

## **Impact of oxygen-depleted water on the vertical distribution of chaetognaths in the Northeastern Arabian Sea**

Kusum KK <sup>a,\*</sup>, Vineetha G <sup>a</sup>, Raveendran TV <sup>a</sup>, Muraleedharan KR <sup>a</sup>, Nair M <sup>a</sup>, Achuthankutty CT <sup>a,b</sup>

a - National Institute of Oceanography, Kochi-18, Kerala, India

b – National Centre for Antarctic and Ocean Research, Vasco-da-gama, Goa – 403804, India

For the sixth author ‘a’ denotes the address at which the work was actually done and ‘b’ denotes the present address.

**Corresponding author:** Kusum KK

National Institute of Oceanography, Salim Ali Road, Kochi-18, India

Phone number: 91 0484 23908141 Fax number: 91 0484 2390618;

E mail address – kusum.kk1@gmail.com

### **Abstract**

The influence of a thick layer of oxygen-depleted water ( $< 0.2 \text{ ml l}^{-1}$ ) on the abundance and distribution of chaetognaths was investigated in the northeastern Arabian Sea (NEAS), a natural oxygen-deficient system in the global ocean. The species and maturity stage-wise distribution of this group were studied at five discrete depths down to 1000 m. A total of 22 species belonging to four genera were observed, and the genus *Sagitta* dominated, representing 60% (500 – 1000 m) to 89% (Mixed layer depth) of the total chaetognath population. Based on their vertical distribution limits, four groups were recognized, as follows: I: species abundant in surface water with a maximum distribution limit up to 300 m; II: species confined mainly to deeper waters ( $> 500 \text{ m}$ ); III: species present throughout the water column (0 – 1000 m); and IV: species present in most layers, but with a preference for a specific depth stratum. A positive correlation ( $P < 0.01$ ) was observed in the abundance of chaetognaths and their main prey copepods, emphasising the strong trophic relationship between these groups. It was found that the intensely oxygen-deficient waters of the NEAS play a crucial role in the vertical distribution and abundance of chaetognath species of all four genera. This report presents information on the maturity stages and ontogenetic migration of this important planktonic group in relation to the oxygen-depleted water in the study region for the first time. The results obtained are also important for understanding the biological processes associated with a major oxygen minimum zone (OMZ) in the global ocean.

**Keywords (6 Nos):** Chaetognaths; vertical distribution; dissolved oxygen; oxygen-depleted water; species diversity; Northeastern Arabian Sea

## 1. INTRODUCTION

Chaetognaths have drawn significant research interest as a major marine zooplankton taxon. Their abundance has been estimated to represent up to 30% of the wet weight biomass of copepods in the global ocean (Ryther, 1969; Reeve, 1970; Bone et al., 1991). The trophodynamics of this group in the pelagic realm are known to play an important role in global ocean ecology (Froneman and Pakhomov, 1998).

Vertical gradients in physico-chemical characteristics of the marine system play a key role in controlling the abundance, distribution limits and diversity of zooplankton (Banse, 1964; Röpke, 1993; Gallagher et al., 2004). Like all other zooplankton groups, chaetognaths respond to different physical characteristics of the marine system through the process of dispersion (Nagai et al., 2008). Vertical migration, as a means of dispersion, helps chaetognaths to locate prey, escape predators (Stuart and Verheye, 1991; Batistić et al., 2003) and avoid stressed environments (Hardy, 1935; Besiktepe and Unsal, 2000).

The north eastern Arabian Sea (NEAS) in the northern Indian Ocean is a natural oxygen-deficient system (Naqvi et al., 2006, 2009) bounded by the western Indian continental shelf in the east and the Eurasian continent in the north. The oxygen minimum zone (OMZ,  $< 0.5 \text{ ml l}^{-1}$ ) in the northern Arabian Sea is the thickest ( $\sim 1 \text{ km}$ ) of the global oceans (Naqvi et al., 2009) and has persisted for thousands of years (Reichart et al., 1998). The existence of a thick oxygen-depleted water (ODW,  $< 0.2 \text{ ml l}^{-1}$ ) layer (Helly and Levin, 2004) is a natural phenomenon of this area and shows a tendency for north south variation (Naqvi, 2008, Naqvi et al., 2009). The ecological sequelae of the OMZ and ODW persisting in this area are very intense, and only a few species can tolerate this extreme oxygen deficiency, thereby constraining the vertical habitat of most marine organisms (Prince and Goodyear, 2006; Bertrand et al., 2010). The relationship between oxygen deficiency and organisms that inhabit the pelagic realm has become a subject of great interest at the global level as it influences the distribution (Judkins, 1980; Fenchel et al., 1990; Saltzman and Wishner, 1997) and subsequently leads to physiological changes in these organisms (Lutz et al., 1994; Childress and Seibel, 1998). In the Indian Ocean, there have been few detailed studies on this important topic (Herring et al., 1998, Wishner et al., 1998; Levin, 2002; Madhu et al., 2003). In spite of the strong prevalence of the OMZ in the Arabian Sea, most earlier investigations have focused mainly on its effect on copepods (Gowing and Wishner, 1998; Wishner et al., 2000). Studies on chaetognaths in the Arabian Sea are limited and have generally

focused on their distribution based on samples collected during the International Indian Ocean Expedition (IIOE, 1960-1965) more than four decades ago (Nair, 1972, 1978). A recent report on chaetognaths from the Andaman Sea also deals with their general diversity in a restricted region (Nair and Gireesh, 2010). The role of physical characteristics of the water column in this group of plankton is largely unknown in this area. The impact of a thick oxygen-deficient layer on the chaetognath distribution and its effect on different life and maturity stages are also not well understood in other parts of the global ocean (Giesecke and González, 2004).

The present study was designed to determine how the oxygen-deficient water column in the NEAS affects the vertical distribution of chaetognaths and whether their main prey copepods have any major influence on their abundance and distribution. Our hypothesis was that heterogeneity in the thickness of the ODW layer will have a direct impact on the vertical distribution of chaetognaths. To test this hypothesis, the following parameters were considered: 1) species-level identification of chaetognaths to understand the species-specific vertical distribution profile; 2) categorisation of chaetognaths into different life stages based on sexual maturity to determine whether the ODW has a different impact on different life stages; 3) vertical characteristics of the water column based on determining temperature, salinity, density and dissolved oxygen; and 4) trophic relationships to understand active biotic interactions in the system.

## 2. METHODS

### 2.1 Sampling

Sampling was carried out in the NEAS between 29<sup>th</sup> November and 20<sup>th</sup> December 2006 (early winter monsoon) onboard the FORV *Sagar Sampada* (Cruise #251) as part of the Marine Research on Living Resources (MR-LR) programme. Stations were distributed along four zonal transects from 15° N to 21° N (Fig. 1). The transects were fixed at a 2° latitude interval, and in each transect, five stations were sampled at intervals of 1° longitude, extending from the coast to offshore. Diurnal observations were performed at one coastal station and one oceanic station along each transect (Fig. 1) at 6 hour intervals for 24 hr. The sampling times for all other stations were noted, to obtain a better understanding of temporal variations. **(Preferred position of Fig. 1)**

At all stations, a CTD (SBE Seabird 911 plus) was used to obtain the temperature and salinity profiles of the water column. This instrument was operated close to the bottom at coastal stations and down to a depth of 1000 m at oceanic stations. The potential density ( $\sigma_t$ ) was computed from the

pressure, temperature and salinity obtained from the CTD. To estimate dissolved oxygen (DO), water samples were collected using a Rosette sampler from standard depths to 1000 m (surface, 10, 20, 30, 50, 75, 100, 150, 200, 300, 500, 750 and 1000 m) and analysed using Winkler's method (Grasshoff *et al.*, 1983). Mesozooplankton sampling was performed using a multiple plankton net (Hydrobios, Germany) with a mouth area of 0.25 m<sup>2</sup> and a mesh size of 200 µm. Samples were collected from five discrete depth zones, including the mixed layer depth (MLD), the thermocline (TC), the base 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. The MLD was determined as the depth up to which a temperature decrease of 0.5° C occurred from the sea surface temperature. The thermocline was defined as the depth where the temperature reached 15°C. The net was towed vertically at a speed of 1 m. sec<sup>-1</sup> and was operated at prefixed depth zones by shipboard control with electronic sensors. Samples were passed through a 200-µm mesh; excess water was removed with absorbent paper; and the displacement volume was measured (Harris *et al.*, 2000). Copepods and chaetognaths were sorted from the whole sample or from an aliquot (50%) using a Folsom splitter and counted under a stereomicroscope. Their abundance was calculated based on the volume of water filtered through the net and expressed as [ind. (1000 m)<sup>-3</sup>]. Based on ovarian development, the chaetognaths were grouped into 3 maturity stages, including Stage I, or immature (specimens with no visible ovaries); Stage II, or maturing (those with developing ova); and Stage III, or matured (individuals with one or more mature ova) (McLaren, 1969; Zo, 1973). All spent individuals were considered under stage III.

