

Spatial structuring of zooplankton communities through partitioning of habitat and resources in the Bay of Bengal during spring intermonsoon

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Abstract:

Despite advances in oceanographic investigations in the Indian Ocean, zooplankton ecology is still poorly known from the open waters of the Bay of Bengal. In order to understand the vertical and horizontal distribution of zooplankton in the Bay of Bengal during spring intermonsoon, stratified sampling was conducted using the multiple plankton net. We found that higher zooplankton biomass was often associated with mesoscale cold-core eddies. The biomass in the mixed layer was lesser in the central Bay and the near- absence of organisms beneath this layer was attributed to the very low dissolved oxygen levels including suboxia in the northern extent. The copepod diversity was severely reduced here and only a few species specialized to thrive in minimum oxygen concentrations were found in this zone. However, *Pleuromamma indica* is another copepod that seems to have adapted to the OMZ as seen from its increased numbers and by its strong vertical migrating ability to cross the low oxygen barrier. Highly diverse copepod assemblages comprising 129 identified species were found to be vertically structured, mostly through partitioning of habitat and food resources.

Key words: Copepods, biomass, mesoscale cold-core eddies, oxygen minimum zone, diversity

1. Introduction

The Bay of Bengal is a semi-enclosed northeastern basin of the Indian Ocean characterized by seasonally reversing monsoon currents. Excessive precipitation over the ocean and runoff from rivers of the Indian subcontinent keeps the surface layers of the Bay permanently stratified (PrasannaKumar et al., 2004, 2007, 2010). As vertical exchange of water is constrained, the surface chlorophyll *a* concentrations are usually less than 0.1 mg m^{-3} (Madhupratap et al., 2003). Mesoscale cold-core eddies occur frequently at many locations in the central and western Bay, boosting productivity and higher abundances of zooplankton in these rings (Fernandes, 2008; Fernandes and Ramaiah, 2009, 2013). Due to the closed northern boundary and stratification, dissolved oxygen (DO) is acutely depleted at intermediate depths (Sen Gupta and Naqvi, 1984). Since many zooplankton species are sensitive and susceptible to low DO concentrations, their biomass is usually severely low at the core of the oxygen minimum zone (OMZ; Wishner et al., 2008). Unlike in shallow areas where only the surface layer can serve as a refuge, in deep waters many organisms ought to develop vertical migration strategies to cope with the OMZ as it sets the limits to their vertical distribution (Ekau et al., 2010). In the equatorial tropical north Pacific Ocean (Saltman and Wishner, 1997) and Arabian Sea (Madhupratap et al., 2001), permanent hypoxia/suboxia extending from ~100-1000m is found to hamper the horizontal and vertical distribution as well as migrations of zooplankton. Sub-lethal responses such as lesser egg production can have important repercussions on zooplankton population dynamics and food web (Marcus et al., 2004).

Vertical structure of zooplankton in the Bay of Bengal is poorly studied. Available information is mostly on the epipelagic species and their biomass, collected during the 1960s when the first International Indian Ocean Expedition (IIOE) took place. IIOE data during March- April (SpIM) shows a huge variability in zooplankton biovolume distribution ranging from 0.05 to $10 \text{ ml } 100 \text{ m}^{-3}$ in the Bay of Bengal (Panikkar and Rao, 1973). Recently, Karati et al. (2018) found high biomass of zooplankton associated with high chl *a* in frontal regions in the Bay of Bengal. Zooplankton biomass in the mixed layer during SpIM in the Arabian Sea was found to be on par with the biomass during the more (primary) productive monsoons because of the microbial loop (Madhupratap et al., 1996). Mukherjee et al. (2018) in a study off the Bay of Bengal coast has found that detrital organic matter is a major source of zooplankton diet.

While the existence of OMZ in the Bay has been known for decades (Wyrтки, 1971; Sen Gupta and Naqvi, 1984), its impact on zooplankton is not clear. Our earlier studies (Fernandes, 2008;

Fernandes and Ramaiah, 2009, 2013) provided some details on zooplankton distribution and copepod communities up to the mesopelagic zone in the central and western Bay of Bengal during the summer monsoon and fall intermonsoon seasons. We observed that copepods often dominate mesozooplankton communities in terms of abundance and biomass in this region as is the pattern from other parts of the world ocean. Copepods are of prime importance as a link between marine primary producers and upper trophic levels, including fish. Few studies describe *Pleuromamma indica* as one copepod adapted to the OMZ of the Indian Ocean (Goswami et al., 1992; Saraswathy and Iyer, 1986). There is mostly a lack of information on copepods adapted to thrive in oxygen deficient waters of the Bay of Bengal. We investigated the vertical distribution of zooplankton in general and copepod species in particular during the spring intermonsoon season 2003. The role of relevant hydrographic factors including low dissolved oxygen influencing the vertical distribution of copepod species was looked into. As such, documentation of existing zooplankton diversity in the water column is useful variously.

2. Materials and methods

2.1. Sampling and sample processing

This study was carried out as a part of the Bay of Bengal Process Studies (BOBPS), onboard ORV *Sagar Kanya* cruise 191 in the central and western Bay of Bengal during April- May (spring intermonsoon) 2003. A multiple plankton net (Multinet®, Hydro-bios, Kiel, Germany; mouth area of 0.25 m² and mesh size of 200 µm) was used to collect samples during day and night from nine stations (Figure 1). The net was deployed at 500 m and based on profiles of conductivity, temperature and depth (CTD; Sea-Bird Electronics Inc., Bellevue, WA, USA) four depth strata were sampled: the mixed layer, the thermocline, the base of the thermocline to 300 m, and 300m to 500 m (mesopelagic zone). The net was retrieved at a speed of 0.8 m s⁻¹, and the volume of water filtered was taken as the product of the sampling depth and the mouth area of the net.

Zooplankton biovolume was measured by the displacement volume method (Harris et al., 2000) and expressed in ml 100 m⁻³ of water filtered. Biovolume of mixed zooplankton was converted to carbon equivalents as per Madhupratap et al. (1981). For gelatinous forms, carbon conversion was done as per Harris et al., (2000). Samples were immediately fixed and preserved in a 4% formaldehyde/seawater solution buffered with hexamine. When the sample size was small, the whole sample was counted and when it was large, it was split in a Folsom plankton splitter and used. The identification and enumeration into different taxonomic groups was done under a stereozoom microscope (Olympus, Japan) and

expressed as individuals per cubic meter (ind. m⁻³) of water filtered. Standard identification keys (UNESCO, 1968; Kasturirangan, 1963; Tanaka, 1956) as well as websites such as “*The marine Species Identification Portal* (<http://copepodes.obs-banyuls.fr>)”, the “*Integrated Taxonomic Information System online database* (<http://www.itis.gov>)” and the “*World Register of Marine Species* (<http://www.marinespecies.org>)” were used to aid in the identification of copepod species.

Seawater was collected by 12-L GO-Flo bottles (General Oceanics, Miami, FL, USA) mounted on a CTD rosette and analyzed for dissolved oxygen (DO) by Winkler titration (Grasshoff et al., 1983). The physical and chemical data was obtained from the CSIR-NIO Data Center (NIODC). Chl *a* was measured from the top 120 m by fluorometric method (Turner Designs, Sunnyvale, CA, USA, 10-AU-005-CE; UNESCO 1994).

2.2. Data analysis

Differences between day and night were tested using Student’s *t*-test. Non-parametric Kruskal Wallis anova was used to compare differences between stations and between depths (*Statistica 6.0*). The copepod families contributing to $\geq 5\%$ and species $\geq 2\%$ of the total copepod abundance were considered as dominant ones. Mesozooplankton diversity was estimated using a range of univariate diversity measures such as alpha diversity based on species richness per sample (*S*), Shannon diversity index (*H'*) and Pielou’s evenness index (*J'*) (Pielou, 1977).

Beta diversity which is the intragroup β -dissimilarity/ within-area heterogeneity was calculated using the multivariate dispersion index (MVDISP).

Multivariate numerical ordination techniques were used to classify stations into groups with different zooplankton community structures. Similarity among samples was determined by standardized, square root transformed copepod species abundance to generate a Bray-Curtis similarity matrix using the program package Primer 5 (Clarke and Warwick, 1994). The Group average method was used to cluster samples into Groups depending on the similarity in assemblages that was also confirmed by multi-dimensional scaling (MDS). Analysis of similarity (One way ANOSIM) was used to test the significant differences between Groups of zooplankton assemblages. The SIMPER (similarity of percentages) test was used to identify those species that contributed the most to similarities within Groups and between Groups.

3. Results

3.1. Hydrographic parameters

Sea surface temperature (SST) was 29- 30.5°C (Fig 2) and the mixed layer 15- 40 m in the study area during spring intermonsoon period. Weak thermocline oscillations were observed at CB2, CB3, CB5, WB2 and WB3 mostly within the upper 200 m and in some locations even deeper. Sea surface salinity (SSS) varied from 32.8 to 33.9 psu. There was not much variation in salinity between sampling locations and the vertical salinity gradient in the top 100 m was only 1-2 psu.

Dissolved oxygen concentration was low between depths 80 and 500 m ($<50 \mu\text{M}$). Subsurface hypoxia intensified northwards in both transects. At stations CB3 and CB5, the DO was about $10 \mu\text{M}$ at 120 m and a narrow band of intensely suboxic ($\leq 5 \mu\text{M}$) water was found between depths 200 and 300 m.

3.2. Chlorophyll *a*

Surface chlorophyll (chl) *a* in the central Bay was 0.1 mg m^{-3} (Figure 2). Subsurface chlorophyll maxima (SCM) were prominent between 60 and 80m with a maximum concentration of 0.3 mg m^{-3} . The SCM were shallower at stations CB1 and CB5. The 0-120 m column concentrations varied from 13.4 to 18.3 mg m^{-2} with the values increasing northwards.

In the western Bay, the surface chl *a* concentrations varied from 0.06 to 0.21 mg m^{-3} . SCM ranged from 0.16 to 1 mg m^{-3} at depths ranging from 40 to 80 m. The highest concentration of chl *a* was found in the shallowest SCM at WB3. Column chl *a* concentrations varied between 11 and 43 mg m^{-2} with the highest value at WB3.

3.3. Mesozooplankton biovolume/biomass and abundance

The biovolume in the mixed layer varied from 28 to $70 \text{ ml } 100 \text{ m}^{-3}$ in the central Bay during the day (Figure 3). In the night, it was higher, ranging from 18 - $230 \text{ ml } 100 \text{ m}^{-3}$. Nearly 95 - 99% of the biovolume in the sampled water column was in the mixed layer. In the western Bay, the variation of biovolume in the mixed layer was much larger ranging from 7 to $400 \text{ ml } 100 \text{ m}^{-3}$ during day and from 20 to $667 \text{ ml } 100 \text{ m}^{-3}$ in the night (Figure 4). About 80% of the biovolume was in the mixed layer and unlike in the central Bay, quantifiable biovolume was observed even up to 500 m.

The biovolumes were greater at stations CB3, CB4, WB3 and WB4. Swarms of scyphomedusae were common at many stations. Since there was no data at some stations and negligible biomass at many subsurface depths, the abundance data was combined for the day and night samples. The abundance of

zooplankton varied from 0.1 to 248 ($\times 10^3$) ind. 100 m^{-3} in the central and 0.2 to 534 ($\times 10^3$) ind. 100 m^{-3} in the western Bay. Similar to the biovolume, the abundance was more in the mixed layer accounting for 96% of the total in the upper 500 m in the central Bay and 86% in the western Bay (Table 1). The abundance was higher at CB3, CB5 and WB4.

There was little diel difference in zooplankton biovolume and abundance even as both decreased significantly with increasing depth ($p < 0.05$). The 0-500 m column integrated zooplankton carbon biomass in the central Bay (Figure 5), varying from 24 to 197 (av. 75) mM C m^{-2} and abundance from 0.7 to 5 (av. 3.3) $\times 10^4$ individuals m^{-2} was lesser than that in the western Bay, where the biomass ranged from 35 to 480 (av. 224) mM C m^{-2} and the abundance from 3.8 to 18.2 (av. 9.6) $\times 10^4$ individuals m^{-2} .

3.4. Mesozooplankton groups and their vertical distribution

Twenty eight groups of zooplankton were found during this study (Table 2). The total number of groups decreased significantly ($p < 0.05$) at deeper depths but remained similar between stations (Figure 6). Copepoda was the predominant group at all stations and depths, ranging from 70 to 85% (Figure 7). Their proportion increased with depth but for their least abundance in the 200-300 m stratum in the western Bay. In this stratum, ostracoda (9.5%) and foraminifera (11.5%) were found in higher proportion. These two groups, chaetognatha (1.5 to 4.3%) and appendicularia (0.4-2.5%) were commonly found at all depths in both transects. Abundance of invertebrate eggs (1.2-6.5%) in the upper 300 m was conspicuous while polychetes (0.76-1.82%) occurred in small numbers throughout the 500 m column in the central Bay. In contrast, salps (0.8-1.4%) were found throughout the water column in the western Bay.

3.5. Vertical distribution of Copepoda

3.5.1. Orders

Copepods observed during this study were from four Orders viz. Calanoida, Cyclopoida, Mormonilloida and Harpacticoida in decreasing order of abundance (Figure 8). Copepods of the Order Calanoida averaging 36-64% of the total copepod abundance in the central Bay and 45-76% in the western Bay were minimum in the 200-300m stratum. This coincided with the highest proportion of Mormonilloid copepods (31 & 28% in CB & WB) in this stratum. Cyclopoida abundance averaged 30% in the water

column with relatively higher abundance in the thermocline in the western Bay. Harpacticoid percentage was negligible.

3.5.2. Families

From the 34 families of copepods that were recorded during this study, individuals of only eight families (Clausocalanidae, Eucalanidae, Lucicutiidae, Metridinidae, Paracalanidae, Oithonidae, Mormonillidae and Oncaeiidae) were dominant during this study. Copepods from 25-30 families were found in the first two strata compared to just 20-24 in the last two strata (Table 3). In general, Clausocalanidae, Paracalanidae and Corycaeiidae were abundant in the top 200 m and Oncaeiidae in all three strata. Copepods from families of Oithonidae, Metridinidae (in central Bay) and Sapphirinidae (in western Bay) peaked in the thermocline. Mormonillidae were dominant in the 200-300 m and Eucalanidae (central Bay) and Lucicutiidae (in western Bay) proportions increased with depth.

3.5.3. Genera and species

Copepods from 50 genera were identified in the central Bay (Table 3), of which 42 each were present in the mixed layer and the thermocline and just 28 in the 200-300 m stratum. The number of copepod species found in these strata was 72, 61 and 39 respectively. In the western Bay, 59 genera were identified (Table 3) with 48 genera each in the mixed layer and thermocline, 33 in the 200-300 m stratum and 31 in the 300-500 m stratum. The number of species in each of these strata was 80, 84, 49 and 37 respectively.

3.6. Dominant copepod species

Out of the total 129 copepod species recorded during this study, 96 were found in the central Bay, of which only 12 species considered as dominant contributed to 65% of the copepod abundance (Table 3). The species *Acrocalanus gracilis*, *Calocalanus pavo*, *Clausocalanus furcatus*, *Corycaeus speciosus* and *Oncaea mediterranea* were restricted to the upper two strata (Figure 9). The others such as *Clausocalanus arcuicornis*, *Oncaea venusta*, *Oithona similis*, *Lucicutia flavicornis*, *Pleuromamma indica*, *Mormonilla minor* and *Corycaeus catus* were abundant till 300m.

From the western Bay, 111 copepod species were identified, of which nine species were the most dominant, contributing 59% to the total copepod abundance. *Acrocalanus gracilis* was abundant in the mixed layer (Figure 10). *C. arcuicornis* was most abundant in the top 200 m, rarely occurring in the deeper strata and *P. robusta* in moderate abundance exhibited similar pattern. *Centropages furcatus* and

E. monachus were abundant mostly in the northern stations. *L. flavicornis*, *O. venusta*, *O. similis* and *P. indica* were present at all stations and depths sampled.

