

Influence of upwelling on distribution of chaetognath (zooplankton) in the oxygen deficient zone of the eastern Arabian Sea

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Abstract

The study addresses the coupled spatial scales in the physico-chemical variables and chaetognaths in the upwelling system of the eastern Arabian Sea during the 2005 summer monsoon. We studied the taxon between 0 and 1,000 m depth along seven zonal sections between 8° and 19° N and especially observed the vertical stratification of the animals. In the upwelling regions, higher chaetognath abundance was observed resulted by the local population growth and advection of the upwelling preferred epipelagic species. Abundance weight (Aw) value further helped to understand the mode of distribution of the chaetognath community around the upwelling locations. The variation in the depth-weighted average values of different species between the upwelling and non-upwelling sites helped to identify the dissimilarity in their coupling with the abiotic components. As this eastern boundary current region further draws research interest as one of the major natural oxygen deficient system in the global ocean, the role of this hypoxia was shelved separately from the influence of upwelling in the heterogeneity of distribution of chaetognaths. In our study, two mesopelagic species *Eukrohnia fowleri* and *E. minuta* were identified as the indicator species of this upwelling process. Our observation suggests that the temporal physical event (upwelling) plays a decisive role in the heterogeneity of the spatial abundance, community composition and diversity of chaetognaths in this least studied eastern boundary current system.

Keywords (5 Nos): Chaetognaths; upwelling; oxygen minimum zone; indicator species; eastern Arabian Sea.

1. Introduction

The eastern boundary current systems (EBCs) in the oceans are well known for their close association with upwelling, and plays a vital role in the spatial variability of physico-chemical variables and biological components (Escribano and Morales, 2012; Hidalgo et al., 2012). Upwelling regions have immense global significance (Peterson et al., 1988; Bostford et al., 2003) as they form biologically the richest parts of the oceans and in turn produce about half of the world's fish supply (Ryther, 1969). The eastern Arabian Sea (EAS) is one of the major EBCs in the Indian Ocean, which experiences intense upwelling induced by the westerly-northwesterly monsoonal winds during summer monsoon (Banse, 1959; Mathew, 1983; Mohan Kumar et al., 1995; Smitha et al., 2008). This temporal phenomenon has persisted for millions of years (Sirocko et al., 1991) and has a strong impact on the biological production of the Arabian Sea (Curry et al., 1992; Rostec et al., 1997). Zooplankton plays a pivotal role in the pelagic food web as they transfer the energy from primary producers to higher trophic levels (Banse, 1995). Chaetognaths, a major carnivorous taxon, form an important component of the food web in the upwelling regions (Giesecke and González, 2004; Ulloa et al., 2004) and often are taken as valuable indicators of different hydrographic conditions as well as water masses (Bieri, 1959; Sund and Renner, 1959; Nagai et al., 2006). Recently, the variability in the abiotic and biotic components in the EBCs of Pacific and Atlantic Oceans has been an important area of study (Cornejo and Farías, 2012; Correa-Ramírez et al., 2012; Morales and Anabalón, 2012; Roura et al., 2012). Among zooplankton, several comprehensive studies have been carried out on the copepod community of the upwelling systems (Boyd et al., 1980; Hidalgo and Escribano, 2007; Hidalgo et al., 2010, 2012) and groups like euphausiid, fish and decapod larvae have also received wide attention (Lindsey and Batchelder, 2011; Riquelme-Bugueño et al., 2012; Parada et al., 2012; Soto-Mendoza et al., 2012; Yannicelli et al., 2012), whereas studies on chaetognaths are scanty (Giesecke and González, 2004; Ulloa et al., 2004). In EBCs of the Indian Ocean, earlier studies on chaetognath community were mostly limited to the geographic (Nair, 1972; Nair and Rao, 1973) and vertical distribution (Nair, 1978; Balamurugan et al., 2011; Kusum et al., 2011). Earlier, Srinivasan (1974) studied the chaetognath community of this upwelling region and suggested the possibility of using *Sagitta decipiens* as an indicator of upwelling process from the total 14 species identified. Though the work gave an account of the distributional pattern of chaetognaths and their preferences between shelf and oceanic region, the coupling between chaetognaths and the physico-chemical variables associated with upwelling process was mostly overlooked. Later, Nair (1977) while describing the chaetognath community of the Indian Ocean mentioned the association of mesopelagic

species *Eukrohnia fowleri* with upwelling event. Though these earlier observations gave an account of the chaetognath community in this region, the modulating processes for the heterogeneity in their distribution remained poorly understood.

The EAS also forms an area of immense ecological interest as one of the prominent natural oxygen deficient systems in the global ocean (Vinogradov and Voronina, 1962; Morrison et al., 1999; Naqvi et al., 2006, 2009). The northern part of EAS in particular has greater significance as the oxygen minimum zone (OMZ, $< 0.5 \text{ mL L}^{-1}$) of this region is the thickest (~1 km) among the world oceans (Naqvi et al., 2009). The ecological impact of the OMZ is the shrinking of the available habitats, and only a few species can tolerate the extreme oxygen deficient condition (Prince and Goodyear, 2006; Bertrand et al., 2010; Kusum et al., 2011). Thus to have a better understanding on the ecology of this dynamic system, the need to understand the critical role of the oxygen deficient waters along with the influence of upwelling on zooplankton distribution is a prerequisite.

In the present study, our aim was to identify the active upwelling zones and to assess the influence of this physical process on the abundance and diversity pattern of chaetognath community in this oxygen deficient system. We intended to identify this process along both surface and subsurface layers to verify whether any fine scale coupling occur in the biotic and abiotic components of this environment. As the earlier studies had dissimilar views on the indicator species in this upwelling region (Srinivasan, 1974; Nair 1977), an attempt was also made to reevaluate this aspect. The present study depicting the responses of an important zooplankton taxon to the upwelling phenomenon will provide vital information regarding the ecology and dynamics of this important upwelling zone in the Indian Ocean.

2. METHOD

2.1. Sampling

Sampling locations in the EAS are shown in Fig. 1. Starting from near the coast, sampling was carried out during 26 May – 24 June 2005 (summer monsoon) on board FORV *Sagar Sampada* (cruise 235) on seven zonal transects along 8° N to 19° N (Fig. 1). Stations were spaced by 1° of longitude. For diurnal observation, one coastal and one offshore station were monitored along each transect (only one diurnal station at 10°, 15° and 19° N) and the sampling was done at 6-hour intervals for 24-hours. The day and night was determined based on the local times of sunrise and sunset during the cruise. **(Preferred position of Fig. 1)**

Vertical profiles of temperature and salinity were obtained by a SBE Seabird 911 plus CTD. It was operated from the sea surface to close to the bottom in coastal stations, and down to 1000 m in offshore stations. For expressing the salinity value, the practical salinity scale was used which has no physical unit (UNESCO, 1985). The potential density (σ_t) was computed from the temperature, salinity and pressure obtained from the CTD. To estimate dissolved oxygen (DO) water samples were collected using a CTD Rosette sampler, fitted with 1.8 L Niskin bottles, from standard depths down to 1000 m (surface, 10, 20, 30, 50, 75, 100, 150, 200, 300, 500, 750, 1000 m), and were analyzed using Winkler's method (Grasshoff, 1983) with visual endpoint detection.

A multiple plankton net (Hydrobios, Germany) with a mouth area of 0.25 m² and a mesh area of 200 μ M, with an electronic depth sensor was operated vertically to sample mesozooplankton. As each net is opened and closed independently, contamination is apt to be negligible (Weikert and John, 1981). One disadvantage of similar net system i.e. MOCNESS is that the slow speed of vertical hauling can lead to avoidance of some of the larger zooplankton (www.whoi.edu/instruments/viewInstrument.do?id=10008). Hence, to avoid this problem we maintained a towing speed of 1 m. sec⁻¹. We sampled at five depth strata: mixed layer (MLD), top to base of thermocline (TC), base of thermocline (BT) to 300 m, 300–500 m and 500–1000 m based on temperature and density characteristics (see Table 1). MLD was fixed as the depth at which a temperature decrease of 0.5°C occurred from the sea surface temperature, and BT was taken as the depth where temperature fell to 15°C. Chaetognaths were counted by species in the whole sample or from an aliquot (50%) using a Folsom splitter. The volume strained was figured from the distance towed (m) \times 0.25 m², and the abundance expressed as ind / 1000 m³. To have a better understanding on the influence of upwelling on chaetognaths, the upwelling regions were categorized as i.e. i) surface upwelling site, where deep water had been uplifted into the mixed layer, ii) upper subsurface upwelling site, where upwelling was prominent in TC layer and iii) lower subsurface upwelling site, where upwelling was most evident at BT–300 m layer. **(Preferred position of Table 1)**

2.2 Statistical analysis

Multivariate statistics, principal components analysis (PCA) was carried out for the abiotic (physicochemical variables) and biotic component (chaetognath abundance) as it helped in the reduction and interpretation of large multivariate data sets with some underlying linear structure. For plotting and clustering, the important aspect of this analysis is the simple reduction of the data set to only two most

important components. The mean values of the abiotic parameters for the particular depth stratum at each station were considered for the analysis. As all the variables are measured in different units, they were normalized and analysis was done based on the correlation matrix using the statistical program PAST version 2.02 (Hammer et al., 2001). The biplot was drawn according to the correlation biplot of Legendre and Legendre (1998).

