

The distribution of the chaetognath population and its interaction with environmental characteristics in the Bay of Bengal and the Arabian Sea

VIJAYALAKSHMI R. NAIR^{1*}, KARATI KOMAL KUSUM¹, RAGHAVAN GIREESH^{1,2}, MAHESWARI NAIR¹

¹CSIR-National Institute of Oceanography, Kochi-18, Kerala, India.

²Central Marine Fisheries Research Institute, Kochi-18, Kerala, India.

Running head: Influence of environmental variables on chaetognaths

*Corresponding author: Vijayalakshmi R. Nair, CSIR-National Institute of Oceanography, Salim Ali Road, Kochi-18, India. E-mail: vijayalakshmi40@hotmail.com
Phone: 91 0484 2390814; Fax: 91 0484 2390618

Abstract

The Bay of Bengal (BoB) and the Arabian Sea (AS), the two major ocean basins in the north Indian Ocean, share similarities in geographical and meteorological characteristics but differ in hydrographic characteristics and biological production. The BoB is traditionally considered a less productive region than the AS. Chaetognatha, a major taxon of carnivorous mesozooplankton, often rank second in abundance to copepods and thus play a pivotal role in the pelagic food web of this region. We studied the influence of environmental variables on the distribution and the diversity of chaetognaths in these two ocean basins. Of the twenty one species observed during the study, *Flaccisagitta enflata* dominated in the mixed layer to the thermocline, *Decipisagitta decipiens*, from the bottom of thermocline to 500 m and *Eukrohnia fowleri* below 500 m. Mesoscale and basin scale processes such as eddies, gyres and upwelling had a profound influence on the abundance in the upper layer while the presence of an oxygen minimum zone in the mid-depth layers had a crucial effect on the vertical distribution of the chaetognath population. Despite the variation in the controlling factors on chaetognath populations in the BoB and AS, the patterns of depth-specific abundance were similar.

Keywords: Chaetognaths, Bay of Bengal, Arabian Sea, environmental characteristics, community structure

Introduction

The Bay of Bengal (BoB) and the Arabian Sea (AS) are the two major ocean basins of the northern Indian Ocean and are separated by the Indian subcontinent. These tropical basins are located in the same latitudes and are landlocked to the North, but open into the equatorial Indian Ocean to the South (Shenoi et al. 2002). The hydrography and productivity in both the BoB and the AS are greatly influenced by the seasonally reversing monsoon winds. Despite these similarities, the basins exhibit large contrasts in their hydrographic characteristics and biological productivity (Nair 1986; Prasanna Kumar et al. 2002; Nair & Srinivasa Kumar 2006). The BoB receives higher volumes of river influxes compared to the AS. As a result, the BoB surface waters are 3 - 7 psu less saline than the AS surface waters (Prasanna Kumar et al. 2002). Excessive evaporation over precipitation also leads to higher surface salinities in the AS (about 36 psu), this water sinks and renews deep waters (Dietrich 1973). The strong westerly winds during the southwest monsoon result in coastal and open ocean upwelling in the AS. Both basins experience seasonal atmospheric forcing, leading to regular oscillations in biological productivity. Open ocean upwelling (Brock et al. 1991), wind driven mixing (McCreary et al. 1996; Lee et al. 2000) and lateral advection (Young & Kindle 1994; Prasanna Kumar et al. 2001) make the open ocean waters of the AS more productive. With the exception of the inter monsoon period, the 120 m water column primary production in the AS is $> 500 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Prasanna Kumar et al. 2000, 2001; Gauns et al. 2005). Heavy cloud cover, high turbidity, and the narrow shelf result in lower production in the BoB (mostly $< 500 \text{ mg C m}^{-2} \text{ d}^{-1}$; see Table 1, Prasanna Kumar et al. 2010), though physical processes like cyclones can play an important role in elevating production in this basin ($> 1000 \text{ mg C m}^{-2} \text{ d}^{-1}$; Madhu et al. 2002).

Mesozooplankton biomass and abundance in each basin varies both spatially and temporally. Mesozooplankton biomass in the upper 1000 m of the water column in the AS has been found to range between $1 - 2.6 \text{ mg C m}^{-3}$ (Smith & Madhupratap 2005). In the BoB, biomass is generally lower ($< 2 \text{ mg C m}^{-3}$, Fernandes & Ramaiah 2009), though the influence of physical processes often leads to higher production ($> 2 \text{ mg C m}^{-3}$, Fernandes 2008). Chaetognaths often rank second in abundance in the zooplankton (Nair et al. 1977, 1978) in both the BoB and the AS, and being exclusively carnivorous they play a significant role in transferring energy from copepods to higher trophic levels. Although the global biogeography of chaetognaths is well-known (Alvariño 1965; Pierrot- Bults & Nair 1991), researches on the biodiversity of chaetognaths of the northern Indian Ocean is limited to the International Indian Ocean Expedition period (Nair 1976, 1977a, 1978; Nair & Rao 1973) along with a few subsequent more local reports (Nair 1977b; Nair & Madhuprathap 1984; Nair et al. 2000, 2002;

Kusum et al. 2011). Although the Indian Joint Global Ocean Flux Study (JGOFS) in the AS and the Bay of Bengal Process study (BoBPS) in the BoB were carried out to understand the ecology and biogeochemistry of these regions, information regarding species diversity and community structure of chaetognaths remains scarce. To properly understand the patterns of distribution and community structure of this ecologically important planktonic group in the BoB and the AS, a detailed investigation on the interaction of the chaetognath community with different environmental variables is required.

In this context, this paper is an attempt to (1.) address the patterns in the biodiversity of chaetognaths in two biologically contrasting tropical basins, the BoB and the AS; (2.) study the effects of environmental characteristics that govern stratification of chaetognath species and (3.) investigate the relationship between community structure and depth.

Material and Methods

Sampling

In both the BoB and the AS, sampling was carried out over two seasons from the FORV *Sagar Sampada* as part of the Marine Research on Living Resources (MR-LR) programme. In the BoB, along the eastern part of the exclusive economic zone of India, sampling was done during July and August 2003 (summer monsoon, SM) and February to March 2005 (spring inter monsoon, SIM). In the AS, along the western part of the exclusive economic zone of India, sampling was done during September and October 2003 (fall inter monsoon, FIM) and August to September 2005 (SM). Stations were distributed along zonal transects from 11° N to 20.5° N (up to 17° N during SM) in the BoB and 8° N to 21° N in the AS (Fig. 1). The transects were fixed at a 2° latitude interval and in each transect, the stations were distributed at intervals of 1° longitude, extending from the coast to offshore. A total of 31 and 41 stations were considered from the BoB and the AS, respectively.

A CTD (SBE Seabird 911 plus) was deployed at each sampling station to obtain temperature and salinity profiles of the water column. The CTD was operated close to the bottom at coastal stations and down to a depth of 1000 m at oceanic stations. For estimation of dissolved oxygen (DO), water samples were collected with Niskin bottles in a rosette around the CTD from standard depths (surface, 10, 20, 30, 50, 75, 100, 150, 200, 300, 500, 750 and 1000 m) and analyzed using Winkler's method (Grasshoff 1983).

Mesozooplankton was collected using a Multiple Plankton Net (Hydro-Bios, mouth area 0.25m², mesh size 200 µm) at five discrete depth zones; the mixed layer depth (MLD), the thermocline (TC), the

bottom of the thermocline (BT) to 300 m, 300 – 500 m and 500 – 1000 m, based on the temperature and density characteristics of the water column. In the BoB, MLD was determined as the depth where the density difference from the surface was 0.2 kg m^{-3} (Shetye et al. 1996) and in the AS, it was determined as the depth up to which a temperature decrease of 0.5° C occurred from the sea surface temperature. In both the BoB and the AS, the bottom of thermocline was defined as the depth where the temperature reached 15° C .

The plankton net was hauled vertically from depth towards the surface, at a speed of 1 m.sec^{-1} to prevent larger zooplankton escaping. The advantage of this net is the negligible rate of contamination among the samples between depth layers (Weikert & John 1981). Samples from each depth were filtered, excess water was removed using absorbent paper and the displacement volume was estimated (Harris et al. 2000). Zooplankton samples were preserved in 4% formaldehyde for later enumeration and identification. Detailed taxonomic identification of chaetognaths was done from 50 - 75% aliquots for the upper layers and entire samples for deeper layers following Nair (2003).

Statistical analysis

Community indices (species diversity (H') and species evenness (J')) were calculated using PRIMER version 5.2.8 (Clarke & Warwick 1994). Cluster analyses were performed based on distribution of chaetognaths in the total water column at different stations and calculated using the Bray-Curtis similarity index with standardized $\log_{10}(x + 1)$ data. The Mann-Whitney U test was used to test for significant differences in chaetognath abundance between the two basins. The average abundances at different depth layers over the inter-monsoon and SM were used for this purpose. This test was done as a nonparametric test, not assuming Gaussian distributions, with two tailed P-values and 99% confidence interval.

