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Ecohydrographic control on the community structure and vertical distribution of pelagic Chaetognatha in the Red Sea

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Disclosure statement

BK and AA conceived the study. BK, ME, RD and AA carried out fieldwork, analyzed the
zooplankton samples, and processed the data. KK provided taxonomic identifications of
Chaetognatha, interpreted the data, and drafted the manuscript. BK, US, and BJ provided
editorial advice.

Abstract

The present study details the effects of basin-scale hydrographic characteristics of the Red Sea on the macroecology of Chaetognatha, a major plankton component in the pelagic realm. The hydrographic attributes and circulation of the Red Sea as a result of its limited connection with the northern Indian Ocean make it a unique ecohydrographic region in the world ocean. Here, we aimed to identify the prime determinants governing the community structure and vertical distribution of the Chaetognatha in this ecologically significant world ocean basin. The intrusion of Gulf of Aden Water influenced the Chaetognatha community composition in the south, whereas the overturning circulation altered their vertical distribution in the north. The existence of hypoxic waters ($<100 \mu\text{mol kg}^{-1}$) at mid-depth also influenced their vertical distribution. The detailed evaluation of the responses of the different life stages of Chaetognatha revealed an increased susceptibility of adult individuals to hypoxic waters compared to immature stages. Higher oxygen demands of the adults for the egg and sperm production might have prevented them from inhabiting the oxygen deficient mid-depth zones. The carbon and nitrogen content of the Copepoda and Chaetognatha communities and the quantification of the predation impact of Chaetognatha on Copepoda based on the feeding rate helped in corroborating the significant trophic link between these two prey-predator taxa. The observed influences of physical and chemical attributes on the distribution of Chaetognatha can be used as a model example for the role of the hydrography on the zooplankton community of the Red Sea.

Keywords: Biogeography; Chaetognatha; Ecohydrography; Macroecology; Red Sea; Zooplankton

Introduction

The phylum Chaetognatha embraces a major component of pelagic plankton in the global oceans and their marginal seas (Nair 1978; Bohata and Koppelman, 2013; Terazaki 2013; Kürten et al. 2014). As carnivores, chaetognaths are known to consume ~1 to 12 prey day⁻¹ ranging from oligotrophic to productive environments (Kimmerer 1984; Kehayias 2003) and therefore play a pivotal role in the trophodynamics of marine ecosystems. Their sensitivity to the physical and chemical environment leading to their association with specific water masses makes them suitable bioindicators of ecohydrographic provinces (Nagai et al. 2006; Buchanan and Beckley 2016) and for regions with increased primary productivity and the underlying physical processes (e.g. eddies, fronts, and upwelling) (Kusum et al. 2014; Lima 2014; Nair et al. 2015).

The Red Sea, geographically positioned between the Asian and African continents and characterized by an area of $4.51 \times 10^5 \text{ km}^2$ and a length of ~2000 km is a semi-enclosed inlet of the Indian Ocean (Sofianos and Johns 2002). The high evaporation rates ($>2 \text{ m yr}^{-1}$), low precipitation ($0.05 - 0.15 \text{ m yr}^{-1}$) and negligible river discharges makes the Red Sea one of the saltiest ocean basins with a salinity range of 36 to 41 (Miller 1964; Grasshoff 1969; Maillard and Soliman 1986). Moreover, an exchange-flow between the Red Sea and the Indian Ocean in the south and the overturning circulation in the north influence the salinity, sea surface temperature, and nutrient availability of the Red Sea (Sofianos and Johns 2002, 2003). Thus, a detailed understanding about the influence of its ocean dynamics on the biotic community is utmost important to delineate the ecosystem status, health, and trophic dynamics of this unique ocean basin.

The goal of the present study was to understand the integrated effects of both abiotic (hydrographic regime) and biotic components structuring Chaetognatha community in the Red

Sea. The study is sequel to latitudinal assessments of phytoplankton and zooplankton biodiversity and trophic dynamics in nearshore coral reefs (Kürten et al. 2015; Al-Aidaros et al. 2017; Devassy et al. 2017). Most other recent studies focused on the detailed taxonomic and biogeographic descriptions of the dominant zooplankton taxon Copepoda (e.g. Al-Aidaros et al. 2016; El-Sherbiny et al. 2007, 2017). However, comprehensive studies pertaining to the macroecology of Chaetognatha with 19 species from this region are scarce and limited to their distribution in the upper water column in coral reefs (Ducret 1973; Halim 1984; Casanova 1985, 1986; Al-Aidaros et al. 2017).

We hypothesized that the oceanographic features i.e. the northward intrusion of Gulf of Aden Water (GAW), the anti-estuarine overturning circulation, and vertical gradients in physical and chemical variables play a crucial role in the macroecology of Chaetognatha in the Red Sea. To address our goals, the latitudinal and vertical distribution of the Chaetognatha community and their life stages were related to abiotic variables (temperature, salinity, dissolved oxygen and depth) to identify the influence of the hydrography on their distribution. Following the β -diversity approach, we aimed to identify biotic dissimilarities generated by the variability in the physical and chemical attributes of the basin.

Materials and Methods

Study area and sampling

Sampling was carried out from 8th to 20th April, 2012 onboard RV *Pelagia* (cruise 64PE351) (Fig. 1). Considering the geographical position of the basin, the sampling sites were selected to cover the ecohydrographic gradients of the Red Sea over a distance of ~1300 km.

Physical and chemical variables

At all stations, a SBE 911 CTD (Sea-Bird Electronics, USA) was deployed to obtain vertical profiles of temperature and salinity. The CTD was equipped with a SBE 43 dissolved oxygen (DO) sensor to obtain DO profiles of the water column. A detailed description of water mass characteristics (excluding DO) has been presented by Kürten et al. (2016).

Biological variables

A multiple opening-closing net (type Midi; Hydro-Bios, FRG) with mesh size of 330 µm and mouth area of 1 m² was used for meso- and macrozooplankton sampling. The net was hauled in stratified oblique mode (sensu Wiebe et al., 2014) to obtain samples from five depths strata i.e., 0 – 100 m, 100 – 200 m, 200 – 300 m, 300 – 500 m, and 500 – 1000 m at a tow speed of 1 knot. At sampling locations with depth less than 1000 m, the deeper waters were sampled from near bottom to 500 m (Supplementary Table 1). On deck, zooplankton samples were immediately preserved in 4% buffered formalin for detailed taxonomic evaluation. Copepoda and Chaetognatha were sorted and enumerated under a stereomicroscope (SMZ168, Motic, FRG) and abundances were calculated based on the volume of water filtered and expressed as Ind m⁻³ (Harris et al., 2000). The identification of the Chaetognatha community at the species level was carried out following standard identification protocols (Nair 2003) and available literature for the Red Sea (Casanova 1986; Echelman and Fishelson 1990).