To analyze the difference in the assemblages of chaetognath community in upwelling and non-upwelling zones, the diversity indices such as species diversity (H'), and species evenness (J') were done using PRIMER version 5.2.8 (Clarke and Warwick, 1994). Wilcoxon matched pair test was performed between the datasets of day and night abundance of chaetognath community to estimate the diel variation. Based on the test for the normality distribution (D'Agostino and Pearson omnibus normality test; Result: $P < 0.0001$, non Gaussian distribution), the matched pair test was done as nonparametric, with two tailed P-values and 95% confidence intervals using the Graph Pad Prism (version 5.01). To understand the spatial variability on the vertical scale, one way analysis of variance was carried out on station wise abundance data of each depth strata using the same statistical software. Relative frequency of occurrence of chaetognath at different depths along different transects was expressed using statistical program PAST version 2.02.

To better understand the heterogeneity of the distribution of chaetognath community, we assessed the abundance weight (Aw) at each location for a particular depth stratum as,

$$Aw_{ik} = A_{ik} / \left(\sum_{i=1}^n A_{ik} / n \right)$$

Where Aw_{ik} is the abundance weight of sampling location i at stratum k

A_{ik} is the abundance of sampling location i at stratum k

n is the total number of samplings at stratum k

To check whether significant variation lies in the Aw values of different depth strata, Kruskal-Wallis analysis of variance was performed among the upper three layers. Additionally, a t-test was done between the Aw values of upwelling and non-upwelling sites for upper three depth strata.

In order to understand the preferred depth along the vertical axis of distribution of chaetognaths, depth-weighted averages –DWA (m) were calculated for each species according to Escribano et al. (2009) as,

$$DWA = \left[\sum_{i=1}^n (x_i z_i) \right] / \sum_{i=1}^n x_i$$

Where x_i is the abundance of each chaetognath species in stratum i (ind / m³), z_i is the corresponding mid depth (m) of stratum i and n is the total number of sampled strata.

3. Results

3.1. Physiochemical environment

The northern part (15° - 19° N) of the EAS, exhibited higher sea surface temperature (SST) ($\geq 31^\circ\text{C}$) than the southern part (8° - 13° N $\sim 30^\circ\text{C}$). An uplifting of the isotherm was evident in surface, upper subsurface and lower subsurface layers in four locations denoting clear signatures of upwelling (Fig. 2). The surface upwelling site was observed along 10° N 75.5° E (station 24), where the uplifting of the isotherms (19° to 27° C) was most prominent. In the upper subsurface layer, upwelling signatures were observed along 13° N 72° E (station 16) where the uplifting of isotherms was evident. In the lower subsurface upwelling zone, the up-sloping of the isotherms of $\leq 15^\circ\text{C}$ was prominent along 8° N 75° E (station 31) and 17° N 71° E (station 8). **(Preferred position of Fig. 2)**

The vertical profile of potential density (σ_t) exhibited an increasing trend towards depth (Fig. 3). The occurrence of upwelling identified through temperature profile was further supported by the uplifting of isobars along these locations. **(Preferred position of Fig. 3)**

Sea surface salinity varied between 34.2 and 37 and showed an increasing trend towards the north with lesser gradients (Fig. 4). In the vertical profiles of salinity, the up-sloping of the isohalines in the upwelling sites gave clear indication of the upward movement of the subsurface water towards the surface layer. **(Preferred position of Fig. 4)**

Surface dissolved oxygen values did not show much variation and ranged between 4.7 and 5.7 mL L⁻¹ with an average of 5.1 ± 0.2 mL L⁻¹. A pronounced OMZ layer (< 0.5 mL L⁻¹) was observed in varying thickness along all transects (Fig. 5). At 8° N, the OMZ was less prominent whereas at 10° N it got thicker and extended between 300 m and 400 m. An increase in the thickness of the OMZ layer was evident between 150 – 350 m and 250 – 800 m along 11.5° and 13° N, respectively (Fig. 5). Towards north along 15° N, the OMZ layer further thickened and extended from 140 – 800 m. An acute hypoxic layer (< 0.2 mL L⁻¹) (Kamykowski and Zentara, 1990; Helly and Levin, 2004), termed as oxygen depleted water (ODW) (Naqvi et al., 2009) was observed between 150 – 200 m depth at the location

close to the coast. The 17° N transect experienced a thicker OMZ (150 – 1000 m) and thicker ODW layer (180 – 250 m and 450 – 750 m). The upper OMZ boundary deepened slightly along 19 °N (180 – 1000 m) and the ODW layer was quite thick mainly in the coastal stations (Fig. 5). Thus an increasing tendency in the thickness of OMZ was observed from south to north of the EAS. **(Preferred position of Fig. 5)**

Hence, based on the physical properties, a total of four upwelling sites were observed in this oxygen deficient zone of EAS.

3.2. Relative frequency of occurrence of chaetognath

Relative frequency of occurrence (RFO) profile of chaetognath exhibited a clear difference from south to north transects (Fig. 6). Along 8° N and 10° N, it was 100% throughout the water column whereas along 11.5° N, it reduced to 80% at the 300 – 500 m layer. Along 13°, 15° and 17° N, it was < 100% at all depth strata except at MLD and 500-1000 m layer. The lowest RFO (33%) was recorded at 500 – 1000 m depth along 19° N (Fig. 6). **(Preferred position of Fig. 6)**

3.3. Chaetognath abundance

A vertically stratified distribution was observed with maximum abundance in the MLD and a gradual decrease towards deeper layers. In the MLD, the abundance ranged between 121 – 56600 (ave. 12600 ± 2726) ind / 1000 m³ (Fig 7). MLD of the upwelling site (Station 24 at 10° N) experienced 5.6 times higher abundance than the non-upwelling regions. In TC layer, the abundance ranged between 0 – 10520 (ave. 2960 ± 555) ind / 1000 m³. They were absent at some stations in central and northern transects along 13°, 15° and 17°N. The effect of upwelling on abundance of chaetognaths was clearly evident in this layer also with a 3.9 fold increase compared to non-upwelling regions. In BT – 300 m layer, they were absent at some stations in northern part of EAS and the abundance ranged between 0 - 4465 (ave. 630 ± 225) ind / 1000 m³ (Fig. 7). The influence of upwelling in the lower subsurface layer was apparent with a 12.8 fold higher abundance in the upwelling sites. In both 300 – 500 m and 500 – 1000 m depth layers, most of the stations of southern part exhibited higher abundance compared to the northern part (Fig. 7). **(Preferred position of Fig. 7)**

Figure 8 displays the A_w of different sampling locations in the upper three layers. As abundances of zooplankton can vary in a wide range due to the influence of different temporal and meso-scale processes, A_w will be beneficial in the fine-scale understanding of the relative variation in their spatial

distribution. In MLD, A_w ranged between 0.01 - 4.49 and in TC layer between 0.02 - 3.75. In BT – 300 m layer, this value was between 0.07 and 7.12 (Fig. 8). In general, in all these depth layers higher values were observed in the upwelling sites. Though significant variation was not evident among the A_w values of upper three layers ($P > 0.05$), the variation was significant between the A_w values of upwelling and non-upwelling sites in all three upper depth strata ($P < 0.0001$). **(Preferred position of Fig. 8)**

Day and night collections in the diurnal stations showed no significant variation ($P > 0.05$). Nevertheless, the spatial abundance decreased significantly ($P < 0.001$) with depth. **(Preferred position of Fig. 9)**

3.4. Composition of chaetognath species

We followed the classical taxonomy where the phylum chaetognath is directly divided into genera and species (Alvariño, 1964 a, b; Nair, 1978, 2003; Pierrot-Bults and Nair, 1991; Nagai, 2006). We observed a total of 26 species belonging to 4 genera in the entire water column (0 – 1000 m) (Table 2). The genus *Sagitta* shared 87% of the total population and in different depth strata sampled, contribution of this genus ranged between 63% (500 – 1000 m) and 93% (BT – 300 m) of the respective depth stratum. While the total number of species encountered varied between 10 (500 – 1000 m) to 21 (TC), the number of species belonging to the genus *Sagitta* ranged from 6 (500 – 1000 m) to 16 (TC). Except the upwelling stations, deeper water species of the genus *Eukrohnia* (4 species) were observed only below 300 m depth. The higher abundance in the surface upwelling site (station 24) was contributed by twelve species of which *Sagitta enflata* dominated (25.9%) (Fig. 9). The other abundant species were *S. neglecta* (16.5%), *S. ferox* (15.3%), and *Krohnitta subtilis* (10.8%) (Fig. 9). As it was a diurnal coastal station, it further helped to add information on the temporal variation in species composition of this surface upwelling site. At night, apart from *S. enflata*, the other abundant species were *S. bipunctata*, *S. bedoti*, *S. ferox*, *S. neglecta*, *S. hexaptera*, *S. bedfordii* and *S. robusta* (Fig. 10). During day, the abundance of *S. enflata* decreased, while the opposite was true for *K. subtilis* and *S. ferox*. *S. bipunctata*, *S. bedoti*, *S. bedfordii* and *S. decipiens* were found only during night where as during day they were found in the TC layer (Fig. 10). **(Preferred position of Fig. 10)**

Though a total of 15 species were recorded in the upper subsurface upwelling site, the abundant species were *S. hexaptera*, *S. enflata*, *S. ferox*, *S. decipiens*, *S. neglecta*, *S. pacifica*, *S. regularis* and *K. pacifica* (Fig. 9). The lower subsurface upwelling sites were comprised of total 10 species and among

them *S. ferox*, *S. regularis* and *S. enflata* dominated. The mesopelagic species *E. fowleri* and *E. minuta* shared a lesser percentage of abundance (0.3 – 1.6 %) in lower and upper subsurface upwelling sites.