Results

Environmental characteristics

Bay of Bengal

The SIM of the BoB was characterized by relatively less saline ($32.6 \pm 1.2 \text{ psu}$ and $33.8 \pm 0.5 \text{ psu}$ during SIM and SM, respectively) and cool surface waters ($27.3 \pm 0.9^\circ \text{ C}$ and $28.5 \pm 0.9^\circ \text{ C}$ during SIM and SM, respectively) compared to the SM period. During SIM, both the sea surface temperature (SST) and the sea surface salinity (SSS) gradually increased towards the South (Fig. 2). The vertical profile of

temperature showed a wide variation along depths with relatively higher gradients in the upper 200 m (Fig. 2). The vertical distribution of salinity showed stratification in the upper 100 m with more intensity towards the north (Fig. 2). During SM, the signature of coastal upwelling, as indicated by the uplifting of isothermal lines, was observed along all transects from 11° to 15°N (Fig. 2). Along the 13° and 15°N transects, oceanic stations experienced higher SST than coastal stations, where a warm gyre was observed (For detail environmental characteristics see Muraleedharan et al. 2007). Along 17°N, SST was relatively lower at 17°N 84°E and the doming of the temperature profile was also observed in this region. An uplifting of the isohaline (34.5 psu) was observed along the coastal stations of 11° to 15°N and this further supported the signatures of upwelling in the coastal stations (Fig. 2). Along 17°N, SSS was relatively higher at 17°N 84°E. The low SST and higher SSS along with the doming of temperature profile indicated the occurrence of a cold core eddy in this region. The vertical profile of DO showed a marked decrease of the DO value within the upper 150 m during both the SM and SIM (Fig. 2), although the surface DO was relatively higher during the SIM period. Along all transects, an oxygen minimum zone (OMZ, $< 0.5 \text{ ml l}^{-1}$) was observed and its thickness gradually increased towards the North (Fig. 2). During the SIM, the oxygen depleted water (ODW, $< 0.2 \text{ ml l}^{-1}$) layer was observed only along the 20.5° N transect, whereas during the SM a relatively thin layer of ODW was present along the coastal stations at all transects except at 11°N. During the SIM, the MLD was relatively shallower than for the SM period ($23 \pm 13 \text{ m}$ and $51 \pm 19 \text{ m}$ during SIM and SM, respectively) but the depth of the bottom of the thermocline layer was mostly similar ($180 \pm 45 \text{ m}$ and $168 \pm 19 \text{ m}$ during SIM and SM, respectively).

Arabian Sea

During the SM, the SST was relatively less than during the FIM in the AS ($27.6 \pm 0.7 \text{ }^{\circ}\text{C}$ and $28.8 \pm 0.5 \text{ }^{\circ}\text{C}$ during SM and FIM, respectively). During both periods, the upsloping of isothermal lines was observed towards the coastal region from 8° to 17°N indicating the occurrence of coastal upwelling in the SM and its continuation into the FIM period (Figs. 3 and 4). The average SSS during the SM ($35.8 \pm 0.9 \text{ psu}$) was similar to that of the FIM ($35.9 \pm 0.8 \text{ psu}$). During both periods, the SSS showed an increasing trend towards the North, which was in contrast to what was observed in the BoB (Figs. 2 – 4). The DO in the surface layer did not show much variation between the two periods ($4.5 \pm 0.2 \text{ ml l}^{-1}$ and $4.4 \pm 0.2 \text{ ml l}^{-1}$ during SM and FIM, respectively). The OMZ was observed along all transects and its thickness gradually increased towards the North (Figs. 3 and 4). In the northern AS, the ODW layer occupied a major part of the mid-depth water during both periods, whereas in the southern AS a relatively thin layer was present only during the SM period. The average depth of MLD was similar

during both seasons (45 ± 18 m and 45 ± 19 m during SM and FIM, respectively) whereas the depth of the bottom of the thermocline was relatively deeper during the FIM (164 ± 56 m and 180 ± 53 m during SM and FIM, respectively)

Abundance of Chaetognatha

Chaetognaths were most abundant in the MLD in all seasons in both the BoB (70.3% and 79.7% of total chaetognaths in the water column from 0 – 1000 m during SIM and SM, respectively) and the AS (75.7% and 83.4% during SM and FIM, respectively). Abundance gradually decreased with depth and the ratio of the chaetognath population towards deeper layers i.e. MLD : TC : BT – 300 m : 300 – 500 m : 500 – 1000 m did not show much variation between the BoB (142 : 55 : 2 : 1.6 : 1 and 147 : 33 : 1.6 : 2 : 1 at SIM and SM, respectively) and the AS (112 : 29 : 4 : 1.3 : 1 and 157 : 25 : 2 : 4 : 1 at SM and FIM, respectively). During the SM in the BoB and during the FIM in the AS, the abundance in BT – 300 m layer was less than in the layer at 300 – 500 m depth.

In the BoB, the abundance in the MLD was lower during the SIM compared to the SM period (21400 ± 19700 and 31800 ± 19900 ind. $(1000 \text{ m})^{-3}$, during SIM and SM, respectively). During the SIM, abundance at oceanic stations along 17°N was relatively higher than at other stations (Fig. 5). During the SM, maximum abundance was observed in the coastal upwelling stations (along 13° and 15°N). Chaetognaths were also abundant in the cold core cyclonic eddy region of the 17°N transect. Relatively lower abundance was observed in the warm gyre regions of the 13° and 15°N transects (Fig. 5). In the AS, during both the SM and the FIM, coastal upwelling stations along $8^\circ - 11^\circ\text{N}$ had higher abundance at MLD.

Chaetognatha community composition

A total of 21 species belonging to thirteen genera were observed in the total study area during the entire study period (Table I). In the BoB, the total number of species observed in the total water column (0 – 1000 m) was mostly similar during the SIM (16) and the SM (18). *Eukrohnia minuta* (Silas & Srinivasan, 1968) was observed only during the SIM whereas *Caecosagitta macrocephala* (Fowler, 1904), *Mesosagitta minima* (Grassi, 1881) and *Zonosagitta pulchra* (Doncaster, 1902) were present only during the SM (Table I). During both seasons, *Flaccisagitta enflata* (Grassi, 1881) was the dominant species in the upper two layers whereas *Decipisagitta decipiens* (Fowler, 1905) dominated in BT – 300 m and 300 – 500 m layers (Fig. 6). In the deeper layer (500 – 1000 m), *Eukrohnia fowleri* (Ritter-Záhony, 1909) was the most abundant species. During the SIM, *Aidanosagitta neglecta* (Aida, 1897),

Sagitta bipunctata (Quoy & Gaimard, 1828) and *Serratosagitta pacifica* (Tokiooka, 1940) were the other dominant species in the upper layer. During the SM, the more abundant chaetognath community in the upper layer of the shallow coastal upwelling stations (<75 m depth) comprised only six species, with *F. enflata* (45%), *Zonosagitta bedoti* (Beraneck, 1895) (20.3%), *A. neglecta* (10.6%) and *S. bipunctata* (10.6%) being dominant. Seven species were present in the cold core eddy region, with *F. enflata* (53%) and *Z. bedoti* (19.7%) being dominant. Although chaetognath abundance in the warm gyre region was lower, a total of twelve species were observed in this region, with *A. neglecta* contributing to 34% of the total population.

More species occurred in the AS during the SM (21) compared to the FIM (17). During both seasons, the most abundant species in the five depth layers were similar to those observed in the BoB except in the BT – 300 m layer where *Serratosagitta pacifica* dominated during the FIM (Fig. 6). The upper layers of the coastal upwelling stations mostly consisted of the epipelagic species. During the SM, the major contributing species were *F. enflata* (38.1%), *Z. bedoti* (29.2%) and *S. bipunctata* (15.4%) whereas during the FIM the abundant species were *F. enflata* (47.7%), *Z. bedoti* (28%) and *Pterosagitta draco* (Krohn, 1853) (20.6%). The mesopelagic species *E. fowleri* was observed mostly in the surface waters of upwelling locations and contributed to a smaller fraction of the chaetognath population.

