. The bubble size is proportional to the number of ind.m<sup>-3</sup>. Contour lines indicate the 50% similarity level of separation. In figure SIM – Spring Intermonsoon; SWM – Southwest Monsoon; NEM – Northeast Monsoon; OVE – *Oncaea venusta*; FGI – *Farranula gibbula*; PAT – *Pareucalanus attenuatus*; COR – *Centropages orsinii*.

Figure 11 - RDA Triplot showing the distribution of seasonal environmental variables as well as dominant and indicator copepods. Samples are displayed by points (small unfilled circles), species and environmental variables are shown by arrows. The direction of the arrow indicates the direction of the increase of that particular factor on spatially assembled sampling locations. During the spring intermonsoon and northeast monsoon periods, there was a clear segregation of the Gulf of Mannar (GoM) and the Palk Bay (PB) locations as highlighted in large dashed circles, which also encompass the dominant and indicator species in respective regions. Such clear segregation was impossible for the Southwest Monsoon as evident in the second panel, which was due to the increased homogeneity of copepod species in the GoM and the PB during the period.

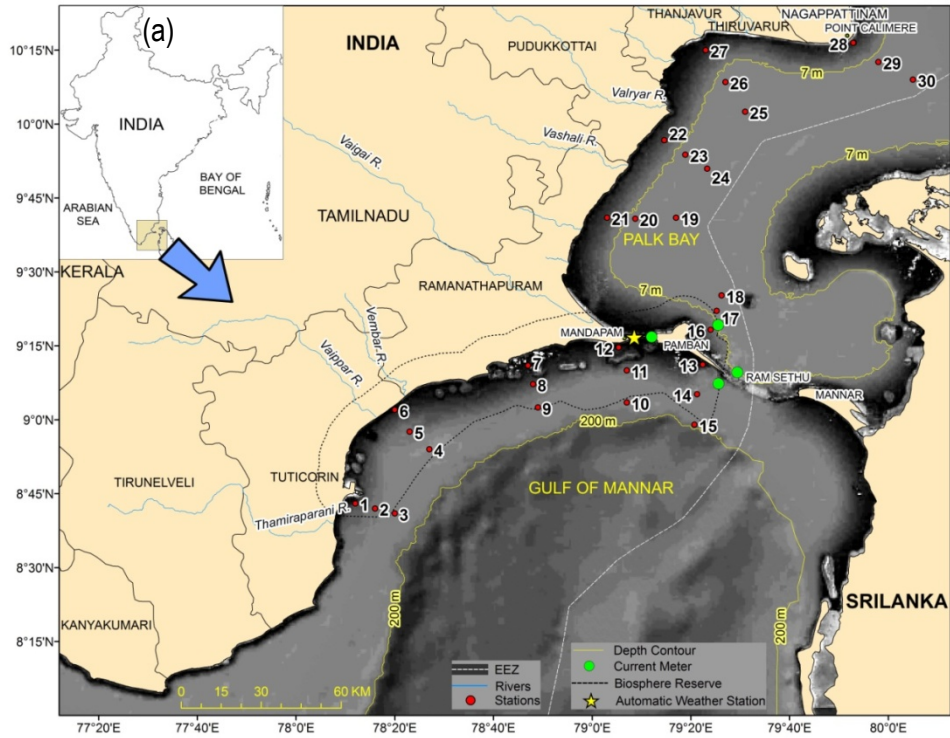


Figure 1a

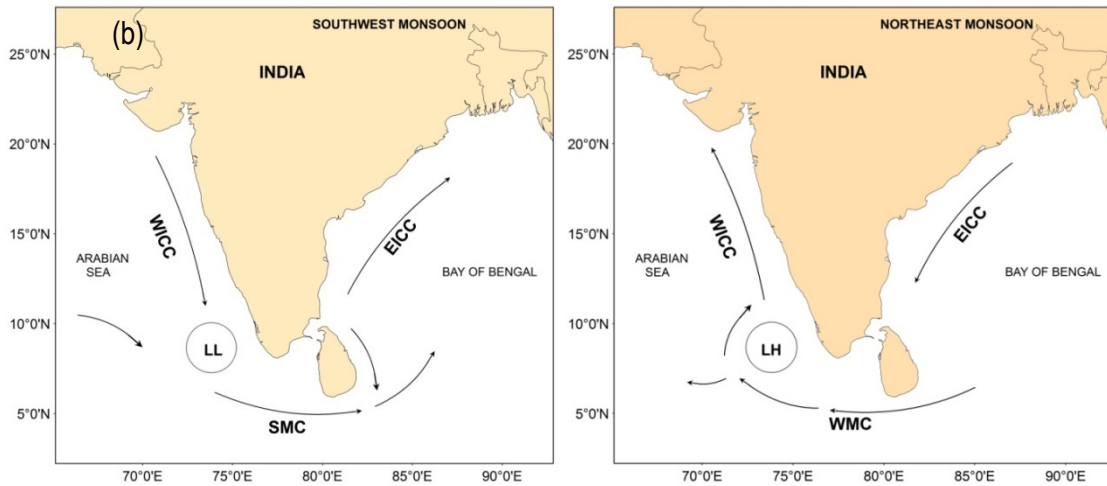


Figure 1b

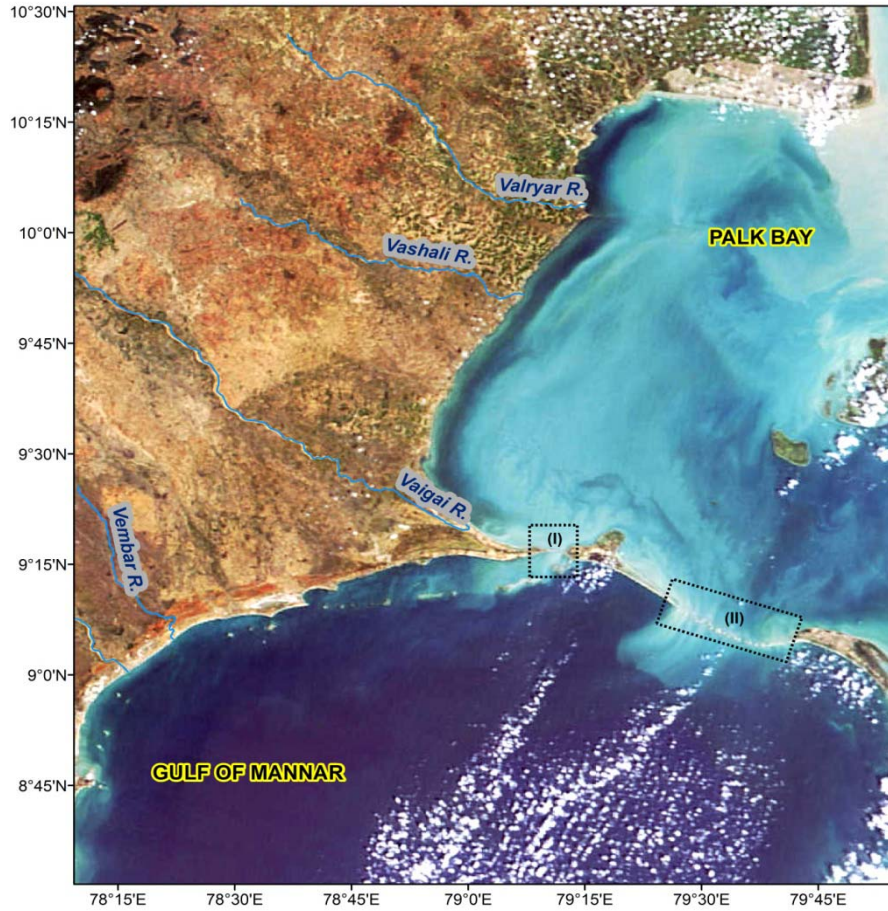


Figure 2a

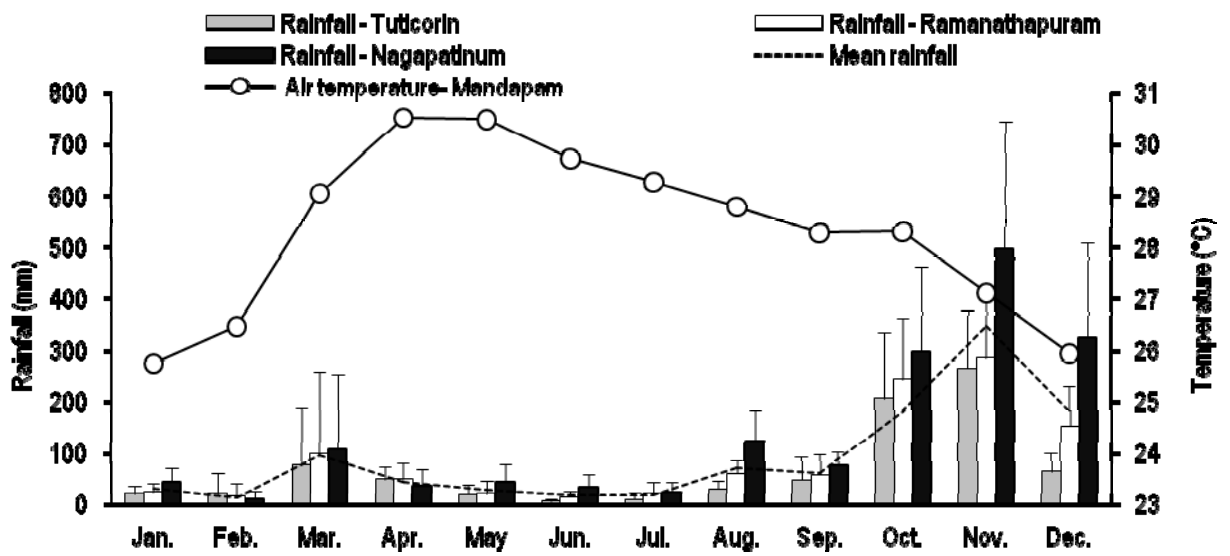


Figure 2b

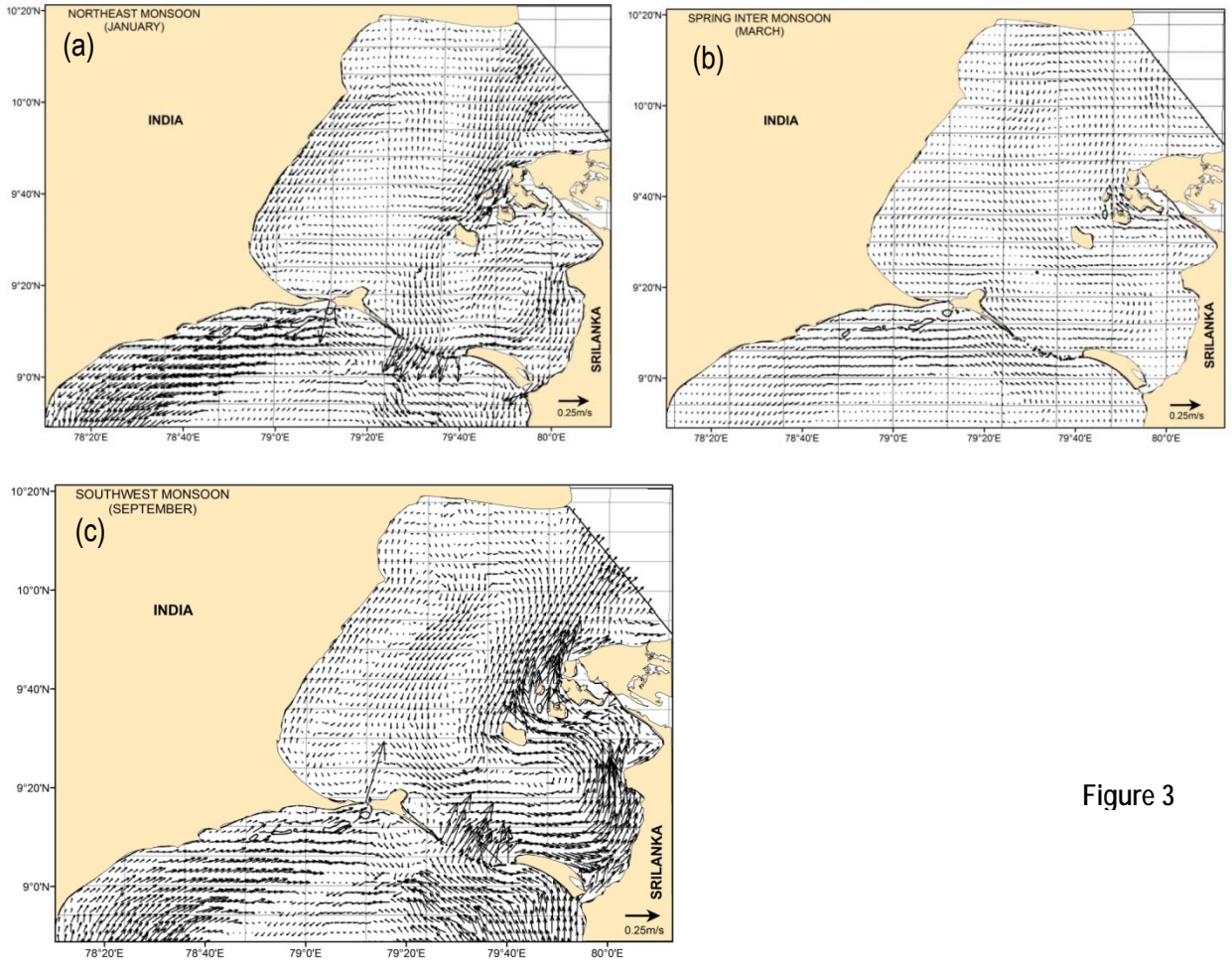


Figure 3

Northeast Monsoon (Nov.- Feb.)    Spring Intermonsoon (Mar.- May)    Southwest Monsoon (Jun. -Sep.)