To have a better understanding of their vertical distribution, the weighted mean depth of the Chaetognatha species was calculated following Dupont and Aksnes (2012) as:

$$Z_m = \frac{\sum_{i=1}^n a_i d_i z_i}{\sum_{i=1}^n a_i d_i}$$

$$Z_s = \sqrt{\left(\frac{\sum_{i=1}^n a_i d_i z_i^2}{\sum_{i=1}^n a_i d_i} \right) - Z_m^2}$$

Where, Z_m is the weighted mean depth (m) of each species, Z_s is the corresponding standard deviation (± 1 SD), a_i is the abundance (ind m^{-3}) of each species along stratum i , d_i is the thickness (m) of the stratum i , z_i is the corresponding mid-depth (m) of stratum i , n is the total number of sampled strata.

Although the maturity period in Chaetognatha varies among species, which can be assessed based on their ovarian development, all Chaetognatha specimens were assigned to one of three maturity stages (McLaren 1969; Zo 1973) to understand the varied responses of the growth stages to hydrographic attributes. In brief, Stage I (immature individuals) lack visible ovaries, in Stage II (maturing) developing ova are present, whereas Stage III (matured) have one or more mature ova. The spent individuals were also included under the stage III category (Kusum et al. 2011).

Carbon and nitrogen (hereafter C and N) content of Chaetognatha and Copepoda was determined using elemental analysis as detailed in Kürten et al. (2016). C and N data were available for dominant Copepoda genera only. In case of Chaetognatha, the total community was considered. The information on the relative trophic position of the Chaetognatha was used from Kürten et al. (2016).

Statistical analyses

Abundances of both Copepoda and Chaetognatha in different depth strata were compared using one-way ANOVAs, with two-tailed P-values and 95% confidence intervals (Graphpad prism version 5.01). Prior to the analysis, the Kolmogorov-Smirnov normality test was performed to determine whether parametric or non-parametric ANOVA was applicable. Relationships between the abundance of Copepoda and Chaetognatha were identified using Pearson correlation with two-tailed P-values and 95% confidence intervals (Graphpad prism).

Unconstrained non-metric multidimensional scaling (NMDS) is often significant in the ordination of biological variables. To explain the similarities in the composition of the Chaetognatha community along different depth strata, we used NMDS analysis using PRIMER 6 (Clarke and Gorley 2006) based on the Bray-Curtis similarity matrix of the fourth-root transformed species-wise abundance of each depth zones. Clusters based on 75% similarity were overlaid on the NMDS plot to describe relationships of the Chaetognatha distribution among the sampling depths. In addition, a second NMDS plot was used to identify the similarity in the distribution of the Chaetognatha species based on their abundance along the horizontal and vertical scale.

The α - and β -diversities of the Chaetognatha community were used to assess the biodiversity and the variation in species identity among the sampling locations (Anderson et al. 2011). First, the Shannon-Wiener species diversity index (H') was estimated using PRIMER 6. Inter-site variability was assessed using the index of multivariate dispersion (MVDISP, Warwick and Clarke 1993).

The constrained Redundancy analysis (RDA) was used as in multivariate space it best explains the linear relationships between response and explanatory variables (Van den Wollenberg 1977).

The advantage of RDA is that it displays a simultaneous representation of the observations of the response variables (Chaetognatha) and explanatory variables (physical and chemical variables and Copepoda), and the position of the variables in the tri-plot helps visualizing their relationships.

Results

Physical and chemical environment

Sea surface temperatures (at 3 m depth) varied between 23.1 and 28.5°C (average $\pm$ SD, 26 ± 1.8 °C) and decreased towards the north (Fig. 2a). In the vertical temperature profile, a strong gradient was observed in the upper 200 m of the water column and more pronounced in the south (Fig. 2a). Sea surface salinity also showed a latitudinal gradient with a marked increase towards the north (range 37.3 – 40.4; average 39 ± 1.1) (Fig. 2b). The stratification in the vertical salinity profile was evident in the upper 200 m with stronger gradient towards the south (Fig. 2b). Spatial variation in the surface DO was marginal (average $253.9 \pm 19.2 \mu\text{mol kg}^{-1}$), with a sharp gradient in the vertical profile below 50 m (Fig. 2c). Low DO ($<100 \mu\text{mol kg}^{-1}$) at depths were evident throughout the study region. In the south, the oxygen minimum layer was observed between 150 – 800 m whereas in the north it was between 400 – 650 m (Fig. 2c).

Copepoda abundance

The upper 100 m contributed 79.3% to the total copepod abundance over the entire 1000 m water column. Copepoda abundances in this layer varied between 37.9 and 74.9 ind m^{-3} with an average abundance of 53.4 ± 14.3 ind m^{-3} (Supplementary Fig. 1). The variation in the abundance along different depth zones was significantly different (one-way ANOVA, $F_{4,25} = 67.63$, $P < 0.001$). While there was a pronounced decrease from the 0 – 100 m stratum to the 100 – 200 m stratum, the further decrease in abundance was not consistent with increasing depth (Supplementary Fig. 1a). The abundance was observed to be lowest at the 200 – 300 m depth at all sampling sites except off Farasan where it was lowest at 300 – 500 m (Supplementary Fig. 1).