3.5. Vertical distribution of chaetognath species

Table 2 illustrates the vertical distribution of chaetognath species observed along the upper 1000 m water column. Numerically *S.enflata* dominated the MLD and TC strata sharing 34 and 17% of the total population respectively. In deeper layers also this species contributed moderately to the total population. Below TC layer, *S. decipiens* formed the dominant species contributing 22% (300 – 500 m) to 47% (500 – 1000 m) of the population. *S. hexaptera* was abundant in the MLD and TC layer whereas both *S. regularis* and *S. bedfordii* had higher abundance up to 300 m depth. The epipelagic species *S. bedoti* and *S. minima* were mostly confined in the upper water column up to TC strata while *P. draco*, *K. pacifica*, *K. subtilis* and *S. ferox* were more abundant up to 300 m depth.

3.6. Depth-weighted average

Figure 11 represents the depth weighted average (DWA) of all chaetognath species in both upwelling and non-upwelling sites. The DWA of different chaetognath species showed a wide range from 16 – 750 m. In majority of the species, DWA in upwelling sites had lower value than the non-upwelling sites. In case of mesopelagic species *E. fowleri* and *E. minuta*, a marked difference was observed in the DWA values at the upwelling and non-upwelling sites. **(Preferred position of Fig. 11)**

3.7. Multivariate analysis

The scatter gram in the PCA helped to visualize all the data points plotted in the coordinate system given by the two most important components (Fig. 12). Based on the interrelation of all four variables (abiotic and biotic) in MLD, station 24 was observed to be positioned separately outside the 95% ellipse. Similarly isolated position were also observed for station 16 in TC layer, and for stations 8 and 31 in BT – 300 m layer indicating dissimilarities in their characteristics from other sampling locations (Fig. 12). The biplot which is another visualization of the PCA loadings showed the projection of the original variables onto the scattergram. In upper three layers, most of the stations having higher chaetognath abundance were correlated with relatively higher dissolved oxygen and low temperature values. **(Preferred position of Fig. 12)**

3.8. Diversity indices

The H' value was slightly higher in TC layer (av. 1.7 ± 0.5) compared to MLD (av. 1.6 ± 0.5). The H' showed a decreasing trend with increasing depth (Fig. 13a). The H' in the upwelling sites did not vary much from the non-upwelling sites in MLD and BT – 300 m layers whereas in TC layer it was relatively higher in upwelling site (Fig. 13a). The J' value was relatively lower in MLD and BT – 300 m layer and higher in the TC layer in the upwelling site (Fig. 13b). **(Preferred position of Fig. 13)**

4. Discussion

While analyzing the influence of upwelling on the variability of spatial distribution of chaetognaths, one important concern was to first identify the effects of the OMZ on the distribution of this important plankton group. During this study, the presence of OMZ layers of varying thickness below the surface water along all transects indicated the existence of oxygen deficient water mass throughout the EAS. The gradual increase in the thickness of OMZ from 8° to 19° N, clearly supports the view of pronounced north–south gradation in oceanographic parameters in the EAS (Wyrski, 1971; Naqvi, 2008). The heterogeneity in the vertical profile of RFO of chaetognath community (Fig. 6) along different latitudes synchronized with the vertical distribution of DO in the system. The thin layer of OMZ along 8° and 10° N did not have much significant effect on the vertical distribution of chaetognath in any depth stratum, indicated by 100% RFO, while the thicker OMZ layer (150 – 350 m) along 11.5° N affected the chaetognath abundance at mid depth. The persisting OMZ in major part of the water column along 13° , 15° and 17° N further affected the distribution and abundance of chaetognath below MLD to 500 m depth emphasizing OMZ as an important factor controlling their vertical distribution. Earlier we demonstrated the impact of oxygen depleted water on distribution of chaetognath in the north-eastern Arabian Sea during winter monsoon (Kusum et al., 2011) and the present study gives clear indication that during summer monsoon also the oxygen deficient water persisting in this environment has important role in limiting their vertical distribution. However, as the detail species specific response of chaetognaths towards this oxygen deficient water was described earlier (Kusum et al., 2011) it was avoided in the present study. The low RFO values (33 – 75%) in deeper layers along 19° N might be the result of the existence of the OMZ along with thick ODW in the deeper layers.

Though oxygen deficient water had influence on the vertical distribution of chaetognaths, pronounced higher abundance of this taxon in upwelling areas in the surface and subsurface layers (3.9 – 12.8 times higher than non-upwelling stations) in both the northern and southern parts of the study area signifies the role of this temporal scale physical process on their spatial abundance. The higher

abundance weight values in the upwelling sites might have resulted by either local population growth (individual growth and reproduction minus predation loss) or advection of chaetognath community towards the upwelling centers. Upwelling regions are considered as one of the most productive region in the world oceans and a higher abundance of copepods, the major prey of the chaetognaths, has been well established in the upwelling regions of the Pacific Ocean (Escribano and Hidalgo, 2000; Escribano et al., 2012). In the Indian Ocean also, Madhupratap et al. (1990) have reported the higher abundance of copepod in response to upwelling which also supports the view of higher chaetognath abundance in the upwelling sites. This in turn results in the spatial heterogeneity in the abundance weight of those regions (Fig. 8). The dominance of epipelagic species *S. enflata*, *S. bipunctata*, *S. bedoti*, *S. ferox*, *S. neglecta* and *K. subtilis* along with *S. hexaptera* in the surface upwelling site corroborates our view of local population growth and advection of the chaetognath species rather than the contribution by vertical mixing as a consequence of upwelling. The ecological and biogeochemical effect of this process is immense as it helps in the accumulation of organic matter towards the center of the upwelling site.

Earlier, *E. fowleri* was reported as mesopelagic in both Indian Ocean (Nair, 1978) and Pacific Ocean (Bieri, 1959) and *E. minuta* has been described as mesopelagic in Arabian Sea (Silas and Srinivasan, 1969) which is evident in our observation also. Because of their mesopelagic nature (Nair, 1978) and also by their presence in subsurface layers of upwelling sites, they can be considered as a good indicator species of the upwelling event. Their occurrence in the subsurface water might have occurred by the upward displacement of the deeper water as a result of upwelling. This view also gets supported by the observation of Nair (1977), who presumed the association of *E. fowleri* with upwelling process. Earlier, Srinivasan (1974) has described *S. decipiens* as an upwelling indicator of this region. Though DWA of *S. decipiens* in upwelling sites was slightly lower than the non-upwelling sites, their abundance did not show much variation in MLD and BT - 300 m layers of the upwelling and non-upwelling sites (Fig. 9). They are also observed as the dominant species below TC layer down to a depth of 1000 m. Hence, a part of their population might have occurred in the upper layers. Therefore describing *S. decipiens* as an upwelling indicator of this region can be deceiving. Upwelling in this region is a temporal event and mostly occurs during summer monsoon and is generally found to be absent during winter monsoon (Banse, 1959). In our earlier study during winter monsoon (Kusum et al., 2011), we have observed *S. decipiens* in MLD and TC layers in sufficient numbers, which further corroborates our view of not considering this species as an upwelling indicator of this region. Of the total 27 species analyzed during the study, the dominance of a few chaetognath species (*S. enflata*, *S.*

bedoti, *S. ferox*, *S. hexaptera*, *S. neglecta*, *S. regularis* and *K. subtilis*) in the upwelling sites might be due to their preference to the food rich upwelling environments and thus can be considered as most preferred species to utilize the productive upwelling environment. As some of the upwelling stations (Station 8) in this study were located in BT - 300 m layer, which was within OMZ, the abundant chaetognath community in this region (*S. ferox*, *S. regularis* and *S. enflata*) might have been adapted to cope with the low oxygen conditions prevailing in the environment. **(Preferred position of Table 2)**

The insignificant variation observed in day and night abundance might have been caused by the limited vertical migration of the chaetognaths due to the presence of the thick OMZ as was found in the distribution of several species of zooplankton in the OMZ region at northern Chile (Escribano and Hidalgo 2000). The significant reduction in the abundance of chaetognath with depth supports the view that the epipelagic chaetognaths were either avoiding the OMZ layer below or were reluctant to migrate towards the food scarce deeper layers. Similar observations at coast of Chile in the Pacific Ocean (Hidalgo et al., 2010; Ulloa et al., 2004) and in Andaman water of the Indian Ocean (Madhu et al., 2003) also support our view.