Vertical distribution of chaetognaths

In both ocean basins, *Flaccisagitta enflata* was the only species that was observed in each depth layer during both seasons (Fig. 7). The other species that were present in the total water column in both basins during the SM were *Krohnitta pacifica* (Aida, 1897), *Sagitta bipunctata*, *Decipisagitta decipiens*, *Flaccisagitta hexaptera* (d'Orbigny, 1836) and *Aidanosagitta neglecta*. Fewer species were observed in each layer of the 1000 m water column during the inter monsoon periods (2 and 3 in the BoB and AS, respectively) than during the SM (10 and 7 in the BoB and AS, respectively). Among the abundant epipelagic species, *Zonosagitta bedoti*, *Serratosagitta pacifica* and *Aidanosagitta regularis* (Aida, 1897) were present in most of the depth layers. *Krohnitta subtilis* (Grassi, 1881), *Mesosagitta minima* and *Zonosagitta pulchra* were mostly restricted to the upper 300 m depth. The species that were mostly found in the deeper water were *Caecosagitta macrocephala*, *Pseudosagitta maxima* (Conant, 1896), *Pseudosagitta lyra* (Krohn, 1853), *Eukrohnia fowleri*, *Eukrohnia hamata* (Möbius, 1875) and *Eukrohnia minuta* (Fig. 7).

Statistical analyses

Species diversity (H') was higher in the upper two layers compared to deeper layers (Table II). In the BoB, during the SIM, maximum H' was found in the TC layer whereas it was highest in the MLD during the SM. In the AS, H' did not vary between the upper two layers during the FIM, but it was higher in the MLD during the SM. The species evenness (J') was generally high in most layers in both basins (Table II).

In both the BoB and the AS, cluster analysis based on the abundance and distribution of chaetognath species at different depth layers revealed some common features during the SM (Fig. 8). Based on 60% similarity, the deeper water species *Pseudosagitta maxima*, *Caecosagitta macrocephala* and *Eukrohnia fowleri* mostly clustered together. In both seasons, the majority of the epipelagic and cosmopolitan species were observed in the same cluster.

The Mann-Whitney U test did not show any significant variation in chaetognath abundances between the BoB and the AS during either the SM or the two inter monsoon periods ($P > 0.05$).

Discussion

The present study presents a detailed description of the influence of environmental characteristics on chaetognath distribution during the SM and the inter monsoon in the BoB and the AS, two major ocean basins in the northern Indian Ocean. In both the BoB and the AS, the pronounced north–south variation observed in the SST and SSS distribution during the present study supports views of a prevalent north–south gradation of oceanographic parameters described earlier (Wyrтки 1971; Naqvi 2008). The gradual increase in the thickness of the OMZ from South to North further corroborates this view. Irrespective of seasons, this thick OMZ persisted along the mid-depth water of both ocean basins. The sudden drop of chaetognath abundance below the TC in both the BoB and the AS thus clearly substantiates the earlier observation of the role of oxygen depleted water on the vertical distribution of chaetognaths in this region (Kusum et al. 2011). Similarly, Giesecke and González (2004) reported that vertical distributions of chaetognaths off Chile were influenced by DO. The temperature gradient and the possible current shear at temperature discontinuities might have also influenced chaetognath distribution by inhibiting a free downward migration (Peter & Nair 1978).

Bay of Bengal

The SIM is less productive than other seasons in the BoB (Prasanna Kumar et al. 2010), possibly because of the high SST and weak winds causing higher stratification. Lower abundance of chaetognaths in the MLD during this season compared to the SM period supports this view (Fig. 5). Lower abundance of the majority of the epipelagic species compared to that in the SM (except in the case of *Sagitta bipunctata* and *Flaccisagitta enflata*), resulted in a lower abundance in this upper layer during this period (Fig. 6). The shallow MLD during this period (23 ± 13 m and 51 ± 19 m at SIM and SM, respectively) might have also contributed to this abundance pattern

During the SM, three concomitant physical processes (coastal upwelling, cold core eddies and warm gyres) were observed along three different parts of the BoB (Muraleedharan et al. 2007). During this period, coastal upwelling has been recorded as a common process in the BoB (Shetye et al. 1991; Naidu et al. 1999; Rao 2002). The uplifting of cool subsurface nutrient rich water leading to high biological production is a characteristic feature (Bhavanarayana & La Fond 1957; Achuthankutty et al. 1980) and higher production in lower trophic levels propagates up the food chain. Higher chaetognath abundance observed in this zone compared to the oceanic region indicates their positive responses to the upwelling phenomenon. Similar observations of relatively higher chaetognath abundance in the upwelling region of the Pacific coast (Noblezada & Campos 2008) supports our view. Of the six species observed in this region, *F. enflata*, *Aidanosagitta neglecta*, *Zonosagitta bedoti* and *S. bipunctata* had relatively high abundance suggesting that they are responsive to these coastal physical processes.

Another prominent feature observed during this period was the occurrence of a high saline cold core cyclonic eddy along 17°N 84°E . The cyclonic eddy also aids in the enhancement of biological production (Prasanna Kumar et al. 2004). As is the case for upwelling regions, the higher abundance of chaetognaths in the cold core eddy indicates a response to this mesoscale physical event. Among the abundant species recorded from the upwelling zone, *F. enflata*, *Z. bedoti* and *S. bipunctata* were also abundant in this environment, although *A. neglecta*, which was abundant in the MLD, was rare in the eddy region.

A warm gyre was also evident during the SM in the oceanic stations of the central BoB. The occurrence of anticyclonic warm cells is common in this region (Somayajulu et al. 2003), generally forming during the SIM and persisting throughout the SM. The anticyclonic warm cell deepens the isothermal layer, resulting in increasing the thickness of the barrier layer and thus preventing vertical mixing. This, in

turn, results in an oligotrophic condition leading to low secondary productivity. Although chaetognath abundance was lower in this region, it supported the existence of a higher number of species (13) compared to the upwelling zone (6) and the cyclonic eddy region (7). Johnson and Terazaki (2003) reported similar low abundances in a warm core ring in Oyashio (Northwest Pacific) water. Pelagic biodiversity is generally negatively correlated with environmental instability, so that in areas of high production such as upwelling areas that are unstable, species richness is lower and unevenness is higher than in stable but less productive areas such as gyres. The dominance of *A. neglecta* (34%) over *F. enflata* (32.6%) in the warm gyre region indicates the former's affinity towards warm oligotrophic waters. The contrasting nature observed in the abundance of *F. enflata* and *A. neglecta* in cool cyclonic eddy and warm gyre regions provides an indication of their temperature preferences.

Arabian Sea

Upwelling is a well-known phenomenon during the summer monsoon along the west coast of India, which significantly influences the biological productivity in this region (Banse 1959; Smitha et al. 2008). In our study, clear signatures of upwelling were evident along the coastal stations from 8° to 17°N during the SM period. Similarly to the BoB, higher chaetognath abundance (especially *Flaccisagitta enflata*, *Zonosagitta bedoti* and *Sagitta bipunctata*) in the upper layer of the upwelling stations indicates the role of this temporal scale physical process on their spatial abundance. The mesopelagic species *Eukrohnia fowleri* was observed in the upper layer only in the upwelling region, which is consistent with the use of this species as an upwelling indicator in this region (Kusum et al. 2014).

The FIM, a short switchover phase from the summer monsoon to the winter monsoon, was characterized by high SST (>28°C) and high saline water (>35.5 psu) in most of the region. During this period, lower cloud cover leads to stronger insolation and high SST (Prasanna Kumar & Narvekar 2005). Along the southwest coast of India, upwelling events that were active during the SM persisted in the FIM but in a receding phase. In this region, these coastal events have been characterized as highly localized features with different forcing mechanisms, and thus differ from uniform wind-driven upwelling systems (Smitha et al. 2008). Along with the abundant *F. enflata* and *Z. bedoti*, *Pterosagitta draco* was identified as another species associated with the receding upwelling event. The upwelling indicator species *E. fowleri* was also noticed in low numbers and thus further validates its significance as an indicator species of this physical process.

Community structure and diversity

The study area appears to be vertically ordered, with the density discontinuity leading to biotic gradients also influenced by their physiological ability to cope with the oxygen deficient mid-depth water. This might have led to the higher species diversity in the upper two layers compared to the less oxygenated deeper layer (Table II). In the BoB during the FIM, although the abundance was higher in the MLD, species diversity was relatively higher in the TC, as previously observed by Nair (1978). Mixing of the epipelagic and mesopelagic species might be responsible for this (Pierrot-Bults & Nair 1991).

The cluster of the deeper water species of the genus *Eukrohnia*, *Pseudosagitta*, and *Caecosagitta* (60% similarity) in every season clearly indicates their preference for similar habitat. The large cluster formed by a higher number of species might have occurred due to their restricted habitat in the upper layer avoiding the oxygen deficient deeper layer. The basic trend observed in the clustering of species was the group of epipelagic species above the TC and another cluster of the meso- and bathypelagic species below the TC. This clearly substantiates the earlier concept of the TC layer acting as an ecological barrier for some zooplankton species (Nair et al. 1977; Peter & Nair 1978).