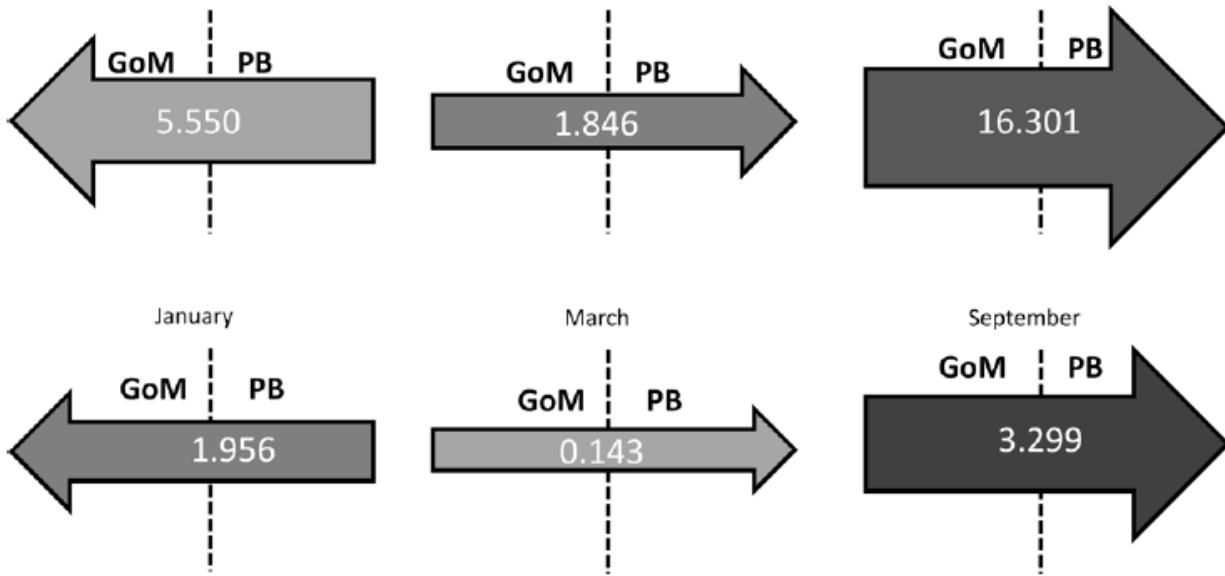


Figure 4

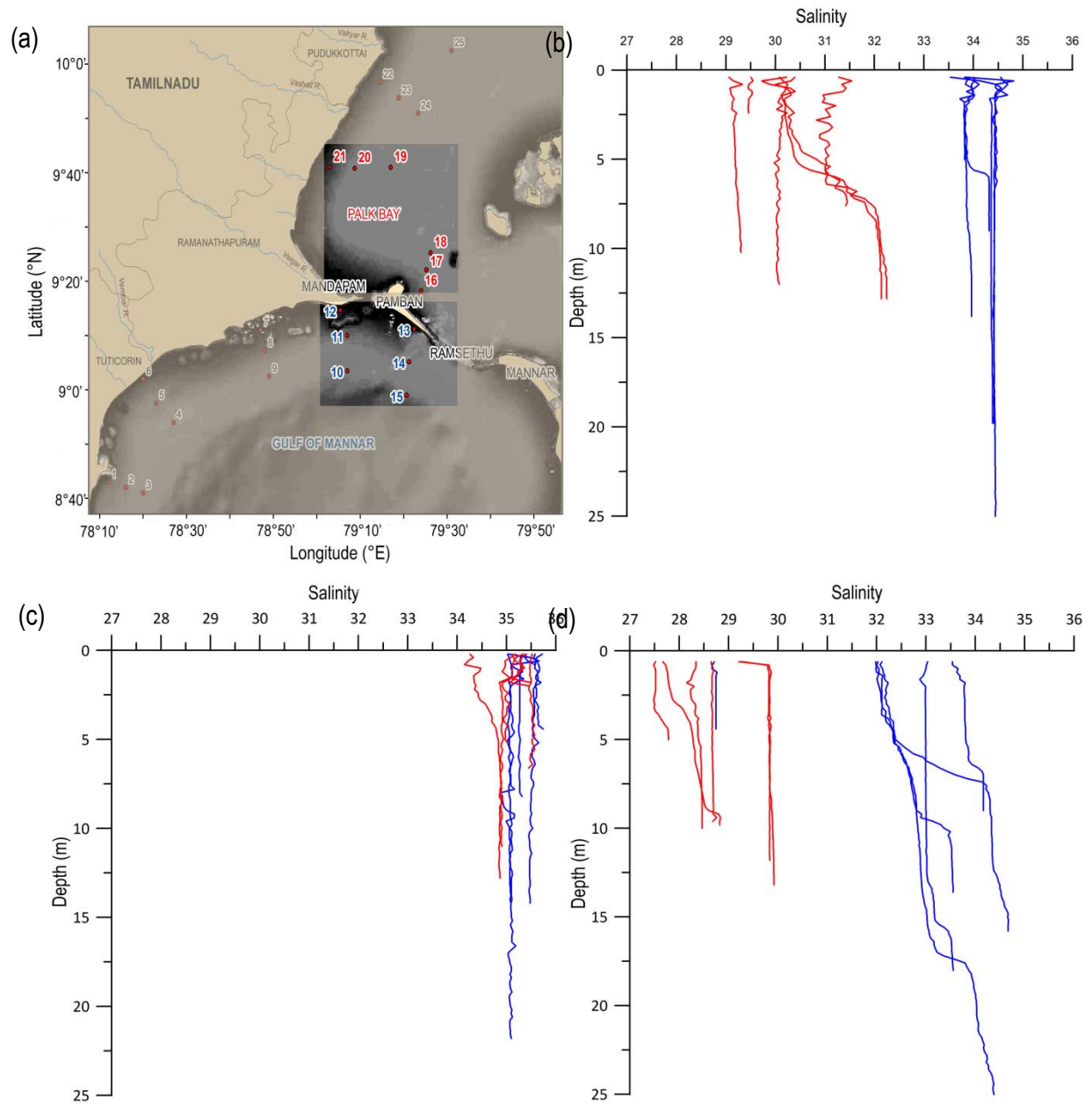


Figure 5



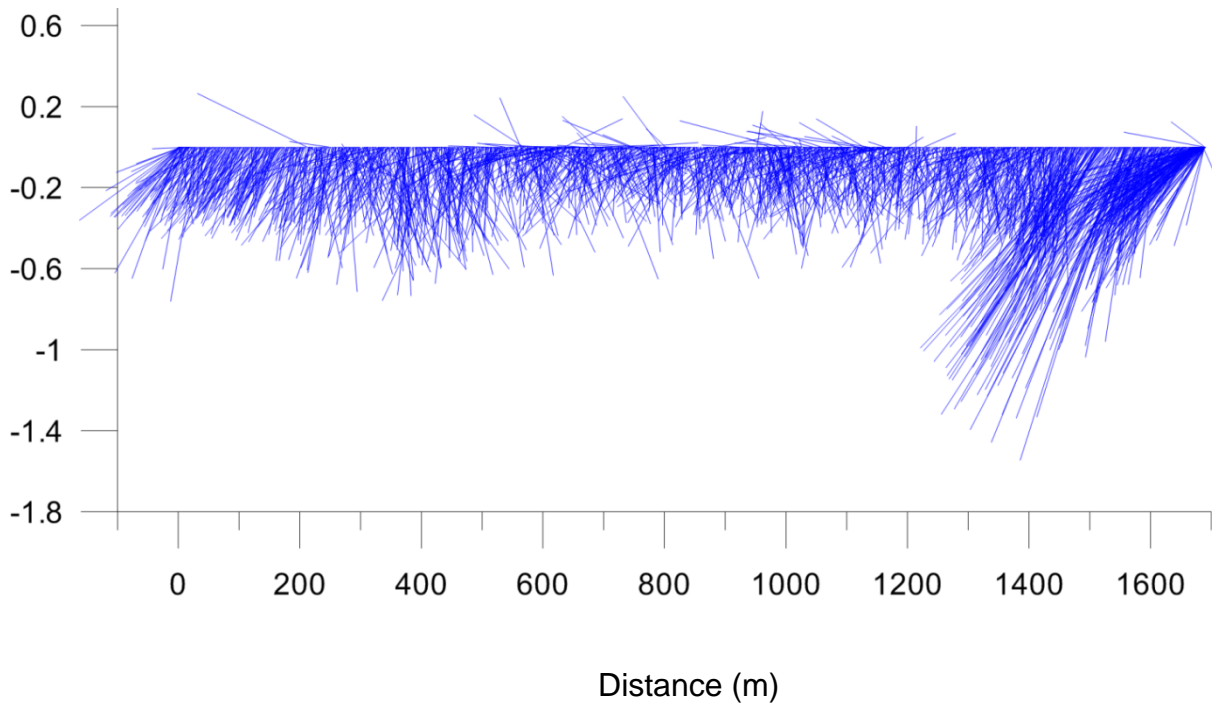