Chaetognath abundance, community structure and vertical distribution

Similar to the copepod community, Chaetognatha were most numerous in the upper 100 m contributing to 74.2% to their total population over the entire sampling depths (Supplementary Fig. 1). The variation in the Chaetognatha abundance over depths were statistically significant

189 (one-way ANOVA, $F_{4,25} = 10.84$, $P < 0.001$). The Chaetognatha abundances sharply decreased
 190 below 100 m at most sites and abundances showed an intermediate low at 100 – 200 m depth
 191 before reaching 500 – 1000 m (Supplementary Fig. 1). A total of 17 species belonging to 11
 192 genera were observed (Table 1). Although Chaetognatha abundance was higher in the upper 100
 193 m, a maximum number of species was recorded from 200 – 300 m (17) and a minimum at 100 –
 194 200 m and 500 – 1000 m (12 each, respectively). *Flaccisagitta enflata* was the dominant species
 195 in the upper two depth strata, whereas *Decipisagitta decipiens* dominated depths below 500 m
 196 (Fig. 3). Nine species (*Krohnitta pacifica*, *Krohnitta subtilis*, *Aidosagitta regularis*,
 197 *Decipisagitta decipiens*, *Flaccisagitta enflata*, *Flaccisagitta hexaptera*, *Ferosagitta ferox*,
 198 *Sagitta bipunctata*, and *Zonosagitta pulchra*) were observed at all stations in one or more depth
 199 strata despite different abundances. Among the epipelagic Chaetognatha, nine species were
 200 observed in the entire 1000 m, and five of them had >75% of their abundance in the upper 100 m
 201 (Table 1 and Supplementary Fig. 2). The epipelagic *Pterosagitta draco* and *Zonosagitta pulchra*
 202 were observed in the upper 500 m, and showed higher abundances in the upper 100 m (>75%),
 203 whereas the distribution of *Zonosagitta bedoti* was restricted to the upper 300 m (Table 1). Of
 204 the mesopelagic species, only *Decipisagitta decipiens* was present throughout the 1000 m and
 205 had higher abundances at 200 – 500 m. *Eukrohnia fowleri* and *Pseudosagitta maxima* were
 206 observed only below 200 m especially with high preferences for waters below 300 m (Table 1).
 207 Although the weighted mean depth (Z_m) of the chaetognaths varied among species, it was less
 208 than 100 m depth for majority of the epipelagic species (Fig. 4). The Z_m of the mesopelagic
 209 species ranged between 352 and 556 m (Fig. 4). Spatially, the occurrence of the majority of the
 210 epipelagic species in the deeper layers was higher in Duba, the northernmost station
 211 (Supplementary Table 2). Based on the maturity stages of the species of chaetognaths, the

immature individuals dominated at most depths (Fig. 5). Both maturing and mature individuals of the majority of the epipelagic species had a preference for surface waters (0 – 100 m) (Fig. 5)

Chaetognatha-Copepoda interrelationship

A positive relation was observed between the abundances of Copepoda and Chaetognatha (Pearson correlation; $R = 0.761$, $P < 0.01$). The ratio of the abundance of the Copepoda and Chaetognatha varied among the depth layers (Fig. 6). It was relatively higher in the upper two layers and in the deeper 500 – 1000 m depth, but lower in the mid-depth waters (median 7.8, 13.9, 1.7, 8, and 14.3, in 0 – 100 m, 100 – 200 m, 200 – 300 m, 300 – 500 m and 500 – 1000 m depth, respectively).

Table 2 displays the C and N content of Chaetognatha and of the dominant genus of the Copepoda. The C and N of Chaetognatha was 34.12 and 9.09% of their dry weight, respectively. In Copepoda, the percentage of C varied between 18.07% to 51.65% of their dry weight, and in case of N it ranged between 4.23% and 12.58% among the different genera. To approximate the C and N content of the total Copepoda community, an average C and N content of the dominant Copepoda genera were used for the remaining Copepoda community. Considering the total volume of the upper 100 m of the Red Sea as $3.433 \times 10^{13} \text{ m}^3$, Chaetognatha contained ~25,222 t C and 3,719 t N, respectively. In case of Copepoda, the elemental content was 95451 t and 21865 t for C and N, respectively. The total amount of C in the Chaetognatha was 26.4% of the total C content of Copepoda and in case of N content this value was 30.7%. The relative trophic position for the Chaetognatha community was 3.2 ± 0.4 (min 2.7 max 4.1; $n = 31$ samples, a composite of 514 specimens, Kürten et al. 2016).

The NMDS plot based on the abundance of Chaetognatha species along the depth layers, exhibited a discrete ordination of the upper 0 – 100 m and deeper 500 – 1000 m from the other

depth zones with a Kruskal stress value of 0 (Fig. 7a). The overlay cluster based on the 75% similarity level revealed a group of the mid-depth zones together (100 – 200 m, 200 – 300 m, and 300 – 500 m) (Fig. 7a). The NMDS plotted to evaluate the similarity in the distribution of the Chaetognatha species revealed a large group with majority of the epipelagic species and another group with two mesopelagic species based on the 40% similarity (Fig. 7b).

α and β -diversity

The species diversity (H') varied both spatially and temporally and based on the depth-wise average value it was maximum at 200 – 300 m (average 2.29 ± 0.45 , 2.3 ± 0.88 , 2.64 ± 0.49 , 2.61 ± 0.54 , and 2.22 ± 0.6 , in 0 – 100 m, 100 – 200 m, 200 – 300 m, 300 – 500 m, and 500 – 1000 m, respectively). The relative variability of the Chaetognatha assemblages within each stations (i.e. intragroup β -dissimilarity) exhibited the lowest value off Duba (Supplementary Table 3, based on the MVDISP analysis). The pairwise inter-station β -dissimilarity based on the index of multivariate dispersion (IMD) showed varying results among sites (Supplementary Table 3). In general, the southernmost two stations had high IMD values with most of the other sampling locations (Supplementary Table 3). The northernmost station had a high dissimilarity with its nearby station Mabahiss (0.62).

Redundancy analysis (RDA)

The RDA triplots indicated the preferred environment of the Chaetognatha species. Most of the epipelagic Chaetognatha were positively correlated with DO and the abundance of their dominant prey Copepoda (Fig. 8a). The abundances of mesopelagic *Eukrohnia fowleri* and *Pseudosagitta maxima* also exhibited a similar result having positive relation with the abundance of Copepoda and DO (Fig. 8b).

Discussion

The ecohydrographic framework of the Red Sea helped to understand the complexity in the biotic-abiotic relationships of the Chaetognatha community. The lower salinity in the upper 100 m, chiefly up to 19°N, relates to the inflow of GAW into the Red Sea and corroborates earlier observations and modeling studies (Stubbings 1939; Maillard and Soliman 1986; Sofianos and Johns 2007). The overturning circulation in the northern Red Sea is another important factor that governs the hydrography of this basin. The outcome of this overturning circulation is the sinking of surface waters in the north which was clearly evident in the salinity structure around 27°N (Fig. 2b). The winter surface cooling leads to deep convection in the northern Red Sea and results in a near-homogeneous water up to subsurface layers (Kürten et al. 2016; Fig. 2). However, the sinking of the isothermal lines at the northernmost location supports the salinity based observation of the sinking of water to deeper layers.