Based on the spatial and vertical distribution, the 21 species observed during the study can be categorized into epipelagic, mesopelagic and bathypelagic (Table I). Among the epipelagic species, the cosmopolitan *Flaccisagitta enflata* remained dominant in the upper two layers during every season in both basins and thus can be considered truly epipelagic, as was found during the IIOE (Nair 1978). Below the TC layer, in the mid-depth oxygen deficient water, the majority of the species had meager abundance. The only species that had relatively high percentage contribution in these layers was *Decipisagitta decipiens*, which indicated their adaptability to survive in the oxygen deficient environment. Similar observations by Batistić et al. (2004) of relatively high abundances of *D. decipiens* in less oxygenated mid-depth waters of the Adriatic Sea corroborate our view. In the northern Indian Ocean, *Eukrohnia hamata* is mostly recorded below 1000 m (Nair 1978). Hence, in the AS during the SM, though *E. hamata* was observed in the depth layer above 1000 m, it was considered as bathypelagic only.

Earlier studies have indicated that the AS and the BoB are two biologically contrasting tropical basins (Prasanna Kumar et al. 2002; Gauns et al. 2005), but our data suggest there is insignificant variation in chaetognath abundance and community structure between these basins.

Acknowledgements

We thank the Director, CSIR - National Institute of Oceanography and the Director, Centre for Marine Living Resources and Ecology, Kochi for providing the facilities for this work. We are indebted to all the participants of FORV *Sagar Sampada* for their help in sampling during the cruises. This study was carried out under the program “Marine Research on Living Resources” (MR-LR) funded by the Department of Ocean Development, Government of India. This is NIO contribution number **** (number to be received after the acceptance of the manuscript).

References

- Achuthankutty CT, Madhuratap M, Nair VR, Nair SRS, Rao TSS. 1980. Zooplankton biomass and composition in the western Bay of Bengal during late southwest monsoon. *Indian Journal of Marine Sciences* 9:201-6.
- Alvariño A. 1965. Chaetognaths. *Oceanography and Marine Biology - An Annual Review* 3:115-94.
- Banse K. 1959. On upwelling and bottom trawling off the southwest coast of India. *Journal of Marine Biological Association of India* 1:33-49.
- Batistić M, Kršinić F, Jasprica N, Carić M, Vilićić D, Lučić D. 2004. Gelatinous invertebrate zooplankton of the South Adriatic: species composition and vertical distribution. *Journal of Plankton Research* 26:459-74.
- Bhavanarayana PV, La Fond EC. 1957. On the replenishment of some plant nutrients during the upwelling period on the East coast off India. *Indian Journal of Fisheries* 4:75.
- Brock J, McClain C, Luther M, Hay W. 1991. The phytoplankton bloom in the north western Arabian Sea during the south west monsoon of 1979. *Journal of Geophysical Research* 96:20623-42.
- Clarke KR, Warwick RM. 1994. *Changes in Marine communities: An Approach to Statistical Analysis and Interpretation*. Plymouth: Plymouth Marine Laboratory. 144 pages.
- Dietrich G. 1973. The unique situation in the environment of the Indian Ocean. In: Zeitzschel B, editor. *The Biology of the Indian Ocean*. Berlin: Springer, p 1-6.
- Fernandes V. 2008. The effect of semi-permanent eddies on the distribution of mesozooplankton in the central Bay of Bengal. *Journal of Marine Research* 66:465-88.
- Fernandes V, Ramaiah N. 2009. Mesozooplankton community in the Bay of Bengal (India): spatial variability during the summer monsoon. *Aquatic Ecology* 43:951-63.
- Gauns M, Madhuratap M, Ramaiah N, Jyothibabu R, Fernandes V, Paul JT, et al. 2005. Comparative accounts of biological productivity characteristics and estimates of carbon fluxes in the Arabian Sea and the Bay of Bengal. *Deep-Sea Research II* 52:2003-17.

- Giesecke R, González HE. 2004. Feeding of *Sagitta enflata* and vertical distribution of chaetognaths in relation to low oxygen concentrations. *Journal of Plankton Research* 26:475-86.
- Grasshoff K. 1983. Determination of oxygen. In: Grasshoff K, Ehrhardt M, Kremling K, editors. *Methods of Sea Water Analysis*. Weinheim: Verlag Chemie, p 61–72.
- Harris R, Wiebe P, Lenz J, Skjoldal HR, Huntley ME. editors 2000. *ICES Zooplankton Methodology Manual*. London: Academic Press. 684 pages.
- Johnson TB, Terazaki M. 2003. Species composition and depth distribution of chaetognaths in a Kuroshio warm-core ring and Oyashio water. *Journal of Plankton Research* 25:1279-89.
- Kusum KK, Vineetha G, Raveendran TV, Muraleedharan KR, Nair M, Achuthankutty CT. 2011. Impact of oxygen-depleted water on the vertical distribution of chaetognaths in the northeastern Arabian Sea. *Deep-Sea Research I* 58:1163-74.
- Kusum KK, Vineetha G, Raveendran TV, Muraleedharan KR, Biju A, Achuthankutty CT. 2014. Influence of upwelling on distribution of chaetognath (zooplankton) in the oxygen deficient zone of the eastern Arabian Sea. *Continental Shelf Research* 78:16-28.
- Lee C, Jones B, Brink K, Fischer A. 2000. The upper ocean response to monsoonal forcing in the Arabian Sea: seasonal and spatial variability. *Deep Sea Research II* 47:1177-226.
- Madhu NV, Maheswaran PA, Jyothibabu R, Sunil V, Revichandran C, Balasubramanian T, et al. 2002. Enhanced biological production off Chennai triggered by October 1999 super cyclone (Orissa). *Current Science* 82:1472-9.
- McCreary JP, Kohler KE, Hood RR, Olson DB. 1996. A four- component ecosystem model of biological activity in the Arabian Sea. *Progress in Oceanography* 37:193-240.
- Muraleedharan KR, Jasmine P, Achuthankutty CT, Revichandran C, Dinesh Kumar PK, Anand P, et al. 2007. Influence of basin scale and mesoscale physical processes on biological productivity in the Bay of Bengal during the summer monsoon. *Progress in Oceanography* 72:364-83.
- Naidu PD, Ramesh Kumar MR, Ramesh Babu V. 1999. Time and space variations of monsoonal upwelling along the west and east coasts of India. *Continental Shelf Research* 19:559-72.
- Nair VR. 1976. Species diversity of chaetognaths along the equatorial region of the Indian ocean with comments on the community structure. *Indian Journal of Marine Sciences* 5:107-12.
- Nair VR. 1977b. Zonation of chaetognath species along the southwest coast of India. *Indian Journal of Marine Sciences* 6:142-6.
- Nair VR. 1978. Bathymetric distribution of chaetognaths in the Indian Ocean. *Indian Journal of Marine Sciences* 7:276-82.
- Nair VR. 1986. Monsoon regime in the Indian Ocean and zooplankton variability. *Pelagic Biogeography*. UNESCO technical papers in marine science. 49. Proceedings of International Conference, The Netherlands, 1985. p 210-13.