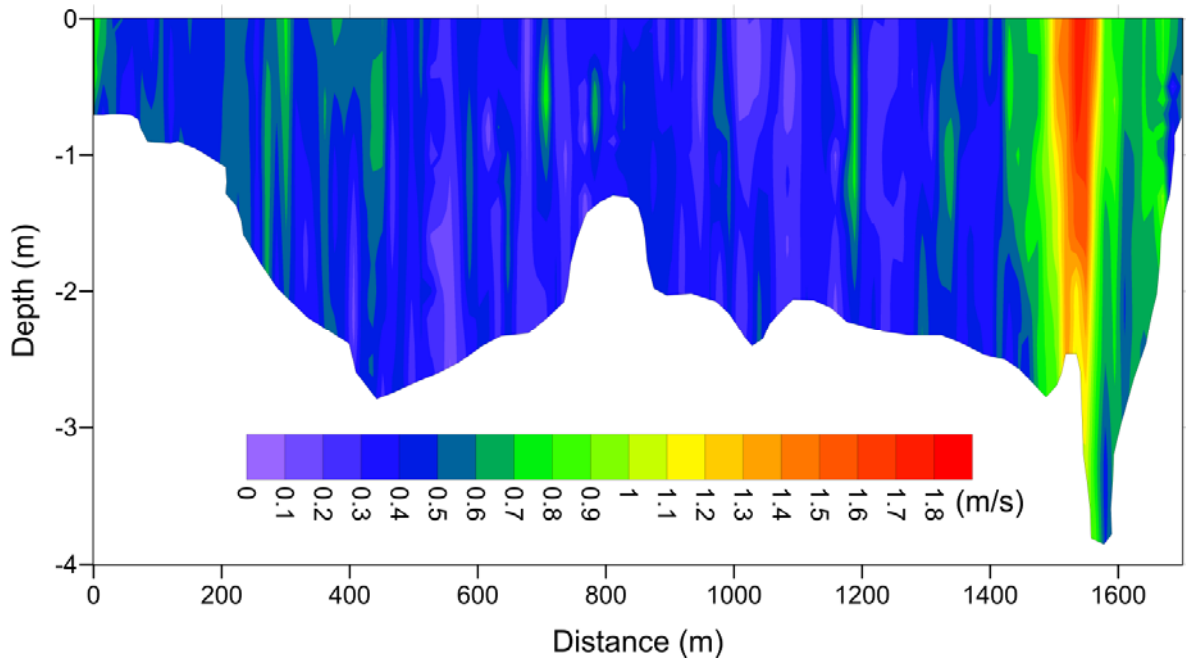


Figure 6

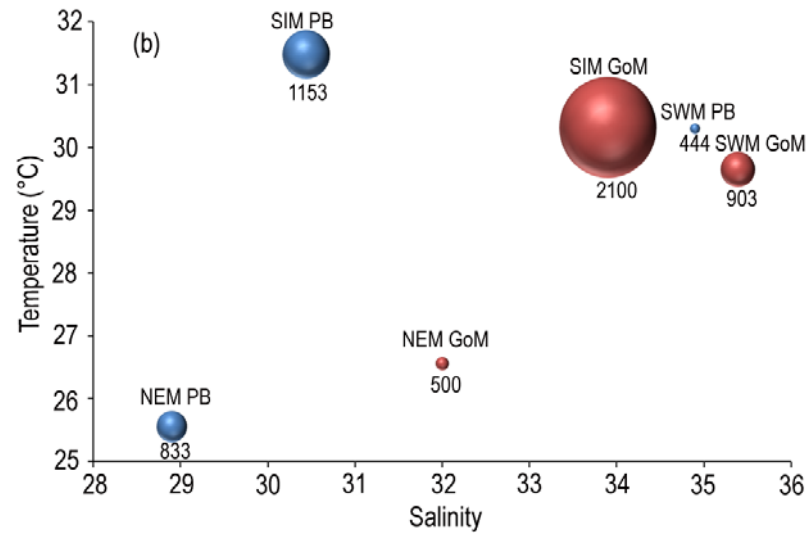
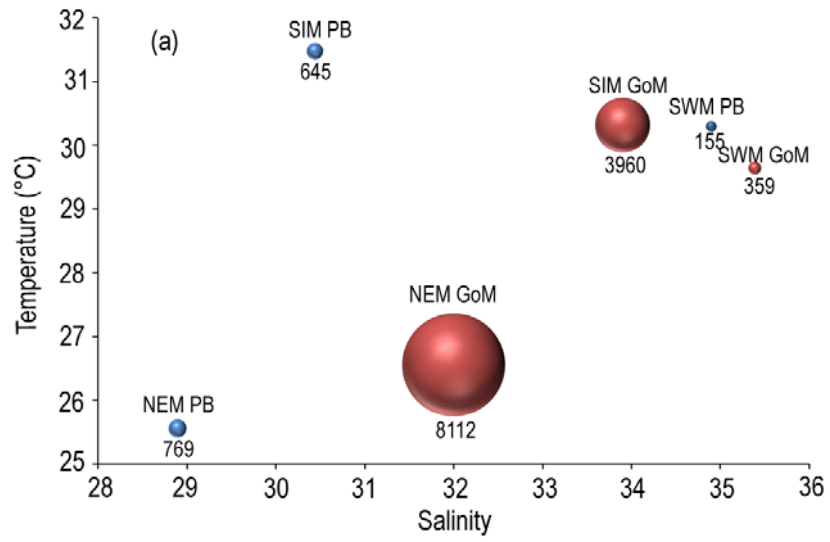