The variability in the physical and chemical characteristics in the Red Sea influenced the plankton distribution. In the upper 100 m water, the Chaetognatha abundance was high in Atlantis II and off Duba. At the Atlantis II, upwelling of nutrient-rich water contributed to the conspicuous preponderance of diatoms (Kürten et al. 2016). It is suggested that the higher availability of diatoms supported increased abundances of Copepoda and in turn sustained higher Chaetognatha abundance in this location. Similarly, the increased abundance of diatoms off Duba also offered sufficient food for zooplankton as indicated by increased chlorophyll *a* and particulate organic nitrogen as proxies for phytoplankton biomass (Kürten et al. 2016).

The existence of hypoxic waters helps explaining the sudden drop in the Chaetognatha abundance below 100 m. Chaetognatha are sensitive to low DO, as was shown, for example, in the adjacent Arabian Sea where Chaetognatha are scarce in oxygen deficient zones (Kusum et al. 2011). Hence,

the sharp gradients in DO leading to hypoxia in the 100 – 200 m in the Red Sea are likely to lower Chaetognatha abundances at this depth. The Z_m of majority of the epipelagic species was less than 100 m indicating their preference to the upper oxygenated water. The Z_s varied among the species and the relatively lower Z_s in epipelagic species like *Zonosagitta bedoti* and *Zonosagitta pulchra* points out their restricted vertical distribution (Fig. 4). The marked positive relation between the abundance of most of the Chaetognatha species and DO corroborates the vital role of DO in structuring the Chaetognatha population (Fig. 8), a relationship typical for plankton distribution in the oxygen minimum zones around the world (Wishner et al. 1995).

The higher abundance of the epipelagic Chaetognatha inhabiting the oxygenated upper 100 m was reflected in the separation of this depth stratum from the aphotic zone (Fig. 7a). Among the nine epipelagic Chaetognatha observed, five species had >75% of their abundance in the upper 100 m, which points towards their preferences for relatively well-oxygenated surface waters. The group of the majority of the epipelagic Chaetognatha species in the NMDS plot (Fig. 7b) corroborated their preferences for the similar environments. The higher abundance of Copepoda, their primary prey at this depth, might have also favored their higher sustenance and abundances. Although gut content analysis of the Chaetognatha was not carried out in the present study, Copepoda are typically the most preferred prey of Chaetognatha (Kehayias 2003; Giesecke and González 2004; Terazaki 2004; Yoon et al. 2016). The marked positive correlation between prey and predators confirms the important trophic link. In the RDA analysis, the observed positive association of the majority of the epipelagic and mesopelagic species of Chaetognatha with the abundance of Copepoda (Fig. 8) further validates their trophic relations. The relative trophic position for the Chaetognatha community in this study was 3.2 ± 0.4 where producer species were assigned to trophic level 1, and the consumer values range from 2 (primary consumers) to 5 or

greater. This relative trophic position exhibits their importance as the secondary consumer in the pelagic ecosystem. The feeding rate of the Chaetognatha has been found to vary among tropical, temperate, and polar organisms (Oresland 2000; Giesecke and González 2012). *Flaccisagitta enflata*, the dominant Chaetognatha in the upper 300 m is capable of consuming up to 10 – 12 prey items day⁻¹, whilst its feeding rate depends on prey availability (Reeve 1980; Kimmerer 1984). The higher values of the ratio of the abundance of the Copepoda and Chaetognatha (median 7.8, and 13.9, in 0 – 100 m, and 100 – 200 m, respectively) indicates a favorable environment for the Chaetognatha. The lower ratios in the mid-depth waters (median 1.7, and 8, in 200 – 300 m, 300 – 500 m, respectively) indicates a food-limited environment for the Chaetognatha compared to the upper layers. This scenario differs from the northern Arabian Sea, where the prey – predator ratio was higher in the acute oxygen depleted mid-depth waters than in surface waters (Kusum et al. 2011).

The abundance of both Copepoda and Chaetognatha in the upper 100 m was > 70% of their total population in the entire 1000 m water column and hence based on the information in the available literature we estimated the predation pressure of the Chaetognatha on the Copepoda in this stratum. We considered the predation impact (the percentage of the copepod standing stock consumed per day) of the dominant species *F. enflata* and also of the total Chaetognatha community. To calculate the predation impact, the prey day⁻¹ for each individual of Chaetognatha was estimated based on the result observed in the upper 100 m by Kehiyas (2003, Tables 4 and 5) in the Mediterranean Sea (*F. enflata*: ave 0.96 ± 0.58 , range 0.46 – 1.8 prey per day; Total Chaetognatha: ave 1.36 ± 1.16 , range 0.64 – 3.9 prey per day). The Mediterranean Sea has many ecohydrographic similarities with the Red Sea, e.g. high salinity, low productivity, and zooplankton stock (Gotsis-Skretas et al. 1999). The predation impact of *F. enflata* varied

between 1.51 and 11.7 (av. 5.8 ± 4) with an increasing trend towards the north (Supplementary Table 4). The average ($\pm$ SD) predation impact was higher than in the Cretan Passage (1.3 ± 0.5) and Rhodes Sea (4.8 ± 1.4), but lower than the Ionian Sea (28.5 ± 2.8) and the Cretan Sea (21.7 ± 6) in the Mediterranean. The predation impact of the total Chaetognatha community (13 ± 9.8 , range 3.6 - 30.6) showed a similar trend to that of the *F. enflata* and clearly indicates the significance of this plankton taxon in the trophic energy transfer.

Interestingly, in the upper 100 m, the C and N contents of the Chaetognatha community were 26.4% and 30.7%, of the Copepoda community, which were higher than the estimated predation impact of the total Chaetognatha on the Copepoda (13 ± 9.8). Compared to the copepods, the relatively larger size of the individuals of Chaetognatha as seen also in the high dry mass per individual (Table 2), might have resulted in asymmetry between the ratio of the elemental composition and the predation pressure of Chaetognatha on the Copepoda.