## 2.2 Statistical analysis

Principal component analysis (PCA) was carried out using the statistical programme PAST version 2.02 (Hammer *et al.*, 2001), to understand the relationships between the biotic and abiotic variables. The mean values of the abiotic parameters for each depth stratum at all stations were considered for the analysis. As potential density is a derived parameter, it was not used in the analysis. Non-metric multidimensional scaling analysis (MDS) was performed for five depth strata based on the distribution of temperature, salinity, dissolved oxygen and chaetognath abundance at different stations and calculated using the Bray- Curtis similarity index with standardised log<sub>10</sub> (x + 1) data using PRIMER version 5.2.8 (Clarke and Warwick, 1994). Community indices, such as species diversity (*H'*), species richness (*d*) and species evenness (*J'*), were analysed for the chaetognaths to detect differences in their vertical assemblages. Species richness (*d*) was calculated only up to the TC layer, as the density below TC layer was <1 ind. (1000 m)<sup>-3</sup>. To establish whether copepod abundance determines the vertical

distribution of chaetognaths, the ratio of chaetognaths and copepods was calculated for each depth zone. The Pearson correlation coefficient ( $r$ ) was calculated between the abundances of copepods and chaetognaths to detect their trophic relationship, followed by linear regression analysis with a 99% confidence band to estimate the magnitude of the relationship using Graph Pad Prism (version 5.01). A Wilcoxon matched pair test was carried out between the day and night abundances of chaetognaths and copepods at different depths at the diurnal stations, to determine whether the diel vertical migrations of these groups affect their abundance. This was done as a nonparametric test, not assuming Gaussian distributions, with two-tailed P-values and a 95% confidence interval. Analysis of variance (ANOVA) was performed on chaetognath abundance to have a better understanding of spatial variability.

### 3. RESULTS

#### 3.1 Physico-chemical environment

Sea surface temperature (SST) showed a gradual decrease from south to north (Fig. 2a). Along 15°N, it was ~ 29° C and at 17° N, it ranged between 28.2 – 28.8° C. A Relatively low SST (~ 27.5° C) was recorded along 19° N, and the lowest value was recorded along 21° N (25.7° C). The upper 200 m layer was intensely stratified, with a strong vertical thermal gradient of 11 - 14° C in the southern and 8 – 9° C in the northern NEAS (Fig. 2a). MLD ranged from 21 m (station 10) to 63 m (station 18), with an average value of  $45 \pm 12$  m. There was a difference in MLD between the northern ( $49 \pm 12$  m) and southern ( $40 \pm 12$  m) regions. The bottom of the thermocline layer varied widely between stations, ranging from 194 (station 2) to 314 m (station 19). The TC layer progressively deepened from south to north ( $217 \pm 29$ ,  $220 \pm 48$ ,  $261 \pm 55$  and  $297 \pm 12$  m along 15°, 17°, 19° and 21° N, respectively) (Fig. 2a). **(Preferred position of Fig. 2)**

Spatial variation in sea surface salinity (SSS) was marginal (34.6 - 36.6), and the gradients decreased towards the north (Fig. 2b). The vertical distribution of potential density ( $\sigma_t$ ) showed higher gradients in the upper 200 m of the water column (Fig. 2c). Dissolved oxygen in surface layers (4.2 – 4.8 ml l<sup>-1</sup>) did not show considerable variation, but a marked gradient was observed in the vertical profile along all transects, with a pronounced OMZ layer (< 0.5 ml l<sup>-1</sup>) being detected below subsurface waters. In the southern region along 15° N, the OMZ occurred between 120 – 1000 m (Fig. 2d). An acute OMZ (ODW < 0.2 ml l<sup>-1</sup>) was observed between 280 – 400 m at coastal stations and from 150 – 400 m at the oceanic stations. Along 17° N, the OMZ prevailed from 150 to 1000 m, and the ODW was detected between 200 – 775 m (Fig. 2d). In the northern region along 19° N, the ODW was found to

extend between 200 – 820 m, while along 21° N, it was found between 180 – 800 m. Thus, an increasing trend in the thickness of the ODW layer was observed from south to north of NEAS.

### 3.2 Copepod abundance

At MLD, copepod abundance was relatively high in the northern region of the NEAS (Fig. 3a) and ranged between 114814 and 1062295 ind. (1000 m)<sup>-3</sup>. A marked difference in abundance was observed at BT – 300 m between the northern [67743 ± 17334 ind. (1000 m)<sup>-3</sup>] and southern sectors [8057 ± 6644 ind. (1000 m)<sup>-3</sup>]. In depth zones below 300 m, the abundance was relatively higher in the southern region (Fig. 3a). The Wilcoxon matched pair test did not show any significant variation ( $P > 0.05$ ) in diel abundance, but the single factor ANOVA revealed significant variation in abundance between different depth zones ( $P < 0.05$ ). **(Preferred position of Fig. 3)**

### 3.3 Chaetognath abundance

Chaetognaths were abundant at MLD (71% of total chaetognaths in the water column from 0 – 1000 m) and ranged between 2274 and 44444 ind. (1000 m)<sup>-3</sup>. In upper three depth zones, their abundance was relatively higher in the northern region (Fig. 3b). At depths of 300 – 500 m, highest abundance was observed at station 19 [129 ind. (1000 m)<sup>-3</sup>], while at depths of 500 – 1000 m, the southern region exhibited relatively higher abundance. Although no significant variation was found in diurnal abundance ( $P > 0.05$ ), a significant decrease in abundance with depth was noted ( $P < 0.05$ ). The ratio of the abundance of chaetognaths and copepods showed a decreasing trend from upper to deeper layers (0.04, 0.039, 0.032, 0.007 and 0.003 at MLD, TC, BT – 300 m, 300 – 500 m and 500 – 1000 m, respectively).

### 3.4 Chaetognath composition

Twenty-two species belonging to 4 genera were recorded during the present study (Table I). *Sagitta* represented the dominant genus (16 species), with a relative abundance of 60 (500 – 1000 m) to 89% (MLD). At MLD, 17 species were observed, among which two belonged to genus *Krohnitta* (9.9%) and one to genus *Pterosagitta* (1.1%). The TC layer was represented by 17 species and the BT – 300 m layer by 10 species. Bathypelagic species of genus *Eukrohnia* (3 species) were sparse and occurred mostly in 500 – 1000 m in the water column (Table I). The maturity stage composition showed dominance of Stage I (> 60%) (Fig. 4). In the deeper layer, the less abundant species were represented by a higher immature population percentage (84% in 500 – 1000 m). The maximum mature (Stage III) population

percentage occurred at MLD (20%) and gradually decreased in deeper layers (9, 7, 4 and 3% at TC, BT – 300 m, 300 – 500 m and 500 – 1000 m, respectively). **(Preferred position of Fig. 4)**

### **3.5 Vertical distribution and ontogenetic migration of different species of chaetognaths**

Based on their vertical distribution limits, the observed chaetognath species were grouped into four categories.

(I) Species abundant in surface layers with a maximum distribution limit up to 300 m, such as *Sagitta neglecta*, *S. bedfordii*, *S. minima*, *S. pulchra*, *S. bipunctata*, *S. planktonis*, and *Pterosagitta draco*. *S. neglecta* was one of the major components in upper layers, representing 13, 11 and 10.5% of the chaetognath population in the MLD, TC and BT – 300 m zones, respectively (Fig. 5). The immature population dominated (> 80%) the upper two strata, whereas mature specimens formed the major part of the population (47.3%) in the BT – 300 m layer (Fig. 6). *S. bedfordii* comprised 3 – 8% of the population, with maximum abundance at MLD [av. 402 ind. (1000 m)<sup>-3</sup>]. Figure 7 depicts the ontogenetic vertical migration of different species, considering the total abundance (including day and night) of a particular stage of a species as 100%. Among the species in this group, mature specimens of *P. draco* were abundant in the TC layer and immature specimens at MLD, whereas immature specimens of *S. pulchra* were more abundant in the TC layer, and the maturing (stage II) population was mostly collected from MLD. Regardless of maturity stages, the abundance of most of the other species (except *S. planktonis*) was high at MLD. **(Preferred position of Fig. 5)**

(II) Species such as *Sagitta maxima*, *Eukrohnia bathypelagica*, *E. minuta* and *E. fowleri* were mostly confined to deeper waters (> 500 m). The bathyplanktonic species *S. maxima* was only observed in the southern region at depths of 500 – 1000 m, contributing 15% of the total chaetognath population of this layer (Fig. 5). Most of the species of *Eukrohnia* were restricted to depths below 500 m. They were mainly observed in the southern region (Fig. 8), and only immature stages were encountered during the study (Figs. 6 and 7). **(Preferred position of Fig. 6)**