- Nair VR. 2003. Digitized inventory of marine bioresources. Chaetognatha. National Institute of Oceanography, Kochi. www.nio.org/index/option/com_nomenu/task/show/tid/2/sid/18/id/6 (accessed 5 September 2012).
- Nair VR, Rao TSS. 1973. Chaetognaths of the Arabian Sea. In: Zeitzschel B, editor. *The Biology of the Indian Ocean*. Berlin-Heidelberg-New York: Springer, p 293-317.
- Nair VR, Peter G, Paulinose VT. 1977. Zooplankton studies in the Indian Ocean. 1. From Bay of Bengal during southwest monsoon period. *Mahasagar-Bulletin of the National Institute of Oceanography* 10:45-54.
- Nair VR, Peter G, Paulinose VT. 1978. Zooplankton studies in the Indian Ocean II. From the Arabian Sea during the postmonsoon period. *Mahasagar-Bulletin of the National Institute of Oceanography* 11:35-43.
- Nair VR, Madhupratap M. 1984. Latitudinal range of Chaetognatha and Ostracoda in the western tropical Indian Ocean. *Hydrobiologia* 112:209-16.
- Nair VR, Jayalakshmi KV, Terazaki M. 2000. Abundance and diversity of chaetognaths from the Rodriguez triple junction area of the Indian Ocean. *The Deccan Geographer* 38:41-51.
- Nair VR, Terazaki M, Jayalakshmy KV. 2002. Community structure of chaetognaths in the northern Indian Ocean. *Plankton Biology and Ecology* 49:27-37.
- Nair VR, Srinivasa Kumar T. 2006. The Indian Ocean : Oceanic Properties that conceptualise zooplankton variability. Abstract No.41.. GODAE Symposium on ocean data assimilation and prediction in Asia-Oceania, 16-8 October 2006, Beijing, China. p 56.
- Nair VR, Panampunnayil SU, Pillai HUK, Gireesh R. 2008. Two new species of Chaetognatha from Andaman Sea, Indian Ocean. *Marine Biology Research* 4:208-14.
- Naqvi SWA. 2008. The Indian Ocean. In: Capone DG, Bronk DA, Mulholland MR, Carpenter EJ, editors. *Nitrogen in the Marine Environment*. New York: Elsevier, p 631-81.
- Noblezada MMP, Campos WL. 2008. Spatial distribution of chaetognaths off the northern Bicol Shelf, Philippines (Pacific coast). *ICES Journal of Marine Science* 65:484-94.
- Peter G, Nair VR. 1978. Vertical distribution of zooplankton in relation to thermocline. *Mahasagar-Bulletin of the National Institute of Oceanography* 11:169-75.
- Pierrot-Bults AC, Nair VR. 1991. Distribution patterns in Chaetognatha. In: Bone Q, Kapp H, Pierrot-Bults AC, editors. *The Biology of Chaetognaths*. Oxford: Oxford University Press, p 86–116.
- Prasanna Kumar S, Madhuprathap M, Dileep Kumar M, Gauns M, Muraleedharan PM, Sarma VVSS, et al. 2000. Physical control of primary productivity on a seasonal scale in central and eastern Arabian Sea. *Proceedings of the Indian Academy of Sciences-Earth and Planetary Sciences* 109:433-41.
- Prasanna Kumar S, Madhuprathap M, Dileep Kumar M, Muraleedharan PM, de Souza SN, Gauns M, et al. 2001. High biological productivity in the central Arabian Sea during summer monsoon driven by Ekman pumping and lateral advection, *Current Science* 81:1633–8.

- Prasanna Kumar S, Muraleedharan PM, Prasad TG, Gauns M, Ramaiah N, de Souza SN, et al. 2002. Why is the Bay of Bengal less productive during summer monsoon compared to the Arabian Sea? *Geophysical Research Letters* 29:2235, doi:10.1029/2002GL016013. 88 pages.
- Prasanna Kumar S, Nuncio M, Narvekar J, Ajoy Kumar S, Sardesai S, Desouza SN, et al. 2004. Are eddies nature's trigger to enhance biological productivity in the Bay of Bengal? *Geophysical Research Letters* 31:L07309, doi:10.1029/2003GL019274
- Prasanna Kumar S, Narvekar J. 2005. Seasonal variability of the mixed layer in the central Arabian Sea and its implication on nutrients and primary productivity. *Deep-Sea Research II* 52:1848-61.
- Prasanna Kumar S, Nuncio M, Narvekar J, Ramaiah N, Sardesai S, Gauns M, et al. 2010. Seasonal cycle of physical forcing and biological response in the Bay of Bengal. *Indian Journal of Marine Sciences* 39:388-405.
- Rao TVN. 2002. Spatial distribution of upwelling off the central east coast of India. *Estuarine and Coastal Shelf Science* 54:141-56.
- Shenoi SSC, Shankar D, Shetye SR. 2002. Differences in heat budgets of the near-surface Arabian Sea and Bay of Bengal: Implications for the summer monsoon. *Journal of Geophysical Research* 107, doi: 10.1029/2000JC000679.
- Shetye SR, Shenoi SSC, Gouveia AD, Michael GS, Sundar D, Nampoothiri G. 1991. Wind-driven coastal upwelling along the western boundary of the Bay of Bengal during the southwest monsoon. *Continental Shelf Research* 11:1397-408.
- Shetye SR, Gouveia AD, Shankar D, Shenoi SSC, Vinayachandran P, Sundar N, et al. 1996. Hydrography and circulation in the western Bay of Bengal during the northeast monsoon. *Journal of Geophysical Research* 101:14011-25.
- Smith SL, Madhupratap M. 2005. Mesozooplankton of the Arabian Sea: Patterns influenced by seasons, upwelling, and oxygen concentrations. *Progress in Oceanography* 65:214-39.
- Smitha BR, Sanjeevan VN, Vimalkumar KG, Revichandran C. 2008. On the upwelling off the southern tip and along the west coast of India. *Journal of Coastal Research* 24:95-102.
- Somayajulu YK, Murty VSN, Sarma YVB. 2003. Seasonal and inter-annual variability of surface circulation in the Bay of Bengal from TOPEX/Poseidon altimetry. *Deep Sea Research II* 50:867-80.
- Wyrtki K. 1971. *Oceanographic Atlas of the International Indian Ocean Expedition*, National Science Foundation, Washington, D.C. 531 pages.
- Weikert H, John HC. 1981. Experiences with a modified multiple opening closing plankton net. *Journal of Plankton Research* 3:167-77.
- Young DK, Kindle J. 1994. Physical processes affecting availability of dissolved silicate for diatom production in the Arabian Sea. *Journal of Geophysical Research* 99:22619-32.

Tables

Table I. Chaetognath community composition in the BoB and the AS. '+' indicates presence '-' indicates the absence of a particular species. (BoB = Bay of Bengal, AS = Arabian Sea, SIM = spring inter monsoon, SM = summer monsoon, FIM = fall inter monsoon, Epi = epipelagic, Meso = mesopelagic, Bathy = bathypelagic)

| Genus | Species | Category | BoB SIM | BoB SM | AS SM | AS FIM |
|----------------------|--|----------|------------|-----------|----------|-----------|
| <i>Eukrohnia</i> | <i>Eukrohnia fowleri</i> (Ritter-Záhony, 1909) | Meso | + | + | + | + |
| | <i>Eukrohnia hamata</i> (Möbius, 1875) | Bathy | - | - | + | - |
| | <i>Eukrohnia minuta</i> (Silas & Srinivasan, 1968) | Meso | + | - | + | + |
| <i>Krohnitta</i> | <i>Krohnitta pacifica</i> (Aida, 1897) | Epi | + | + | + | + |
| | <i>Krohnitta subtilis</i> (Grassi, 1881) | Epi | + | + | + | + |
| <i>Pterosagitta</i> | <i>Pterosagitta draco</i> (Krohn, 1853) | Epi | + | + | + | + |
| <i>Sagitta</i> | <i>Sagitta bipunctata</i> (Quoy & Gaimond, 1828) | Epi | + | + | + | + |
| <i>Aidanosagitta</i> | <i>Aidanosagitta neglecta</i> (Aida, 1897) | Epi | + | + | + | + |
| | <i>Aidanosagitta regularis</i> (Aida, 1897) | Epi | + | + | + | + |
| <i>Caecosagitta</i> | <i>Caecosagitta macrocephala</i> (Fowler, 1904) | Meso | - | + | + | + |
| <i>Decipisagitta</i> | <i>Decipisagitta decipiens</i> (Fowler, 1905) | Meso | + | + | + | + |
| <i>Ferosagitta</i> | <i>Ferosagitta ferox</i> (Doncaster, 1902) | Epi | + | + | + | + |
| | <i>Ferosagitta robusta</i> (Doncaster, 1902) | Epi | + | + | + | + |
| <i>Flaccisagitta</i> | <i>Flaccisagitta enflata</i> (Grassi, 1881) | Epi | + | + | + | + |
| | <i>Flaccisagitta hexaptera</i> (d'Orbigny, 1836) | Epi | + | + | + | + |
| <i>Mesosagitta</i> | <i>Mesosagitta minima</i> (Grassi, 1881) | Epi | - | + | + | - |

| | | | | | | |
|-----------------------|--|------|---|---|---|---|
| <i>Pseudosagitta</i> | | | | | | |
| | <i>Pseudosagitta lyra</i> (Krohn, 1853) | Meso | - | - | + | - |
| | <i>Pseudosagitta maxima</i> (Conant, 1896) | Meso | + | + | + | - |
| <i>Serratosagitta</i> | | | | | | |
| | <i>Serratosagitta pacifica</i> (Tokiaka, 1940) | Epi | + | + | + | + |
| <i>Zonosagitta</i> | | | | | | |
| | <i>Zonosagitta bedoti</i> (Beraneck, 1895) | Epi | + | + | + | + |
| | <i>Zonosagitta pulchra</i> (Doncaster, 1902) | Epi | - | + | + | + |

Table II: The species diversity (H') and species evenness (J') along different depths in the Bay of Bengal (BoB) and the Arabian Sea (AS). SIM, spring inter monsoon; SM, summer monsoon, FIM, fall inter monsoon; MLD, mixed layer depth; TC, thermocline; BT, bottom of the thermocline.

| | BoB spring inter monsoon | | BoB summer monsoon | | AS summer monsoon | | AS fall inter monsoon | |
|--------------|-----------------------------|------|-----------------------|------|----------------------|------|--------------------------|------|
| | H' | J' | H' | J' | H' | J' | H' | J' |
| MLD | 1.17 | 0.67 | 1.36 | 0.71 | 1.26 | 0.79 | 1.1 | 0.64 |
| TC | 1.24 | 0.67 | 1.17 | 0.67 | 1.18 | 0.78 | 1.1 | 0.65 |
| BT - 300m | 0.69 | 0.8 | 0.92 | 0.67 | 0.91 | 0.7 | 0.61 | 0.88 |
| 300 - 500 m | 0.87 | 0.68 | 1.01 | 0.72 | 0.81 | 0.62 | 0.81 | 0.91 |
| 500 - 1000 m | 0.58 | 0.73 | 0.89 | 0.75 | 1 | 0.84 | 1.1 | 0.89 |

Figure Legends:

Figure 1. Sampling locations in the Bay of Bengal and the Arabian Sea.