Figure 7

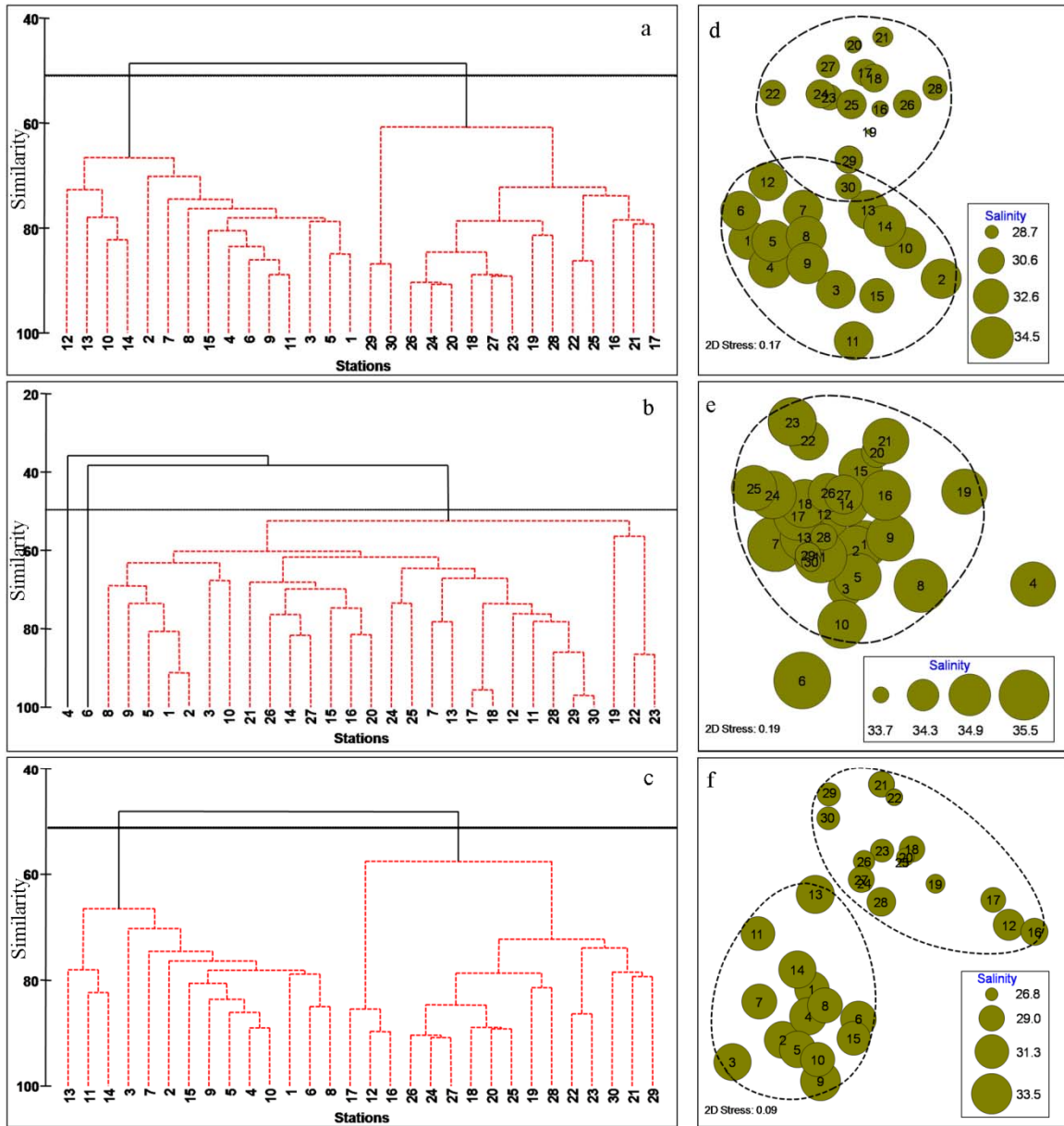


Figure 8

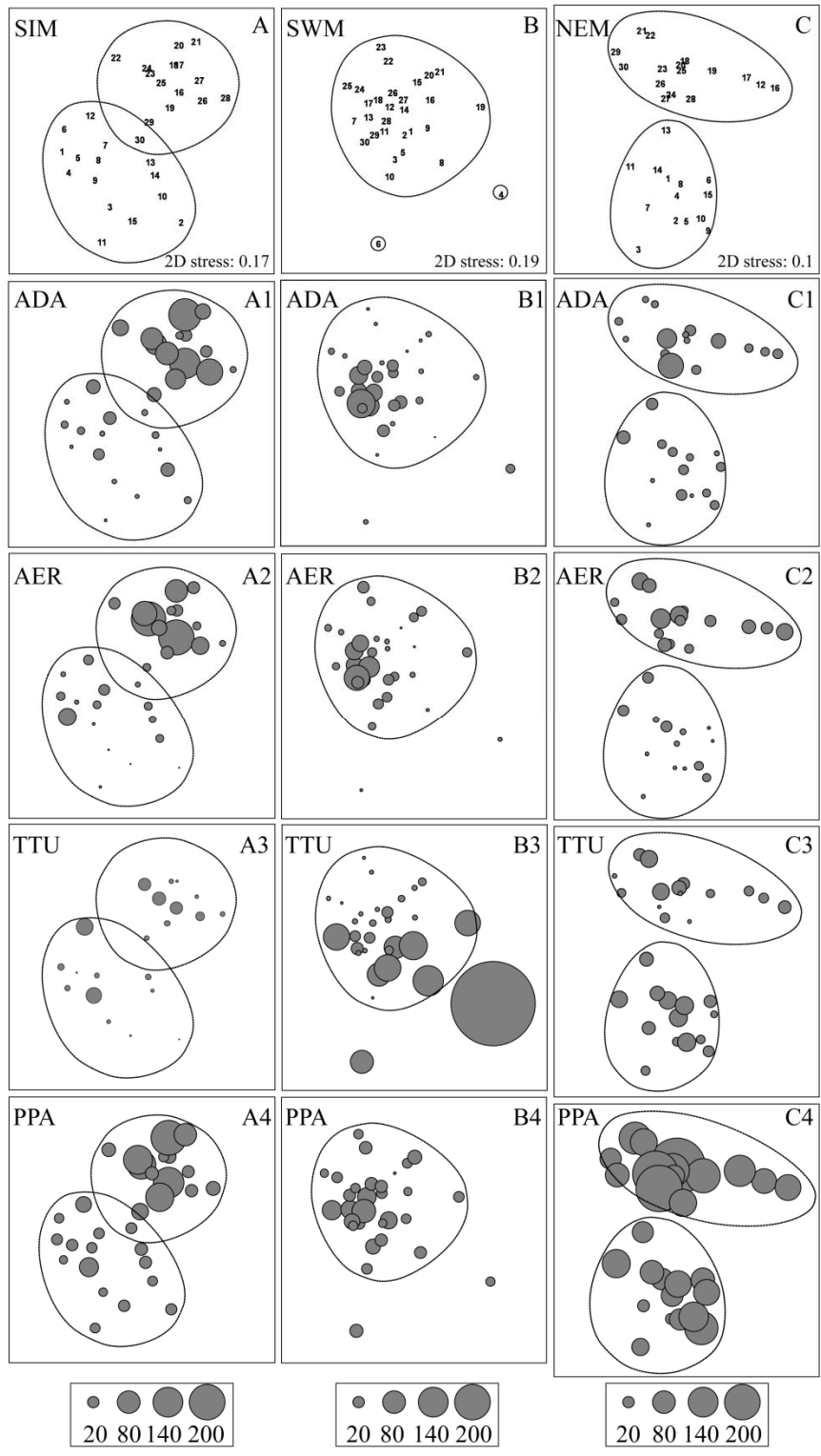


Figure 9

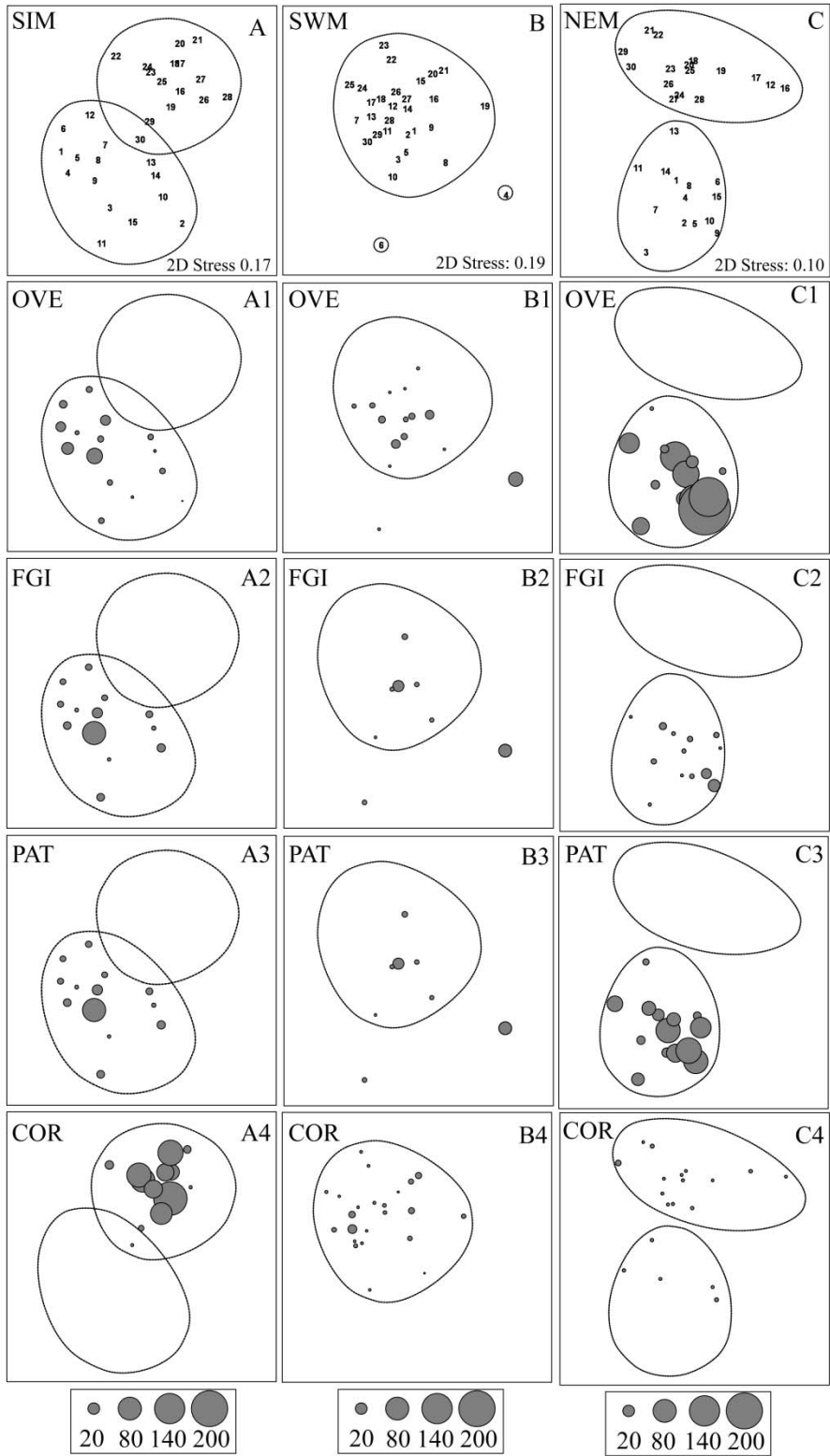


Figure 10

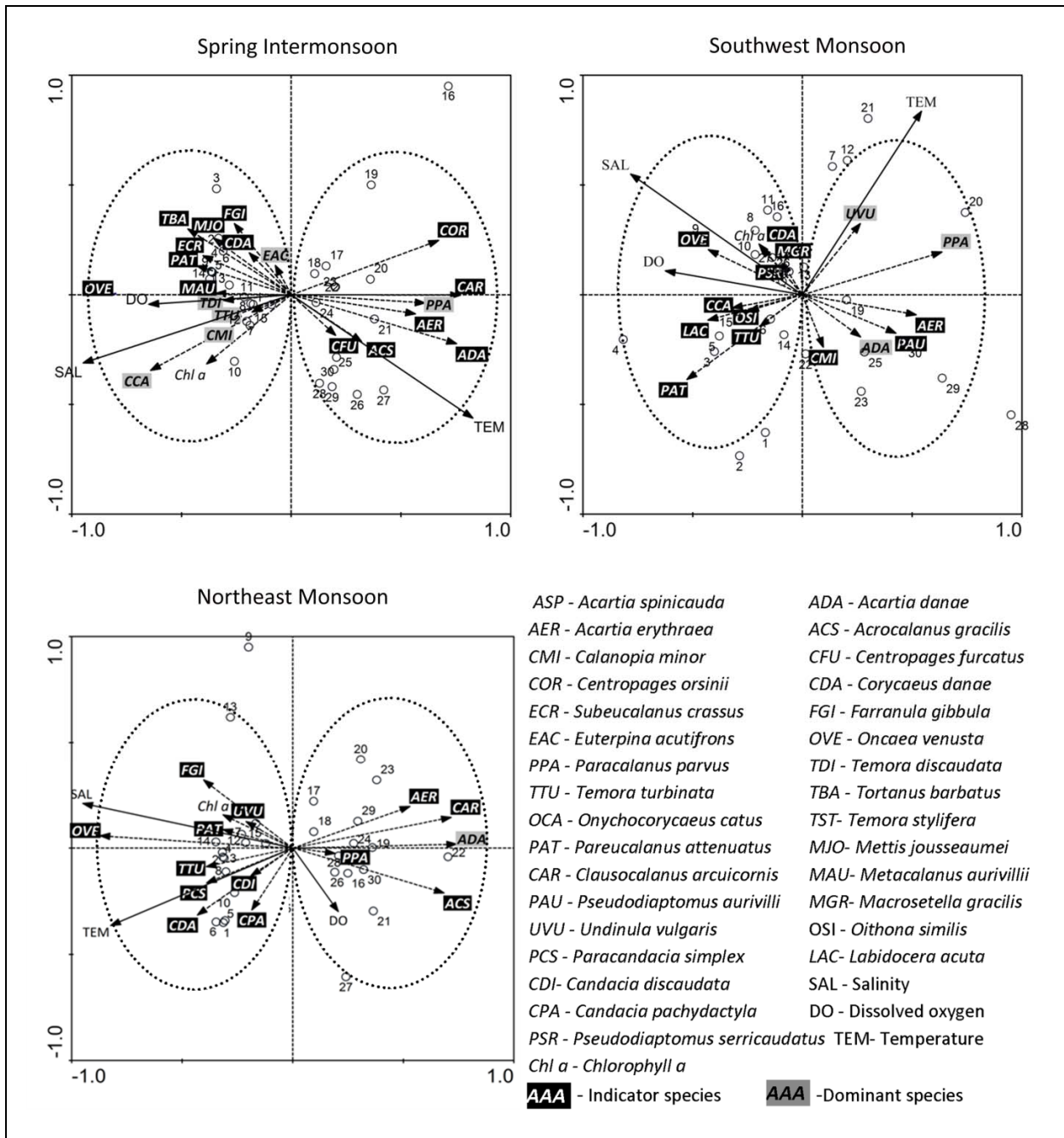


Figure 11

Parameter	Spring intermonsoon (SIM)		Summer monsoon (SM)		Northeast monsoon (NEM)	
	GoM	PB	GoM	PB	GoM	PB
Temperature (°C)	30.31 ± 1.20	31.47 ± 0.81	29.64 ± 1.11	30.29 ± 0.64	26.55 ± 0.49	25.45 ± 0.61
Salinity	33.9 ± 0.54	30.44 ± 1.13	35.39 ± 0.41	34.9 ± 0.60	32.0 ± 0.58	28.9 ± 1.42
Chl. <i>a</i> (mg m <sup>-3</sup> )	0.92 ± 0.45	0.87 ± 0.47	1.6 ± 1.3	0.76 ± 0.4	1.8 ± 1.7	0.75 ± 0.4
DO (mg L <sup>-1</sup> )	7.81 ± 0.93	6.34 ± 0.68	7.92 ± 0.75	6.76 ± 1.11	7.92 ± 0.75	8.12 ± 1.32
<b>Zooplankton</b>						
Biomass (ml. m <sup>-3</sup> )	0.10 ± 0.07	0.15 ± 0.13	0.20 ± 0.23	0.07 ± 0.06	0.26 ± 0.145	0.20 ± 0.15
Shannon Diversity (H')	0.92 ± 0.36	0.57 ± 0.32	0.57 ± 0.38	0.44 ± 0.26	0.41 ± 0.44	0.34 ± 0.23
Pielou's Evenness (J')	0.46 ± 0.18	0.33 ± 0.19	0.29 ± 0.19	0.26 ± 0.14	0.20 ± 0.19	0.19 ± 0.15
Simpson Dominance (C)	0.47 ± 0.20	0.30 ± 0.19	0.25 ± 0.18	0.18 ± 0.16	0.20 ± 0.23	0.13 ± 0.13
<b>Copepod</b>						
Shannon Diversity (H')	3.12 ± 0.26	2.43 ± 0.34	2.6 ± 0.54	2.3 ± 0.41	2.03 ± 0.25	1.69 ± 0.25
Pielou's Evenness (J')	0.93 ± 0.02	0.84 ± 0.06	0.85 ± 0.13	0.81 ± 0.17	0.71 ± 0.06	0.67 ± 0.08
Simpson Dominance (C)	0.94 ± 0.02	0.87 ± 0.04	0.80 ± 0.12	0.76 ± 0.11	0.79 ± 0.06	0.66 ± 0.10

Table 1 - Seasonal data of physico-chemical parameters, zooplankton biomass and diversity indices in the Gulf of Mannar (GoM) and the Palk Bay (PB). Mean and standard deviations are presented.

Major groups	GoM (SIM)	PB (SIM)	GoM (SWM)	PB (SWM)	GoM (NEM)	PB (NEM)
Hydromedusae	8 (1.5)	6 (3.3)	43 (2.37)	6 (3.33)	-	2 (3.5)
Siphonophores	-	-	287 (2.31)	3(4)	16 (3.92)	1(3)
Ctenophores	-	-	8 (1.75)	-	42 (2.62)	-
Thaliacea	-	-	49 (3.92)	-	80 (1.56)	-
Chaetognaths	520 (2.72)	33 (2.27)	1553 (3.0)	58 (1.7)	567 (1.05)	71 (1.89)
Copepods	27873 (1.05)	63158 (1.07)	53059 (1.36)	19823 (1.37)	84220 (0.75)	31629 (0.80)
Cladocerans	220 (0.84)	750 (0.48)	24 (2.38)	-	215 (3.87)	1120 (0.77)
Mysids	20 (2.7)	5 (3.4)	10 (3.7)	135 (4.24)	182 (3.75)	33 (1.36)
Isopods	-	13 (1.15)	-	-	-	7 (1.29)
Amphipods	2 (2)	2 (2)	128 (3.20)	1(5)	5 (2.8)	5 (5)
Lucifers	3960 (1.96)	645 (2.17)	359 (2.79)	155 (2.49)	8112 (3.0)	769 (1.90)
Appendicularians	3 (4)	-	5 (0.32)	9 (1.22)	-	11 (3.73)
Stomatopods	10 (0.5)	2 (3)	7 (2.71)	3 (2)	31 (1.77)	149 (3.32)
Polychaete larvae	3 (3.3)	1 (3)	-	2 (3.5)	-	42 (0.82)