(III) Species distributed throughout the water column (0 – 1000 m) included *Sagitta enflata*, *S. decipiens*, *S. robusta*, *Krohnitta pacifica* and *K. subtilis*. *S. enflata* represented the dominant species up to a depth of 500 m (Table I). It contributed 5% (500 – 1000 m) to 48.4% (BT – 300 m) of the total chaetognath population (Fig. 5). In the upper 300 m, its abundance was relatively high in the northern region (Fig. 8), and all three maturity stages were abundant at MLD (Fig. 7), among which stage III constituted 26.1% of the population (Fig. 6). Although stage I of *S. robusta*, *K. subtilis* and the

mesopelagic species *S. decipiens* were distributed throughout the water column, their mature stages were restricted mainly to the upper layers (Fig. 7) in the northern region (Fig. 8). **(Preferred position of Fig. 7)**

(IV) *Sagitta hexaptera*, *S. ferox*, *S. pacifica*, *S. regularis*, *S. zetesios* and *S. tasmanica* were the species present in most of the layers, but with a preference for a specific depth stratum. The cosmopolitan species, *S. hexaptera* was abundant in all layers except the BT – 300 m zone. In the upper layers, its abundance was relatively high in the northern region while below a depth of 300 m, it was abundant in the southern region (Fig. 8). The immature stage of this species exhibited more active migration than the mature stage and migrated to deeper layers (> 300 m) only during night time (Fig. 7). *S. ferox* showed a similar trend, with a relatively higher migration tendency shown by immature individuals. **(Preferred position of Fig. 8)**

### **3.6 PCA, Multidimensional scaling and diversity indices**

PCA indicated a positive relationship of chaetognath abundance with both dissolved oxygen and temperature. The groups between the depth strata found in the multidimensional scaling analysis based on the distribution of temperature, salinity, dissolved oxygen and chaetognath abundance, showed a high degree of similarity between the last two plots (Fig. 9). Species diversity ( $H'$ ), species evenness ( $J'$ ) and species richness ( $d$ ) were high in the TC layer ( $2 \pm 0.3$ ,  $0.9 \pm 0.02$  and  $7.1 \pm 2.6$ , respectively) (Fig. 10a, b, c).

### **3.7 Relationship of chaetognaths with copepods**

The Pearson correlation coefficient ( $r$ ) calculated based on the abundance of chaetognaths and copepods at different stations and depth zones, revealed a significant positive correlation ( $P < 0.01$ ,  $r = 0.79$ ) between the two groups (Fig. 11).

## **4. DISCUSSION**

The results of the present study indicated a strong impact of ODW on the vertical distribution limit of chaetognath species. The profound OMZ ( $< 0.5 \text{ ml l}^{-1}$ ) and ODW ( $< 0.2 \text{ ml l}^{-1}$ ) in a major part of the water column below the subsurface layer indicate the existence of a pronounced oxygen-deficient water mass in the NEAS. The observed north – south difference in the thickness of the ODW layer ( $15 < 17 < 19 < 21^\circ\text{N}$ ) supports the earlier hypothesis that a more pronounced north – south gradation prevails in oceanographic parameters compared to along an east – west axis (Wyrтки, 1971; Naqvi, 2008). A similar



trend of north – south gradation in the temperature profile resulted in deepening of thermocline layer ( $217 \pm 29$  and  $297 \pm 12$  m at  $15^\circ$  and  $21^\circ$  N, respectively) from south to north. Thus, the system experiences different physical characteristics in the northern and southern parts of the NEAS. In the northern region, the thick ODW extending between depths of 200 - 800 m might be responsible for the zooplankton groups congregating mainly in the upper layers. The relatively higher abundance of copepods and chaetognaths in the upper layers ( $< 300$  m) of the northern NEAS indicates their preference for oxygenated water (Fig. 3 a, b). The higher abundance of chaetognaths [ $16217$  ind. ( $1000$  m) $^{-3}$ ] observed at MLD in the northern region compared to the average abundance ( $< 4500$  ind. ( $1000$  m) $^{-3}$ ] recorded in the upper layer of the entire Indian Ocean (Fig.2 in Nair, 1978) also supports this preference. Compared to the northern region, the relatively higher abundance of chaetognaths in deeper layers in the southern region might have resulted from the absence of the ODW in the majority of the deeper layers ( $> 400$  and  $775$  m along  $15^\circ$ N and  $17^\circ$  N, respectively). In contrast to the characteristics observed in the northern NEAS, a relatively higher abundance of chaetognaths was observed at depths of 300 – 500 m at station 19, and this was mostly contributed by the immature stages of *K. pacifica*, *S. enflata* and *S. robusta*. Additionally, at this station, the chaetognath abundance in the TC layer was not only high but also was mainly contributed by the immature population. The higher abundance in the 300 – 500 m layer might have resulted from the downward migration of a portion of the population to avoid competition. The pocket-like zone (marked in Fig. 2d) around station 19 at depths of 200 – 500 m, exhibiting a relatively higher DO value ( $> 0.25$  ml  $l^{-1}$ ) than the surrounding region ( $< 0.2$  ml  $l^{-1}$ ), might also have been playing a crucial role in sustaining high chaetognath abundance at depths of 300 – 500 m at this station. A similar observation of higher zooplankton abundance at the lower interface of the OMZ in conjunction with an increased DO concentration (0.05 to 0.1 ml  $l^{-1}$ ) in the eastern tropical Pacific Ocean (Wishner et al., 1995) also corroborates our view.

The significant correlation observed between copepod and chaetognath abundance ( $P < 0.01$ ) provides support for the role of copepods in sustaining the population of this important carnivorous planktonic group, as observed in both OMZ and non-OMZ regions of different parts of the world oceans (Øresland, 2000; Kehayias, 2003; Giesecke and Gonzalez, 2004). Although the gut content of chaetognaths was not analysed in the present study to establish the prey-predator relationship, the magnitude of the regression equation and the least squares line (Fig. 11) indicates the trophic relationship that exists between these two major prey and predator groups. The higher abundance of chaetognaths together with copepods in the upper three layers of the northern NEAS provides further

evidence of the role of this trophic relationship. Compared to deeper waters, the relatively high percentage composition of mature chaetognaths (mainly epipelagic) in upper layers suggests that mature stages of some species are more sensitive to the ODW layer than the immature stages. However, this observation contrasts with the earlier observations made by Zo (1973), who found higher abundance of immature *S. elegans* in upper layers of relatively shallow oxygenated basin areas, and made by Johnson and Terazaki (2004), who reported a higher incidence of immature individuals of deeper water species, such as *S. gazellae*, *S. marri* and *E. hamata*, in a relatively oxygenated ( $> 3 \text{ ml l}^{-1}$ ) Australian sector of the Antarctic Ocean. Wishner et al. (2000) indicated that the oxygen demands of mature organisms are higher than those of immature individuals due to egg and sperm production and, thus, might lead to avoidance of oxygen-depleted water. The higher abundance of mature populations of the epipelagic species *K. subtilis*, *S. ferox* and *S. regularis* at MLD found in the present study (Fig. 7) also provides support for the view described above. We observed the presence of a thick ODW below the subsurface layer, and immature individuals showed a relatively stronger and more active migration tendency than mature individuals (Fig. 7). However this observation contradicts the findings of Russell (1931), who observed a greater migration tendency in adults of *S. elegans* in a relatively oxygenated Plymouth area. It appears that because matured individuals are more sensitive, they are reluctant to migrate into oxygen-deficient waters of deeper layers. The occurrence of only immature stages of epipelagic species, such as *S. regularis*, *S. robusta* and *K. pacifica*, at depths of 500 – 1000 m also corroborates this view.

The existence of the ODW appears to have a strong impact on the distributional limit of the four groups of chaetognaths recognised based on their vertical distribution pattern in the study region. Among the species abundant in surface layers, *S. bedfordii*, *S. neglecta* and *S. pulchra* have generally been reported in the upper 200 m of the water column (Nair, 1978), which is in agreement with the present observations. However, species such as *P. draco*, *S. bipunctata* and *S. minima* that have previously been recorded up to depths of 500 m in the non-OMZ region of the southern Arabian Sea and other parts of the Indian Ocean (Nair, 1978) were found to be restricted to the upper 300 m of the water column in the present study, thus indicating the possibility of avoiding the oxygen-deficient waters below. Similarly, the mesopelagic species *S. planktonis*, which has previously been recorded as mesopelagic in the non-OMZ southern part of the Indian Ocean (Nair and Madhupratap, 1984) and off the coast of Chile (Ulloa et al., 2000), was found to be confined to the thermocline layer, thereby avoiding the oxygen-depleted mid-depth waters. **(Preferred position of Table 1)**

Bathypelagic species, such as *S. maxima* and all three species of *Eukrohnia*, were restricted mainly to deeper waters (> 500 m) and were dominated by immature stages, as observed by Duró and Gili (2001) for the Weddell Sea. A likely reason for such a scenario may be that matured individuals of these species are distributed in relatively highly oxygenated waters in deeper layers, below the present depth of sampling. Their abundance only in the southern NEAS (except *E. bathypelagica*) also provides support for their preference for oxygenated waters.