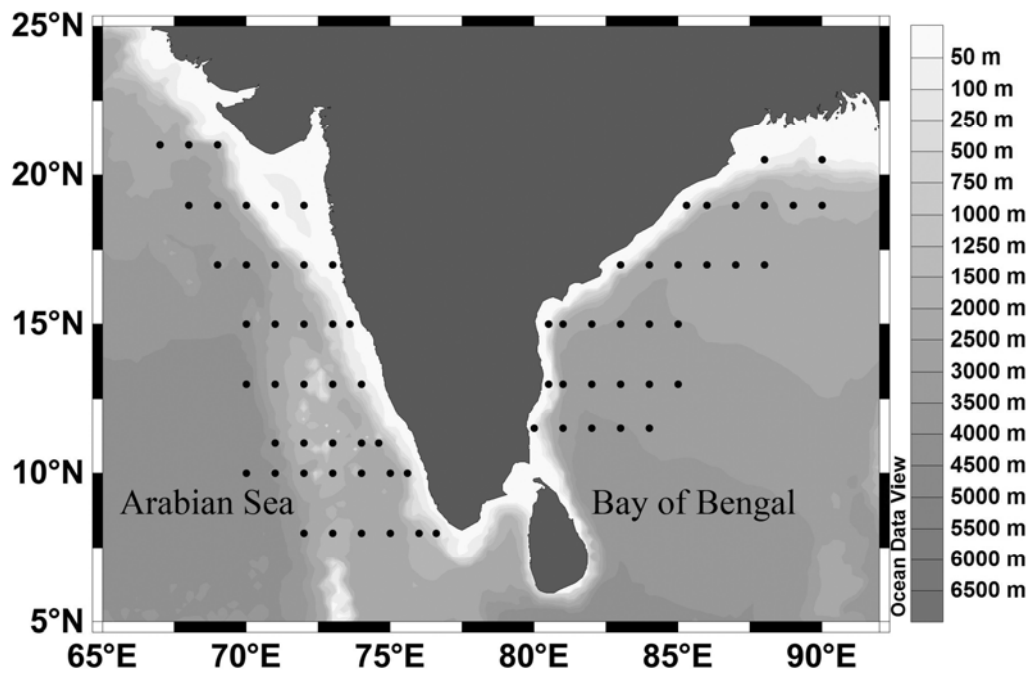


Figure 2. Distribution of (a) temperature ($^{\circ}\text{C}$), (b) salinity and (c) dissolved oxygen (ml l^{-1}) during spring inter monsoon and (d) temperature ($^{\circ}\text{C}$), (e) salinity and (f) dissolved oxygen (ml l^{-1}) during summer monsoon in Bay of Bengal in the upper 1000 m of the water column.

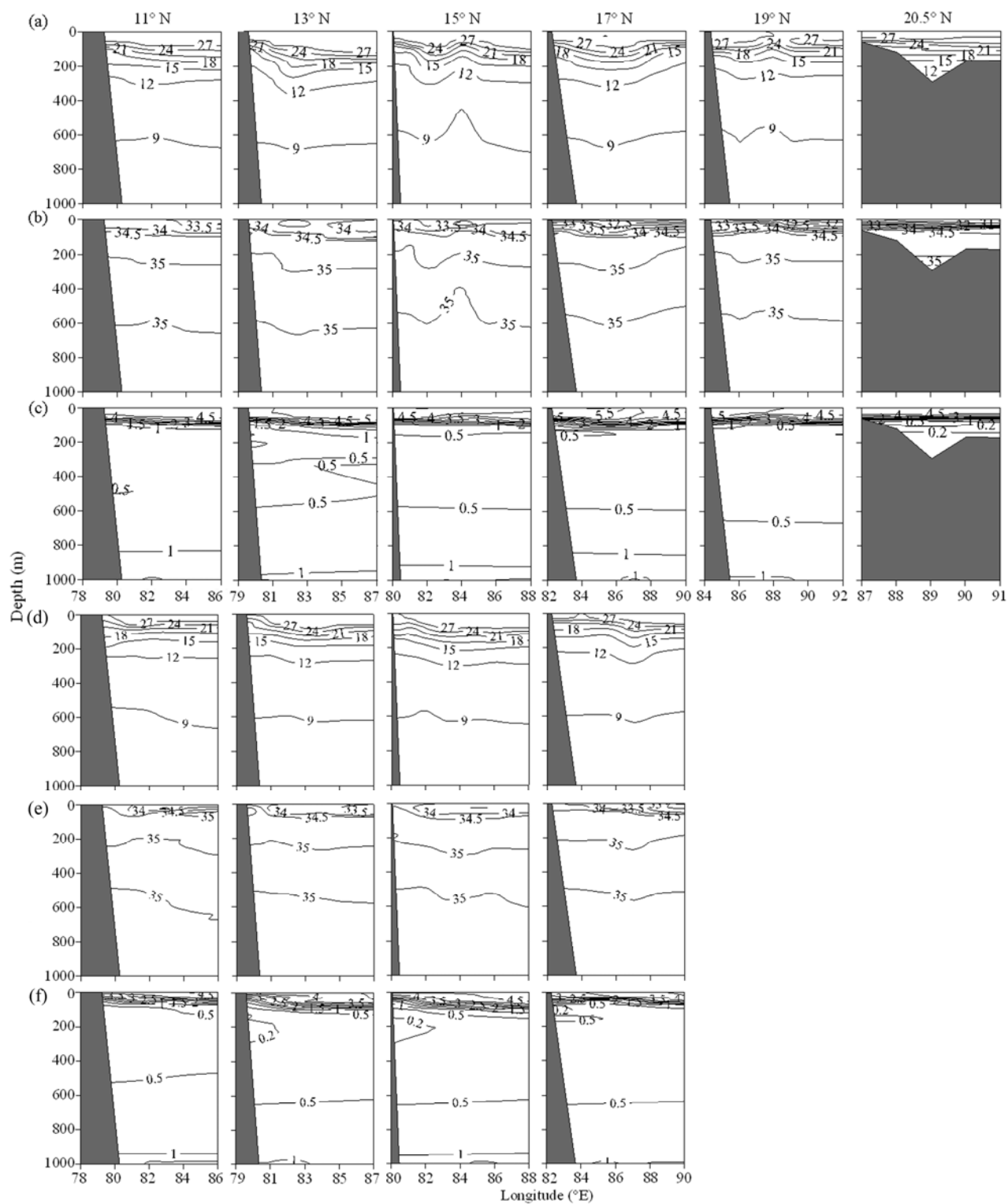


Figure 3. Distribution of (a & d) temperature ($^{\circ}\text{C}$), (b & e) salinity and (c & f) dissolved oxygen (ml l^{-1}) during summer monsoon in Arabian Sea in the upper 1000 m of the water column.