Decapods and larvae	767 (1.58)	844 (1.67)	1035 (2.05)	129 (1.34)	1993 (1.93)	963 (2.0)
Cirriped larvae	-	-	-	10 (4)	-	279 (3.86)
Gastropods, bivalves and larvae	9000 (0.16)	16320 (0.89)	737 (1.89)	5867 (2.67)	3913 (2.87)	100 (2.1)
Fish eggs and larvae	2100 (1.32)	1153 (1.14)	903 (1.44)	444 (1.21)	500 (1.71)	833 (3.18)
<b>Total abundance</b>	<b>56663 (0.93)</b>	<b>82414 (1.03)</b>	<b>58053 (1.24)</b>	<b>26644 (1.29)</b>	<b>99837 (0.64)</b>	<b>34542 (0.83)</b>

Table 2 – Abundance of various mesozooplankton groups in the Gulf of Mannar (GoM) and the Palk Bay (PB) during different seasons. Mean abundance (No. 100 m<sup>-3</sup>) and coefficient of variations (in parenthesis) are presented. Abbreviations: Spring Intermonsoon (SIM), Southwest Monsoon (SWM) and Northeast Monsoon (NEM). Minus sign indicate absence



No.	Copepods	GoM(SIM)	PB(SIM)	GoM(SWM)	PB(SWM)	GoM(NEM)	PB(NEM)
1	<i>Nannocalanus minor</i>	++	+	+	+	+	-
2	<i>Undinula vulgaris</i>	++	-	++	++	++	++
3	<i>Cosmocalanus darwinii</i>	+	-	+	+	+	-
4	<i>Rhincalanus cornutus</i>	+	-	-	-	-	-
5	<i>R. nasutus</i>	+	-	-	-	-	-
6	<i>Eucalanus elongatus</i>	++	-	+	+	++	-
7	<i>Pareucalanus attenuatus</i>	++	-	++	+	+++	++
8	<i>Subeucalanus crassus</i>	++	-	+	+	-	-
9	<i>S. monachus</i>	+	-	+	+	+	-
10	<i>Acrocalanus monachus</i>	+	+	+	+	+	+
11	<i>A. gracilis</i>	+++	+++	+	+++	+	++
12	<i>Clausocalanus arcuicornis</i>	+	+++	+	+	+	++
13	<i>Paracalanus parvus</i>	+++	++++	+++	++++	++++	++++
14	<i>P. aculeatus</i>	+	+	+	+	+	+
15	<i>Centropages orsinii</i>	-	+++	+	+	+	+
16	<i>C. furcatus</i>	++	++	++	+	+	+
17	<i>C. tenuiremis</i>	+	+	-	-	+	-
18	<i>C. calaninus</i>	-	-	++	+	++	+
19	<i>C. elongatus</i>	+	+	-	-	+	+
20	<i>C. dorsispinatus</i>	++	+	+	+	++	++
21	<i>Pseudodiaptomus aurivilli</i>	+	-	+	++	+	+
22	<i>P. serricaudatus</i>	+	-	++	+++	+	+
23	<i>Temora turbinata</i>	++	++	++++	++++	+++	++++
24	<i>T. stylifera</i>	++	++	++	+	-	-
25	<i>T. discaudata</i>	++	+	++	+	+	+
26	<i>T. sp</i>	++	++	++	+	-	-
27	<i>Metacalanus aurivillii</i>	++	+	+	+	+	-
28	<i>Candacia discaudata</i>	-	-	-	-	+	-
29	<i>C. bradyi</i>	-	-	-	-	+	-
30	<i>C. pachydactyla</i>	-	-	-	-	+	-
31	<i>Paracandacia simplex</i>	-	-	-	-	+	-
32	<i>Calanopia elliptica</i>	+	-	+	+	-	-
33	<i>C. aurivilli</i>	+	-	-	-	-	-
34	<i>C. minor</i>	++	++	++	+++	++	+
35	<i>C. thompsoni</i>	-	-	+	+	-	-
36	<i>Labidocera acuta</i>	++	+	++	+	+	+
37	<i>L. pectinata</i>	+	+	++	+	+	++
38	<i>L. bataviae</i>	-	-	+	+	+	+
39	<i>L. madurae</i>	-	-	+	+	-	-
40	<i>L. minuta</i>	+	+	+	+	-	-
41	<i>L. pavo</i>	++	+	+	+	-	-
42	<i>Pontella securifer</i>	+	-	+	+	+	-