Considering the third group, the presence of *S. enflata* and *S. decipiens* throughout the water column might have resulted from the vertical migration of a part of their population. *S. enflata* is a cosmopolitan species and is considered epipelagic, although it has been found in deeper layers (Alvarino, 1965; Furnestin, 1979). Vertical migration of *S. enflata* has been reported in different parts of the world ocean, mostly within upper layers (Pearre, 1974; Pierrot-Bults, 1982), whereas the depth range found in the present study was relatively greater. The difference in the thickness of ODW appears to play a key role in influencing the variation in the abundance and vertical distribution of *S. enflata* in the northern and southern NEAS. In the southern region, where the ODW was thinner, this species was abundant throughout the water column, whereas in the northern region, where the thickness of the ODW was greater, its abundance was restricted to the upper layers. This is also consistent with the observations made by Giesecke and González (2004) in Mejillones Bay, where *S. enflata* was found to be the dominant species but was abundant only above the OMZ layer, where the dissolved oxygen concentration was >1 ml l<sup>-1</sup>. The relatively similar patterns of abundance shown by most species in this group strongly indicate to the effect of ODW on their vertical distribution.

Among the fourth group, *S. tasmanica*, which has previously been recorded mostly at depths of 200 – 1000 m in the non-OMZ region of the central and southern Indian Ocean (Pierrot-Bults and Nair, 1991), showed higher abundance in the upper two layers in the present study (Fig. 7), suggesting that this species might be avoiding the oxygen-deficient waters at deeper layers. Similarly, *S. hexaptera*, which has been reported to occur mostly in the 200 – 500 m depth stratum in the non-OMZ region of the southern Arabian Sea (Nair, 1978), was found in greater abundance in the upper two layers in the NEAS in the present study (Fig. 7). Both of these examples suggest that these species have a tendency to avoid the ODW layer. The presence of mature individuals of the latter species both in upper (MLD) and deeper (500 – 1000 m) layers shows that it is an actively migrating species, but the low oxygen content in the middle layer might be hampering its abundance at mid-depths. This is also supported by earlier reports on the restricted vertical migration of zooplankton groups between the upper and lower interface

of the OMZ in the tropical Pacific Ocean (Wishner et al., 1995). The relatively higher abundance of *S. hexaptera*, *S. regularis* and *S. ferox* in upper layers of the northern NEAS and below a depth of 300 m in the southern NEAS (Fig. 8), provides further evidence that these species exhibit a tendency to avoid the thick ODW in the northern NEAS. **(Preferred position of Fig. 9)**

The PCA biplot indicates a tendency for higher chaetognath abundance associated with high dissolved oxygen and water temperatures, whereas the MDS plot shows a close similarity of abundance only to dissolved oxygen, thus highlighting the role of oxygen in controlling chaetognath abundance (Fig. 9). The depth zones that were found in similar groups in both MDS plots were the upper three layers, where dissolved oxygen values were relatively high, thus supporting the congregated abundance in these layers. The group formed between the deeper two layers, where the ODW was more prominent, further supporting the influence of dissolved oxygen in controlling the vertical distribution of these species. The higher ratio of chaetognath and copepod abundance in the relatively oxygenated upper layers compared to the oxygen-deficient deeper layers provides additional evidences that the presence of dissolved oxygen rather than the abundance of copepods plays a more decisive role in controlling the vertical distribution of chaetognaths. The insignificant relationship ( $P > 0.05$ ) observed between the day and night abundance of chaetognaths might have resulted from the restricted vertical migration of some species in the presence of the thick ODW layer. Similar observations have been made by Fernandes and Ramaiah (2008) with respect to the mesozooplankton biomass and density pattern in the OMZ of the Bay of Bengal. **(Preferred position of Fig. 10)** The observed greater species richness and diversity in the thermocline layer suggest that this niche is suitable for many chaetognath species. Similar reports of maximum species diversity existing at 125 – 250 m water depths in the Indian Ocean (Nair, 1978) and maximum zooplankton biomass and density being found in the TC layer in the Pacific Ocean (Saltzman and Wishner, 1997) are also consistent with the present observations. As suggested by Pierrot-Bults and Nair (1991), the mixing of mesopelagic and epipelagic species in this layer might contribute to the high species richness and diversity in this region (Fig. 10). The existence of the intense ODW layer has also been playing a prominent role in this by controlling the vertical migration of the investigated species towards deeper layers. The high evenness in distribution ( $> 0.6$ ) throughout the water column indicates that strong oxygen deficiency plays a key role in influencing the distribution of most of these species, as none of them dominated at any station. **(Preferred position of Fig. 11)**

## 5. CONCLUSIONS

The present study indicates the impact of oxygen deficiency on the vertical distribution limits of chaetognath species in a natural oxygen-deficient system in the NEAS. Physical factors, such as salinity and temperature, are also responsible for the formation of two physically distinct characteristics in the northern and southern regions of the NEAS, although they had a negligible effect in influencing the distribution limits of chaetognath species. The major phenomenon that has a limiting effect on the vertical migration of chaetognaths in the NEAS can be concluded to be species-specific sensitivity to oxygen-depleted water. The difference in the ODW thickness in the northern and southern regions affected the distribution of copepods and chaetognaths, resulting in relatively higher abundance of both groups in the upper layers of the northern region. The significant relationship observed between copepods (major prey) and chaetognaths (predator) highlights the active trophic relationship existing in this oxygen-deficient system. The results of the present study, which emphasise the effect of ODW on chaetognaths, a major invertebrate predator group, will be useful in designing detailed research focusing on the effect of ODW on other important zooplankton groups.

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## List of Tables:

Table 1. Average abundance of chaetognath species [ind. (1000 m)<sup>-3</sup>] at different depth strata

Species	MLD	TC	BT - 300 m	300 - 500 m	500 - 1000 m
<i>Pterosagitta draco</i>	139	27	-	-	-
<i>Krohnia pacifica</i>	257	270	6	6	1
<i>K. subtilis</i>	1047	369	86	3	1
<i>Eukrohnia bathypelagica</i>	-	-	-	-	1
<i>E. minuta</i>	-	-	11	-	2
<i>E. fowleri</i>	-	-	-	-	3
<i>Sagitta bipunctata</i>	357	215	-	-	-
<i>S. bedfordii</i>	402	169	54	-	-
<i>S. decipiens</i>	142	471	65	7	3
<i>S. enflata</i>	4704	991	417	11	1
<i>S. ferox</i>	190	132	-	3	-
<i>S. hexaptera</i>	701	148	-	1	1
<i>S. maxima</i>	-	-	-	-	3
<i>S. minima</i>	48	45	11	-	-
<i>S. neglecta</i>	1718	494	91	-	-
<i>S. regularis</i>	2415	391	-	-	1
<i>S. robusta</i>	788	458	55	5	1
<i>S. pacifica</i>	148	238	-	1	-
<i>S. planktonis</i>	-	9	-	-	-
<i>S. pulchra</i>	35	22	-	-	-
<i>S. tasmanica</i>	128	30	-	1	-
<i>S. zetesios</i>	27	-	66	-	2

**List of Figures:**

Figure. 1. Sampling locations in the northeast Arabian Sea. The circles denote diurnal stations. Filled squares denote day sampling and filled rectangle denote night sampling in regular stations