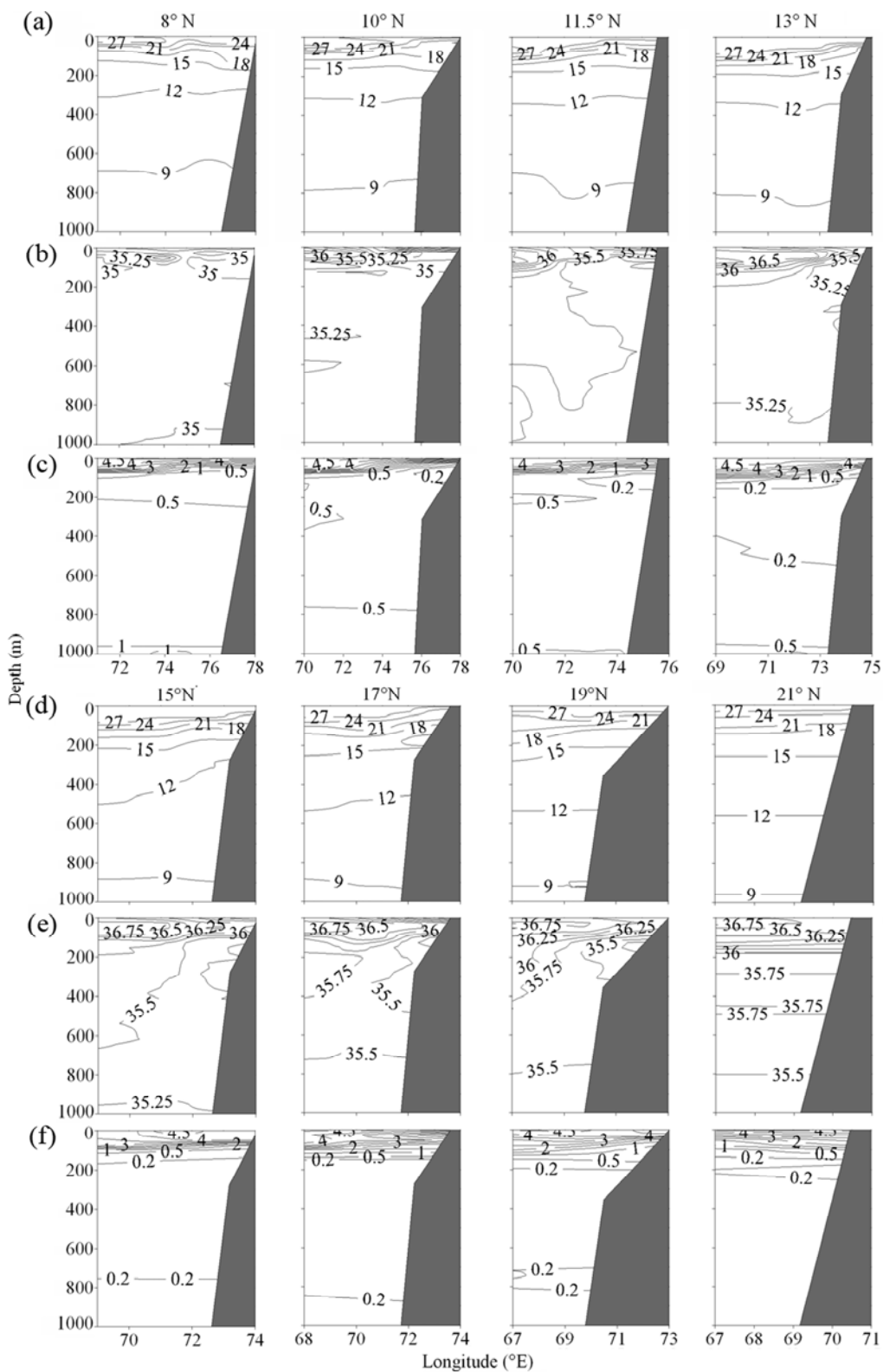


Figure 4. Distribution of (a & d) temperature ($^{\circ}\text{C}$), (b & e) salinity and (c & f) dissolved oxygen (ml l^{-1}) during fall inter monsoon in Arabian Sea in the upper 1000 m of the water column.

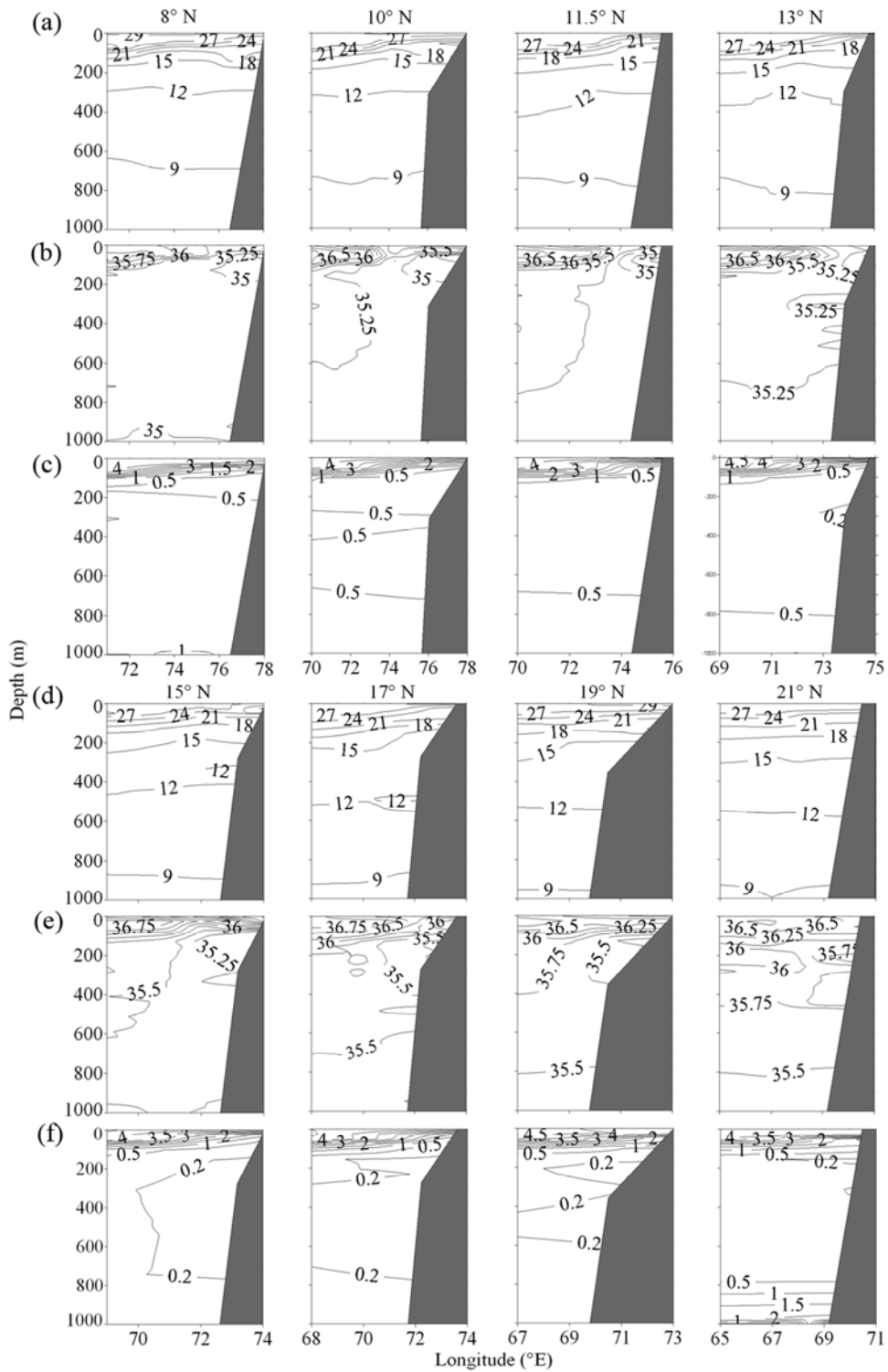


Figure 5. Chaetognath population distribution (ind. (1000 m)⁻³) along Mixed layer depth at different seasons in Bay of Bengal and Arabian Sea (a: BoB- spring inter monsoon, b: BoB – summer monsoon, c: AS – summer monsoon, d: AS – fall inter monsoon).

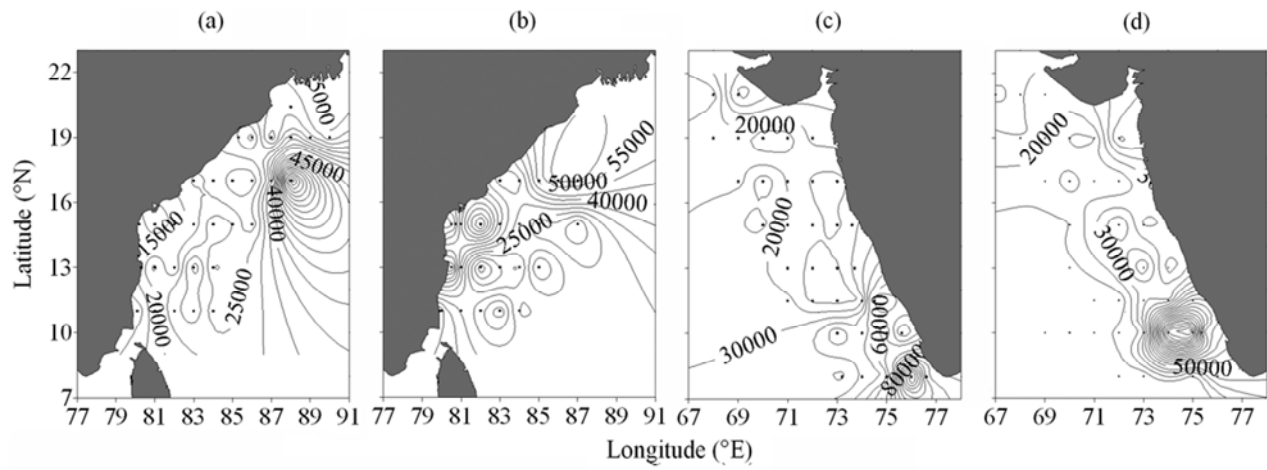


Figure 6. Depth layers and chaetognath species distribution (a) Mixed layer depth, (b) Thermocline, (c) Bottom of thermocline – 300 m, (d) 300 – 500 m and (e) 500 – 1000 m.