3.7. Copepod Diversity Measures

3.7.1. Alpha diversity (Shannon diversity H' , Species richness d , and evenness J)

Alpha diversity for copepod species varied greatly with depth and between stations. Diversity in the central Bay ranged from 1 to 5, was generally higher in the mixed especially at CB1 (Figure 11). In the western Bay H' varied from 1.7 to 4.4 and a steady northward decline was noticed in the thermocline. The H' values were the lowest in the 200-300m strata in both transects with drastically low values in the north in the central Bay.

Species richness ranged from 0.5 to 4.8 in the central and from 1.5-4.4 in the western Bay. The maximum value of species richness was found in the mixed layer at CB1 and in the thermocline at WB1. In both transects, the 'd' was greatly diminished in the 200-300m stratum, decreasing northwards, especially between CB3 and CB5.

3.7.2. Beta diversity

The relative variability of copepod species assemblage within each of the strata sampled showed higher values of MVDISP in the 200-300 m stratum indicating higher beta diversity (Figure 12). Beta diversity was higher also in the central Bay.

3.8. Copepod Community structure

Multivariate analysis of all the 129 copepod species data combined from all the stations and depths in the central and western Bay distinguished through the 30% cut-off level of the Bray-Curtis similarity dendrogram yielded three clusters. Most of the thermocline (T) and OMZ (O) strata clustered into Group I, those from the mixed layer (M) strata and a few thermocline (T) strata into Group II and, OMZ strata from three stations CB3, CB4 and CB5 as Group III (Figure 13). The same was confirmed by two-dimensional ordination of the samples by NMDS (stress: 0.1; Figure 14) suggesting that the depths within each of the three groups shared similar copepod species communities. One-way ANOSIM test further substantiated the observed significant differences between these groups of assemblages (Global R: 0.826; p: 0.1%) in the study area.

Similarity percentage (SIMPER) analysis based on abundance estimates of all copepod species revealed the percent contribution of species to intra- group similarity ('characterizing species') as well

as inter-group dissimilarity ('discriminating species'). Table 4 summarizes information on (characterizing) species that contribute foremost to the average similarity together with their percent contribution to the total copepod abundance, within each group. There was little variation in the intra-group similarities (36.47-82.27%).

Group I characterized 25 species with average similarity 49.6%, of which the top 8 most-contributing species are listed in Table 4. These are *O. venusta*, *C. arcuicornis*, *O. similis*, *P. indica*, *L. flavicornis*, *C. speciosus*, *C. catus* and *E. monachus*, contributing over 50% of the average similarity of Group I. Similarly, 20 species from depths between 200 and 500 m characterized the Group II, of which the top 7 species contributed to over two thirds of the average similarity. The composition of assemblages in the subsurface Group II was not very different from the surface Group I. However the abundances of species in Group II were low and relative importance of *O. venusta* (17%), *M. minor* (15%), *P. indica* (11%) and *O. similis* (10%) was higher. Group III was characterized by just 3 species of copepods with an average similarity of 82.27%. Except for a few specimens of these species that were found in the three stations CB3, CB4 and CB5 at 200-300 m depth, no other copepod was found here. The reason for this is probably the intensely low oxygen concentration in this zone.

Table 5 shows the key copepod species that differentiate between the assemblages within mld –thermocline (Group I) and thermocline-500 m (Group II) strata, thus identifying them as 'discriminating species' in this study. As seen in the Tables, the average dissimilarity between the surface and subsurface groups is smaller than when compared with Group III. Though *O. venusta* is the predominant species at most depths and stations, *M. minor*, *E. monachus*, *C. arcuicornis*, *C. catus*, *O. similis*, *Corycaeus speciosus*, *Acartia negligens*, *A. gracilis*, *O. venusta*, *Cosmocalanus darwinii* and *Acrocalanus monachus* are good discriminating species for being abundant in the mixed layer and having low to nil abundance in the strata below.

Copepods like *Conaea gracilis*, *Heterostylites major*, *Heterorhabdus* sp., *Gaussia princeps* and *Haloptilus acutifrons* are also good discriminators as they were found in deeper waters and never in the surface strata. The exclusive presence of the copepods *Gaetanus kruppii*, *Gaussia princeps* and *Pleuromamma xiphias* in the 200-300 m zone (Figure 15), where dissolved oxygen concentration was 5-10 μM is indicative of them as discriminators of deep water hypoxia.

3.9. Correlation

Zooplankton biomass showed significant positive correlation with abundance, groups and chl *a*. Similarly, chl *a* and the number of zooplankton groups found, correlated negatively with temperature (Table 6).

4. Discussion

We have discussed below how the mesoscale cold-core eddies let the proliferation of mesozooplankton in the mixed layer, OMZ that limits their abundance in the subsurface and how both may be structuring the copepod communities in the upper 500 m.

4.1. Vertical distribution of zooplankton biomass, abundance and groups

The spring intermonsoon which is the transition phase between the Northeast Monsoon and Southwest Monsoon, characterised by maximum solar heating and high SST and SSS, is generally viewed as a low productive season with low zooplankton stock along the southeast coast of India (Jyothibabu et al., 2008). However, during this study, we observed very high standing stocks of zooplankton in the mixed layer, especially where food resources in terms of chlorophyll concentration were abundant. The average biovolume of zooplankton in the central Bay was 95 ml 100 m⁻³ compared to more than double biovolume (230 ml 100 m⁻³) in the western Bay. This value is more than one order of magnitude higher than the average biovolume of 10 ml 100 m⁻³ reported from the Palk Bay (Jagadeesan et al., 2013), in the south western Bay of Bengal and also the range of 3- 52 ml 100 m⁻³ found by Karati et al., (2018) in the western Bay of Bengal.

Since stratification was the least during this season, particularly in the western Bay, cold-core eddies identified from the thermocline oscillations of the isotherms at CB2, CB3, CB5, WB2 and WB3 (Prasanna Kumar et al., 2010) enabled pumping up of inorganic nutrients such as nitrate and silicate from the deep layers into the euphotic zone, enhancing phytoplankton productivity. Therefore higher chl *a* up to 1mg m⁻³ was found in the SCMs at most cold- core eddy locations. Since the eddy effect was felt close to the surface at CB5 and WB3, the column chl *a* and primary productivity were also the maximum here (Ramaiah et al., 2010; Prasanna Kumar et al., 2010). Enhanced productivity in cold-core eddies has been observed by Falkowski et al., (1991), Vaillancourt et al., (2003) etc.

As the generation time of zooplankton is longer than phytoplankton, i.e. 15-30 days (Piontkovski et al., 1995), during the ~4 month life span of the eddy (Nuncio and Prasanna Kumar, 2012),

zooplankton seem to have sustained on the phytoplankton bloom within the eddies. There was also significant positive relationship between zooplankton biomass and chl *a* at stations having relatively lower seawater temperature in the euphotic zone. Significant enhancement of zooplankton biomass was observed within cold core eddies during fall intermonsoon and summer monsoon seasons in our earlier studies (Fernandes, 2008; Fernandes and Ramaiah, 2009; Fernandes and Ramaiah, 2013). Higher copepod abundance was observed in the nutrient replenished upwelling area on the south west coast of India (Madhupratap 1990) and elsewhere (Wiebe, 1976; Beckmann et al., 1987; Huntley et al., 1995).

Jyothibabu et al. (2004) found zooplankton biomass ranging from 30 to 60 mMCm⁻² in the oceanic and, 50-133 mMCm⁻² in the coastal areas of Bay of Bengal (upper 200 m). The average zooplankton carbon biomass in the upper 500 m (40 mMCm⁻²) in the central Bay during present study was ~4 times poorer compared to the central Arabian Sea (161 mMCm⁻²; Madhupratap et al. 1996). However the western Bay (260 mMCm⁻²) was more than twice as rich in zooplankton as the eastern Arabian Sea (105 mMCm⁻²; for the upper 200 m) during the same season. The overwhelming effect of the cold-core eddies helped the western transect of the Bay of Bengal to support ~ 7 times more zooplankton biomass than the central transect, which is also higher than the values recorded during the summer monsoon and fall intermonsoon seasons (Fernandes, 2008; Fernandes and Ramaiah, 2009, 2013).

Generally the biomass and abundance were in good agreement except at WB3 and WB4, where larger gelatinous organisms such as scyphomedusae, siphonophores and salps contributed significantly. As Madin et al. (2001) and Brodeur et al. (2002) noted, they become important component of the plankton, especially during the spring/summer months. Riandey et al. (2005) also observed high abundance of salps or doliolids in cyclonic eddy in the western Mediterranean Sea during summer. They can strongly impact the zooplankton standing stocks as they devour a wide spectrum of zooplankton prey and (Omori et al., 1995; Ishii and Tanaka, 2001) their mass occurrence has been found to reduce local stocks of copepods (Hulsizer, 1976).

The biomass below the mixed layer, especially in the central Bay was very low and so also were the numbers of zooplankton groups which were the least during this study compared to the other seasons even as copepod distribution remained unchanged (Fernandes et al., 2008, Fernandes and Ramaiah, 2013). The larger, faster moving zooplankton such as the euphausiids having capabilities to traverse greater distances (Longhurst, 1976) were present in small numbers. Therefore as Roman et al. (1995)

suggested, due to the dominance of smaller size class of organisms, there was no evidence of diel vertical migration during this study. In a recent study, Karati et al. (2017) observed restricted diel vertical migration mostly due to sharp vertical gradients in physico-chemical parameters. Chaetognaths feed primarily on copepods (Terazaki, 1996) and their distribution profile was similar to that of the copepods. The 200-300 m stratum contained very low DO concentration and dominance by ostracods and foraminifera was observed. This could be attributed to their passive and less selective feeding, mainly on phytodetritus and other organic matter that rains down from the surface production (Maas et al., 2014; Spindler et al., 1984); and their ability to tolerate hypoxia better (Moodley et al., 1997; Gooday et al., 2009).

4.2. Copepod community structure

Calanoids were relatively more abundant in the mixed layer especially in the western transect where higher chl *a* and primary productivity were observed (Ramaiah et al., 2010). This could be related to their preference for diatoms (Frost, 1972; Checkley, 1980) enriched by the high Si:N and Si:P ratios in the cold core eddies (Paul et al., 2008). It is evident from the study of Stephen (1992) that copepods from the families Paracalanidae, Eucalanidae and Calanidae occur along both the coasts of India. In this study, *Clausocalanus arcuicornis* was the most important herbivore (Frost and Fleminger, 1968) in the central Bay and *Eucalanus monachus* in the western Bay. As Stephen (1992) suggested the former feeds on fine- and latter on coarse particles. According to Miyashita et al., (2009), *Clausocalanus* becomes important in spring as it is highly adapted to oligotrophic conditions and can exploit other forms of food besides phytoplankton (Roff et al., 1995). It is believed that copepods sense the amino acids present in phytoplankton cells from long distances (Poulet and Oullet, 1982), that a strong relationship was evident between abundance of phytoplankton and predominance of the two herbivorous species in the mixed layer.

Cyclopoid copepods were abundant throughout the water column and similar to our study, Stephen (1988) found that its most abundant representative *Oncaea* to be abundant in the oceanic regions, away from the high productivity zones. This is possible since their feeding habits are diverse, comprising detritus, larvacean houses and marine snow (Steinberg and Silver, 1994). Abundance of *Oithona* spp. was quite less unlike in other studies (e.g. Paffenhöfer and Mazzocchi, 2003) where smaller mesh sizes were used for sampling. They are ambush feeders and generally do not prefer diatoms (Paffenhöfer, 1993). Their representative *Oithona similis* feeds upon a variety of food sources

like phytoplankton, heterotrophic protists, and copepod nauplius, but primarily on ciliates and heterotrophic dinoflagellates (Nakamura and Turner, 1997). Since their respiration rate is minimally affected by temperature (Lampitt and Gamble, 1982) and feeding habits are more coupled to the microbial loop (Turner, 2004), they are able to peak in the thermocline as well as occupy all depth ranges. The order of abundance of calanoids> cylopoids>mormonilloids>harpacticoids during this study did not differ from our earlier observations for a different time period (Fernandes, 2008; Fernandes and Ramaiah, 2009, 2013).

Despite getting organisms from the top 500 m only, 129 species of copepods were found, typifying the high diversity of this basin. Not more than 12 copepod species were present in abundance greater than 2%. This is typical of tropical systems as also found by Piontkovski et al. (2003) where only a few species are successful in evolution (Briggs, 1974). During the summer monsoon 2001, Fernandes and Ramaiah (2009) listed 163 species of copepods of which 132 represented the Order Calanoida. Similar species and diversity was recorded from this region during the fall intermonsoon (Fernandes, 2008; Fernandes and Ramaiah, 2013). Li et al. (2017) identified 187 zooplankton species including the most diverse copepods from the surface along 10°N in the Bay of Bengal.

Temperature, chl *a* and seasonality are some factors believed to affect copepod diversity (Roy et al., 1998., Rutherford et al., 1999). As they suggest, copepods are ectotherms with short generation times, so warmer temperatures influence metabolic rates and indirectly affect diversity. The Bay of Bengal is a warm pool throughout the year with low chlorophyll *a* that does not change markedly with seasons and according to Woodd-Walker et al. (2002), more species are evidenced to co-occur in such areas with lower seasonal changes in physical properties and primary productivity. Also, as McGowan (1990) and Longhurst (2007) point out, the high species diversity of copepods is found in this basin because it is moderately oligotrophic and the productivity is limited by nutrients. The near surface waters of the Bay are also highly stable which according to Rutherford et al. (1999) provides higher vertical niche availability and therefore supports greater number of species.

4.3. Effect of OMZ on vertical distribution of zooplankton biomass and copepod species

The Bay of Bengal has an equally intense oxygen minimum zone as the more productive Arabian Sea, with hypoxic waters extending from 100 m to 500 m during this season. In the cold-core eddy region, there was even an intrusion of 10µM dissolved oxygen contour to 80 m. Though a general decrease in zooplankton abundance with increasing depth correlating with primary productivity in the upper water

column is a universal feature in tropical oceans (Banse, 1964; Fogg et al., 1985; Vinogradov, 1997), the reduction we observed was quite drastic in the central Bay where there were hardly any organisms netted from below 300 m. The intense oxygen minima and suboxia between 200 and 500 m seems apparently to partition zooplankton groups and is a deterrent for them in this zone.

In the western Bay, the DO concentrations did not fall below 6 μ M and its effect was seen in terms of considerable biomass observed up till 500m. Vinogradov and Voronina (1961) found that the zooplankton in the intermediate layers of the northern Arabian Sea become abnormally low when DO falls below 0.15ml L⁻¹ (6.7 μ M). This effect is also observed in the tropical Pacific and Benguela system (Saltzman and Wishner, 1997; Auel and Verheye, 2007; Wishner et al., 2008).

The copepod diversity was the lowest in the 200-300 m strata of the central Bay, coinciding with the lowest oxygen concentrations of 4-15 μ M. In the narrow band of suboxic water ($\leq 5 \mu$ M) that was observed in this stratum between stations CB3 and CB5, *Gaetanus kruppii*, a species of the family Aetideidae and two species of Metridinidae (*Gaussia princeps* and *Pleuromamma xiphias*) were the only copepods that were found. These are the large, rare deep water species that were reported sporadically in the Arabian Sea (Padmavati et al., 1998). The largest percentage of *Mormonilla minor*, a fragile, cosmopolitan meso-bathypelagic particle-feeding copepod having filter baskets formed by its appendages (Boxshall, 1985), occurred in high numbers in this stratum. *Conaea gracilis*, a deep-water copepod, rarely found in the IIOE collections (Stephen, 1988) was also most abundant here. The relative abundance of *Eucalanus* spp. and *Rhincalanus* spp. was also high as observed in other studies (Auel et al., 2007; Loick et al., 2005). Few species of Aetidedae, Augaptilidae, Heterorhabdidae, Lucicutiidae were also some of the occupants of this zone as also observed in the Arabian Sea (Padmavati et al., 1998).

Their tolerance to oxygen minimum conditions offers them an advantage from predators and competitors (Parker-Stetter and Horne, 2009). These copepods survive hypoxia either by taking up oxygen efficiently from surrounding waters, reduction of metabolic rates or by deriving energy from anaerobic metabolism (Childress and Seibel, 1998). It could also be due to anaerobic pathway supplementing aerobic metabolism by higher activity of enzyme lactate dehydrogenase as reported in copepods such as *E. inermis* and *R. rostrifrons* within other OMZs (González and Quinones, 2002; Cass, 2011). Some more ways of survival are decreased protein utilization and increased lipid catabolism, lower oxygen consumption rates and reduced feeding/ activity when in low-oxygen waters

observed in *Eucalanus inermis*, *Subeucalanus subtenuis* and *Rhincalanus rostrifrons* the copepods adapted to living in the world's most intense OMZ- the eastern tropical North Pacific (Cass and Daly, 2014; Cass et al., 2014).