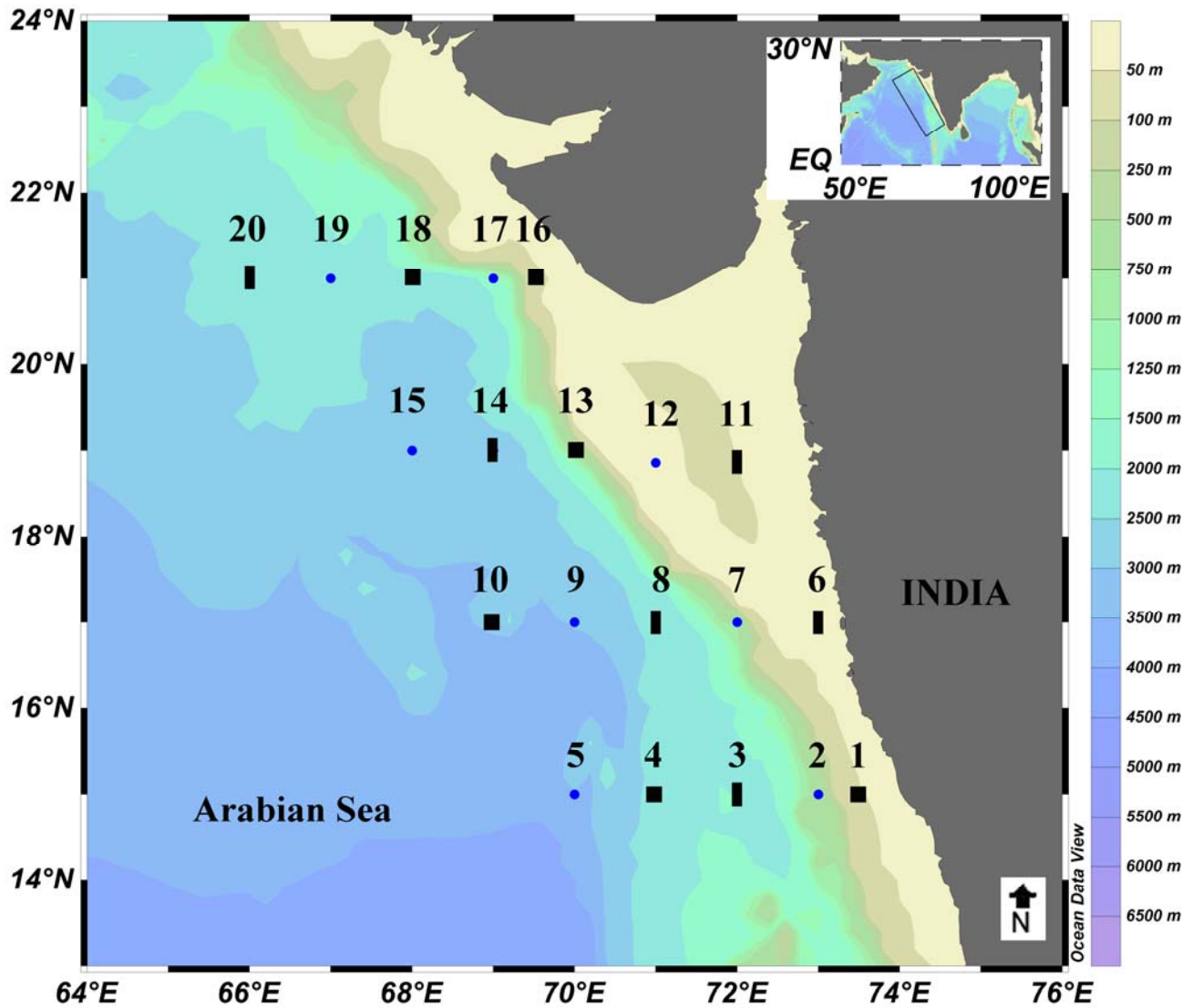


Figure. 2. Distribution of [a] Temperature ( $^{\circ}\text{C}$ ), [b] salinity and [c] potential density ( $\sigma_t$ ) [d] dissolved oxygen ( $\text{ml l}^{-1}$ ) in the upper 1000 m of the northeastern Arabian Sea. Station locations are indicated by the arrows

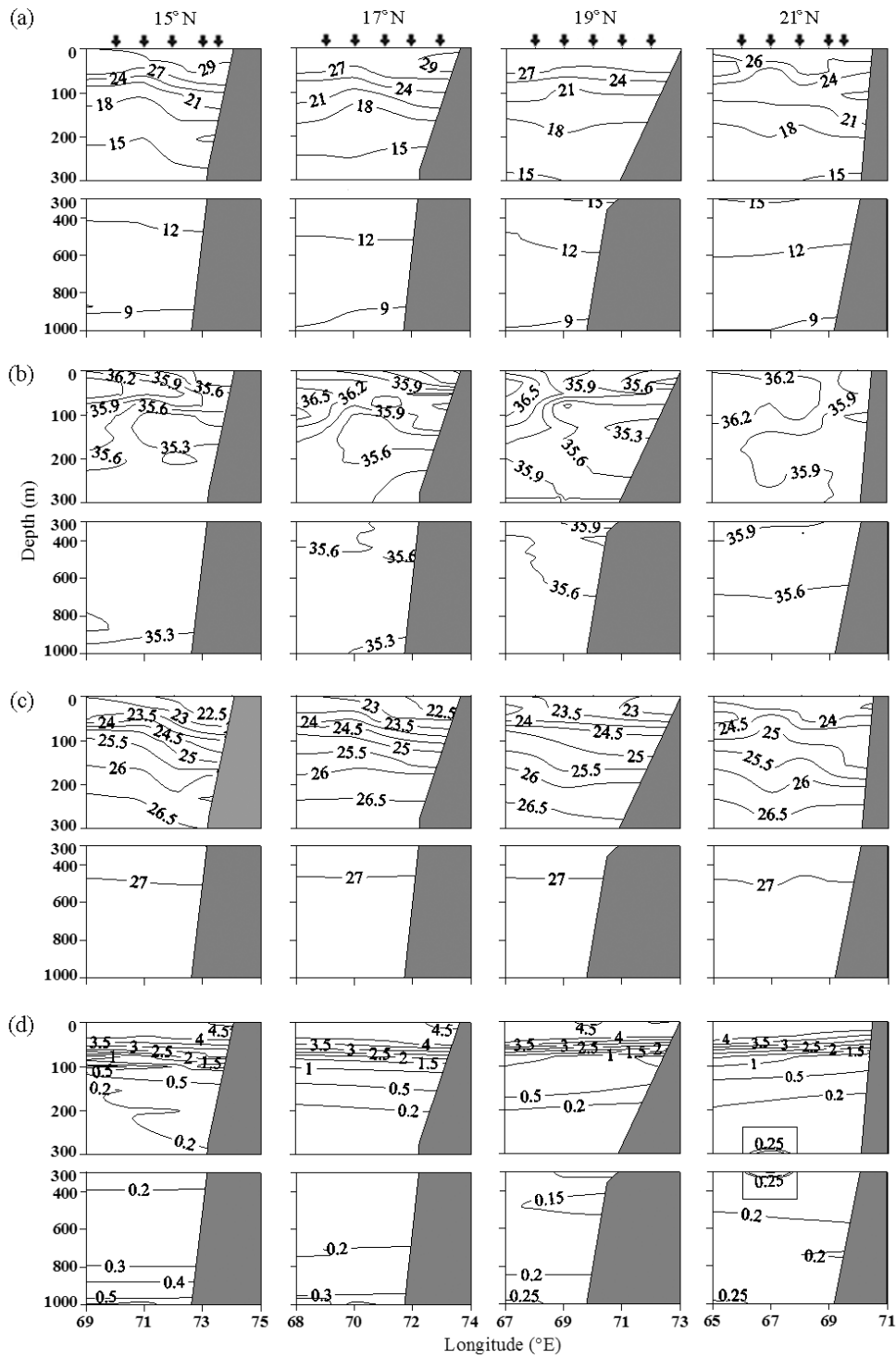


Figure. 3. Abundance [ind. (1000 m)<sup>-3</sup>] of [a] copepods and [b] chaetognaths along different depth at northeastern Arabian Sea (MLD – Mixed layer depth, TC – Thermocline, BT – Base of thermocline)