43	<i>P. danae</i>	+	-	+	+	+	+
44	<i>P. spinipes</i>	+	-	-	-	+	-
45	<i>Pontellopsis herdmani</i>	-	-	+	+	-	-
46	<i>P. armata</i>	+	-	-	-	-	-
47	<i>P. scotti</i>	+	-	+	+	+	-
48	<i>Pontellina plumata</i>	+	-	-	-	+	-
49	<i>Acartia spinicauda</i>	++	++	+	+	-	-
50	<i>A. erythraea</i>	++	+++	+++	++++	++	++
51	<i>A. danae</i>	++	++++	+++	++++	++	+++
52	<i>Tortanus barbatus</i>	++	-	++	++	+	+
53	<i>T. gracilis</i>	+	-	+	+	+	+
54	<i>Microsetella norvegica</i>	++	+	+	+	+	+
55	<i>M. rosea</i>	++	+	+	+	+	+
56	<i>Macrosetella gracilis</i>	+	+	+	+	-	-
57	<i>M. oculata</i>	+	+	+	+	+	+
58	<i>Euterpina acutifrons</i>	++	++	++	+	++	++
59	<i>Mettis jousseaumei</i>	+	-	+	-	+	-
60	<i>Oithona spinirostris</i>	+	+	-	-	-	-
61	<i>O. plumifera</i>	+	+	-	-	-	-
62	<i>O. similis</i>	++	+	+	++	++	+
63	<i>O. rigida</i>	+	+	-	-	+	+
64	<i>O. brevicornis</i>	+	+	-	-	+	+
65	<i>O. simplex</i>	+	-	-	-	-	-
66	<i>O. nana</i>	++	+	++	+	+	+
67	<i>Oncaea venusta</i>	+++	-	+++	+	++++	-
68	<i>O. conifera</i>	++	-	++	-	-	-
69	<i>O. media</i>	++	+	++	+	+	-
70	<i>Corycaeus danae</i>	++	++	+++	+++	++++	+++
71	<i>C. longistylis</i>	-	-	+	+	-	-
72	<i>C. speciosus</i>	++	+	+	+	-	-
73	<i>Onychocorycaeus ovalis</i>	++	+	-	-	++	++
74	<i>O. catus</i>	++	+	++	+	+	+
75	<i>Farranula gibbula</i>	++	+	++	+	++	-
76	<i>Copilia vitrea</i>	-	-	-	-	+	-
77	<i>C. mirabilis</i>	-	-	-	-	+	-
78	<i>Sapphirina ovatolanceolata</i>	+	-	-	-	+	-
79	<i>S. auronitens</i>	+	-	-	-	+	-
80	<i>S. nigromaculata</i>	+	-	-	-	+	-
81	<i>Bomolochus sp</i>	-	-	-	-	+	+
Total		67	41	57	55	60	37

Table 3 – Species of copepods recorded in the Gulf of Mannar (GoM) and the Palk Bay (PB) during different seasons. Minus sign indicates absence, + indicates <1% contribution, ++ indicates 1-5% contribution, +++ indicates 5-10 % contribution, ++++ indicates >10% contribution. Abbreviations: SIM - Spring Intermonsoon, SWM - Southwest Monsoon and NEM - Northeast Monsoon

	GoM	PB
SIM	<i>Acrocalanus gracilis</i> (0.065) <i>Paracalanus parvus</i> (0.047) <i>Temora turbinata</i> (0.028) <i>Temora discaudata</i> (0.023) <i>Calanopia minor</i> (0.027) <i>Acartia</i> ( <i>Odontacartia</i> ) <i>spinicauda</i> (0.024) <i>Acartia</i> ( <i>Odontacartia</i> ) <i>erythraea</i> (0.027) <i>Acartia danae</i> (0.021) <i>Euterpina acutifrons</i> (0.028) <i>Oncaea venusta</i> (0.102) <i>Corycaeus danae</i> (0.030) <i>Onychocorycaeus catus</i> (0.031)	<i>Acrocalanus gracilis</i> (0.16) <i>Clausocalanus arcuicornis</i> (0.129) <i>Paracalanus parvus</i> (0.134) <i>Centropages orsinii</i> (0.08) <i>Centropages furcatus</i> (0.027) <i>Acartia</i> ( <i>Odontacartia</i> ) <i>erythraea</i> (0.08) <i>Acartia danae</i> (0.143) <i>Corycaeus danae</i> (0.032)
SWM	<i>Undinula vulgaris</i> (0.023) <i>Pareucalanus attenuatus</i> (0.022) <i>Paracalanus parvus</i> (0.067) <i>Pseudodiaptomus serricaudatus</i> (0.032) <i>Temora turbinata</i> (0.222) <i>Calanopia minor</i> (0.033) <i>Acartia</i> ( <i>Odontacartia</i> ) <i>erythraea</i> (0.025) <i>Acartia danae</i> (0.05) <i>Oncaea venusta</i> (0.023) <i>Coryceus danae</i> (0.05)	<i>Undinula vulgaris</i> (0.034) <i>Paracalanus parvus</i> (0.157) <i>Pseudodiaptomus aurivilli</i> (0.023) <i>Pseudodiaptomus serricaudatus</i> (0.023) <i>Temora turbinata</i> (0.163) <i>Calanopia minor</i> (0.083) <i>Acartia</i> ( <i>Odontacartia</i> ) <i>erythraea</i> (0.03) <i>Acartia danae</i> (0.099) <i>Corycaeus danae</i> (0.066)
NEM	<i>Undinula vulgaris</i> (0.036) <i>Pareucalanus attenuatus</i> (0.059) <i>Paracalanus parvus</i> (0.293) <i>Temora turbinata</i> (0.126) <i>Acartia danae</i> (0.13) <i>Oncaea venusta</i> (0.10) <i>Coryceus danae</i> (0.129)	<i>Undinula vulgaris</i> (0.02) <i>Paracalanus parvus</i> (0.45) <i>Temora turbinata</i> (0.03) <i>Acartia danae</i> (0.06) <i>Acartia erythraea</i> ( 0.03) <i>Coryceus danae</i> (0.09)

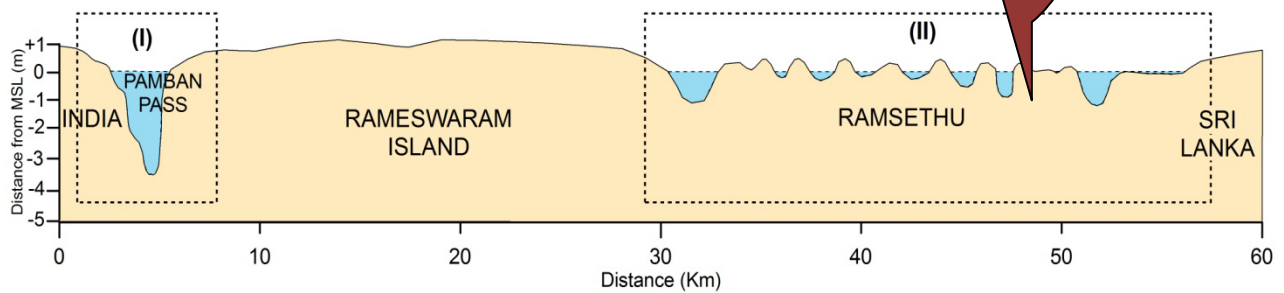
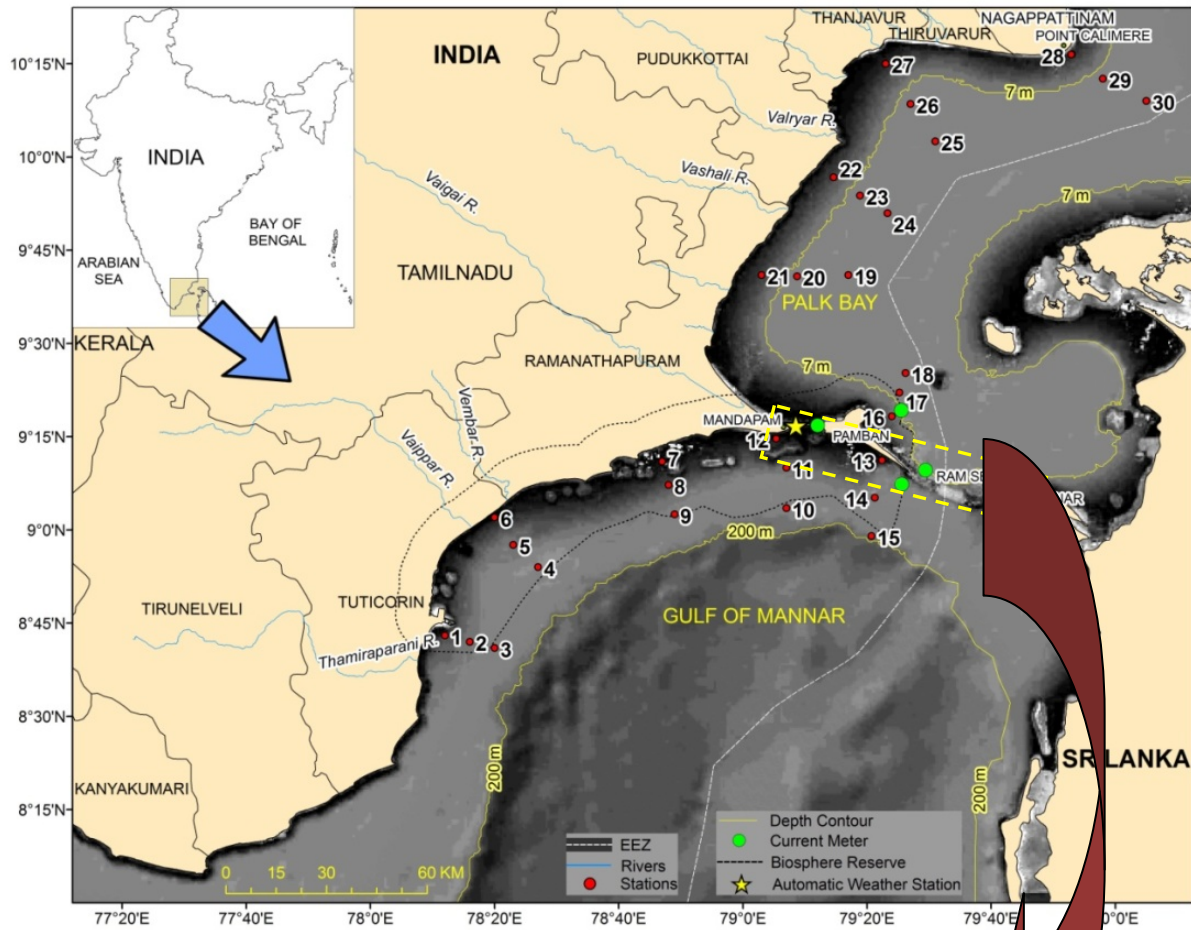
Table 4 – Details of dominant copepods and dominance values (in parenthesis) in the Gulf of Mannar (GoM) and the Palk Bay (PB) during different seasons. Abbreviations: SIM - Spring Intermonsoon, SWM - Southwest Monsoon and NEM - Northeast Monsoon