In the subsurface and deeper waters, the Chaetognatha populations of the three mid-depth zones between 100 – 500 m were closely ordinated in the NMDS plot (Fig. 7), most likely attributable to the hypoxic conditions at the mid-depths strata. Similar to the observation in the Arabian Sea, the hypoxic waters exerted a profound impact on the vertical distribution of the Chaetognatha community of the Red Sea, but species like *Sagitta bipunctata* and *Serratosagitta pacifica* which were found to be mostly restricted to upper waters in the northern Arabian Sea (Kusum et al. 2011), were present in most of the depth zones of the Red Sea. Unlike the northern Arabian Sea, the absence of the acute oxygen depleted waters ($DO < 9 \mu\text{mol kg}^{-1}$) in the mid-depth zones of the study region might have permitted these species to inhabit these waters.

The intrusion of GAW plays a role in the spatial variability of the Chaetognatha community in the Red Sea, similar to other plankton taxa, e.g. Foraminifera (Siccha et al. 2009). The upper 150 m

of the southernmost two stations were characterized by relatively low saline, warm, and oxygenated waters which indicated the inflow of GAW into the Red Sea. The importance of the inflow of GAW for the spatial distribution in the Red Sea was also reflected in the high IMD at the two stations in the south with the other sampling locations (Supplementary Table 3). The intragroup β -dissimilarity was also higher in these southernmost stations. The presence of both low saline waters from the Gulf of Aden in the surface and conversely high saline Red Sea Deep Water at depths may contribute to intra-station community dissimilarity at these two stations compared to other locations where salinity was higher (>40). Earlier Casanova (1985) reported *Zonosagitta bedoti* as an indicator of the surface inflow of GAW. The limitation of this species' presence to the southern stations up to 18° N supports this view. In contrast to previous observations which documented the presence of *Pterosagitta draco* mostly in the southern part of the Red Sea (Casanova 1986), *P. draco* was found also in the northern part of the Red Sea in the present study. This implies that the northward advection of GAW influences the distribution of this species farther than expected. This observation also refutes the view of Halim (1969), who noted that the seasonal and geographic distribution of Chaetognatha affords no evidence of dependence on the southern inflow.

In the Red Sea, the gradual increase in salinity from south to north is known to set ecophysiological boundaries for faunal assemblage along the basin's axis, e.g. Foraminifera (Fenton et al. 2000; Siccha et al. 2009). Additionally, the wind jet near the Tokar Gap at 19°N also plays a role in the ecohydrographic division in the Red Sea as it influences the regional circulation (Stubbings 1939; Zhai and Bower 2013; Abdullah et al. 2018). Although, these factors contributed to the β -dissimilarity between the locations of the north and south, the majority of species were observed

at most of the sampling locations in varying abundances. These Indo-Pacific species, due to their euryhaline nature, might have survived in this ocean basin.

Another interesting feature that modulated the vertical distribution of the Chaetognatha community was the convective mixing in the northern Red Sea. The downward inclination of the isolines of salinity, temperature and DO at the northernmost station Duba (Fig. 2) corroborates this notion. Association of Chaetognatha with upwelled or downwelled water has been documented before ascertaining their role as indicators of physical processes (Thiriot 1978; Kusum et al. 2014; Nair et al. 2015; Al-Aidaros et al. 2016). Here, the sinking of water masses associated with the deep water formation in the northern Red Sea is a plausible explanation for higher epipelagic Chaetognatha abundances in deeper layers (Supplementary Table 2).

A total of 17 Chaetognatha species were observed during the present study in the Red Sea. The observed species are all common in the northern Indian Ocean and many of them have Indo-Pacific affinity and are absent from the Atlantic Ocean (Table 1). The importance of *Flaccisagitta enflata* and *Decipisagitta decipens*, the dominant species of the upper 300 m and 300 – 500 m strata, respectively, concurs with the observation in the northern Indian Ocean (Nair et al. 2015) and suggests similarity in Chaetognatha community structure between these two tropical ecoregions. But, the mesopelagic *Eukrohnia fowleri* and *Pseudosagitta maxima*, which often dominate the Chaetognatha community in the 500 – 1000 m depth of the northern Indian Ocean (Kusum et al. 2014), were less numerous. The shallow sill of the Bab-al-Mandab (160 m) connecting the Red Sea and the Arabian Sea is considered to limit the presence of the deeper water species in the Red Sea (Casanova 1986). Nevertheless, the occurrence of mesopelagic species in the upper waters in association with upwelling has been reported before (Kusum et al. 2014, Nair et al. 2015). This process offers a plausible explanation for their presence in the Red

Sea. In fact, the bathypelagic Chaetognatha in the Arabian Sea like *Eukrohnia hamata*, *E. minuta* and *E. bathypelagica* were absent in the Red Sea, indicating the restriction imposed by the shallow sill on their distribution. The scenario of the restricted abundance of mesopelagic species and absence of bathypelagic species in the Mediterranean Sea (Casanova 1986), which is also connected through a shallow sill to the Atlantic Ocean supports that such barriers are important to understand the distribution of the Chaetognatha.

The number of species recorded from the 1000 m of Red Sea was relatively low compared to the northern Indian Ocean or the Pacific Ocean (Nair 1978; Pierrot-Bults and Nair 1991). The less variability in the physical variables in this basin compared to that of Indian Ocean or Pacific Ocean might be the reason for the low diversity in the Chaetognatha community of the Red Sea. Similarly, the lower diversity of Chaetognatha in the Persian Gulf (total 12, Furnestin and Codaccioni 1968; Haghi et al. 2010), another hyperhaline semi-enclosed inlet of the Indian Ocean, further supports the view.

The patterns in vertical abundance and the species diversity distribution seem contradictory as both number of species and the species diversity index reached their maximum not at 0 – 100 m depth, but at 200 – 300 m. The higher abundance in the euphotic zone was mainly attributable to epipelagic species, whereas the abundance at 200 – 300 m was the result of mixed populations of both epipelagic and mesopelagic Chaetognatha species (Table 1), leading to a higher species diversity at this depth compared to the surface waters. This subsurface diversity maximum of Chaetognatha was in accordance with the earlier observation in the Indian Ocean (Nair 1978; Kusum et al. 2011), as well as with those of Copepoda in the Pacific Ocean (Saltzman and Wishner 1997).