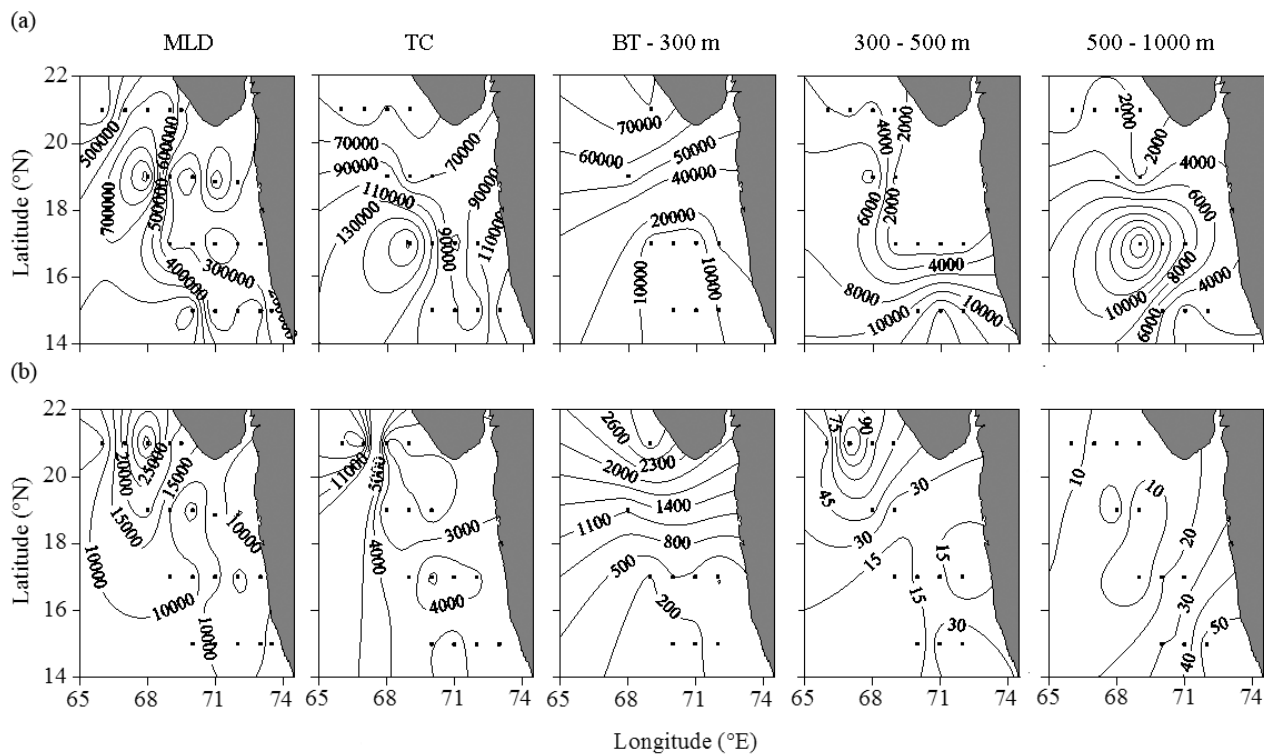


Figure 4. Depth wise percentage composition of different maturity stages of chaetognaths (MLD – Mixed layer depth, TC – Thermocline, BT – Base of thermocline).

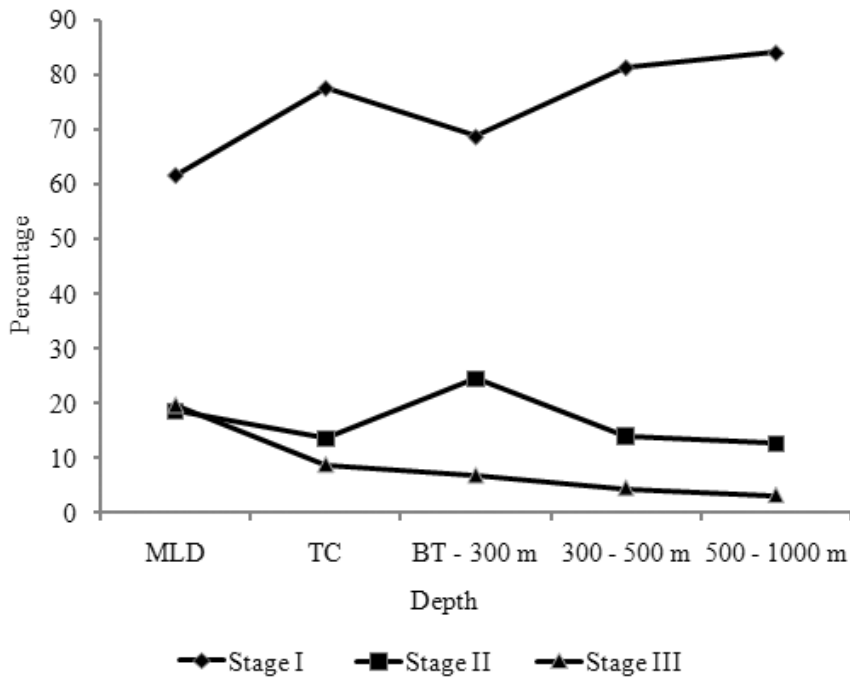


Figure 5. Relative abundance (%) of each chaetognath species to total chaetognaths in each depth layer sampled (MLD – Mixed layer depth, TC – Thermocline, BT – Base of thermocline)

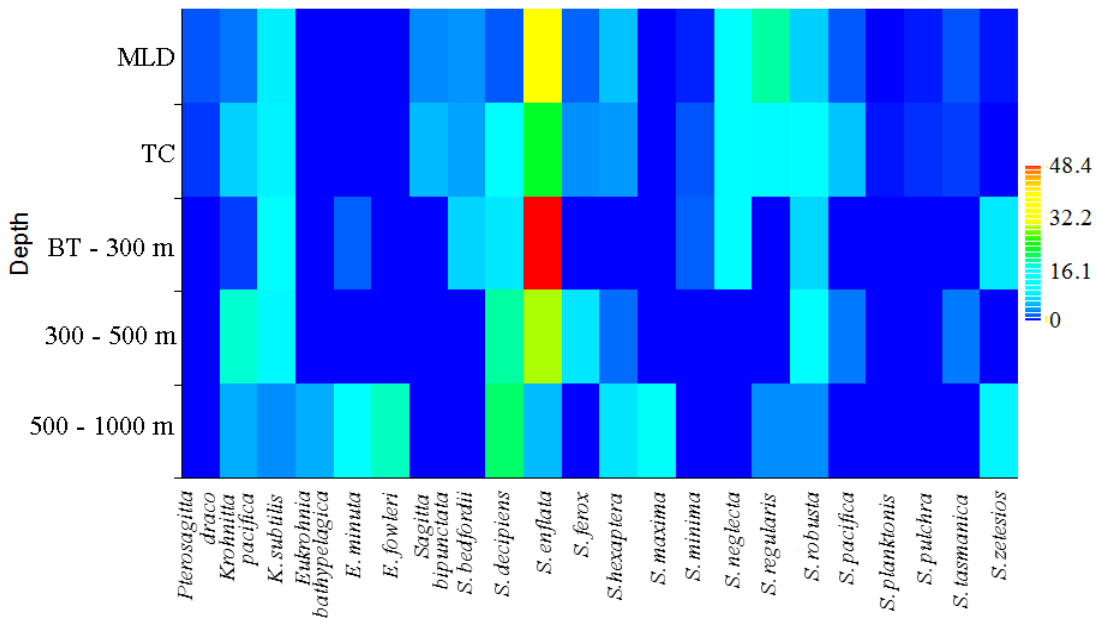


Figure. 6. Maturity stage wise percentage composition of different chaetognath species at [a] Mixed layer depth, [b] Thermocline, [c] Base of thermocline – 300 m, [d] 300 – 500 m and [e] 500 – 1000 m