The DWA values calculated in our study illustrate the variation in the centre of gravity over the vertical axis of distribution in different species between the upwelling and non-upwelling sites and thus also helps to identify the species-specific variation in coupling with the changes in the abiotic component in this EBCs. In general, most of the epipelagic species showed relatively low DWA values in the upwelling locations compared to the non-upwelling locations. Except *S. hexaptera* and *S. regularis*, the upwelling preferred species (*S. bedoti*, *S. enflata*, *S. ferox*, *S. neglecta* and *K. subtilis*) had relatively lower DWA values in upwelling locations. Though these five species are epipelagic, a part of their population is observed in most of the deeper layers also (Table 2). As upwelling regions are highly productive these epipelagic species might have preferred to retain their position in the food rich surface and sub-surface layers thus resulting in the lower DWA compared to the non-upwelling sites. The marked difference in the DWA values of mesopelagic species *E. fowleri* and *E. minuta* in upwelling and non-upwelling sites might have been caused by the upward displacement of mid-depth water towards upper layers in the upwelling sites and thus further confirms them as indicator species of upwelling event (Fig. 11).

Based on the interrelation of the abiotic and biotic variables, the isolated position of four upwelling sites in the PCA scatter gram along surface and subsurface layers clearly indicates a distinct

abiotic and biotic environment between the upwelling and non-upwelling sites. The surface upwelling site characterized by relatively less temperature and dissolved oxygen, was the result of the uplifting of less oxygenated cold water from the subsurface layer clearly supports the occurrence of upwelling in this region. Similarly, relatively less temperature observed in the subsurface upwelling sites was due to the presence of cold deeper water (Fig. 12). Generally high chaetognath abundance was observed in regions with relatively high DO values, but in food rich upwelling sites, the relative difference in DO value had no profound impact on the abundance of the chaetognath community. The local population growth and advection of the upwelling preferred species might have contributed towards the higher abundance in these sites.

In spite of higher abundance of chaetognaths in MLD, the higher diversity index was observed at TC layer in both upwelling and non-upwelling sites (Fig. 13). Mixing of both epipelagic and mesopelagic species in this layer might have facilitated the higher diversity in TC layer supporting the earlier observation of maximum species diversity at 125 – 250 m depth in Indian Ocean (Nair, 1978, Pierrot-Bults and Nair, 1991). In this oxygen deficient environment, the mesopelagic species inhabited relatively upper layers avoiding the OMZ of middle and deeper layers and thus resulted in the mixing of epipelagic and mesopelagic species in TC layer (Kusum et al., 2011). The diversity index in upwelling and non-upwelling sites did not vary much in MLD and BT – 300 m layers. Though the abundance in the upwelling sites were much higher than other locations, only a few species contributed towards the abundance in the upwelling sites especially in MLD and BT – 300 m layer leading to less variation in these locations. The relatively lower evenness index in the upwelling sites compared to other locations in MLD and BT – 300 m layer might be due to the higher proportion of a few species in the upwelling locations.

As upwelling has been described as a key process determining the biological production in the EBCs (Escribano et al., 2012; Manríquez et al., 2012), the intensity of the upwelling will have significant role in the variability of the biotic components. The global rate of greenhouse gases is reported to be increasing and it is playing a crucial role in the intensification of coastal ocean upwelling in both tropical and temperate region (Bakun, 1990; Bakun and Weeks, 2004). As observed in our study, the responses to upwelling process vary among species which in turn produces heterogeneity in spatial abundance in the upwelling locations. Thus, the increase in the upwelling intensity can lead to the dominance of the upwelling preferred species thus inducing a change in the community structure in the

pelagic system. Hence the decadal scale variability in the abiotic components that induce this physical process and its response to the biotic components will require more attention in further research.

In summary, the characteristics of the coupled spatial scale variability in the physico-chemical variables and the chaetognath population in the upwelling system depends on the varying response of different species towards this physical process leading to the heterogeneity in the spatial abundance and diversity in the surface and subsurface layers. The high abundance in the upwelling sites might be the result of the local population growth and advection of the upwelling preferred epipelagic species. The study further helped to reevaluate and identify the most suitable indicator species (*E. fowleri* and *E. minuta*) of upwelling in the EBC of the Indian Ocean. As compared to the Pacific and Atlantic Ocean, the upwelling system in the EBCs of Indian Ocean are least studied, our findings will be relevant in the understanding of the ecology of this important plankton taxa in this region and will be useful in designing detailed research focusing on the response of other important zooplankton groups towards this physical process.

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List of Tables:

Table 1: Sampling depth on stations. An asterisk (*) marks the diurnal stations (MLD – Mixed layer depth, TT – Top of thermocline, TC – Thermocline, BT – Bottom of thermocline)

Station	MLD (0 - TT) m	TC (TT - BT) m	BT - 300 m	300 - 500 m	500 - 1000 m
1	0 - 27	---	---	---	---
2	0 - 36	---	---	---	---
3	0 - 30	30 - 226	226 - 300	---	---
4	0 - 38	38 - 240	240 - 300	300 - 500	500 - 1000
*5	0 - 33	33 - 273	273 - 300	300 - 500	500 - 1000
6	0 - 25	---	---	---	---
*7	0 - 29	29 - 170	---	---	---
8	0 - 29	29 - 214	214 - 300	300 - 500	500 - 1000
9	0 - 35	35 - 244	244 - 300	300 - 500	500 - 1000
*10	0 - 34	34 - 272	272 - 300	300 - 500	500 - 1000
*11	0 - 36	36 - 191	---	---	---
12	0 - 33	33 - 203	203 - 300	300 - 500	---
13	0 - 36	36 - 214	214 - 300	300 - 500	500 - 1000
*14	0 - 46	46 - 169	---	---	---
15	0 - 33	33 - 179	179 - 300	300 - 500	500 - 1000
16	0 - 33	33 - 201	201 - 300	300 - 500	500 - 1000
17	0 - 34	34 - 218	218 - 300	300 - 500	500 - 1000
*18	0 - 33	33 - 217	217 - 300	300 - 500	500 - 1000
*19	0 - 31	31 - 170	170 - 300	---	---
20	0 - 36	36 - 173	173 - 300	300 - 500	500 - 1000
21	0 - 33	33 - 196	196 - 300	300 - 500	500 - 1000
22	0 - 36	36 - 208	208 - 300	300 - 500	500 - 1000
*23	0 - 21	21 - 181	181 - 300	300 - 500	500 - 1000
*24	0 - 22	22 - 158	158 - 300	---	---
25	0 - 33	33 - 175	175 - 300	300 - 500	500 - 1000
26	0 - 53	53 - 150	150 - 300	300 - 500	500 - 1000
27	0 - 35	35 - 174	174 - 300	300 - 500	500 - 1000
28	0 - 33	33 - 192	192 - 300	300 - 500	500 - 1000
*29	0 - 29	29 - 152	---	---	---
30	0 - 20	20 - 149	149 - 300	300 - 500	500 - 1000
31	0 - 26	26 - 163	163 - 300	300 - 500	500 - 1000
32	0 - 37	37 - 161	161 - 300	300 - 500	500 - 1000
*33	0 - 30	30 - 190	190 - 300	300 - 500	500 - 1000

Table 2: Average abundance of chaetognath species (abundance \pm std. error, unit - ind / 1000 m³) at different depth strata