The OMZ zone in the central Bay had the largest number of species of Metridinid copepod inhabitants (Table 3) similar to the OMZs of the eastern Pacific, Benguela current system and also the Arabian Sea (Escribano et al., 2009; Smith, 1998). Several species of *Pleuromamma* are thought to be vertical migrators and tolerant to low oxygen. Of the 7 species that were found during the IIOE, *P. indica* was the most abundant comprising ~84% of the *Pleuromamma* population (Saraswathy, 1986). Their largest concentration of $>500 \text{ ind.}100 \text{ m}^{-3}$ was observed in the northern Arabian Sea and the Central Bay of Bengal. Smith et al. (2005) argued that their numbers increased in the Arabian Sea in 30 years since then, indicating an increase in the OMZ or its intensity. Much higher numbers of *P. indica* of $\sim 1821 \text{ } 100\text{m}^{-3}$ in the central Bay and $\sim 9852 \text{ } 100\text{m}^{-3}$ in the western Bay of Bengal in the present study may apparently be linked to further deoxygenation of the OMZ.

As revealed by clustering, vertical zonation of copepod species was evident based on the hydrographic characteristics in the Bay. The copepod assemblages were found to be of three types, depending on their occurrence in strata within the 500 m water column during SpIM. Most of the assemblages from the mixed layer and a few from the thermocline formed one cluster that thrived in a warm, low- salinity, well- oxygenated and resource rich environment. Assemblages from thermocline to 500 m were similar at most stations, with the environmental characteristics being cold, more saline, and poor in oxygen and nutrition. An exception was the assemblages in the OMZ of the northern stations in the central Bay that were distinctly in a separate cluster in being able to thrive in suboxic condition.

As indicated from the higher beta diversity in this 200-300 m stratum, the copepod species composition is relatively unstable here compared to the more homogeneously distributed species in waters above and below it. Between 200 and 300 m where the DO concentration is lowest compared to anywhere in the water column, the copepod species in this stratum are unique, probably have low turnover and are least similar to those in the mixed layer and also in the deeper strata sampled. Similarly, higher beta diversity in the central Bay means lower predictability of the copepod species compared to the coastal waters.

4.4. Summary: Cold-core eddies exert positive control on the zooplankton and copepod assemblages and allow them to reach their highest biomass and abundance during the spring intermonsoon. The OMZ exerts negative control on zooplankton thereby drastically diminishing the biomass below 200 m especially in the northern extent of the central Bay. The warm, stable moderately oligotrophic waters are rich in copepod species that diminish very much in the 200- 300 m stratum. However the OMZ core has a high diversity of Metridinid copepods. *Pleuromamma indica* is one such copepod that was adapted to the OMZ by migrating through low oxygen conditions and maintaining greater abundance above the core of OMZ. Increased abundances of this copepod compared to the past studies apparently indicate an expansion of the OMZ in size and or intensity.

From this study, we observed three types of copepod assemblages in the Bay of Bengal during the SpIM season: 1) Surface species such as *O. venusta*, *C. arcuicornis*, *O. similis*, *C. speciosus*, *C. catus*, *E. monachus*, *Undinula vulgaris*, *Centropages furcatus*, *Clausocalanus furcatus* and *Calocalanus pavo* living in waters of higher temperature, oxygen and resources 2) Species adapted to live in oxygen minimum zones such as *Gaetanus krupii*, *Pleuromamma xiphias*, *P. indica*, *Gaussia princeps*, *Eucalanus elongatus*, *E. crassus* and *Rhincalanus cornutus* and 3) the mesopelagic/deep cold water species such as *Conaea gracilis* and *Mormonilla minor*. The highly diverse copepod assemblages in this tropical basin appear to be vertically structured, mostly through partitioning of habitat and food resources. Intensification and expansion of OMZ is likely to affect the communities by habitat compression of the epipelagic species, further reduction in biomass in the subsurface and increase in diversity of the species adapted to live in the OMZ.

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References

- Acuna JL, Deibel D, Saunders PA, Booth B, Hatfield E, Klein B, Mei ZP, Rivkin RB (2002). Phytoplankton ingestion by appendicularians in the North Water. *Deep-Sea Res II* 49: 5101–5115.
- Auel H, Verheye HM (2007). Hypoxia tolerance in the copepod *Calanoides carinatus* and the effect of an intermediate oxygen minimum layer on copepod vertical distribution in the northern Benguela Current upwelling system and the Angola-Benguela Front. *J Exp Mar Biol Ecol* 352: 234–243.
- Banse K (1964). On the vertical distribution of zooplankton in the sea. *Prog Oceanogr* 2:53 -125.
- Barange M. 1990. Vertical migration and habitat partitioning of six euphausiid species in the northern Benguela upwelling system. *J Plankton Res* 12: 1223–1237.
- Beckmann W, Auras A, Hemleben Ch (1987). Cyclonic cold-core eddy in the eastern North Atlantic. 111. Zooplankton. *Mar Ecol Prog Ser* 39: 65-173.
- Bograd SJ, Castro CG, Di Lorenzo E, Palacios DM, Bailey H, Gilly W, Chavez FP (2008). Oxygen declines and the shoaling of the hypoxic boundary in the California Current. *Geophys Res Lett* 35: L12607.
- Boxshall GA (1985). The comparative anatomy of two copepods, a predatory calanoid and a particle-feeding mormonilloid. *Philosophical Transactions of the Royal Society of London, (B, Biological Sciences)* 311: 303-377.
- Boyd SH, Ortner PB, Cox JL (1976). Gulf Stream cold core rings: large-scale interaction sites for open ocean plankton communities. *Deep-Sea Res* 23: 685-710.
- Briggs JC (1974). *Marine Zoogeography*. McGraw–Hill, New York, NY. 475 pp.
- Brodeur RD, Sugisaki H, Hunt GL (2002). Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. *Mar Ecol Prog Ser* 233: 89-103.
- Checkley DM, Jr (1980). Food limitation of egg production by a marine planktonic copepod in the sea off southern California. *Limnol Oceanogr* 25: 991-998.
- Childress JJ, Seibel BA (1998). Life at stable low oxygen levels: adaptations of animals to oceanic oxygen minimum layers. *J Exp Biol* 201: 1223–1232.
- Cass CJ (2011). A comparative study of eucalanoid copepods residing in different oxygen environments in the Eastern Tropical North Pacific: An emphasis on physiology and biochemistry. University of South Florida, Tampa, FL.
- Cass CJ, Daly KL (2014). Eucalanoid copepod metabolic rates in the oxygen minimum zone of the eastern tropical North Pacific: effects of oxygen and temperature, *Deep-Sea Res I* 94: 137–149.
- Cass CJ, Daly KL, Wakeham SG (2014). Assessment of storage lipid accumulation patterns in eucalanoid copepods from the eastern tropical Pacific Ocean. *Deep- Sea Res I* 93: 117–130.

- Clarke KR, Warwick RM (2001). Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. PRIMER-E, Plymouth.
- Conover RJ, Lalli CM (1972). Feeding and growth in *Clione limacina* (Phipps), a pteropod mollusc. *J Exp Mar Biol Ecol* 9: 279–302.
- Cornet C, Gili JM (1993). Vertical distribution and daily migrations of hyperiid amphipods in the northern Benguela in relation to water column stratification. *Deep-Sea Res I* 40: 2295–2306.
- Dadon JR, Cidre LLD (1992). The reproductive cycle of the thecosomatous pteropod *Limacina retroversa* in the western South Atlantic. *Mar Biol* 114: 439–442.
- Diaz RJ, Rosenberg R (2008) Spreading dead zones and consequences for marine ecosystems. *Science* 321: 926–929.
- Ekau W, Auel H, Portner HO, Gilbert D (2010). Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish) *Biogeosciences* 7: 1669–1699.
- Escribano R, Hidalgo P, Krautz C (2009). Zooplankton associated with the oxygen minimum zone system in the northern upwelling region of Chile during March 2000, *Deep-Sea Res II*, 56: 1049–1060.
- Fernandes V (2008). The effect of semi-permanent eddies on the distribution of mesozooplankton in the central Bay of Bengal. *J Mar Res* 66: 465–488.
- Fernandes V, Ramaiah N (2009). Mesozooplankton community in the Bay of Bengal (India): spatial variability during the summer monsoon. *Aquat Ecol* 43: 951–963.
- Fernandes V, Ramaiah N (2013). Mesozooplankton community structure in the upper 1,000 m along the western Bay of Bengal during the 2002 fall intermonsoon. *Zool Stud* 52: 31.
- Falkowski PG, Ziemann D, Kolber Z, Bienfang PK (1991). Role of eddy pumping in enhancing primary production in the ocean. *Nature* 352: 55–58.
- Fogg GE, Egan B, Floodgate GD, Jones DA, Kassab JY, Lochte K, Rees E I S, Scrope-Howe S, Turley CM (1985). Biological studies in the vicinity of a shallow sea tidal mixing front. VII. The frontal ecosystems. *Phil Trans R Soc B* 310: 555–571.
- Frost BW (1972). Effects of size and concentration of food particles on the feeding behaviour of the marine planktonic copepod *Calanus pacificus*. *Limnol Oceanogr* 17: 805–815.
- Frost BW, Fleminger A. 1968. A revision of the genus *Clausocalanus* (Copepoda: Calanoida) with remarks on distributional patterns in diagnostic characters. *Bull Scripps Inst Oceanogr* 12: 1–235.
- González RR, Quinones RA (2002). *Ldh* activity in *Euphausia mucronata* and *Calanus chilensis*: implications for vertical migration behaviour. *J Plankton Res* 24: 1349–1356.

- Gooday AJ, Levin LA, Aranda da Silva A, Bett BJ, Cowie GL, Dissard D et al (2009). Faunal response to oxygen gradients on the Pakistan Margin: a comparison of foraminiferans, macrofauna and megafauna. *Deep Sea Res II* 56: 488–502.
- Goswami SC, Gajbhiye SN, Padmavati G (1992). Distribution of *Pleuromamma* (Copepoda: Metridinidae) along a north-south transect in the Indian Ocean. In: Desai BN, editor. *Oceanography of the Indian Ocean*, Oxford and IBH, New Delhi, pp. 159-166.
- Grasshoff K, Ehrhardt M, Kremling K (1983). Methods of seawater analysis. In: Ehrhardt M, Kremling K, editors. Second revised, extended edition. Verlag Chemie, Weinheim, Germany, pp. 419
- Harris RP, Wiebe P, Lenz J, Skjoldal HR, Huntley M (2000). In: Harris RP, Wiebe PH, Lenz J, Skjoldal HR, Huntley M, editors. *ICES Zoo plankton methodology manual*. California, USA, Academic Press.
- Hulsizer EE (1976). Zooplankton of lower Narragansett Bay, 1972 1973. *Ches Sci* 17: 260-270.
- Huntley ME, Zhou M, Nordhausen W (1995). Mesoscale distribution of zooplankton in the California Current in late spring, observed by optical plankton counter. *J Mar Res* 53: 647–674.
- Ishii H, Tanaka F (2001). Food and feeding of *Aurelia aurita* in Tokyo Bay with an analysis of stomach contents and a measurement of digestion times. *Hydrobiologia* 451: 311–320.
- Jagadeesan L, Jyothibabu R, Anjusha A, Mohan AP, Madhu NV, Muraleedharan KR, Sudheesh K (2013). Ocean currents structuring the mesozooplankton in the Gulf of Mannar and the Palk Bay, southeast coast of India. *Prog Oceanogr* 110:27–48.
- Jyothibabu R, Madhu NV, Maheswaran PA, Jayalakshmya KV, Nair KKC, Achuthankutty CT. (2008). Seasonal variation of microzooplankton (20–200 μ m) and its possible implications on the vertical carbon flux in the western Bay of Bengal. *Cont Shelf Res* 28: 737–755.
- Jyothibabu R, Maheswaran PA, Madhu NV, Mohammed Ashraf TT, Gerson VJ, Haridas PC, Venugopal P, Revichandran C, Nair KKC and Gopalakrishnan TC. (2004). Differential response of winter cooling on biological production in the northeastern Arabian Sea and northwestern Bay of Bengal. *Curr Sci* 87: 783-791.
- Karati KK, Vineetha G, Raveendran TV, Muraleedharan, Achuthankutty CT (2017). Plankton and the Invisible Barriers in the Tropical Ocean. *J Aquac Mar Biol* 6: 00162.
- Karati KK, Vineetha G, Raveendran TV, Muraleedharan, KR, Habeebrehman H, Philson KP, Achuthankutty CT. 2018. River plume fronts and their implications for the biological production of the Bay of Bengal, Indian Ocean. *Mar Ecol Prog Ser* 597: 79–98.
- Kasturirangan, LR (1963). A key for the identification of the more common planktonic Copepoda of Indian coastal waters. In: Panikkar NK, editor. *Indian National Committee on Oceanic Research, Council of Scientific and Industrial Research, New Delhi Publication No 2*, pp. 1-87.

- Lampitt RS, Gamble JC (1982). Diet and respiration of the small planktonic marine copepod *Oithona nana*. *Mar Biol* 66: 185-190.
- Loick N, Ekau W, Verheye HM (2005). Water body preferences of dominant calanoid copepod species in the Angola-Benguela frontal zone. *Afr J Mar Sci* 27: 597–608.
- Longhurst AR (1976). Interactions between zooplankton and phytoplankton profiles in the eastern tropical Pacific Ocean. *Deep-Sea Res.* 23: 729-75.
- Longhurst A (2007). *Ecological geography of the sea*. London, UK: Academic Press.
- Li K, Yin J, Huang L, Tan Y, Lin Q (2017). A Comparison of the Zooplankton Community in the Bay of Bengal and South China Sea during April-May, 2010. *J Ocean Univ China (Oceanic and Coastal Sea Research)* 16: 1206-1212.
- Maas AE, Frazar SL, Outram DM, Seibel BA, Wishner KF (2014). Fine-scale vertical distribution of macroplankton and micronekton in the Eastern Tropical North Pacific in association with an oxygen minimum zone. *J Plankton Res* 0: 1–19.
- Madhupratap M, Achuthankutty CT, Nair, Nair VR (1981). Zooplankton abundance of the Andaman Sea. *Indian J Mar Sci* 10: 258-261.
- Madhupratap M (1987). Status and strategy zooplankton of tropical Indian estuaries: a review. *Bull Plankton Soc Japan* 34: 65-81.
- Madhupratap M, Haridas P (1990). Zooplankton, especially calanoid copepods, in the upper 1000 m off the Southeast Arabian Sea. *J Plankton Res* 12: 305-321.
- Madhupratap M, Nair SRS, Haridas P, Padmavati G (1990). Response of zooplankton to physical changes in the environment: coastal upwelling along the central West coast of India. *J Coast Res* 6:413-426.
- Madhupratap M, Nair KNV, Gopalakrishnan TC, Haridas P, Nair KKC, Venugopal P, Gauns M. 2001. Arabian Sea oceanography and fisheries of the west coast of India. *Curr Sci* 81: 355-361.
- Madin LP, Horgan EF, Steinberg DK (2001). Zooplankton at the Bermuda Atlantic Time-series Study (BATS) station: diel, seasonal and interannual variation in biomass, 1994-1998. *Deep-Sea Res II* 48: 2063-2082.
- Marcus NH, Richmond C, Sedlacek C, Miller GA and Oppert C (2004). Impact of hypoxia on the survival, egg production and population dynamics of *Acartia tonsa* Dana. *J Exp Mar Biol Ecol* 301: 111–128.
- McGowan JA. 1990. Species dominance –diversity patterns in oceanic communities. In: Woodwell GM editor. *The Earth in transition*, pp. 395 –421. New York, NY: Cambridge University Press.
- Miyashita LK, de Melo JM, Lopes RM (2009). Estuarine and oceanic influences on copepod abundance and production of a subtropical coastal area. *J Plankton Res* 31: 815–826.