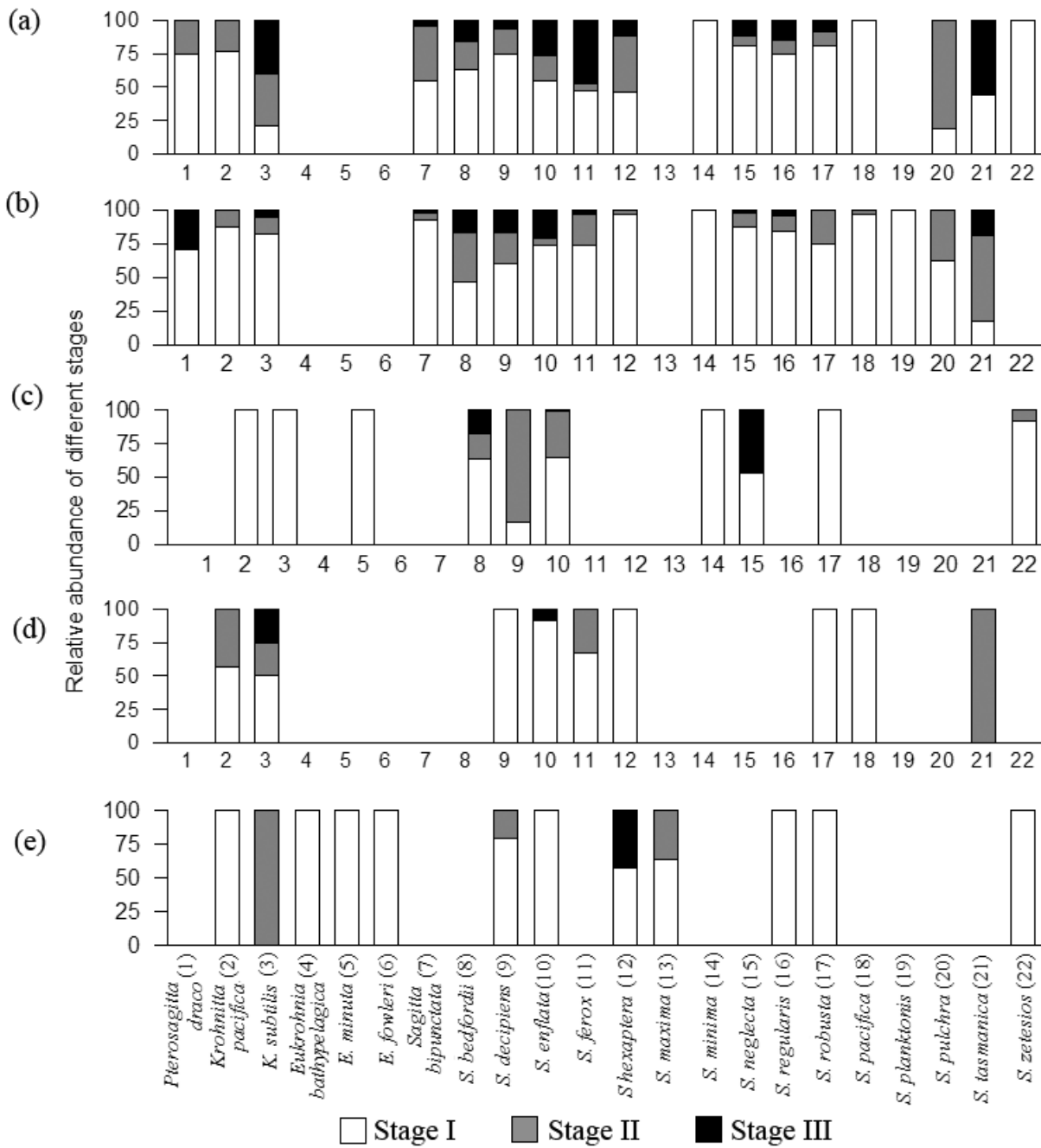


Figure. 7. Vertical distribution of different maturity stages of chaetognath species at different depth layers during day (grey) and night (black) (MLD – Mixed layer depth, TC – Thermocline, BT – Base of thermocline)

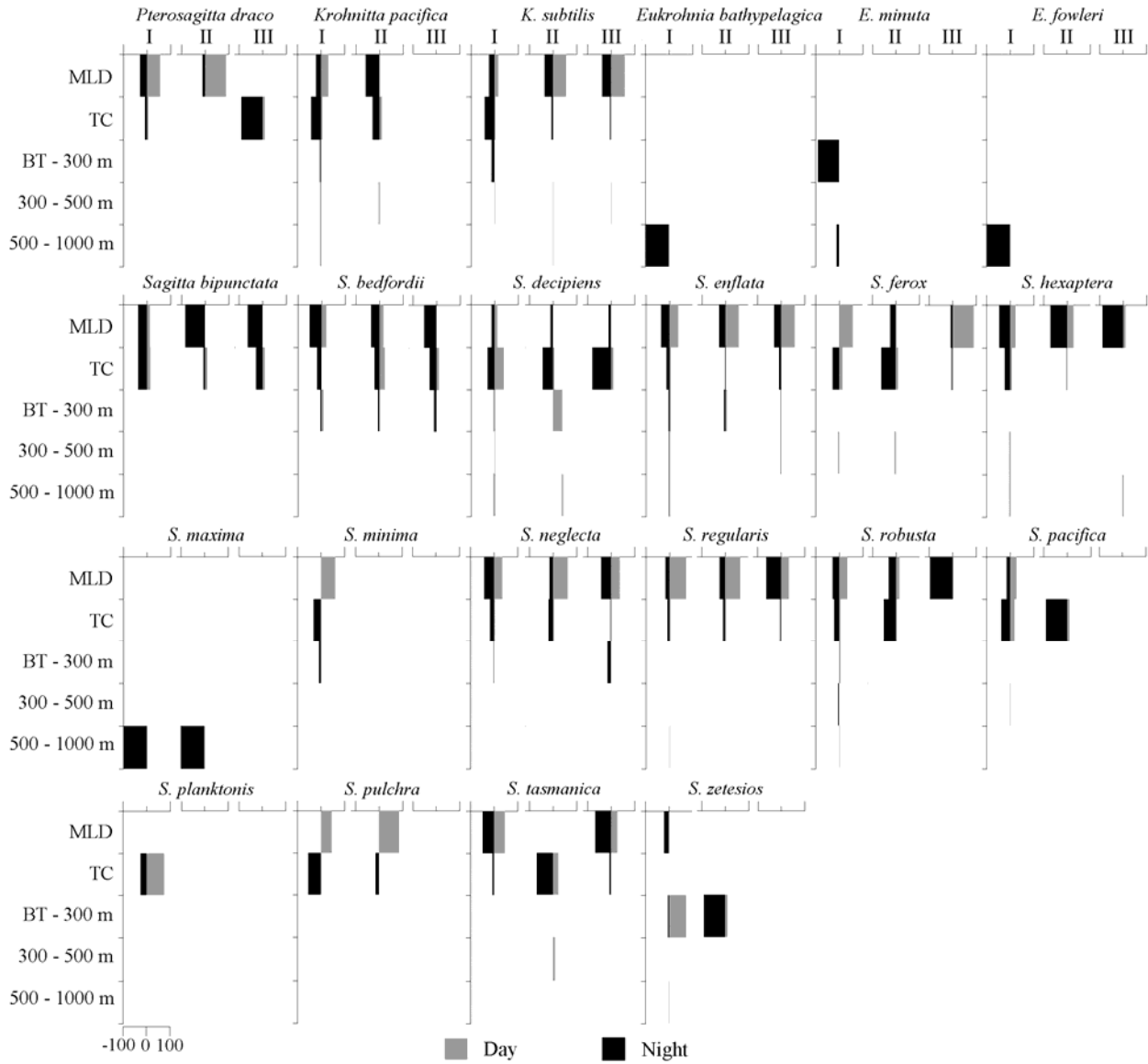




Figure. 8. Abundance of different chaetognath species at northern and southern part of the northeastern Arabian Sea along [a] Mixed layer depth, [b] Thermocline, [c] Base of thermocline – 300 m, [d] 300 – 500 m and [e] 500 – 1000 m

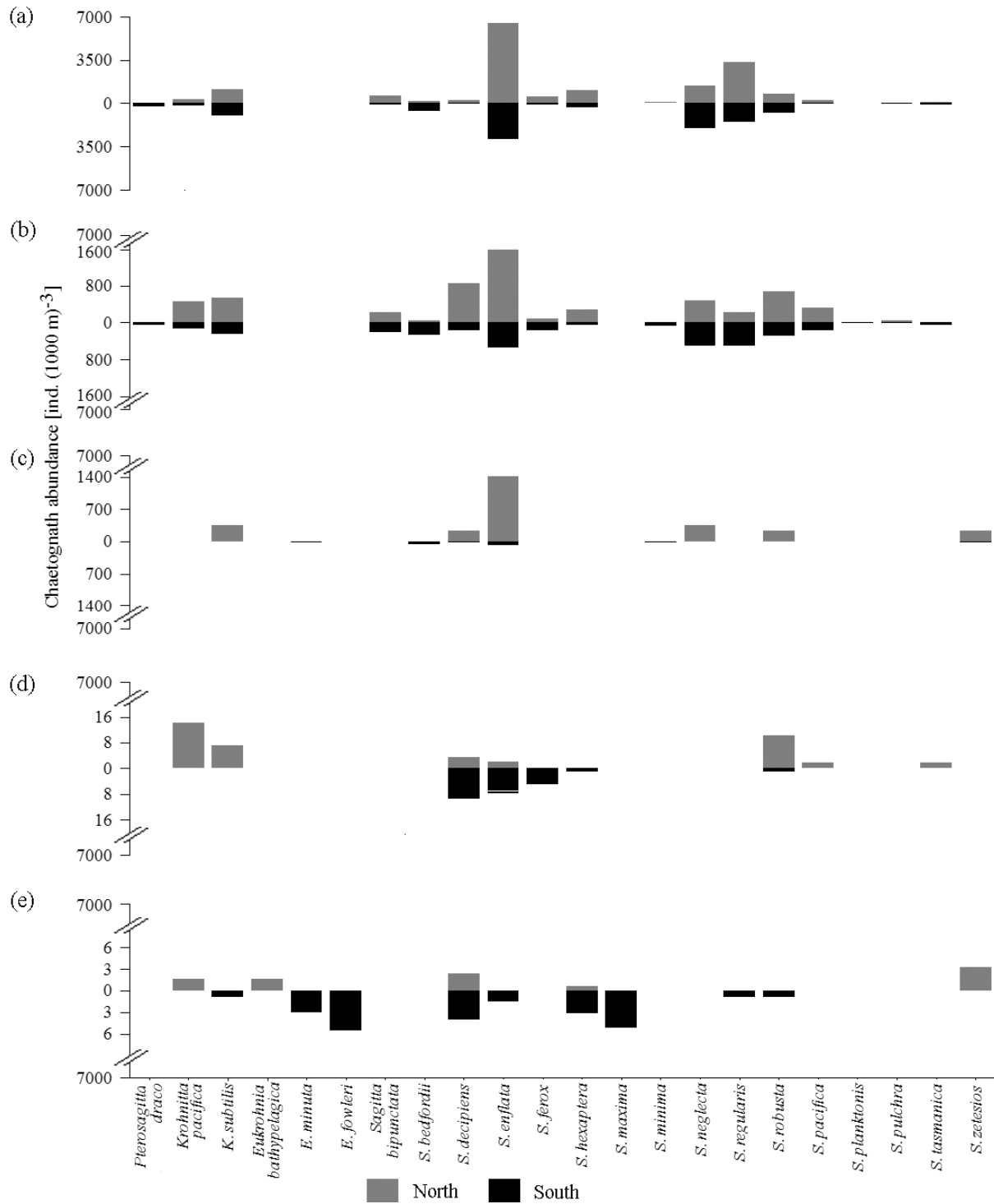


Figure. 9. MDS analyses showing similarity between different depth strata based on the biotic and abiotic parameters and PCA biplot showing the internal relationships of those parameters.