The varied physiology and the ecohydrographic interrelations of the different maturity stages of the plankton community can be the discernible factors affecting their vertical distributions in the water column (Capitanio and Esnal 1998). The dominance of the immature population throughout the water column observed in the study was consistent with the earlier observation in the surface water from this basin (Al-Aidaroos et al. 2017). The question if mature stages of Chaetognatha are more sensitive to oxygen deficient waters compared to immature stages was also assessed in the present study. Among the five depth layers, the relatively higher abundances of maturing and matured individuals of epipelagic species in the well-oxygenated upper layer may corroborate the notion that mature organisms, due to their higher oxygen demands for egg and sperm production (Wishner et al. 2000) avoid the hypoxic mesopelagic zones and therefore congregate the upper and deeper waters with higher DO.

In brief, the macroecology of the Chaetognatha community of the Red Sea was governed by a multitude of indigenous characteristics of this unique ocean basin. The distinct water mass characteristics of GAW, characterized by low salinity, high CDOM and low DO concentration (Zarokanellos and Jones 2018), exerted an important role in structuring the Chaetognatha community. The presence of *Zonosagitta bedoti*, for instance, can be viewed as an indicator of the surface inflow of GAW as described by Casanova (1985). The evident high β -dissimilarity between the Chaetognatha community of the southern regions and other sampling locations corroborate the importance of GAW intrusions. The overturning circulation and the sinking of water mass in the north is another physical characteristic of the Red Sea which influenced the vertical distribution of the Chaetognatha community. In addition to this, hypoxic waters in the mid-depth zones of the Red Sea had an important role in the vertical distribution of Chaetognatha. The results of the predation impact and the elemental analysis of Copepoda and

Chaetognatha confirmed the important trophic link between these two prey-predator taxa. The present study providing detailed information on the ecohydrographic drivers that govern the distribution and community structure of a major plankton component of the Red Sea will be important to unravel the macro ecology of this topographically unique but ecologically significant ocean basin in the world ocean.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval

All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

References

- Abdulla CP, Alsaafani MA, Alraddadi TM, Albarakati AM (2018) Mixed layer depth variability in the Red Sea. *Ocean Sci* 14:563-573.
- Al-Aidaros AM, Salama AJ, El-Sherbiny MM (2016) New record and redescription of *Calanopia thompsoni* A. Scott, 1909 (Copepoda, Calanoida, Pontellidae) from the Red Sea, with notes on the taxonomic status of *C. parathompsoni* Gaudy, 1969 and a key to species. *ZooKeys* 552:17-32. doi:10.3897/zookeys.552.6180.
- Al-Aidaros AM, Karati KK, El-Sherbiny MM, Devassy RP, Kürten B (2017) Latitudinal environmental gradients and diel variability influence abundance and community structure of Chaetognatha in Red Sea coral reefs. *Syst Biodivers* 15:35-48.
- Alvariño A (1964). Bathymetric distribution of chaetognaths. *Pac Sci* 18:64-82.
- Anderson MJ, Crist TO, Chase, JM, Vellend M, Inouye BD, Freestone AL, Sanders NJ, Cornell HV, Comita LS, Davies KF, Harrison SP (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecol Lett* 14:19-28.
- Bohata K, Koppelman R (2013) Chaetognatha of the Namibian upwelling region: taxonomy, distribution and trophic position. *PloS one*, 8:e53839.
- Buchanan PJ, Beckley LE (2016) Chaetognatha of the Leeuwin Current system: oceanographic conditions drive epi-pelagic zoogeography in the south-east Indian Ocean. *Hydrobiologia* 763:81-96.
- Capitanio FL, Esnal GB (1998) Vertical distribution of maturity stages of *Oikopleura dioica* (Tunicata, Appendicularia) in the frontal system off Valdés Peninsula, Argentina. *B Mar Sci* 63:531-539.

486 Casanova JP (1985) Les Chaetognathes de la Mer Rouge. Rapp. P.-v. Reun Commn Int Explor
487 Scient Mer Mediterr 29:269-274.

488 Casanova JP (1986) Similarity of plankton distribution patterns in two nearly land-locked seas:
489 the Mediterranean and the Red Sea. In: Pierrot-Bults AC, van der Spoel S, Zahuranec BJ,
490 Johnson RK (Eds.) UNESCO technical paper in Marine Science, 49:42-46.

491 Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/Tutorial. Plymouth, UK: PRIMER-E
492 Ltd.

493 Devassy RP, El-Sherbiny MM, Al-Sofyani AM, Al-Aidaros AM (2017) Spatial variation in the
494 phytoplankton standing stock and diversity in relation to the prevailing environmental
495 conditions along the Saudi Arabian coast of the northern Red Sea. Mar Biodivers 47:995-
496 1008.

497 Ducret F (1973). Contribution à l'étude des chaetognathes de la Mer Rouge. Beaufortia 20: 135-
498 153.

499 Echelman T, Fishelson L (1990) Surface zooplankton dynamics and community structure in the
500 Gulf of Aqaba (Eilat), Red Sea. Mar Biol 107:179-190.

501 El-Sherbiny MM, Hanafy MH, Aamer MA (2007) Monthly Variations in Abundance and
502 Species Composition of the Epipelagic Zooplankton off Sharm El-Sheikh, Northern Red
503 Sea. Res J Environ Sci 1:200-210.

504 El-Sherbiny MM, Al-Aidaros AM (2017) A new species of *Calanopia* (Copepoda, Calanoida,
505 Pontellidae) from the plankton of the central Red Sea. Mar Biodivers 47:1137-1145.

506 Fenton M, Geiselhart S, Rohling EJ, Hemleben C (2000) A planktonic zones in the Red Sea. Mar
507 Micropaleontol 40:277-294.

508 Furnestin ML, Codaccioni JC (1968) Chaetognathes du Nord-Ouest de l'Océan Indien (golfe
509 d'Aden, Mer d'Arabie, golfe d'Oman, golfe Persique). Cah ORSTOM Sér Océanogr
510 6:143-171.

511 Giesecke R, González HE (2004) Feeding of *Sagitta enflata* and vertical distribution of
512 Chaetognatha in relation to low oxygen concentrations. J Plankton Res 26:475-486.

513 Giesecke R, González HE (2012) Distribution and feeding of chaetognaths in the epipelagic zone
514 of the Lazarev Sea (Antarctica) during austral summer. Polar Biol 35:689-703.