	GoM	PB
SIM	<i>Subeucalanus crassus</i> <i>Pareucalanus attenuatus</i> <i>Metacalanus aurivilli</i> <i>Tortanus barbatus</i> <i>Mettis jousseamei</i> <i>Oncaea venusta</i> <i>Corycaeus danae</i> <i>Farranula gibbula</i>	<i>Acrocalanus gracilis</i> <i>Clausocalanus arcuicornis</i> <i>Centropages orsinii</i> <i>Centropages furcatus</i> <i>Acartia (Odontacartia) erythraea</i> <i>Acartia danae</i>
SWM	<i>Pareucalanus attenuatus</i> <i>Pseudodiaptomus serricaudatus</i> <i>Labidocera acuta</i> <i>Macrosetella gracilis</i> <i>Temora turbinata</i> <i>Oncaea venusta</i> <i>Corycaeus danae</i> <i>Onychocorycaeus catus</i> <i>Oithona similis</i>	<i>Pseudodiaptomus aurivilli</i> <i>Calanopia minor</i> <i>Acartia (Odontacartia) erythraea</i>
NEM	<i>Undinula vulgaris</i> <i>Pareucalanus attenuatus</i> <i>Temora turbinata</i> <i>Oncaea venusta</i> <i>Corycaeus danae</i> <i>Farranula gibbula</i> <i>Candacia pachydactyla</i> <i>Candacia discaudata</i> <i>Paracandacia simplex</i>	<i>Paracalanus parvus</i> <i>Acartia (Odontacartia) erythraea</i> <i>Acrocalanus gracilis</i> <i>Clausocalanus arcuicornis</i>

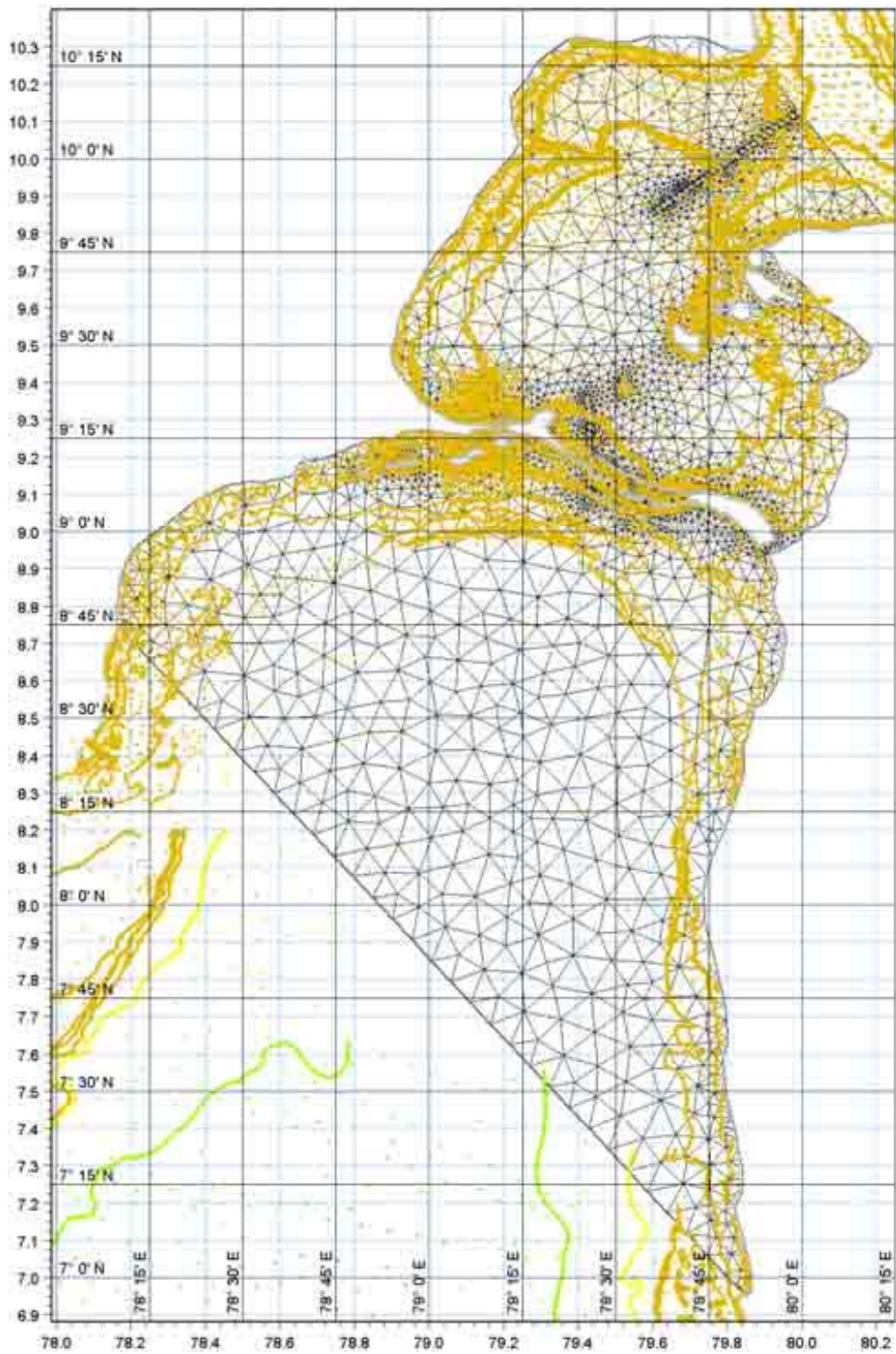
Table 5 – Details of indicator species of copepods in the Gulf of Mannar (GoM) and the Palk Bay (PB) during different seasons. Abbreviations: SIM - Spring Intermonsoon, SWM - Southwest Monsoon and NEM - Northeast Monsoon

GoM	Earlier records	PB	Earlier records
<i>Acartia erythraea</i>	Inshore BoB <sup>1,2</sup>	<i>Acartia danae</i>	Inshore BoB <sup>2</sup>
<i>Acartia danae</i>	Inshore BoB <sup>2</sup>	<i>Acartia erythraea</i>	Inshore BoB <sup>1</sup>
<i>Acartia spinicauda</i>	In & offshore BoB <sup>2,3</sup> & AS <sup>4</sup>	<i>Acrocalanus gracilis</i>	Inshore BOB <sup>1,5,10</sup>
<i>Acrocalanus gracilis</i>	Inshore BoB <sup>1,5</sup>	<i>Calanopia minor</i>	Inshore AS <sup>6</sup>
<i>Calanopia minor</i>	Inshore AS <sup>6</sup>	<i>Centropages furcatus</i>	Inshore AS <sup>9,16</sup>
<i>Candacia discaudata</i>	Offshore BoB <sup>5</sup>	<i>Centropages orsinii</i>	Inshore AS <sup>10,11</sup>
<i>Candacia pachydactyla</i>	Offshore AS <sup>7</sup>	<i>Clausocalanus arcuicornis</i>	Inshore AS <sup>7</sup>
<i>Paracandacia simplex</i>	Offshore BoB <sup>5</sup>	<i>Corycaeus danae</i>	Inshore BOB <sup>1,5</sup>
<i>Corycaeus danae</i>	Inshore BoB <sup>1,5</sup>	<i>Paracalanus parvus</i>	Inshore BoB <sup>5,10</sup>
<i>Euterpina acutifrons</i>	Inshore BoB <sup>1,5,8</sup> & AS <sup>9</sup>	<i>Pseudodiaptomus aurivilli</i>	Inshore AS <sup>16</sup>
<i>Farranula gibbula</i>	Off shore BoB <sup>5</sup>	<i>P.serricaudatus</i>	Inshore AS <sup>10,15,16</sup>
<i>Labidocera acuta</i>	Inshore AS <sup>10</sup> & BoB <sup>5</sup>	<i>Temora turbinata</i>	Inshore AS <sup>7</sup>
<i>Macrosetella gracilis</i>	Offshore BoB <sup>1</sup>	<i>Undinulla vulgaris</i>	In & offshore BoB <sup>3</sup> AS <sup>16</sup>
<i>Metacalanus aurivilli</i>	Inshore AS <sup>11</sup>	<i>Euterpina acutifrons</i>	Inshore BOB <sup>6</sup>
<i>Mettis jousseaumei</i>	Inshore BoB <sup>12</sup>		
<i>Oithona similis</i>	Offshore BoB <sup>3,13</sup>		
<i>Oncaea venusta</i>	Shelf & offshore BoB <sup>5,13</sup> , AS <sup>14</sup>		
<i>Onychocorycaeus catus</i>	Shelf & offshore AS <sup>14</sup>		
<i>Paracalanus parvus</i>	Inshore BoB <sup>5,10</sup> & AS <sup>6</sup>		
<i>Pareucalanus attenuates</i>	Offshore AS <sup>7</sup>		
<i>Pseudodiaptomus serricaudatus</i>	Inshore AS <sup>10, 15, 16</sup>		
<i>Subeucalanus crassus</i>	Offshore AS <sup>11</sup>		
<i>Temora discaudata</i>	Inshore & Shelf AS <sup>7,9</sup>		
<i>Temora turbinata</i>	Inshore BoB <sup>1</sup> AS <sup>7,15</sup>		
<i>Tortanus barbatus</i>	Inshore AS <sup>5,9</sup>		
<i>Undinulla vulgaris</i>	Inshore & offshore BoB <sup>3</sup> AS <sup>16</sup>		