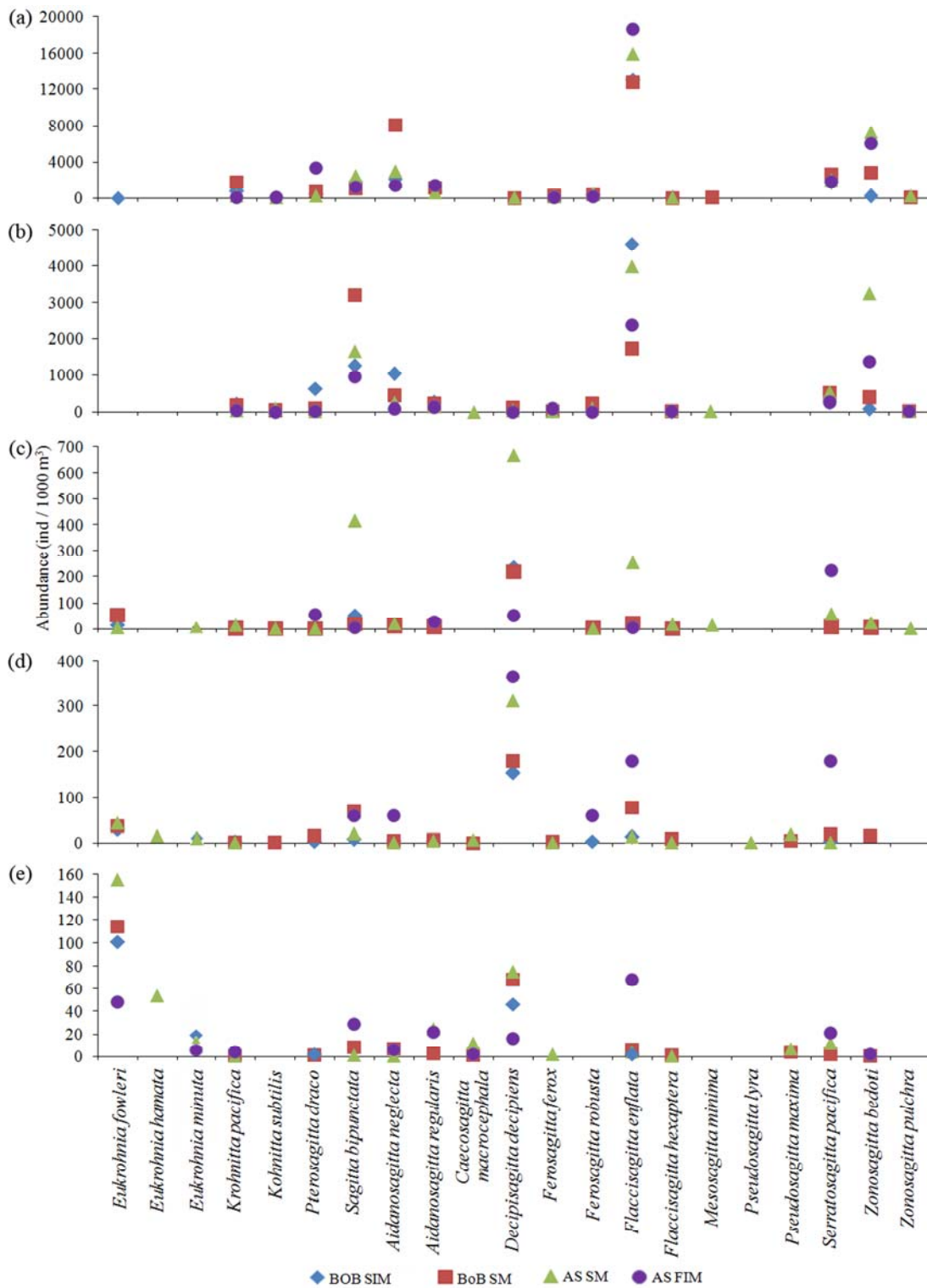


Figure 7. Vertical distribution of different chaetognath species at different depth layers (a: BoB- spring inter monsoon, b: BoB – summer monsoon, c: AS – summer monsoon, d: AS – fall inter monsoon; MLD – Mixed layer depth, TC – Thermocline, BT – Bottom of thermocline). The percentage contribution of less than 2% being incapable to express by the bar diagram, are expressed by symbols.

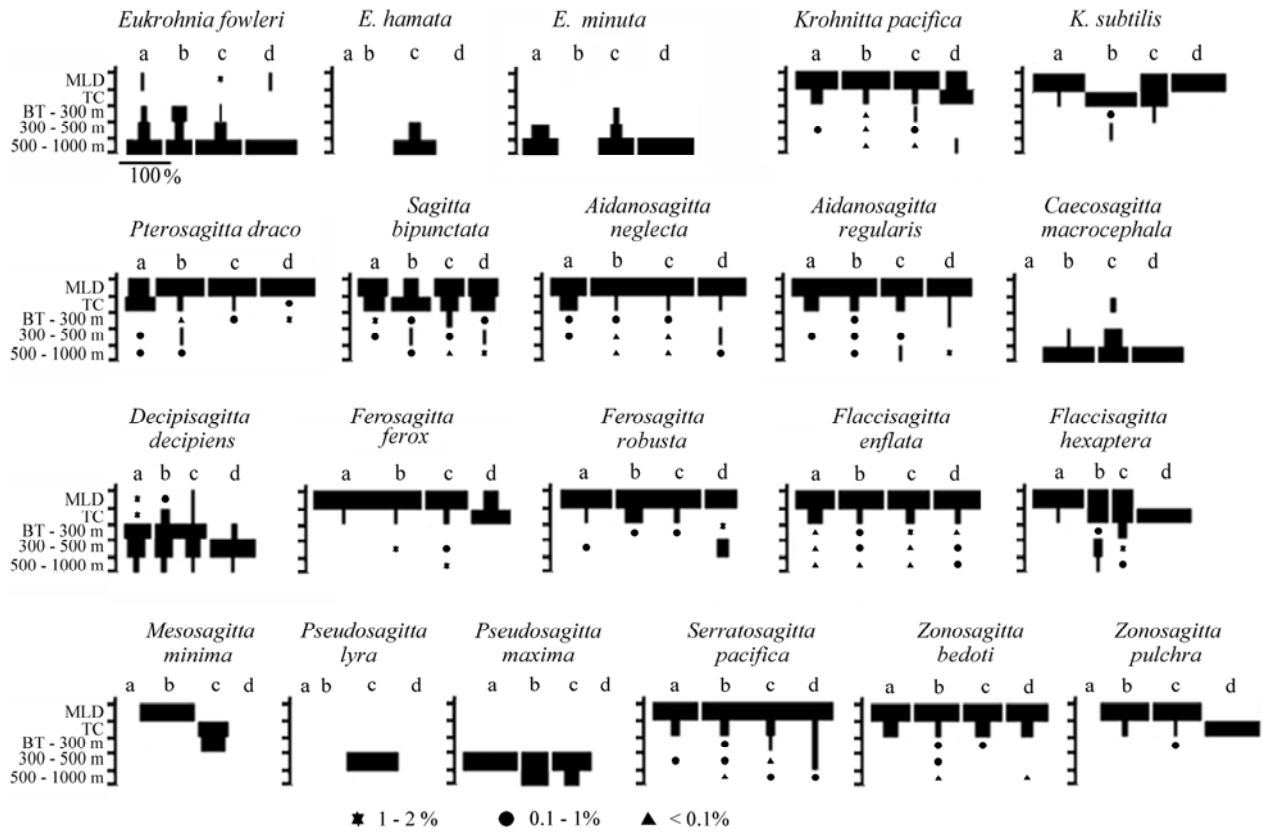


Figure 8. Cluster analyses showing similarity between different chaetognath species based on their habitat preferences in the Bay of Bengal and the Arabian Sea