515 Gotsis-Skretas O, Pagou K, Moraitou-Apostolopoulou M, Ignatiades L (1999) Seasonal
516 horizontal and vertical variability in primary production and standing stocks of
517 phytoplankton and zooplankton in the Cretan Sea and the Straits of the Cretan Arc
518 (March 1994–January 1995). Prog Oceanogr 44:625-649.

519 Grasshoff K (1969) Zur Chemie des Roten Meeres und des Inneren Golfs von Aden nach
520 Beobachtungen von FS "Meteor" während der Indischen Ozean Expedition 1964/65
521 Meteor Forschungsergebnisse, Deutsche Forschungsgemeinschaft, Reihe A Allgemeines,
522 Physik und Chemie des Meeres. Gebrüder Bornträger, Berlin, Stuttgart, pp 1-76.

523 Haghi M, Savari A, Madiseh SD, Zakeri M (2010) Abundance of pelagic chaetognaths in
524 northwestern Persian Gulf. Plankton Benthos Res 5:44-48.

525 Halim Y (1984) Plankton of the Red Sea and the Arabian Gulf. Deep Sea Res I 31:969-982.

526 Harris R, Wiebe P, Lenz J, Skjoldal HR, Huntley ME (eds) 2000. ICES Zooplankton
527 Methodology Manual. Academic Press, London.

528 Kehayias G (2003) Quantitative aspects of feeding of chaetognaths in the eastern Mediterranean
529 pelagic waters. J Mar Biol Ass UK 83:559-569.

530 Kimmerer WJ (1984) Selective predation and its impact on prey of *Sagitta enflata*
531 (Chaetognatha). Mar Ecol Prog Ser 15:55-62.

532 Kürten B, Khomayis HS, Devassy R, Audritz S, Sommer U, Struck U, El- Sherbiny MM, Al-
533 Aidaroos AM (2014) Ecohydrographic constraints on biodiversity and distribution of
534 phytoplankton and zooplankton in coral reefs of the Red Sea, Saudi Arabia. Mar Ecol
535 36:1195-1214.

536 Kürten B, Khomayis HS, Devassy R, Audritz S, Sommer U, Struck U, El-Sherbiny MM, Al-
537 Aidaroos AM (2015) Ecohydrographic constraints on biodiversity and distribution of
538 phytoplankton and zooplankton in coral reefs of the Red Sea, Saudi Arabia. Mar Ecol
539 36:1195-1214.

540 Kürten B, Al-Aidaroos AM, Kürten S, El-Sherbiny MM, Devassy RP, Struck U, Zarokanellos N,
541 Jones BH, Hansen T, Bruss G, Sommer U (2016) Carbon and nitrogen stable isotope
542 ratios of pelagic zooplankton elucidate ecohydrographic features in the oligotrophic Red
543 Sea. Prog Oceanogr 140:69-90.

544 Kusum KK, Vineetha G, Raveendran TV, Muraleedharan KR, Nair M, Achuthankutty CT
545 (2011) Impact of oxygen-depleted water on the vertical distribution of Chaetognatha in
546 the northeastern Arabian Sea. Deep Sea Res Part I 58:1163-1174.

547 Kusum KK, Vineetha G, Raveendran TV, Muraleedharan KR, Biju A, Achuthankutty CT (2014)
548 Influence of upwelling on distribution of Chaetognatha (zooplankton) in the oxygen
549 deficient zone of the eastern Arabian Sea. Cont Shelf Res 78:16-28.

550 Lima ME (2014) Characterization of zooplankton communities associated with an anticyclonic
551 Eddy in the northeast of the islands of Cabo Verde. Doctoral dissertation, Universidade
552 de Cabo Verde.

553 Maillard C, Soliman G (1986) Hydrography of the Red-Sea and exchanges with the Indian-
 554 Ocean in summer. *Oceanol Acta* 9:249-269.

555 McLaren IA (1969). Population and production ecology of zooplankton in Ogac Lake, a
 556 landlocked fiord on Baffin Island. *J Fish Res Board Canada* 26:1485-1559.

557 Miller AR (1964) Highest salinity in the world ocean. *Nature* 203:590-591.

558 Nagai N, Tadokoro K, Kuroda K, Sugimoto T (2006) Occurrence characteristics of
 559 Chaetognatha species along the PM transect in the Japan Sea during 1972–2002. *J*
 560 *Oceanogr* 62:597-606.

561 Nair VR (1978) Bathymetric distribution of Chaetognatha in the Indian Ocean. *Indian J Mar Sci*
 562 7:276–82.

563 Nair VR (2003) Digitized inventory of marine bioresources. Chaetognatha. National Institute of
 564 Oceanography. www.nio.org/index/option/comnomenu/task/show/tid/2/sid/18/id/6

565 Nair VR, Kusum KK, Gireesh R, Nair M (2015) The distribution of the Chaetognatha population
 566 and its interaction with environmental characteristics in the Bay of Bengal and the
 567 Arabian Sea. *Mar Biol Res* 11:269-282.

568 Øresland V (2000) Diel feeding of the chaetognath *Sagitta enflata* in the Zanzibar Channel,
 569 western Indian Ocean. *Mar Ecol Prog Ser* 193:117-123.

570 Pierrot-Bults AC, Nair VR (1991) Distribution patterns in Chaetognatha. In: Bone Q, Kapp H,
 571 Pierrot-Bults AC (Eds.) *The Biology of Chaetognatha*. Oxford University, pp 86-116.

572 Reeve MR (1980) Comparative experimental studies on the feeding of chaetognaths and
 573 ctenophores. *J Plank Res* 2:381-393.

574 Saltzman J, Wishner KF (1997) Zooplankton ecology in the eastern tropical Pacific oxygen
 575 minimum zone above a sea- mount: 1. General trends. *Deep-Sea Res I* 44:907–930.

576 Siccha M, Trommer G, Schulz H, Christoph H, Kucera M (2009) Factors controlling the
 577 distribution of planktonic foraminifera in the Red Sea and implications for the
 578 development of transfer functions. *Mar Micropaleontol* 72:146-156.

579 Sofianos SS, Johns WE (2002) An oceanic general circulation model (OGCM) investigation of
 580 the Red Sea circulation, 1. Exchange between the Red Sea and the Indian Ocean. *J*
 581 *Geophys Res: Oceans*, 107(C11).

582 Sofianos SS, Johns WE (2003) An oceanic general circulation model (OGCM) investigation of
 583 the Red Sea circulation: 2. Three- dimensional circulation in the Red Sea. *J Geophys*
 584 *Res: Oceans*, 108(C3).