- Moodley L, Van der Zwaan GJ, Herman PMJ, Kempers L, Van Breugel P (1997). Differential response of benthic meiofauna to anoxia with special reference to foraminifera (Protista: sarcodina). *Mar Ecol Prog Ser* 158: 151-163.
- Mukherjee J, Naidu SA, Sarma VVS S, Ghosh T (2018). Influence of river discharge on zooplankton diet in the Godavari estuary (Bay of Bengal, Indian Ocean). *Adv Oceanogr Limnol* 9: 1-12.
- Nakamura Y, Turner JT (1997). Predation and respiration by the small cyclopoid copepod *Oithona similis*: how important is feeding on ciliates and heterotrophic flagellates? *J Plankton Res* 19: 1275-1288.
- Nuncio M, Prasanna Kumar S (2012). Life cycle of eddies along the western boundary of the Bay of Bengal and their implications. *J Mar Syst* 94: 9–17.
- Omori M, Ishii H, Fujinaga Ai (1995). Life history strategy of *Aurelia aurita* (Cnidaria, Scyphomedusae) and its impact on the zooplankton community of Tokyo Bay. *ICES J Mar Sci* 52: 597–603.
- Padmavati G, Haridas P, Nair KKC, Gopalakrishnan TC, Shiney P, Madhupratap M (1998). Vertical distribution of mesozooplankton in the central and eastern Arabian Sea during the winter monsoon. *J Plankton Res* 20: 343-354.
- Paffenhöfer GA (1993). On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). *J Plankton Res* 15: 37–55.
- Paffenhöfer GA, Mazzocchi MG (2003). Vertical distribution of subtropical epiplanktonic copepods. *J. Plankton Res* 25: 1139–1156.
- Panikkar NK, Rao TSS (1973). Zooplankton investigation in Indian waters and the role of the Indian Ocean Biological Centre, Handbook to the international zooplankton collections Volume V, National Institute of Oceanography, Cochin, pp. 111–162.
- Parker-Stetter SL, Horne JK (2009). Nekton distribution and midwater hypoxia: a diel, seasonal prey refuge? *Est Coast Shelf Sci* 81: 13-18.
- Paul JT, Ramaiah N, Sardesai, S (2008). Nutrient regimes and their effect on distribution of phytoplankton in the Bay of Bengal. *Mar Environ Res* 66: 337–344.
- Pielou, EC (1977). *Mathematical ecology*. Wiley, New York, 385.
- Piontkovski, SA, Williams, R, Peterson W, Kosnirev VK (1995). Relationship between oceanic mesozooplankton and energy of eddy fields. *Mar Ecol Prog Ser* 128: 35–41.
- Piontkovski SA, Williams R, Melnik TA (1995). Spatial heterogeneity, biomass and size structure of plankton of the Indian Ocean: some general trends. *Mar Ecol Prog Ser* 117: 219-227.

- Piontkovski SA, Landry MR, Finenko ZZ, Kovalev AV, Williams R, Gallienne CP, Mishonov AV, Skryabin VA, Tokarev YN, Nikolsky VN (2003). Plankton communities of the South Atlantic anticyclonic gyre. *Oceanol Acta* 26: 255–268.
- Poulet SA, Oullet G (1982). The role of amino acids in the chemosensory swarming and feeding of marine copepods. *J Plankton Res* 4: 341-361.
- Prasannakumar S, Nuncio M, Narvekar J, Kumar A, Sardessai S, DeSouza SN, Gauns M, Ramaiah N, Madhupratap M (2004). Are eddies nature's trigger to enhance biological productivity in the Bay of Bengal? *Geophys Res Lett* 31: L07309.
- Prasannakumar, S, Nuncio, M, Ramaiah N, Sardessai S, Narvekar J, Fernandes V, Paul, JT (2007). Eddy-mediated biological productivity in the Bay of Bengal during fall and spring intermonsoons. *Deep-Sea Res I* 54: 19–1640.
- Prasanna Kumar, S, Nuncio, M, Narvekar J, Ramaiah N, Sardessai S, Gauns M, Fernandes V, Paul JT, Jyothibabu R, Jayraj KA (2010). Seasonal cycle of physical forcing and biological response in the Bay of Bengal. *Indian J Mar Sci* 39: 388-405.
- Ramaiah N, Fernandes V, Paul JT, Jyothibabu R, Gauns M, Jayraj KA (2010). Seasonal variability in biological carbon biomass standing stocks and production in the surface layers of the Bay of Bengal. *Indian J Mar Sci* 39: 369-379.
- Riandey V, Champalbert G, Carlottia F, Isabelle TL, Thibault-Bothac D (2005). Zooplankton distribution related to the hydrodynamic features in the Algerian Basin (western Mediterranean Sea) in summer 1997 *Deep-Sea Res I* 52: 2029–2048.
- Roff JC, Turner JT, Webber MK et al. (1995). Bacterivory by tropical copepod nauplii: extent and possible significance. *Aquat Microb Ecol* 9: 165–175.
- Roman MR, Dam HG, Gauzens AL, Urban-Rich, J, Foley DG, Dickey TD (1995). Zooplankton variability on the equator at 140°W during the JGOFS EqPac study. *Deep-Sea Res II* 42: 673-693.
- Roy K, Jablonski D, Valentine JW, Rosenberg G (1998). Marine latitudinal diversity gradients: tests of causal hypotheses. *Proc Natl Acad Sci USA* 95: 3699–3702.
- Rutherford, S, D'Hondt S, Prell W (1999). Environmental controls on the geographic distribution of zooplankton diversity. *Nature* 400: 749–753.
- Saltzman J, Wishner KF (1997). Zooplankton ecology in the eastern tropical Pacific oxygen minimum zone above a seamount: 2. Vertical distribution of copepods. *Deep-Sea Res.* 44: 931-954.
- Saraswathy, M (1986). *Pleuromamma* (Copepoda- Calanoida) in the Indian Ocean. *Mahasagar–Bulletin of the National Institute of Oceanography* 19: 185-201.
- Saraswathy M, Iyer H (1986). Ecology of *Pleuromamma indica* Wolfenden (Copepoda-Calanoida) in the Indian Ocean. *Indian J Mar Sci* 15: 219-222.

- Sen Gupta R, Naqvi SWA (1984). Chemical oceanography of the Indian Ocean, north of the equator, Deep-Sea Res. 31:671-706.
- Smith, SL (ed) 1998. 1994–1996 Arabian Sea Expedition: Oceanic response to monsoonal forcing Part 1. Deep-Sea Res II 45:1905–2501.
- Spindler M, Hemleben C, Salomons J, Smit L (1984). Feeding behavior of some planktonic foraminiferas in laboratory cultures. J Foramin Res 14:1–3.
- Stephen R (1988). Oncaeidae (Copepoda: Poecilostomatoida) in the Indian Ocean with comments on the species of *Lubbockia* and *Conaea*. Mahasagar 21: 35-43.
- Stephen R, Saraladevi K, Meenakshikunjamma PP, Gopalakrishnan TC, Saraswathy M (1992). Calanoid copepods of the International Indian Ocean Expedition collections. In: Desai BN, editor. Oceanography of the Indian Ocean. Oxford and IBH Publishing Company, New Delhi pp. 143–156.
- Steinberg DK, Silver MW (1994). Midwater zooplankton communities on pelagic detritus (giant larvacean houses) in Monterey Bay, California. Limnol Oceanogr 39: 1606-1620.
- Stramma L, Johnson GC, Sprintall J, Mohrholz V (2008). Expanding oxygen minimum zones in the tropical oceans. Science 320: 655–658.
- Tanaka O (1956). The pelagic copepods of the Izu region, middle Japan. Systematic Account I. Families Calanidae and Eucalanidae. Publications of the Seto marine Biological Laboratory, Volume V (2).
- Terazaki M (1996). Vertical distribution of pelagic chaetognaths and feeding of *Sagitta enflata* in the Central Equatorial Pacific. J Plankton Res 18: 673-682.
- Turner JT (2004) The importance of small planktonic copepods and their roles in pelagic marine food webs. Zool Stud 43: 255-266.
- UNESCO (1994). Protocols for the Joint Global Ocean Flux Study (JGOFS). Manual and Guides 29, pp. 170
- UNESCO 1968. Zooplankton sampling. Monographs on oceanographic methodology, UNESCO Publication No. 2, pp 174.
- Vaillancourt RD, Marra J, Barber RT, Smith WO. Jr. (2003). Primary productivity and in situ quantum yields in the Ross Sea and Pacific Sector of the Antarctic Circumpolar Current. Deep-Sea Res. II 50: 559-578.
- Vinogradov ME, Voronina NM (1962). The influence of oxygen deficit upon the plankton distribution in the Arabian Sea. (In Russian). Okeanologiat 1:670-678. Translation: Deep-Sea Res. 9:523-530.
- Vinogradov ME (1997). Some problems of vertical distribution of meso- and macroplankton in the ocean. Adv Mar Biol 32: 1–92.
- Wiebe PH (1976). The biology of cold-core rings. Oceanus 19: 69-76.

Wishner KF, Gelfman C, Gowing MM, Outram DM, Rapien M, Williams RL (2008). Vertical zonation and distributions of calanoid copepods through the lower oxycline of the Arabian Sea oxygen minimum zone. *Prog Oceanogr* 78: 163-191.

Woodd-Walker RS, Ward P, Clarke A (2002). Large-scale patterns in diversity and community structure of surface water copepods from the Atlantic Ocean. *Mar Ecol Prog Ser* 236: 189–203.

Wyrtki K (1971). *Oceanographic Atlas of the International Indian Ocean Expedition*, Natl Sci Found Washington DC, 531 pp.

Figure legends

Figure 1 Map of the sampling site in the Bay of Bengal. Stations CB1 to CB5 are located along the central (88° E) and WB1 to WB4 along the western margin of the Bay.

Figure 2. Vertical distribution of temperature, salinity, dissolved oxygen and chlorophyll *a* concentrations in the central and western Bay of Bengal during spring intermonsoon season.

Figure 3 Vertical profiles of day (D) and night (N) zooplankton biovolume from Multinet tows in the central Bay of Bengal during spring intermonsoon. Ng: negligible biovolume; NO DATA is where the net failed to open/close. *Swarms of medusae were observed at CB3 (their biovolume 90 ml 100 m⁻³) and CB4 (200 ml 100 m⁻³) in the surface at night.

Figure 4 Vertical profiles of day (D) and night (N) zooplankton biovolume from Multinet tows in the western Bay of Bengal during spring intermonsoon. Ng: negligible biovolume; NO DATA is where the net failed to open/close. *At WB3, medusae (100 ml 100 m⁻³), and at WB4, salps (200 ml 100 m⁻³) were observed in the surface during the day.

Figure 5 Station-wise variation in the 0-500 m column integrated mesozooplankton abundance/density and biomass in the central (a) and western (b) Bay of Bengal during spring intermonsoon.

Figure 6 Depth- wise variation in the number of zooplankton groups at each station in the central (a) and western (b) Bay of Bengal during spring intermonsoon. “MLD” is mixed layer depth, TT: Top of thermocline, BT: Bottom of thermocline

Figure 7 Distribution of dominant (> 1%) zooplankton taxonomic groups in different depth strata in the central (a) and western (b) Bay of Bengal during spring intermonsoon. The percentages at every depth are averages from 5 stations in the central- and 4 stations in the western Bay.

Figure 8 Vertical distribution of the various types (Orders) of copepods in the central (a) and western Bay (b) of Bengal during the spring intermonsoon. The percentages at every depth are averages from 5 stations in the central and 4 stations in the western Bay. Data is unavailable at 300-500 m in the central Bay due to negligible abundance.

Figure 9 Vertical distribution of abundance (log number 100 m⁻³) of the major copepod species in the central Bay of Bengal during spring intermonsoon. “MLD” is mixed layer depth, TT: Top of thermocline, BT: Bottom of thermocline

Figure 10 Vertical distribution of abundance (log number 100 m^{-3}) of the major copepod species in the western Bay of Bengal during spring intermonsoon. “MLD” is mixed layer depth, TT: Top of thermocline, BT: Bottom of thermocline.

Figure 11 Variation in Shannon diversity (H'), species richness (d) and evenness (J') of copepods in different depth strata in the upper 500 m of the central (a) and western (b) Bay of Bengal.

Figure 12 Variation in Multivariate Dispersion (MVDISP) indices between different depth strata (9 stations data combined) and between the central and western transects in the Bay of Bengal.

Figure 13 Multivariate cluster analysis of all the 129 copepod species data combined from all the stations and depths in the central and western Bay using the 30% cut-off level of the Bray-Curtis similarity. Cluster/Group I are assemblages mostly from the mixed layer (M) and thermocline (T) from central and western transects. Group II comprises assemblages found between the thermocline and 500m and Group III included only few species found exclusively from 200-300 m depth at stations CB3-CB5.

Figure 14 Two-dimensional ordination of the copepod species data combined from all depth strata and stations by non-metric multidimensional scaling (NMDS) method. Group I are surface dwelling species, II from subsurface i.e. top to thermocline to 500 m and III from the OMZ core of the northern stations in the central Bay.

Figure 15 Microphotographs of copepods viz. *Pleuromamma indica* (A), *P. xiphias* (B), *Gaetanus kruppii* (C) and *Gaussia princeps* (D) from the 200-300 m stratum (oxygen minimum zone) between CB3-CB5. The scale bar is in millimeters.