Species	MLD	TC	BT – 300 m	300 – 500 m	500 – 1000 m
<i>Pterosagitta draco</i>	430 \pm 138	153 \pm 42	2 \pm 2	4 \pm 4	0
<i>Krohnitta pacifica</i>	313 \pm 93	147 \pm 52	22 \pm 11	1 \pm 1	0
<i>K. subtilis</i>	802 \pm 231	146 \pm 54	14 \pm 7	1 \pm 1	0
<i>Eukrohnia bathypelagica</i>	0	0	0	0	8 \pm 5
<i>E. hamata</i>	0	0	0	8 \pm 4	7 \pm 6
<i>E. minuta</i>	0	5 \pm 3	3 \pm 3	17 \pm 7	4 \pm 1
<i>E. fowleri</i>	0	3 \pm 2	5 \pm 6	0	4 \pm 3
<i>Sagitta bipunctata</i>	533 \pm 300	170 \pm 69	3 \pm 3	16 \pm 12	0
<i>S. bedoti</i>	359 \pm 302	58 \pm 48	0	0	0
<i>S. bedfordii</i>	181 \pm 76	28 \pm 11	4 \pm 3	2 \pm 2	1 \pm 1
<i>S. decipiens</i>	680 \pm 177	320 \pm 70	166 \pm 154	25 \pm 9	28 \pm 9
<i>S. enflata</i>	4243 \pm 1232	505 \pm 106	113 \pm 67	5 \pm 2	3 \pm 2
<i>S. ferox</i>	567 \pm 309	82 \pm 40	118 \pm 127	6 \pm 4	0
<i>S. hexaptera</i>	1146 \pm 263	303 \pm 86	4 \pm 4	6 \pm 3	1 \pm 1
<i>S. macrocephala</i>	0	0	7 \pm 6	1 \pm 1	0
<i>S. maxima</i>	0	0	0	1 \pm 1	4 \pm 2
<i>S. minima</i>	137 \pm 97	21 \pm 11	0	2 \pm 2	0
<i>S. neglecta</i>	1420 \pm 341	392 \pm 92	38 \pm 17	1 \pm 1	0
<i>S. oceania</i>	150 \pm 76	31 \pm 26	4 \pm 4	0	0
<i>S. regularis</i>	897 \pm 264	298 \pm 115	99 \pm 80	6 \pm 5	1 \pm 1
<i>S. robusta</i>	524 \pm 157	126 \pm 50	3 \pm 3	0	0
<i>S. pacifica</i>	183 \pm 87	100 \pm 40	16 \pm 8	1 \pm 1	0
<i>S. planctonis</i>	0	30 \pm 20	3 \pm 3	0	0
<i>S. pulchra</i>	0	12 \pm 9	0	0	0
<i>S. sibogae</i>	0	0	0	8 \pm 7	0
<i>S. zetios</i>	8 \pm 8	31 \pm 24	3 \pm 4	3 \pm 3	0
Unidentified	37 \pm 36	0	0	0	0

Figure 1. Sampling locations in the EAS. The squares denote diurnal stations and circles denote regular stations. In the regular stations only one sampling was done for each depth layers.

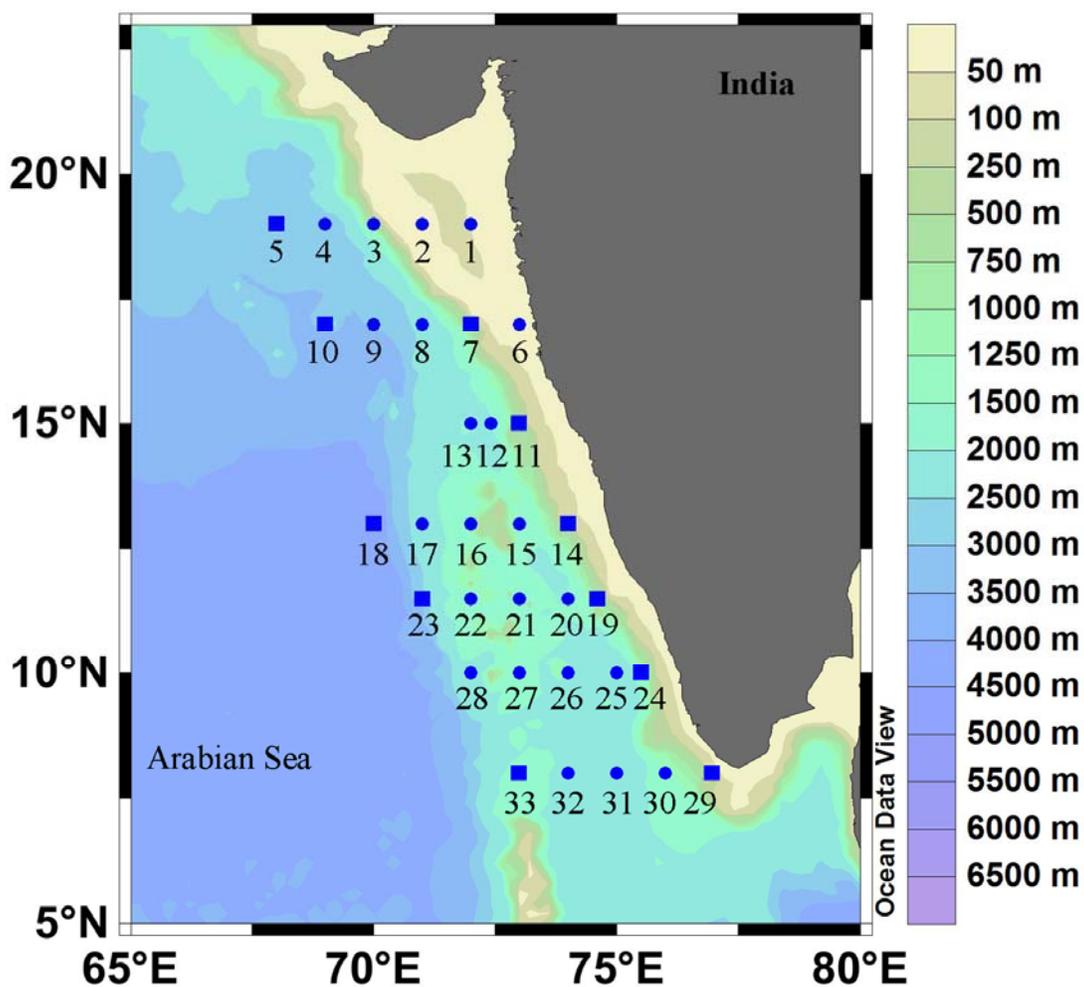


Figure 2. Distribution of temperature ($^{\circ}\text{C}$) in the upper 1000 m of the EAS. Upwelling sites are indicated by the boxes. Station locations are indicated by the arrows

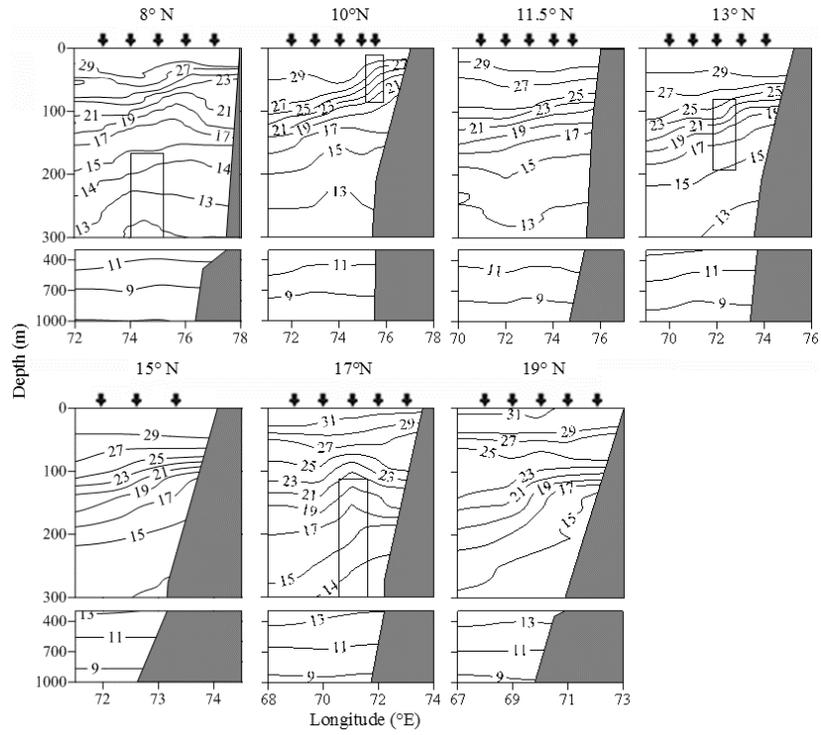


Figure 3. Distribution of potential density (σ_t) of water in the upper 1000 m of the EAS. Station locations are indicated by the arrows.