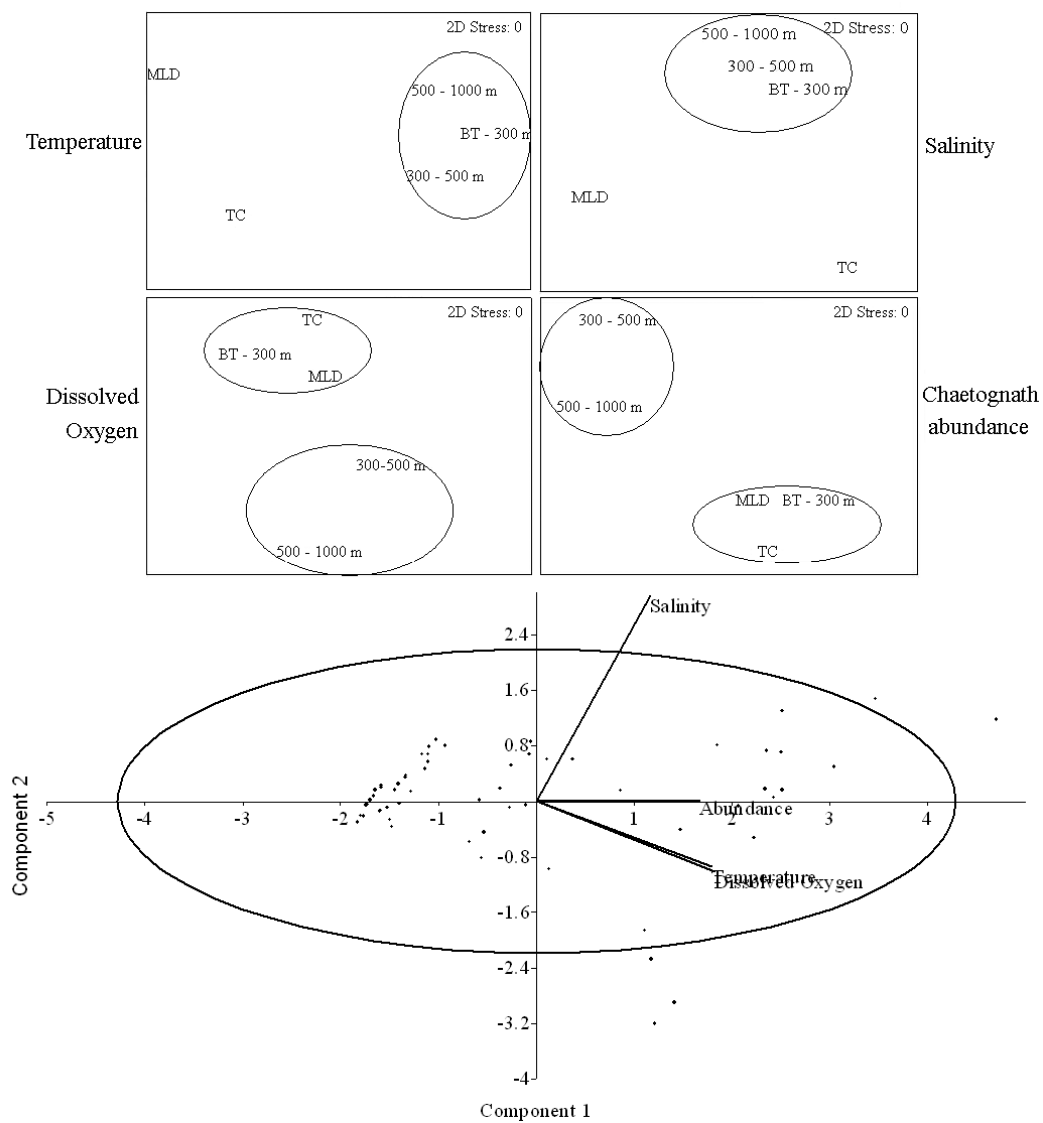


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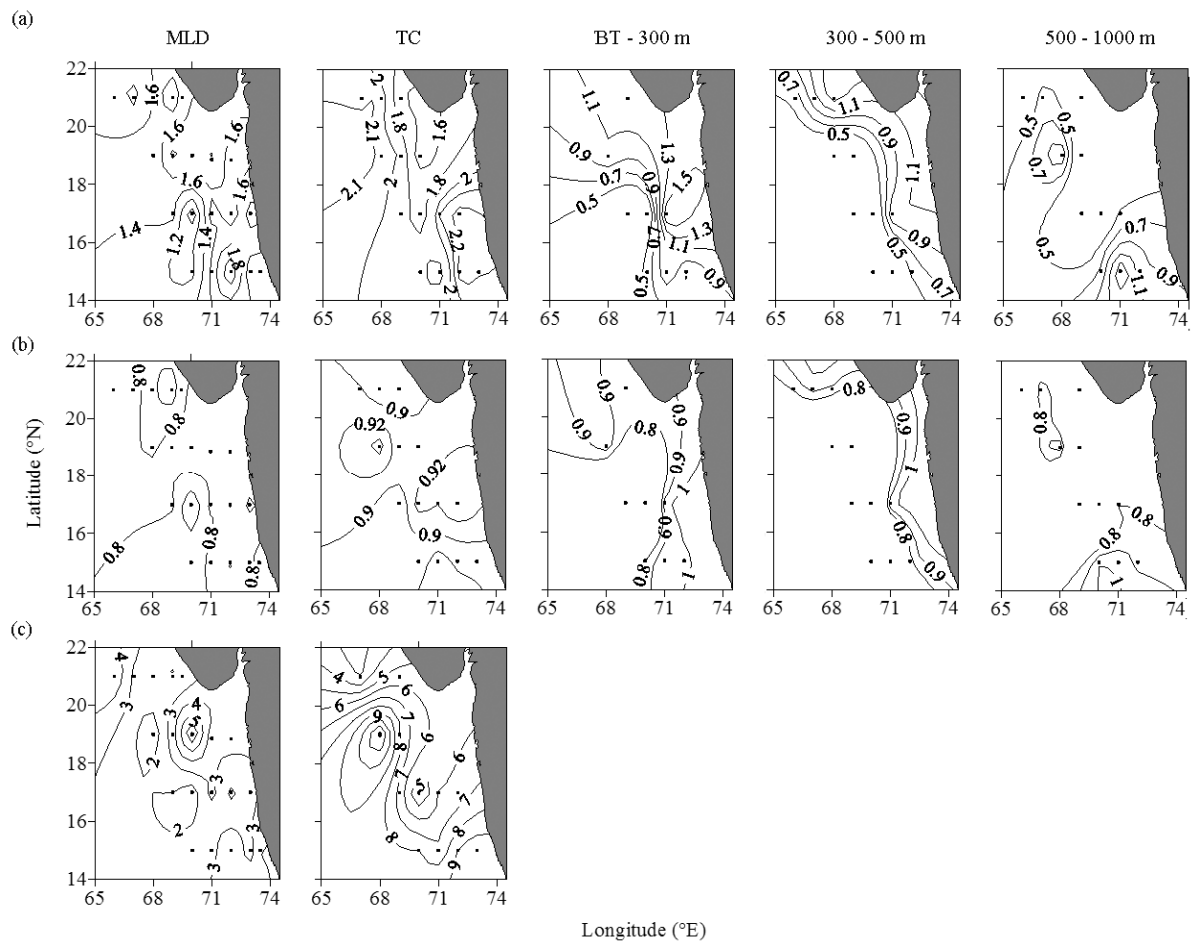


Figure. 11. Relationship between copepods and chaetognaths. The regression equation and the 99% confidence band are shown.