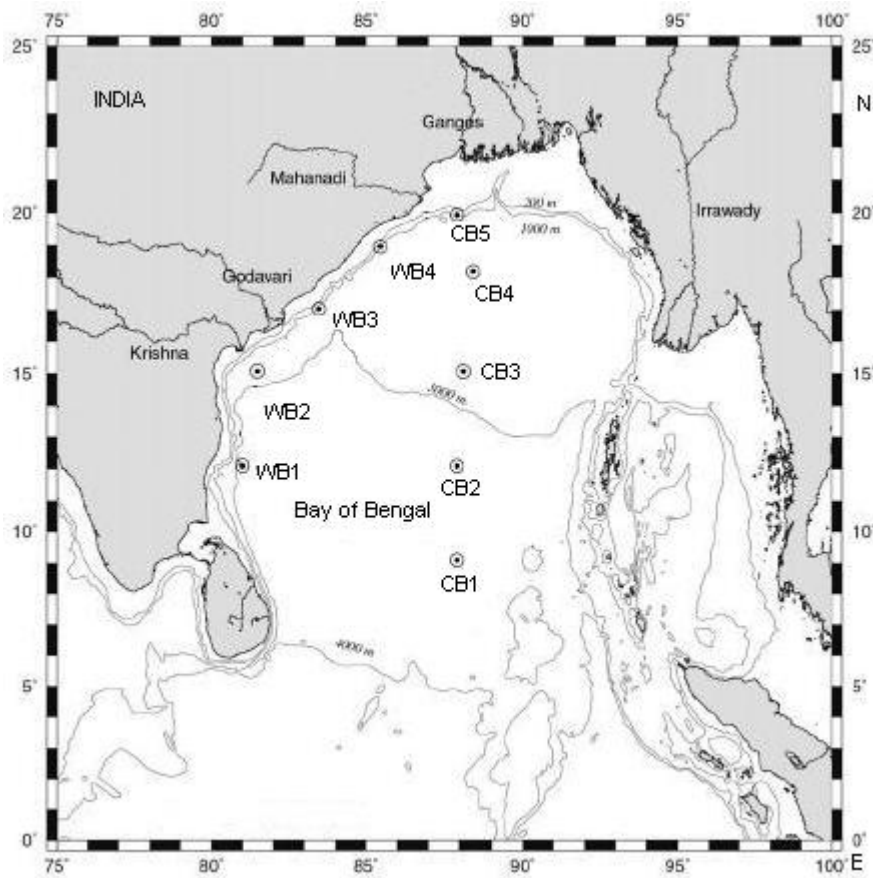


Figure 1

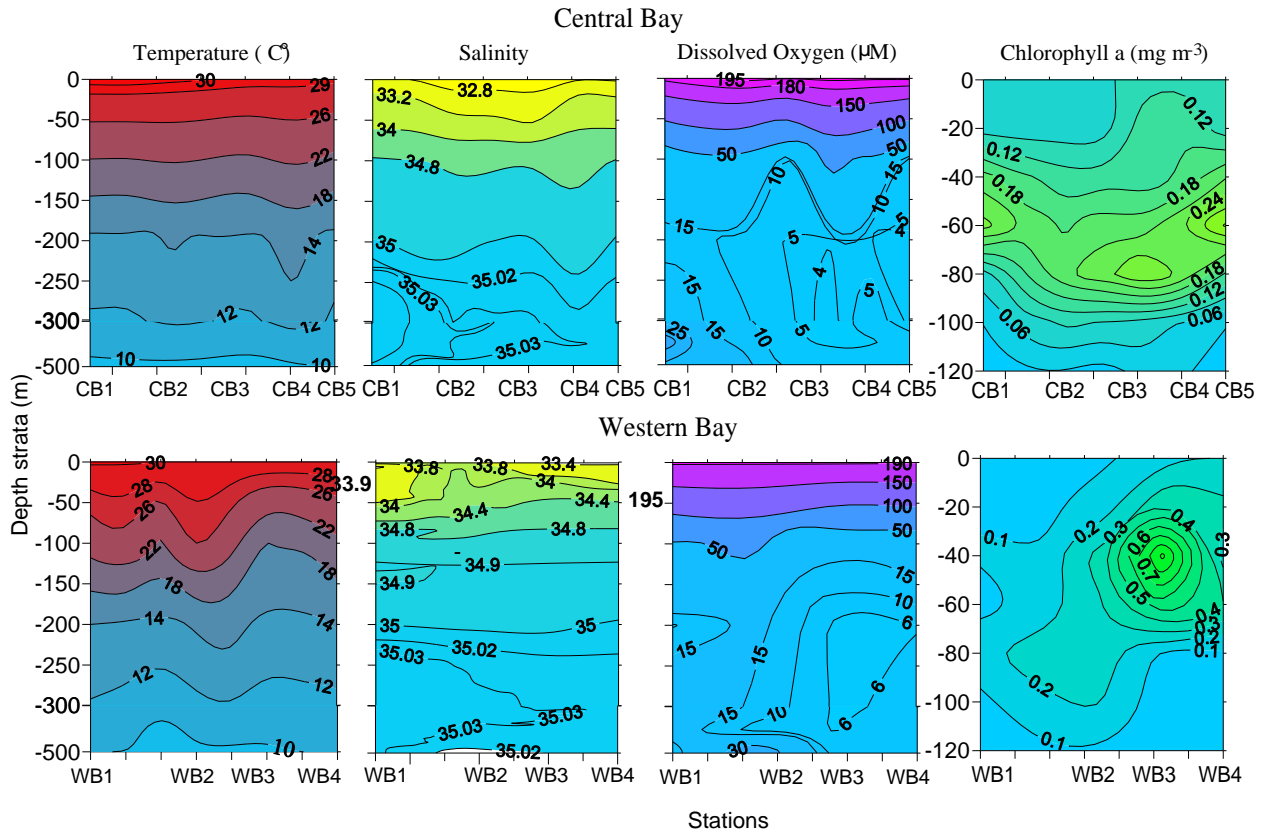


Figure 2

Biovolume (ml 100 m⁻³)