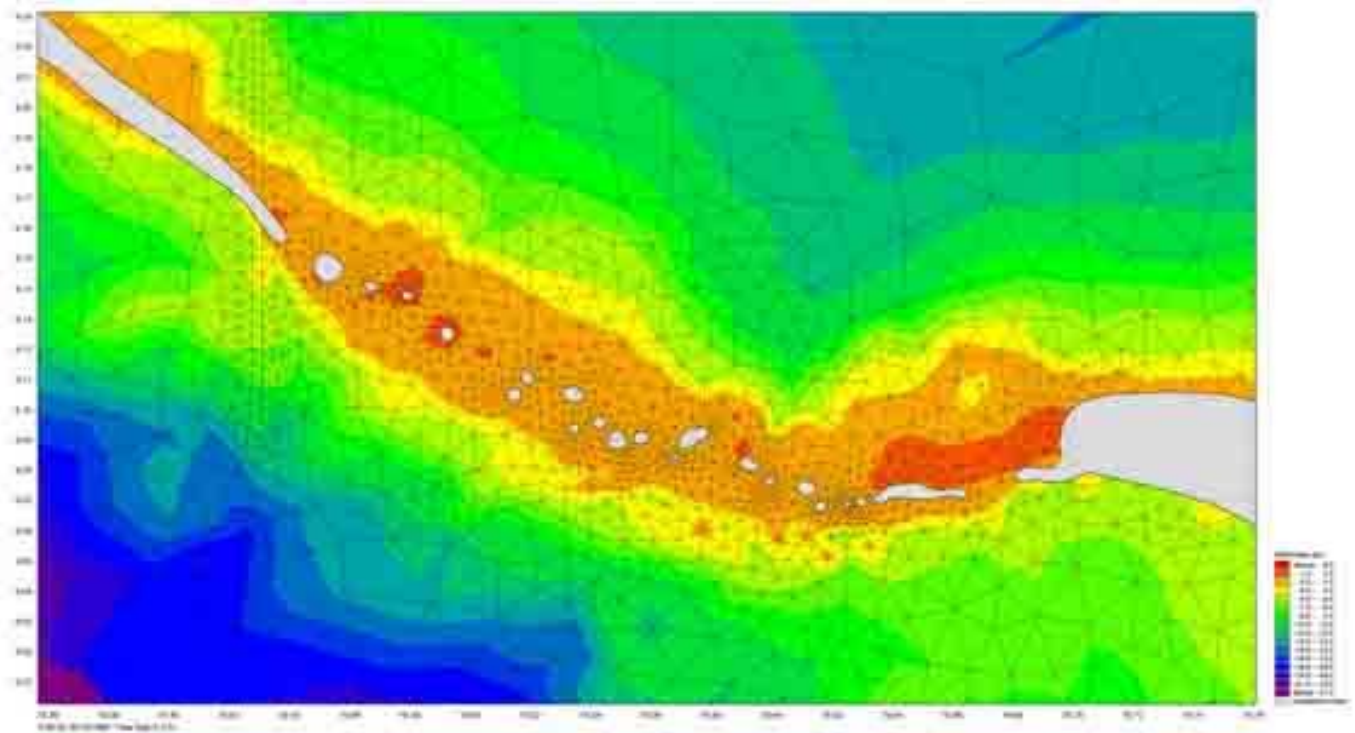
Table 6 – Dominant and indicator species of copepods in the Gulf of Mannar (GoM) and the Palk Bay (PB) and their earlier records from Indian waters: AS and BoB indicate the Arabian Sea and the Bay of Bengal respectively. Literature cited: (1) Rakesh et al., 2008, (2) Perumal et al., 2009, (3) Fernandes, 2008, (4) Madhupratap et al., 1990, (5) Rakesh et al., 2006, (6) Padmavati et al., 1997, (7) Madhupratap et al., 1990, (8) Krishnamurthy, 1967, (9) Gaonkar et al., 2010, (10) Jyothibabu and Madhu, 2007, (11) Madhupratap et al., 1992, (12) Santhanam and Perumal., 2003, (13) Fernandes and Ramaiah, 2009, (14) Martin Thompson, 1990 (15) Madhu et al., 2007 (16) Madhupratap, 1987.



Supplementary material 1 – Study area and a diagrammatic representation of the sea bed from Mandapam (India) to Mannar Island (Sri Lanka) based on ADP measurements in Pamban Pass (Square I) and hydrography chart No. 358 in the Ramsethu Region. Also see in Sivalingam (2005).

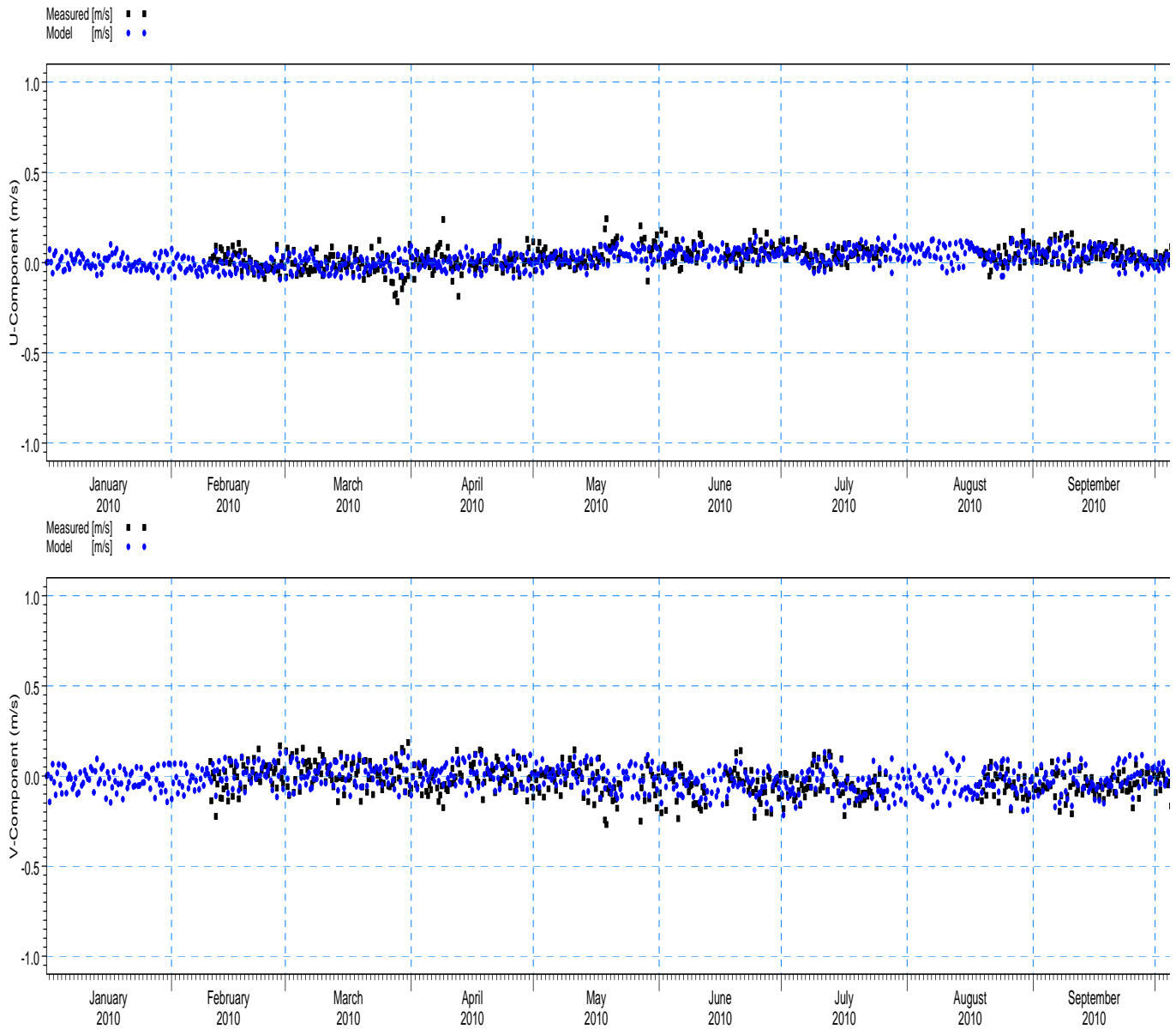


Supplementary materials 2a: Model domain with flexible mesh and bathymetry data points



Supplementary materials 2b: Fine resolution flexible mesh in the Ram Sethu region





Supplementary material 2c: Comparison between measured (black colour) and MIKE 21 modeled (blue colour) current components at the Ramsethu region (a) u-component and (b) v-component. The observed and MIKE 21 simulated currents showed very good correlation