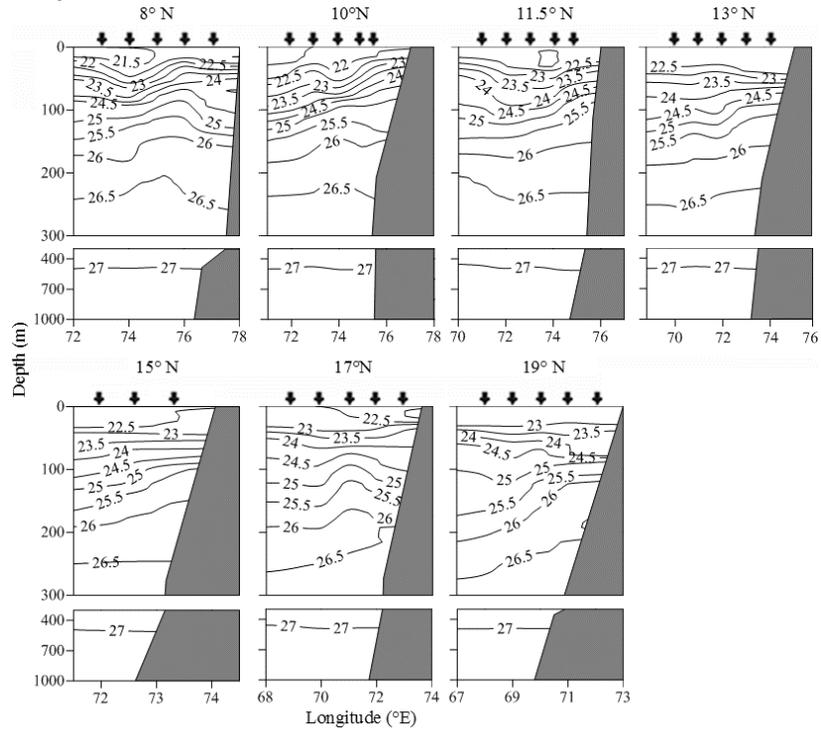


Figure 4. Distribution of salinity in the upper 1000 m of the EAS. Station locations are indicated by the arrows.

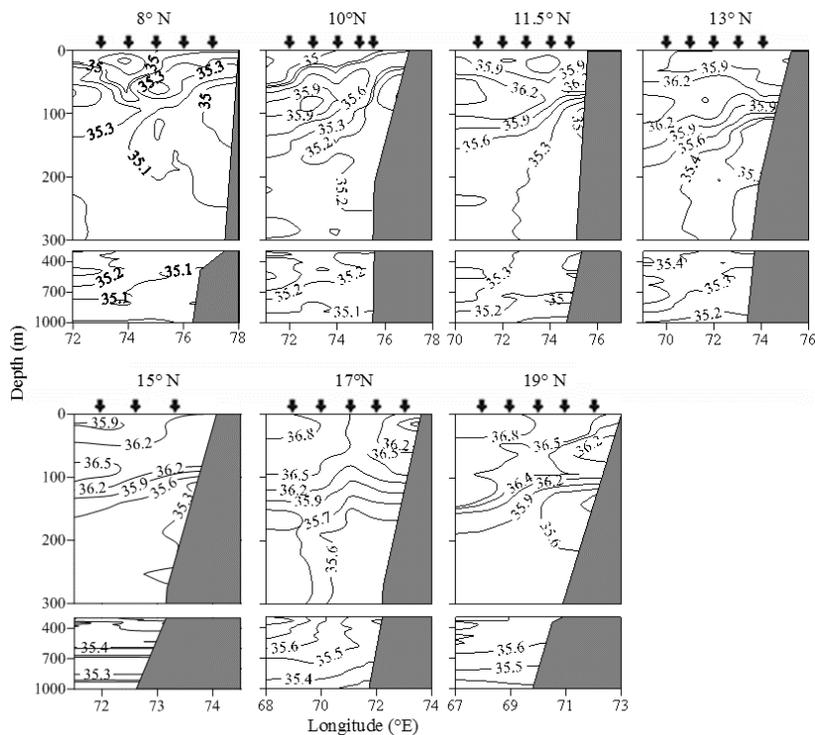


Figure 5. Distribution of dissolved oxygen (mL L^{-1}) in the upper 1000 m of the EAS. Station locations are indicated by the arrows.

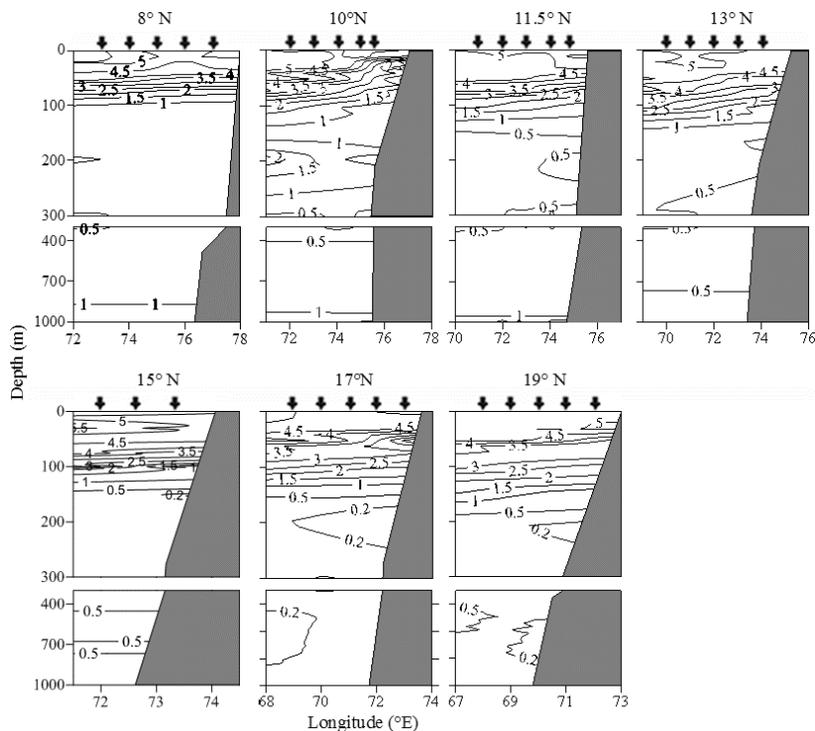


Figure 6. Vertical relative frequency of occurrence profile of chaetognath community along the transects from 8° N to 19° N.

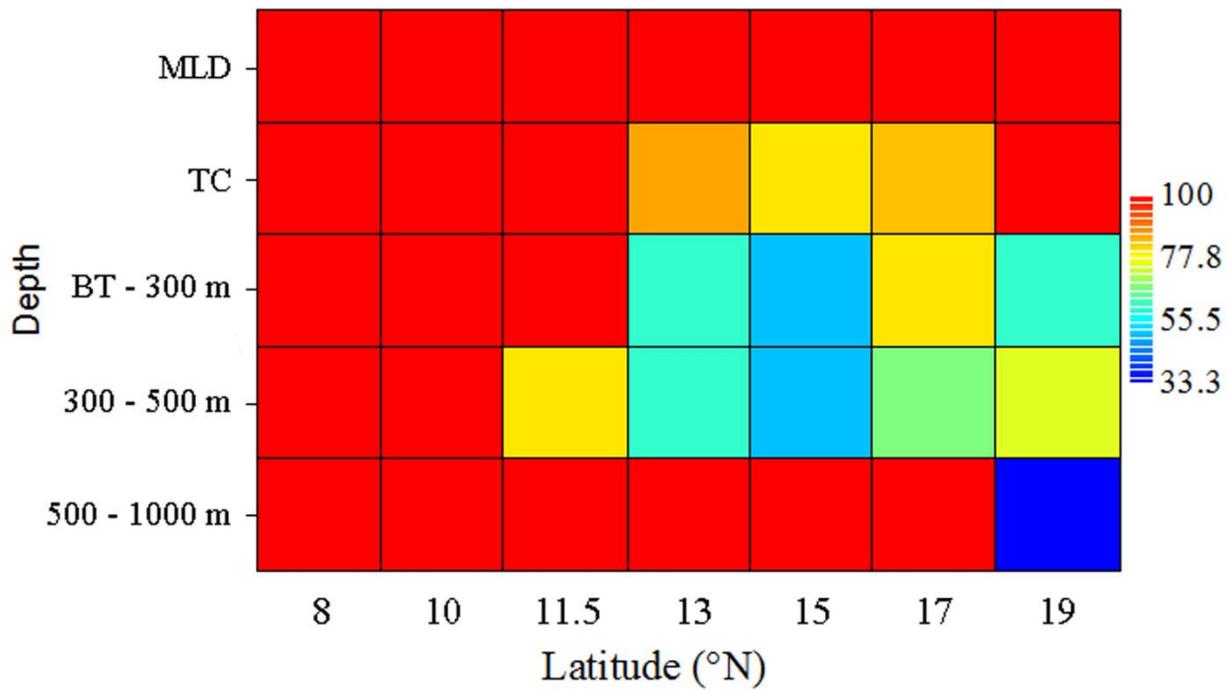


Figure 7. Abundance (ind / 1000 m³) of chaetognaths along different depth at EAS.