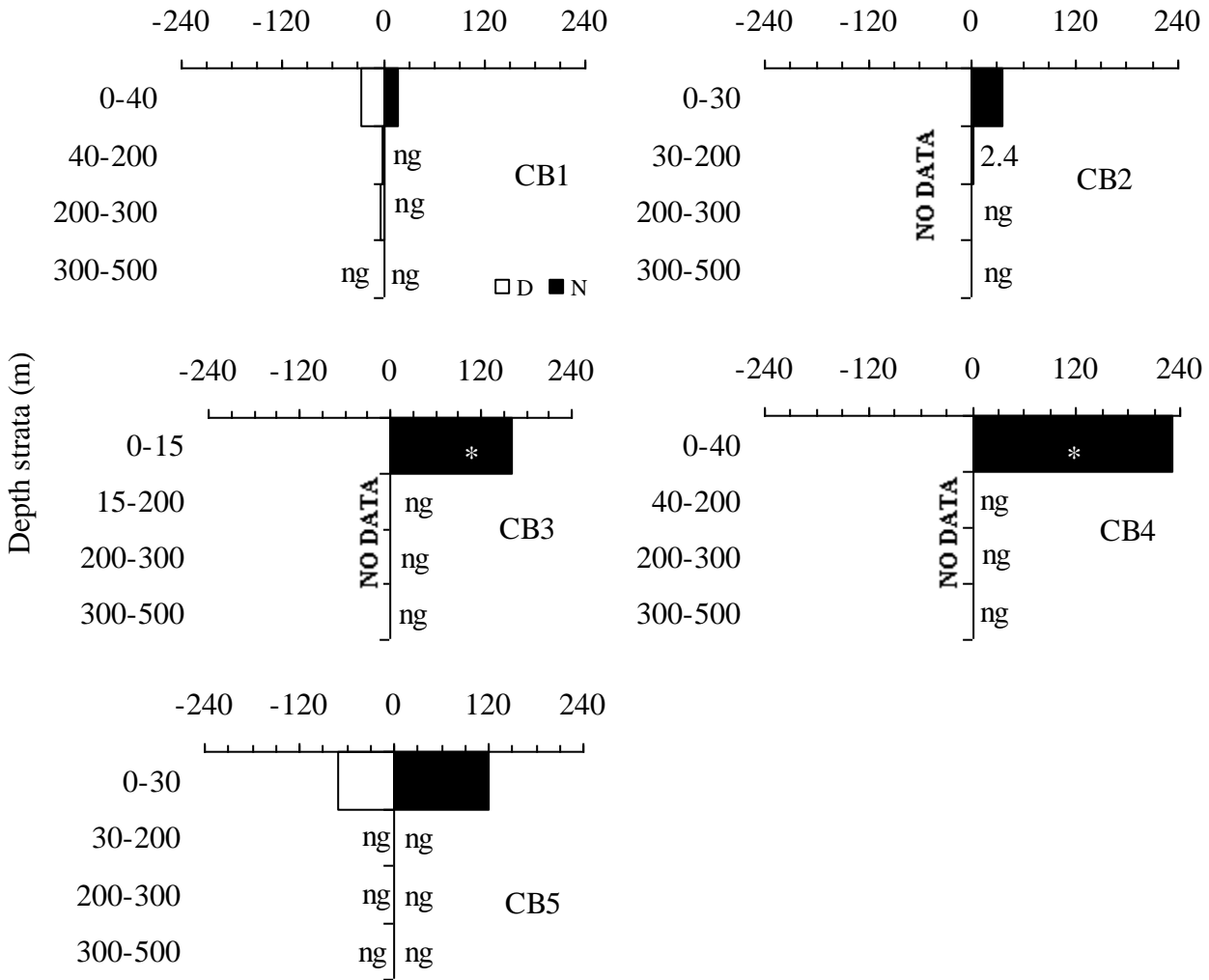


Figure 3

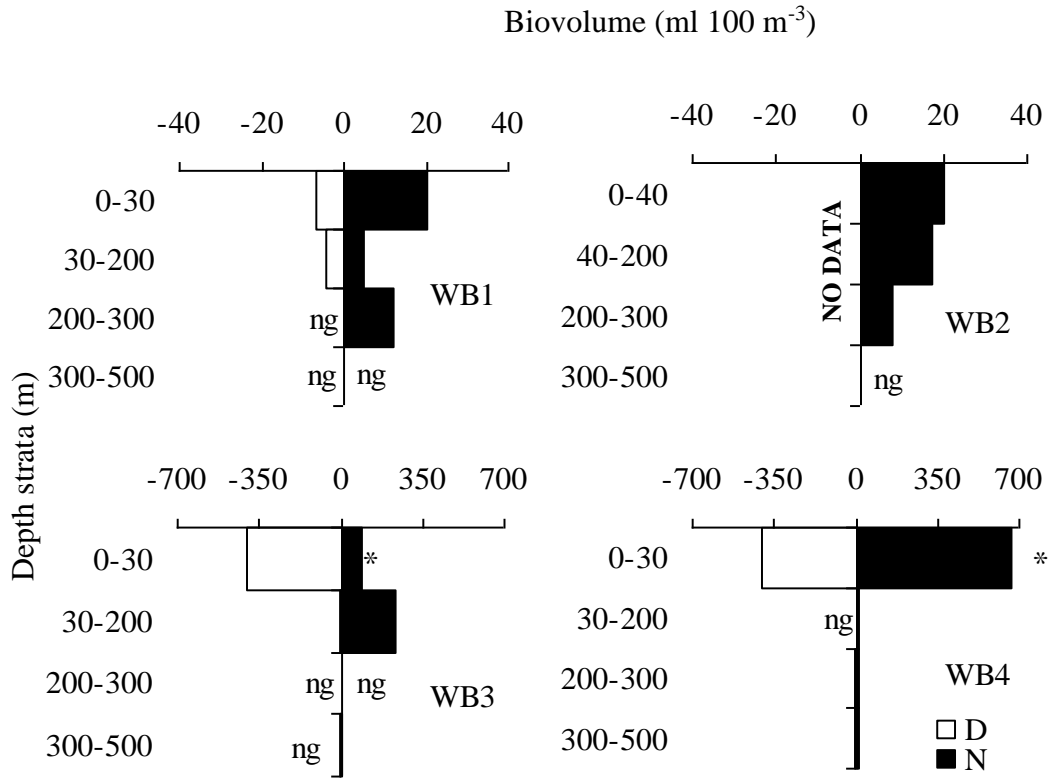


Figure 4

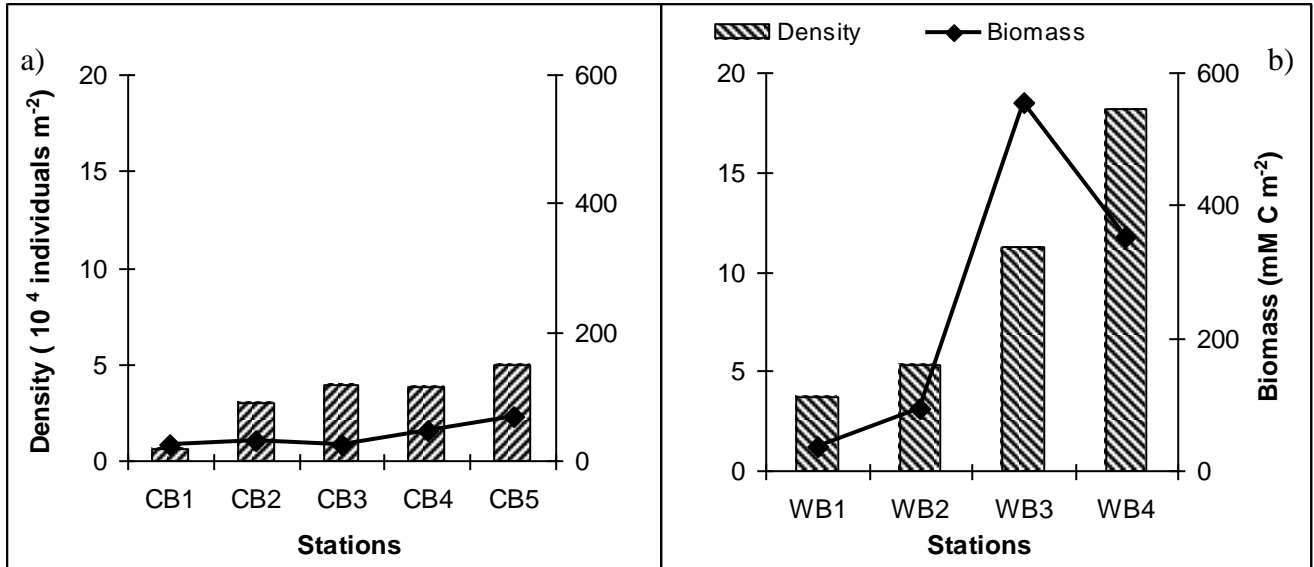


Figure 5

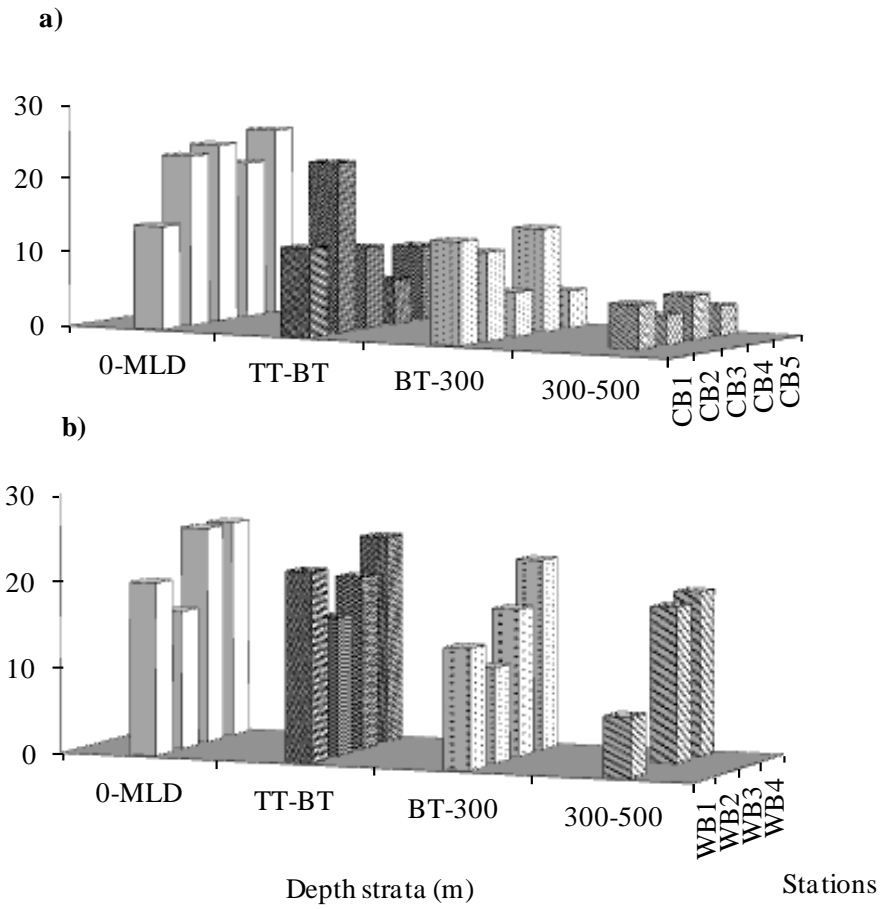


Figure 6

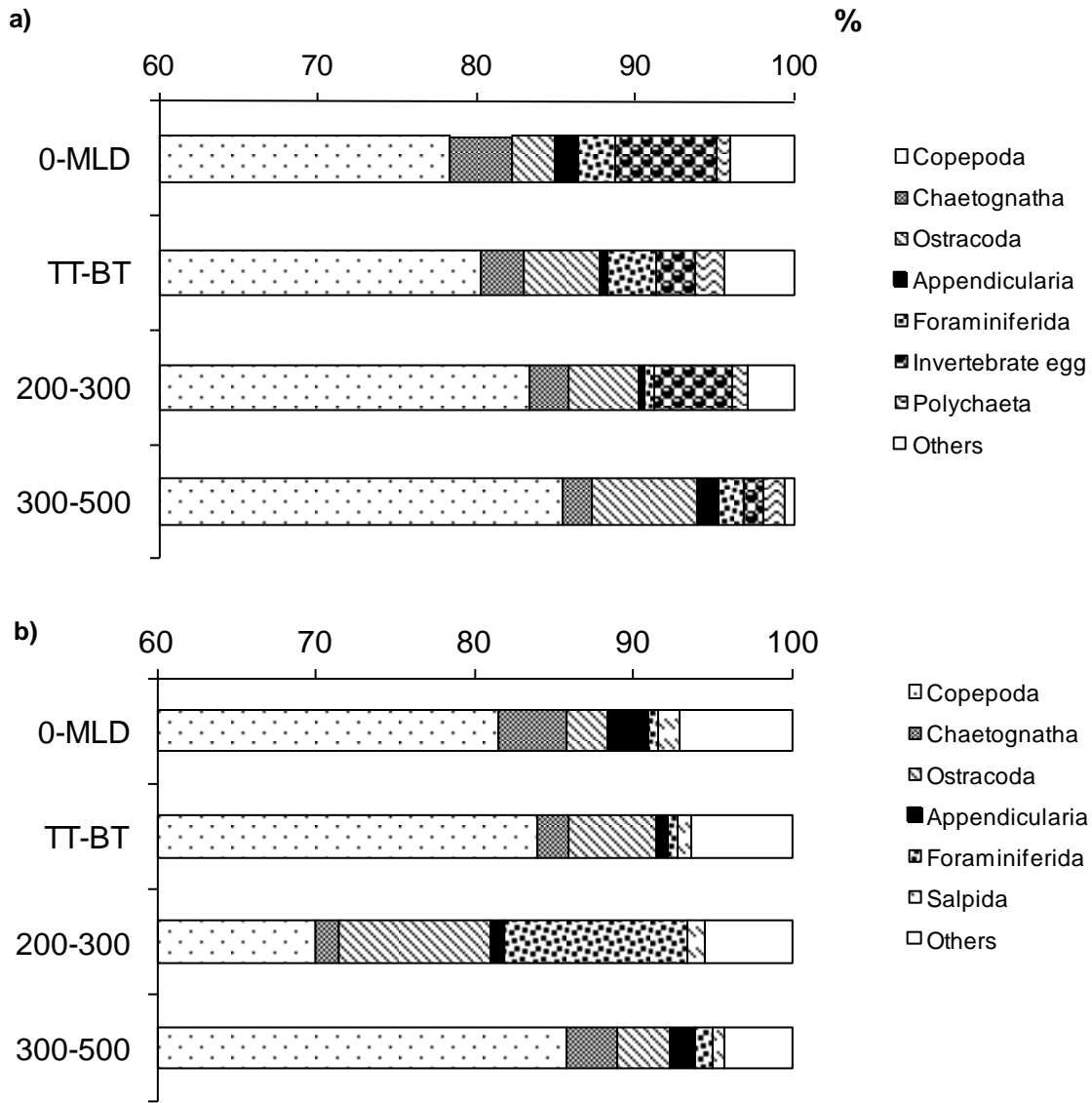


Figure 7

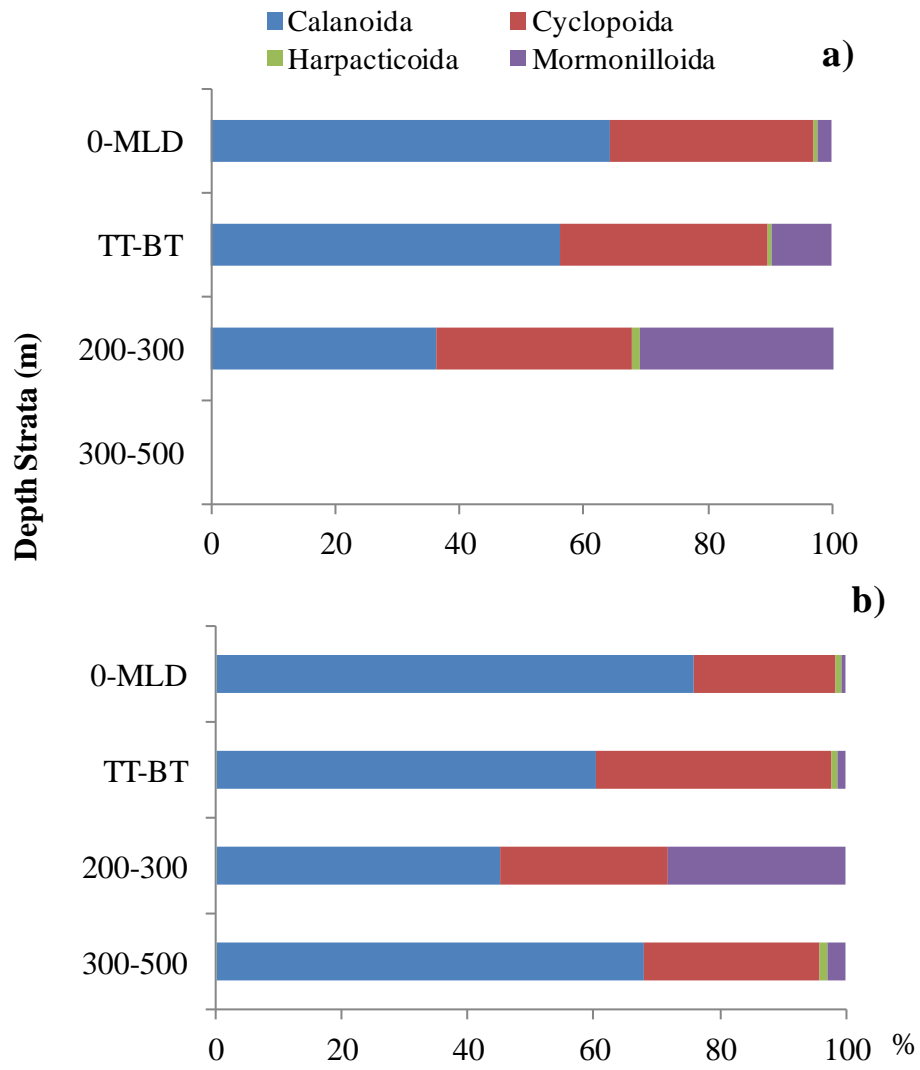


Figure 8

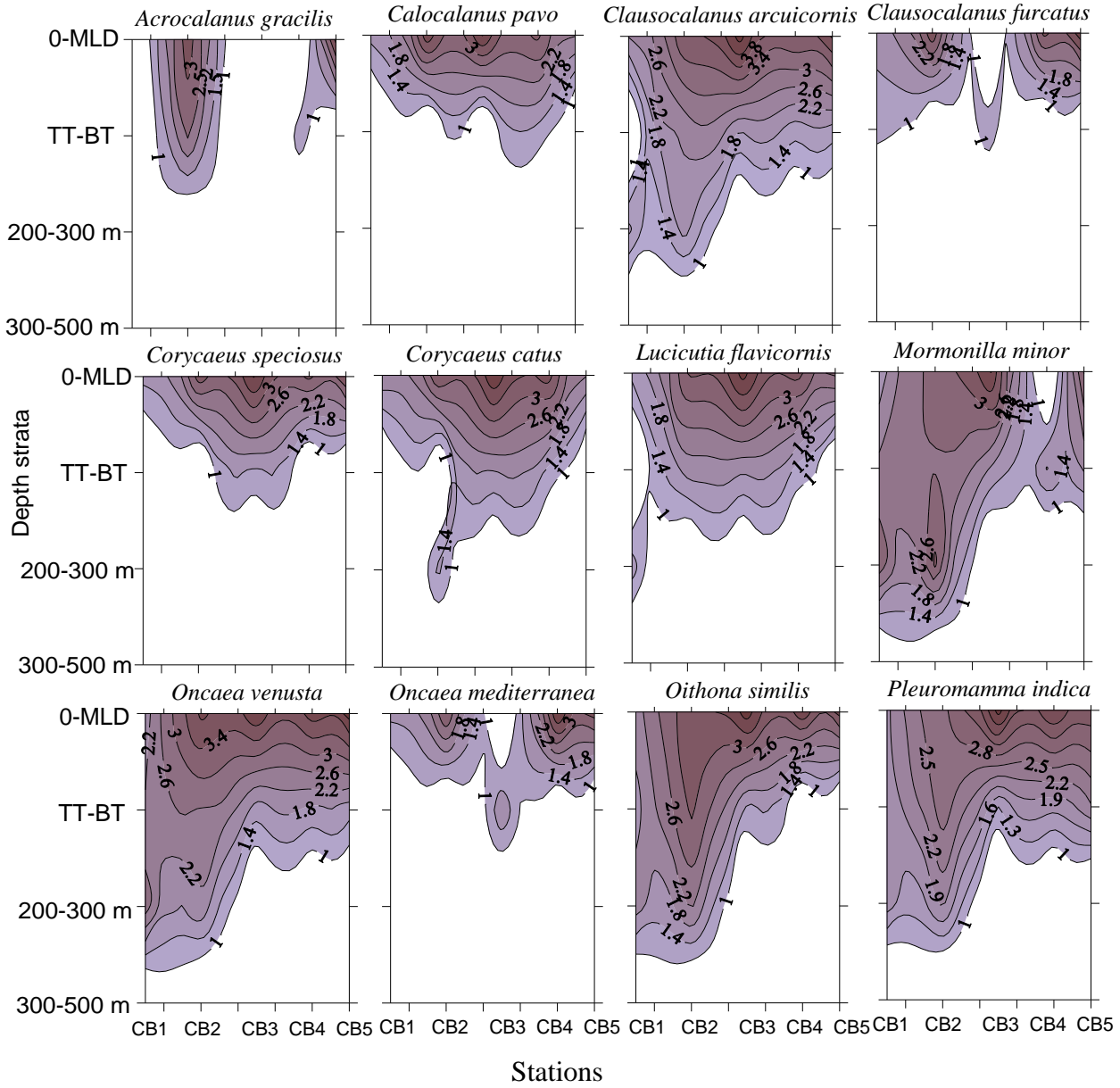


Figure 9

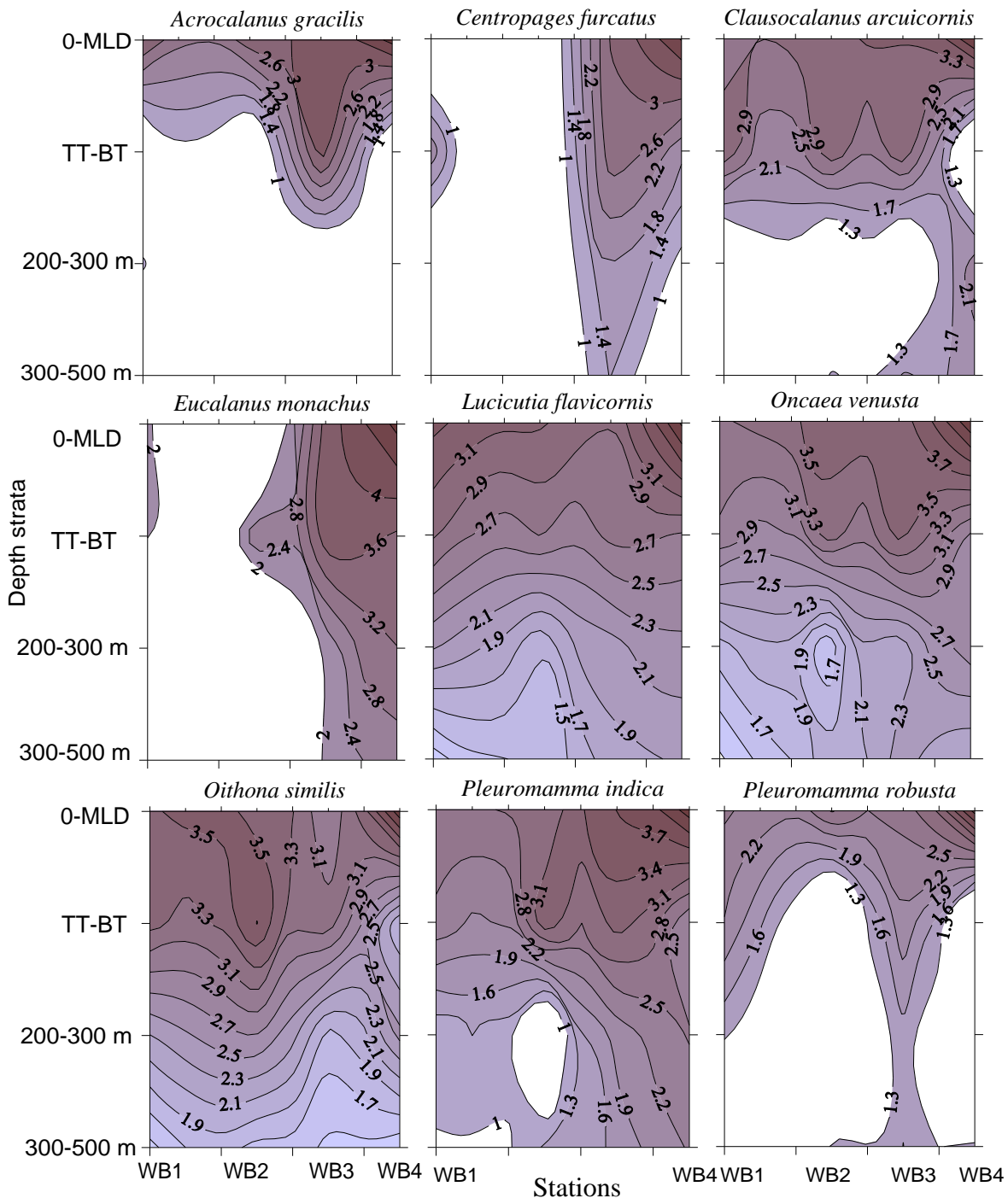


Figure 10

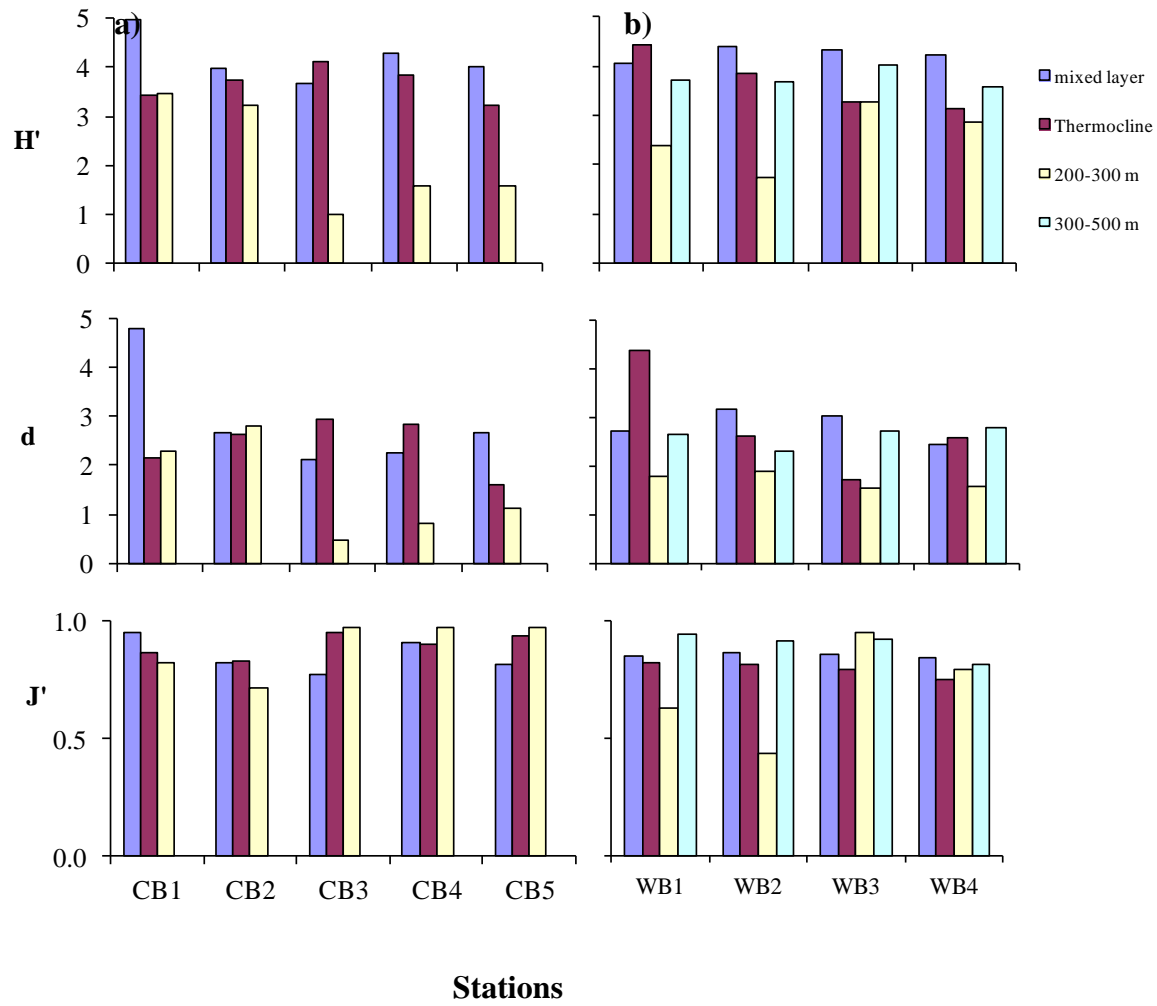


Figure 11

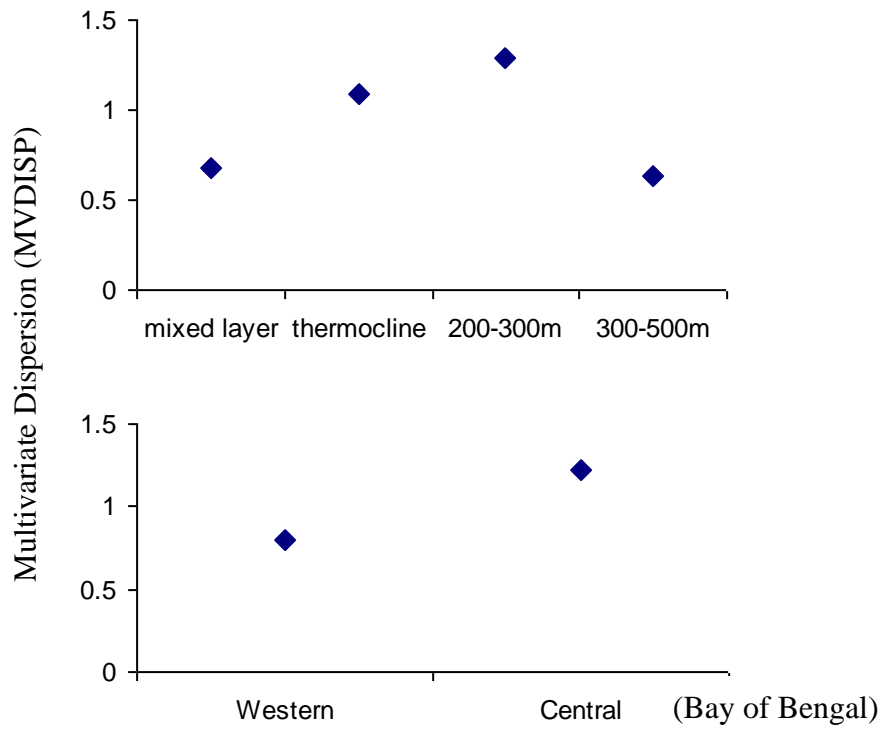


Figure 12

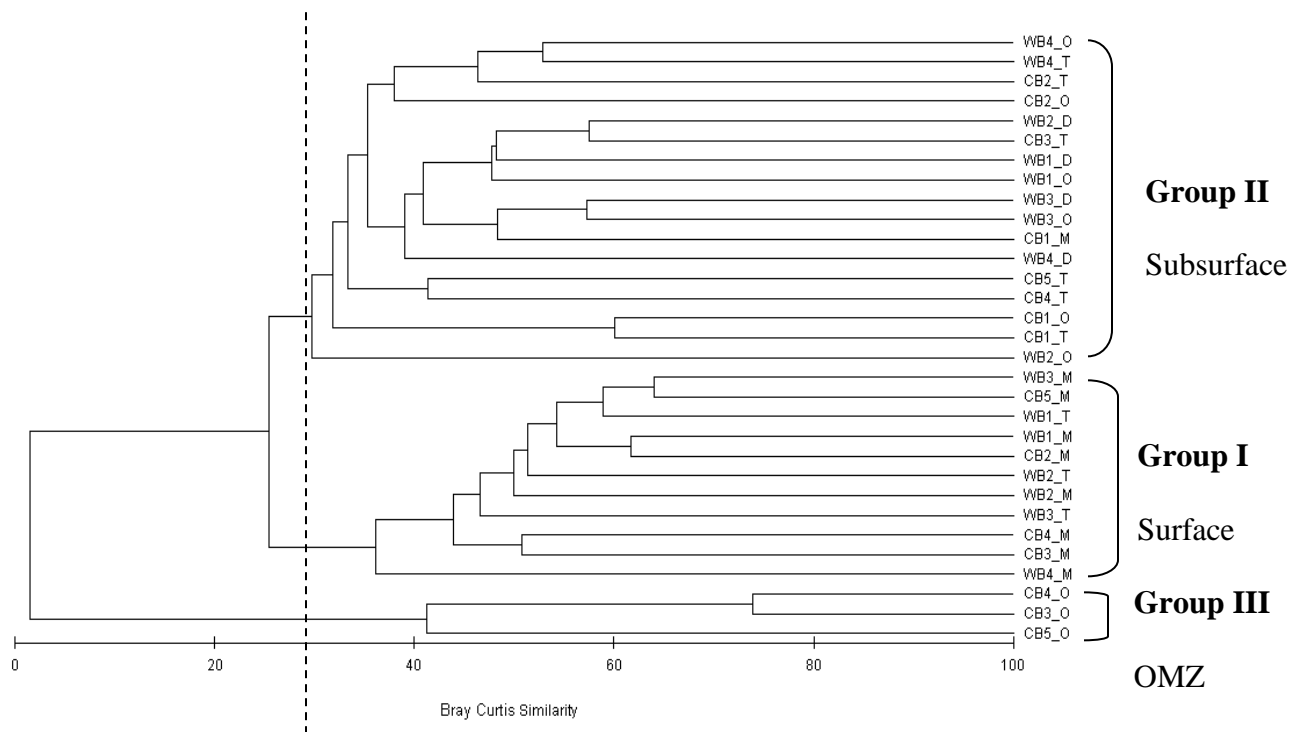


Figure 13

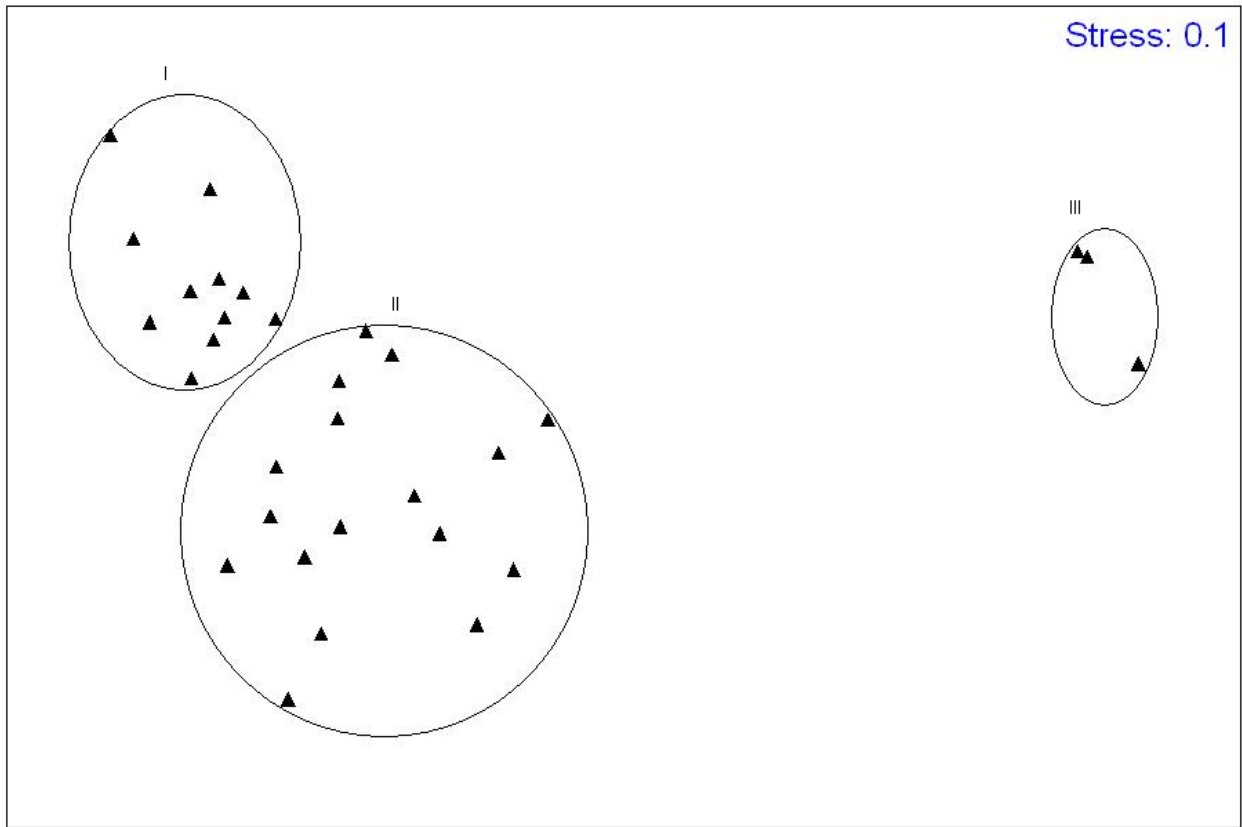


Figure 14



Figure 15

Table 1. Abundance ($\times 10^3$ ind. 100m^{-3}) of zooplankton in various strata in the top 500 m of the central and western Bay (WB) of Bengal. Note that the abundance is very low below the mixed layer in the central Bay (CB).

Depth Strata	CB1	CB2	CB3	CB4	CB5	WB1	WB2	WB3	WB4
Mixed layer	4	48	248	86	125	31	37	50	534
Thermocline	0.8	6.6	0.8	0.8	0.6	15.6	23.0	39.9	8.2
200-300m	3.8	3.6	0.6	2.2	0.4	3.1	4.2	1.4	5.1
300-500m	0	0.3	0.1	0.4	0.04	0.2	0.8	1.6	1.7

Table 2. List of zooplankton groups and their percentage abundance in the central and western Bay of Bengal. “-“ denotes absent.

	Groups	Central	Western
1	Acantharia	0.03	-
2	Amphipoda	0.18	0.13
3	Appendicularia	0.88	1.44
4	Bivalvia	0.02	0.14
5	Amphioxus	-	<0.01
6	Carinaria	0.01	-
7	Cephalopoda	0.01	0.01
8	Chaetognatha	2.75	2.73
9	Cladocera	0.11	0.07
10	Copepoda	81.98	80.37
11	Decapoda	0.17	0.39
12	Doliolida	0.02	0.64
13	Euphausiacea	0.38	1.12
14	fish eggs	-	0.09
15	Fish larva	0.14	0.06
16	Foraminiferida	1.91	3.46
17	Gastropoda	0.20	0.03
18	Halobates	0.00	0.00
19	Invertebrate egg	3.76	0.61
20	Isopoda	0.02	0.00

21	Medusae	0.13	0.53
22	Mysidacea	0.04	0.01
23	Ostracoda	4.63	5.22
24	Polychaeta	1.27	0.94
25	Pteropoda	0.10	0.34
26	Radiolaria	0.78	0.03
27	Salpida	0.07	1.02
28	Siphonophora	0.18	0.52

Table 3. Vertical distribution of copepod species abundance (% average of stations) in the central and western Bay of Bengal during spring intermonsoon. “MLD” is mixed layer depth, TT: Top of the thermocline, “BT”: Bottom of the thermocline, “A” denotes species absent

Sr. No	Species	0-MLD	TT-BT	200-300m	0-MLD	TT-BT	200-300m	300-500m
	CALANOIDA	<u>Central Bay</u>			<u>Western Bay</u>			
	Acartiidae							
1	<i>Acartia negligens</i> Dana, 1849	0.51	0.23	1.04	1.80	0.30	0.11	3.22
	Aetideidae							
2	<i>Aetideus armatus</i> Boeck, 1872	A	0.21	0.28	A	A	A	A
3	<i>A. giesbrechtii</i> Cleve, 1904	A	A	A	A	0.06	A	A
4	<i>Euchirella amoena</i> Giesbrecht, 1888	A	A	A	0.08	A	A	A
5	<i>E. bitumida</i> With, 1915	A	A	0.66	0.56	0.07	0.04	A
6	<i>E. indica</i> Vervoort, 1949	0.26	A	A	A	0.06	A	A
7	<i>E. latirostris</i> Farran, 1929	A	A	A	A	0.00	A	A
8	<i>Euchirella</i> sp.	0.27	0.45	A	2.26	0.08	A	A
9	<i>Gaetanus kruppii</i> Giesbrecht, 1903	A	A	0.69	A	A	A	A
10	<i>G. miles</i> Giesbrecht, 1888	A	A	A	A	A	0.11	A
	Arietellidae							
11	<i>Arietellus giesbrechtii</i> Sars, 1905	A	A	A	A	0.002	A	A
	Augaptilidae							
12	<i>Euaugaptilus angustus</i> Sars, 1905	0.01	A	A	A	A	0.23	A
13	<i>E. facilis</i> Farran, 1908	A	0.21	0.35	A	A	A	A
14	<i>E. hecticus</i> Giesbrecht, 1889	A	A	A	A	0.002	A	A
15	<i>E. laticeps</i> Sars, 1905	A	A	A	A	0.002	A	A
16	<i>Haloptilus acutifrons</i> Giesbrecht, 1892	A	0.20	1.18	A	A	A	A
17	<i>H. longicornis</i> Claus, 1863	0.01	1.36	1.18	0.02	0.52	0.97	0.72
18	<i>Pseudhaloptilus pacificus</i> M. W. Johnson, 1936	A	A	A	0.001	A	A	A

	Calanidae							
19	<i>Canthocalanus pauper</i> Giesbrecht, 1888	0.63	0.45	A	0.77	0.93	A	0.60
20	<i>Cosmocalanus darwini</i> Lubbock, 1860	A	A	A	0.08	0.16	A	A
21	<i>Undinula vulgaris</i> Dana, 1849	1.60	1.15	A	0.78	2.59	A	A
	Candaciidae							
22	<i>Candacia bradyi</i> Scott, 1902	0.31	A	A	0.13	0.77	0.02	0.72
23	<i>C. catula</i> Giesbrecht, 1889	A	A	A	A	0.06	A	A
24	<i>C. discaudata</i> A. Scott, 1909	A	A	A	0.58	0.06	A	0.60
25	<i>C. pachydactyla</i> Dana, 1849	0.04	A	A	0.00	0.22	A	A
26	<i>Paracandacia truncata</i> Dana, 1849	0.00	1.14	A	0.04	0.22	0.11	A
27	<i>Candacia</i> sp.	0.71	0.23	0.66	0.63	1.57	A	A
	Centropagidae							
28	<i>Centropages calaninus</i> Dana, 1849	0.05	A	A	0.82	A	A	A
29	<i>C. furcatus</i> Dana, 1849	1.08	0.45	A	3.55	1.23	0.68	0.97
30	<i>C. gracilis</i> Dana, 1849	0.12	A	A	A	A	A	A
	Clausocalanidae							
31	<i>Clausocalanus arcuicornis</i> Dana, 1849	21.60	3.83	2.89	6.91	6.97	1.94	4.50
32	<i>C. furcatus</i> Brady, 1883	1.86	0.41	A	0.28	1.21	0.31	3.28
33	<i>C. pergens</i> Farran, 1926	A	A	A	0.56	A	A	A
	Eucalanidae							
34	<i>Eucalanus crassus</i> Giesbrecht, 1888	A	0.21	3.59	2.29	0.00	A	A
35	<i>E. elongatus</i> Dana, 1849	0.27	2.32	3.27	A	0.28	0.42	2.55
36	<i>E. monachus</i> Giesbrecht, 1888	1.31	A	A	17.36	15.61	17.26	14.50
37	<i>E. mucronatus</i> Giesbrecht, 1888	0.04	1.14	0.52	0.04	0.90	0.37	0.60
38	<i>Pareucalanus attenuatus</i> Dana, 1849	1.30	1.14	A	1.19	1.05	0.31	0.72
39	<i>Eucalanus</i> sp.	0.58	A	A	0.04	0.12	A	0.60
	Euchaetidae							
40	<i>Euchaeta concinna</i> Dana, 1849	A	A	A	A	A	A	0.72
41	<i>E. indica</i> Wolfenden, 1905	0.04	A	A	0.56	0.06	0.97	A
42	<i>E. marina</i> Prestandrea, 1833	2.07	1.14	A	1.91	0.06	0.13	2.89