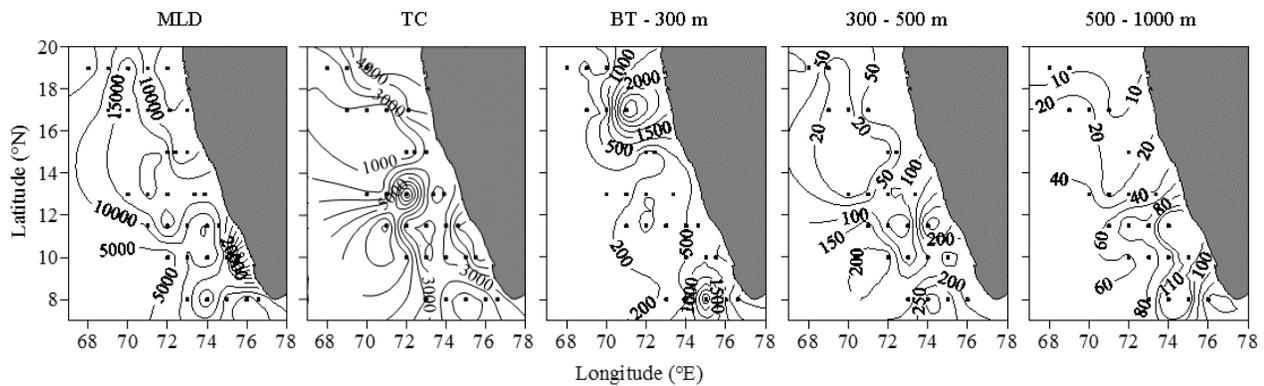


Figure 8. Abundance weight profile in the upper three layers. The red circle denotes the upwelling locations

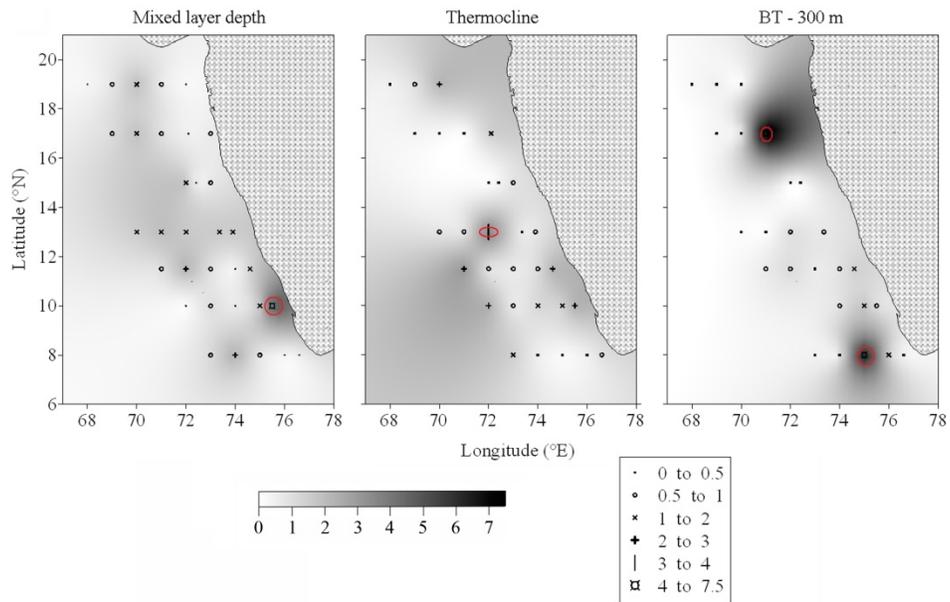


Figure 9. Average abundance (ind / 1000 m³) of chaetognaths at [a] mixed layer depth, [b] thermocline and [c] base of thermocline – 300m strata in non-upwelling and upwelling sites. The vertical line on the bar diagram indicates the standard deviation.

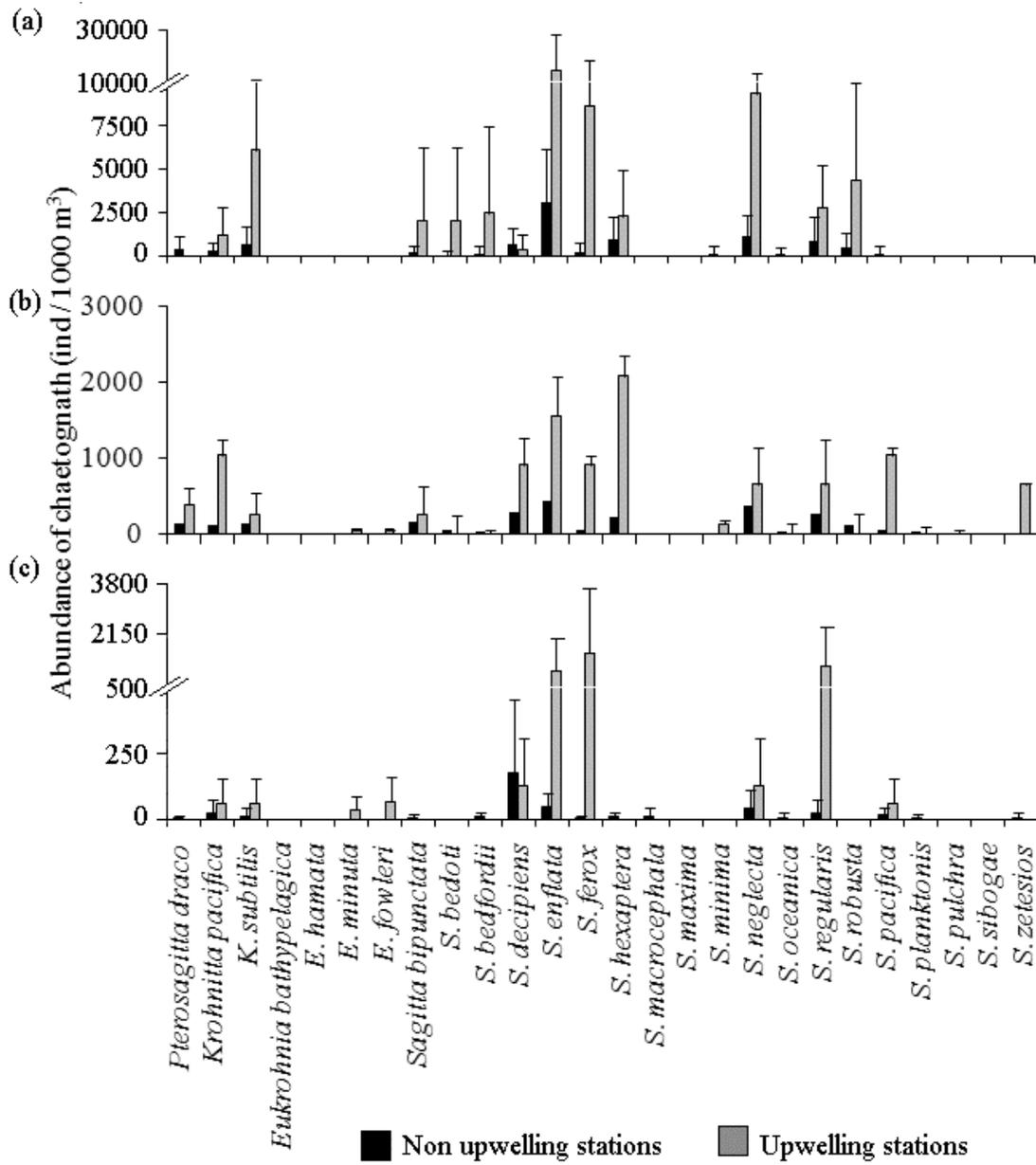


Figure 10. Diurnal variation in chaetognath abundance (ind / 1000 m³) at [a] mixed layer depth, [b] thermocline and [c] base of thermocline – 300 m strata of surface upwelling station (station 24).