43	<i>Euchaeta</i> sp.	A	0.23	A	0.02	0.74	A	A
	Fosshageniidae							
44	<i>Temoropia mayumbaensis</i> T. Scott, 1894	0.52	0.62	0.28	0.73	0.96	0.33	1.69
	Heterorhabdidae							
45	<i>Heterorhabdus papilliger</i> Claus, 1863	A	0.41	A	0.56	0.89	0.27	0.60
46	<i>H. spinifrons</i> Claus, 1863	A	1.36	0.28	A	0.28	0.56	A
47	<i>Heterorhabdus</i> sp.	A	0.65	A	A	0.02	0.33	A
48	<i>Heterostylites longicornis</i> Giesbrecht, 1889	A	0.67	A	A	0.00	A	0.72
49	<i>H. major</i> Dahl, 1894	0.01	0.90	A	A	A	A	1.44
	Lucicutiidae							
50	<i>Lucicutia flavicornis</i> Claus, 1863	7.39	2.29	0.66	2.53	3.48	4.50	5.14
51	<i>L. maxima</i> Steuer, 1904	A	0.17	1.32	A	0.02	A	A
52	<i>L. ovalis</i> Giesbrecht, 1889	0.32	A	A	A	0.06	A	A
	Mecynoceridae							
53	<i>Mecynocera clausii</i> Thompson, 1888	0.12	0.17	A	0.08	0.13	0.31	A
	Megacalanidae							
54	<i>Megacalanus princeps</i> Brady, 1883	A	A	A	0.56	A	A	A
	Metridinidae							
55	<i>Gaussia princeps</i> T. Scott, 1894	0.02	0.03	0.69	A	A	0.06	0.25
56	<i>Metridia brevicauda</i> Giesbrecht, 1889	0.01	0.21	2.93	0.56	A	A	A
57	<i>M. cuticauda</i> Giesbrecht, 1889	A	A	0.52	A	A	A	A
58	<i>M. princeps</i> Giesbrecht, 1889	A	A	1.32	A	A	A	A
59	<i>Pleuromamma gracilis</i> Claus, 1863	0.81	0.73	0.94	1.17	0.20	0.84	1.71
60	<i>P. indica</i> Wolfenden, 1905	4.96	8.95	2.51	6.88	6.00	4.59	7.10
61	<i>P. quadrangulata</i> F. Dahl, 1893	A	A	0.52	0.02	A	A	A
62	<i>P. robusta</i> Dahl, 1893	A	0.38	0.94	5.31	0.40	0.54	2.31
63	<i>P. xiphias</i> Giesbrecht, 1889	0.01	A	0.62	A	A	A	A
64	<i>Pleuromamma</i> sp.	A	0.70	A	A	A	A	1.20
	Nullosetigeridae							
65	<i>Nullosetigera</i> sp.	A	A	A	0.56	A	A	A

	Paracalanidae							
66	<i>Acrocalanus gibber</i> Giesbrecht, 1888	0.80	1.14	A	0.12	A	0.23	A
67	<i>A. gracilis</i> Giesbrecht, 1888	1.52	4.75	A	2.38	2.31	0.11	A
68	<i>A. longicornis</i> Giesbrecht, 1888	1.75	A	A	1.74	0.90	A	A
79	<i>A. monachus</i> Giesbrecht, 1888	A	A	A	0.30	0.06	A	A
70	<i>Calocalanus pavo</i> Dana, 1849	3.04	0.20	A	0.23	1.00	0.54	0.98
71	<i>C. plumulosus</i> Claus, 1863	0.27	A	0.52	0.00	0.06	0.69	A
72	<i>Paracalanus indicus</i> Wolfenden, 1905	1.91	3.90	0.52	1.40	1.66	1.34	2.59
73	<i>P. parvus</i> Claus, 1863	A	A	A	A	0.31	A	A
	Phaennidae							
74	<i>Cephalophanes frigidus</i> Wolfenden, 1911	A	A	A	0.04	0.16	A	A
	Pontellidae							
75	<i>Calanopia elliptica</i> Dana, 1849	A	A	A	0.56	A	A	A
76	<i>C. minor</i> Scott, 1902	A	A	A	0.00	0.16	A	A
77	<i>Labidocera acuta</i> Dana, 1849	0.26	A	A	1.12	0.12	A	A
78	<i>L. pavo</i> Giesbrecht, 1889	0.01	A	A	0.06	A	A	A
89	<i>Pontellina plumata</i> Dana, 1849	0.52	1.15	A	0.23	0.16	A	0.72
	Rhincalanidae							
80	<i>Rhincalanus cornutus</i> Dana, 1849	A	0.21	2.65	0.56	0.13	1.65	0.25
81	<i>R. nasutus</i> Giesbrecht, 1888	A	0.21	0.80	A	A	A	A
82	<i>R. rostrifrons</i> Dana, 1849	0.00	A	A	A	0.06	A	A
	Scolecitrichidae							
83	<i>Amallothrix gracilis</i> Sars, 1905	0.52	0.17	A	0.13	0.74	A	A
84	<i>Lophothrix frontalis</i> Giesbrecht, 1895	0.00	0.62	0.94	A	A	0.04	0.39
85	<i>Scaphocalanus elongatus</i> A. Scott, 1909	0.01	A	A	A	A	A	A
86	<i>S. magnus</i> Scott, 1894	A	0.03	A	0.56	A	0.04	A
87	<i>Scaphocalanus</i> sp.	A	0.20	A	0.56	A	A	A
88	<i>Scolecithricella bradyi</i> Giesbrecht, 1888	0.80	A	A	A	A	A	A
89	<i>S. dentata</i> Giesbrecht, 1892	A	A	A	0.56	A	A	A
90	<i>Scolecithricella</i> sp.	0.85	A	A	0.08	0.08	A	A

91	<i>Scolecithrichopsis ctenopus</i> Giesbrecht, 1888	0.26	A	A	0.17	0.06	A	A
92	<i>Scolecithrix bradyi</i> Giesbrecht, 1888	0.12	A	A	A	A	A	A
93	<i>S. danae</i> Lubbock, 1856	0.13	A	A	0.69	0.06	A	0.72
94	<i>Scolecithrix</i> sp.	A	A	A	0.04	0.12	A	A
95	<i>Scottocalanus helenae</i> Lubbock, 1856	A	A	A	0.02	A	A	A
	Spinocalanidae							
96	<i>Monacilla gracilis</i> Wolfenden, 1911	A	A	1.04	A	A	A	A
97	<i>M. tenera</i> Sars, 1907	A	A	A	A	A	0.62	A
	Temoridae							
98	<i>Temora discaudata</i> Giesbrecht, 1889	0.01	A	A	0.65	0.28	1.24	A
99	<i>T. stylifera</i> Dana, 1849	A	A	A	0.75	0.06	0.31	1.45
100	<i>T. turbinata</i> Dana, 1849	A	A	A	0.16	0.06	A	0.39
	CYCLOPOIDA							
	Corycaeidae							
101	<i>Corycaeus catus</i> Dahl, 1894	4.76	0.90	0.52	1.58	1.46	1.53	3.96
102	<i>C. danae</i> Giesbrecht, 1891	0.55	1.14	A	1.21	0.44	0.60	1.20
103	<i>C. speciosus</i> Dana, 1849	2.82	0.23	A	1.61	2.59	0.67	0.72
104	<i>C. typicus</i> Krøyer, 1849	0.94	0.44	A	A	A	A	A
105	<i>Corycaeus</i> sp.	0.29	0.20	A	0.59	A	A	0.60
	Lubbockidae							
106	<i>Lubbockia aculeata</i> Giesbrecht, 1891	A	0.17	A	0.13	0.16	0.11	A
	Oncaeidae							
107	<i>Conaea gracilis</i> Dana, 1853	A	1.39	12.23	A	0.02	A	0.50
108	<i>Oncaea mediterranea</i> Claus, 1863	2.05	0.70	A	0.12	2.22	1.36	1.11
109	<i>O. venusta</i> , Philippi, 1843	13.09	8.33	12.85	7.49	11.95	9.26	13.80
110	<i>Oncaea</i> sp.	A	A	A	A	A	A	0.60
111	<i>Pachos punctatum</i> Claus, 1863	A	A	A	A	0.003	A	A
112	<i>Triconia conifera</i> Giesbrecht, 1891	0.00	0.62	0.56	0.56	0.83	A	0.39
	Oithonidae							
113	<i>O. plumifera</i> Baird, 1843	2.43	2.30	A	1.76	1.85	1.30	0.84

114	<i>O. setigera</i> Dana, 1849	A	1.15	A	A	A	A	A
115	<i>O. similis</i> Claus, 1866	4.81	15.75	4.74	4.63	13.20	11.39	3.31
Sapphirinidae								
116	<i>Copilia mirabilis</i> Dana, 1849	A	A	A	0.12	0.90	A	0.72
117	<i>C. quadrata</i> Dana, 1849	0.35	A	A	1.29	0.36	0.02	A
118	<i>Sapphirina auronitens</i> Claus, 1863	0.29	A	A	A	A	A	A
119	<i>S. nigromaculata</i> Claus, 1863	0.04	A	A	0.13	0.74	A	A
120	<i>S. ovatolanceolata</i> Dana, 1849	0.01	A	A	A	0.06	0.33	A
121	<i>Sapphirina</i> sp.	0.26	A	0.52	1.22	0.40	A	A
122	Unidentified	1.36	8.94	0.66	1.14	3.46	2.14	1.19
HARPACTICOIDA								
Aegisthidae								
123	<i>Aegisthus. mucronatus</i> Giesbrecht, 1891	A	A	0.66	A	A	A	A
Clytemnestridae								
124	<i>Clytemnestra scutellata</i> Dana, 1848	A	A	A	A	0.002	A	A
Ectinosomatidae								
125	<i>Microsetella rosea</i> Dana, 1848	0.04	0.45	A	0.04	A	A	A
Miraciidae								
126	<i>Macrosetella gracilis</i> Dana, 1848	0.84	0.23	A	0.08	0.16	A	1.23
127	<i>Miracia efferata</i> Dana, 1849	0.01	A	A	0.13	0.90	A	A
MORMONILLOIDA								
Mormonillidae								
128	<i>Mormonilla minor</i> Giesbrecht, 1891	1.99	9.67	30.99	0.68	1.26	27.87	2.96
129	<i>M. phasma</i> Giesbrecht, 1891	A	A	A	A	A	0.33	A
Total ind. 100 m ⁻³		32200	1705	1917	127830	16143	2378	762

Table 4. Major “Characterizing” copepod species, their average abundances and their contribution to the average similarity of the assemblages in Group I, II and III.

Group I (Surface Species), Average similarity: 49.61%

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%
<i>Oncaea venusta</i>	7786	6.02	5.02	12.13
<i>Clausocalanus arcuicornis</i>	10689	4.77	3.10	9.62
<i>Oithona similis</i>	4628	4.27	3.52	8.60
<i>Pleuromamma indica</i>	5471	3.40	2.54	6.86
<i>Lucicutia flavicornis</i>	4144	3.29	3.10	6.62
<i>Corycaeus speciosus</i>	1843	2.70	2.99	5.43
<i>Corycaeus catus</i>	2709	2.53	1.53	5.11
<i>Eucalanus monachus</i>	9006	1.75	0.92	3.53

Group II (Subsurface Species), Average similarity: 36.47%

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%
<i>Oncaea venusta</i>	213	6.29	3.55	17.25
<i>Mormonilla minor</i>	324	5.43	1.31	14.89
<i>Pleuromamma indica</i>	104	3.86	1.87	10.60
<i>Oithona similis</i>	174	3.74	1.33	10.25
<i>Lucicutia flavicornis</i>	78	2.75	1.23	7.53
<i>Eucalanus elongatus</i>	41	1.92	1.03	5.27
<i>Clausocalanus arcuicornis</i>	62	1.92	0.80	5.27

Group III (Oxygen minimum zone species), Average similarity: 82.27%

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%
<i>Gaetanus krupp</i>	230	35.58	18.30	43.25
<i>Gaussia princeps</i>	230	35.58	18.30	43.25
<i>Pleuromamma xiphias</i>	144	11.11	0.58	13.51

Table 5. Major “Discriminating” copepod species, their average abundances and contribution to the average dissimilarity between the Group I, II and III assemblages (Global R: 0.86, P: 0.1%).

Groups II & I; Average dissimilarity = 63.24

Species	Group II	Group I	Av.Diss	Diss/SD	Contrib%
	Av.Abund	Av.Abund			
<i>Mormonilla minor</i>	323.61	1040.62	2.96	1.13	4.69
<i>Eucalanaus monachus</i>	322.46	9006.22	2.60	1.20	4.11
<i>Clausocalanus arcuicornis</i>	62.30	10688.60	2.03	1.23	3.21
<i>Corycaeus catus</i>	34.33	2709.11	1.57	1.52	2.48
<i>Oithona similis</i>	174.08	4627.59	1.55	1.26	2.46
<i>Corycaeus speciosus</i>	9.39	1842.60	1.48	1.88	2.34
<i>Acartia negligens</i>	15.19	912.56	1.42	0.99	2.24
<i>Acrocalanus gracilis</i>	23.35	1511.78	1.38	1.26	2.17
<i>Oncaea venusta</i>	213.29	7785.37	1.06	1.23	1.68
<i>Cosmocalanus darwinii</i>	0.00	208.24	0.36	0.66	0.56
<i>Acrocalanus monachus</i>	0.00	144.58	0.32	0.48	0.51
<i>Conaea gracilis</i>	47.90	0.00	0.84	0.55	1.32
<i>Heterostylites major</i>	10.53	0.00	0.48	0.51	0.75
<i>Heterorhabdus</i> sp.	5.93	0.00	0.40	0.46	0.64
<i>Gaussia princeps</i>	8.78	0.00	0.39	0.55	0.61
<i>Haloptilus acutifrons</i>	5.38	0.00	0.25	0.45	0.40

Groups II & III; Average dissimilarity = 98.23

Species	Group II		Group III		
	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%
<i>Gaetanus kruppai</i>	1.86	230.44	11.04	5.29	11.23
<i>Gaussia princeps</i>	8.78	230.44	10.53	4.48	10.72
<i>Pleuromamma xiphias</i>	4.83	144.44	6.69	1.39	6.81
<i>Mormonilla minor</i>	323.61	0.00	6.41	1.30	6.53
<i>Oncaea venusta</i>	213.29	0.00	5.42	3.67	5.52
<i>Oithona similis</i>	174.08	0.00	4.18	1.50	4.25
<i>Pleuromamma indica</i>	104.00	0.00	3.97	1.70	4.04
<i>Lucicutia flavicornis</i>	77.66	0.00	3.05	1.65	3.11
<i>Eucalanus monachus</i>	22.46	0.00	2.60	0.58	2.65

Groups I & III; Average dissimilarity = 100.00

Species	Group I		Group III		
	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%
<i>Gaetanus kruppai</i>	0.00	230.44	9.39	6.03	9.39
<i>Gaussia princeps</i>	0.00	230.44	9.39	6.03	9.39
<i>Pleuromamma xiphias</i>	0.00	144.44	5.71	1.37	5.71
<i>Oncaea venusta</i>	7785	0.00	5.22	4.13	5.22
<i>Clausocalanus arcuicornis</i>	10689	0.00	4.66	2.36	4.66
<i>Oithona similis</i>	4628	0.00	4.16	2.48	4.16
<i>Pleuromamma indica</i>	5471	0.00	3.34	2.49	3.34
<i>Lucicutia flavicornis</i>	4144	0.00	3.18	2.52	3.18
<i>Eucalanus monachus</i>	9006	0.00	2.84	1.09	2.84

Table 6 Correlation matrix of zooplankton biomass, abundance and groups v/s temperature, salinity and chlorophyll *a* from the upper 200m.

	Biomass	Abundance	Groups	Temperature	Salinity	Chl <i>a</i>
Biomass	1					
Abundance	0.857	1				
Groups	0.572	0.528	1			
Temperature	-0.378	-0.212	-0.541	1		
Salinity	0.472	0.238	0.048	-0.426	1	
Chlorophyll <i>a</i>	0.507	0.124	0.416	-0.677	0.661	1

Bold values are significant at $p < 0.05$