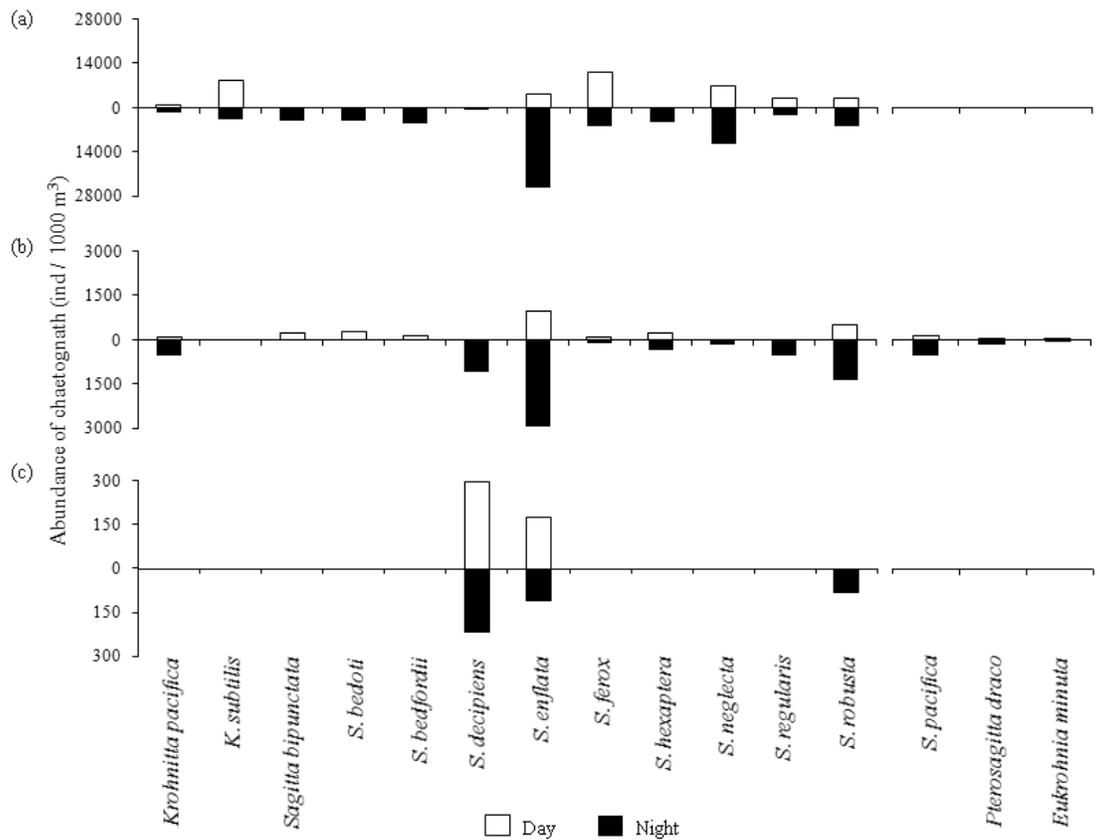


Figure 11. The depth-weighted average values of different chaetognath species in non-upwelling and upwelling sites.

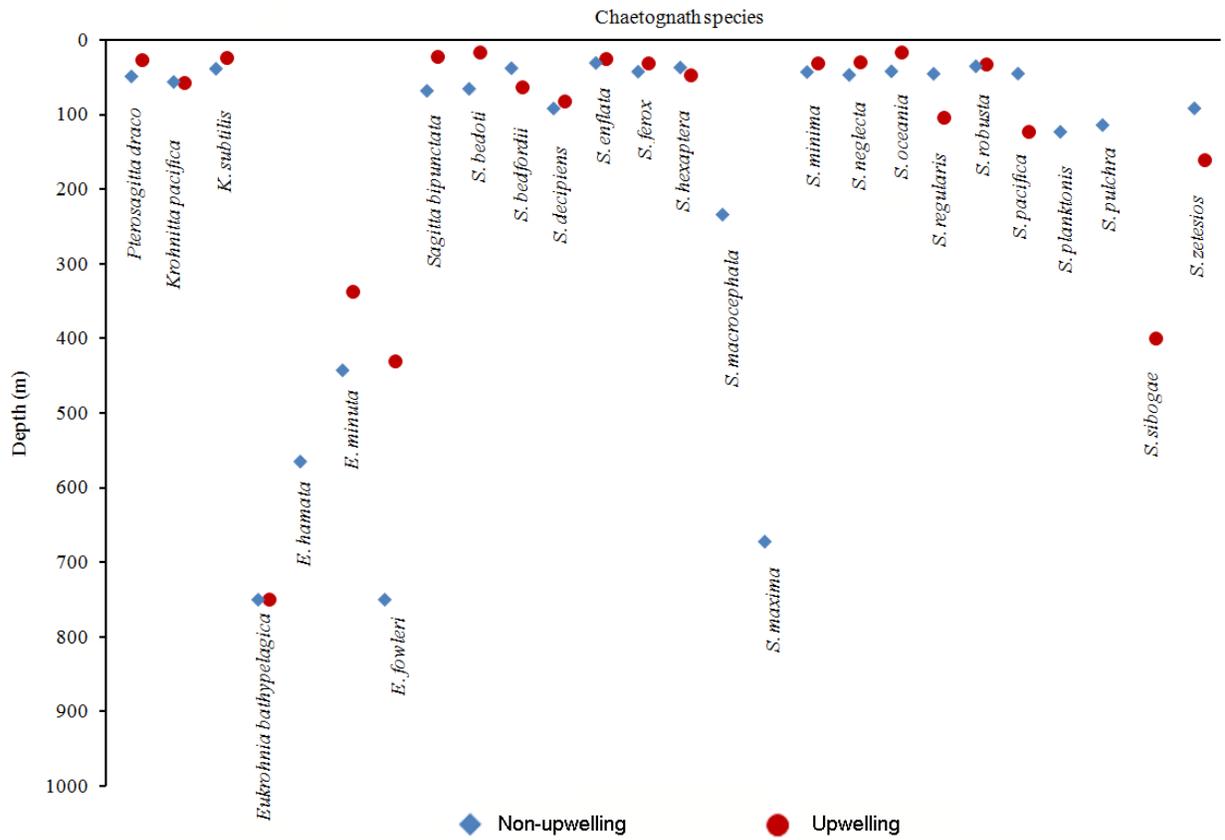


Figure 12. Results of the principal component analysis. Station locations are displayed by points and the biotic and abiotic variables are shown by arrow. The direction of an arrow dictates the direction of increase of that particular variable on spatially assembled sampling locations. The red square denotes the upwelling locations.

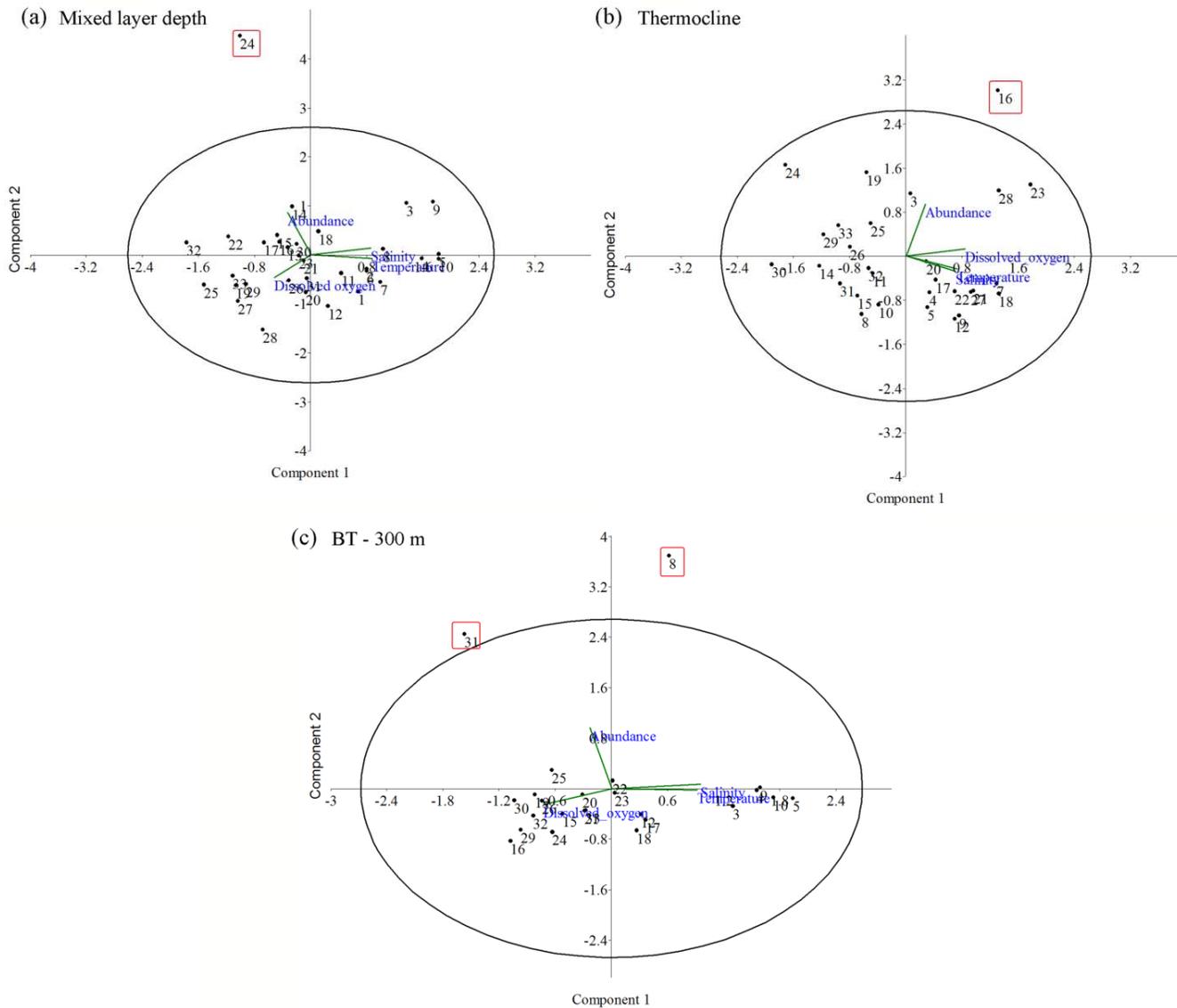


Figure 13. Diversity indices [a] species diversity, [b] species evenness, along discrete depths in the EAS. The vertical line on the bar diagram indicates the standard deviation.