585 Sofianos SS, Johns WE (2007), Observations of the summer Red Sea circulation, *J Geophys Res*
 586 112(C6), C06025, doi:10.1029/2006jc003886.

587 Stubbings HG (1939) The marine deposits of the Arabian Sea: an investigation into their
 588 distribution and biology. Trustees of the British Museum, London.

589 Terazaki M (2013) Feeding of Carnivorous Zooplankton, Chaetognatha. *Dynamics and*
 590 *Characterization of Marine Organic Matter*, 2, p.257.

591 Thiriot A (1978) Zooplankton communities in the west African upwelling area. In: Boje R,
 592 Tomczak M (Eds.) *Upwelling ecosystems*. Springer-Verlag, Berlin, p32-61.

593 Vanden Wollenberg AL. (1977). Redundancy analysis. An alternative for canonical correlation
 594 analysis. *Psychometrika* 42:207–219.

595 Warwick RM, Clarke KR (1993) Taxonomic distinctness and environmental assessment. *J Appl*
 596 *Ecol* 35, 532e543.

597 Wiebe PH, Allison D, Kennedy M, Moncoiffé G (2014) A vocabulary for the configuration of
 598 net tows for collecting plankton and micronekton. *J Plank Res* 37: 21-27

- Wishner KF, Ashjian CJ, Gelfman C, Gowing MM, Kann L, Levin LA, Mullineaux LS,
Saltzman J (1995) Pelagic and benthic ecology of the Eastern Tropical Pacific oxygen
minimum zone. *Deep-Sea Res I* 42:93-115.
- Wishner KF, Gowing MM, Gelfman C (2000) Living in suboxia: ecology of an Arabian Sea
oxygen minimum zone copepod. *Limnol Oceanogr* 45:1576–1593.
- Yoon H, Ko AR, Kang JH, Choi JK, Ju SJ (2016) Diet of Chaetognatha *Sagitta crassa* and *S.*
nagae in the Yellow Sea Inferred from Gut Content and Fatty Acid Analyses. *Ocean*
Polar Res 38:5-46.
- Zarokanellos ND, Jones BH (2018) Winter mixing, mesoscale eddies and eastern boundary
current: Engines for biogeochemical variability of the central Red Sea during winter/early
spring period. *Biogeosciences Discuss* 2018: 1-44 doi 10.5194/bg-2017-544.
- Zhai P, Bower A (2013) The response of the Red Sea to a strong wind jet near the Tokar Gap in
summer. *J Geophys Res Oceans* 118:422-434.
- Zo Z (1973). Breeding and growth of the Chaetognatha *Sagitta elegans* in Bedford basin. *Limnol*
Oceanogr 18:750-756.

Figures

Figure 1: Sampling locations in the Red Sea. At the Nereus deep, only physical and chemical variables were measured.

Figure 2: Distribution of (a) temperature ($^{\circ}\text{C}$), (b) salinity, and (c) dissolved oxygen ($\mu\text{mol kg}^{-1}$),
in the upper 1000 m of the Red Sea in April 2012.

Figure 3: Percentage contribution of each Chaetognatha species to total Chaetognatha abundance in each depth layer.

659 Figure 4: The weighted mean depths (Z_m) of the species of Chaetognatha. (Error bar = ± 1 SD).

Figure 5: Maturity stage-wise percentage (%) composition of the species of Chaetognatha at (a) – 100 m, (b) 100 – 200 m, (c) 200 – 300 m, (d) 300 – 500 m, and (e) 500 – 1000 m.

Figure 6: The ratio of the abundance of the Copepoda and Chaetognatha along the depth layers.
(The lower and upper whiskers display the minimum and maximum values, and the center line in the box indicates the median).

Figure 7: The NMDS plot exhibiting similarity (a) among the depth layers based on the abundance of Chaetognatha species, and (b) among the Chaetognatha species based on their abundance along the depth layers in the station locations. The acronyms of the Chaetognatha species are shown in Table 1.

Figure 8: The RDA triplot of interrelationships of individual Chaetognatha species with abiotic variables, and Copepoda in the (a) upper 200 m, and (b) 200 – 1000 m. The acronyms of the Chaetognatha species are displayed in Table 1.

Table 1: Abundance of the Chaetognatha (ind m⁻³) in five depth strata in the Red Sea. Along with this ocean basin, their presence and nature of habitat in the tropical region of the three major ocean, and in the Persian Gulf are displayed (AC – Acronyms, RS – Red Sea, PO – Pacific Ocean, IO – Indian Ocean, AO – Atlantic Ocean, PG – Persian Gulf; E – epipelagic, M – Mesopelagic). Excluding the present study, the information on the global distribution of Chaetognatha are based on Alvarino 1964, Nair 1978, Pierrot-Bults & Nair 1991, Nair et al. 2015 and other published literatures.

Species	AC	0-100m	100-200m	200-300m	300-500m	500-1000m	PO	IO	AO	PG
<i>Aidanosagitta neglecta</i>	Ane	0.263±0.22	0.043±0.06	0.001±0.004	0	0.004±0.008	E	E	-	E
<i>Aidanosagitta ocellata</i>	Aoc	0	0	0.01±0.02	0	0	E	E	-	-
<i>Aidanosagitta regularis</i>	Are	0.331±0.52	0.008±0.015	0.002±0.005	0.005±0.008	0.004±0.008	E	E	-	-
<i>Decipisagitta decipiens</i>	Dde	0.12±0.11	0.044±0.076	0.230±0.267	0.148±0.13	0.05±0.04	M	M	M	M
<i>Eukrohnia fowleri</i>	Efo	0	0	0.009±0.016	0.07±0.08	0.04±0.05	M	M	M	-
<i>Flaccisagitta enflata</i>	Fen	3.086±2.04	0.169±0.16	0.23±0.19	0.094±0.12	0.01±0.009	E	E	E	E
<i>Flaccisagitta hexaptera</i>	Fhe	0.865±0.6	0.024±0.03	0.045±0.05	0.027±0.018	0.014±0.02	E	E	E	E
<i>Ferosagitta ferox</i>	Ffe	0.469±0.71	0.015±0.02	0.068±0.117	0.03±0.034	0.007±0.01	E	E	-	E
<i>Ferosagitta robusta</i>	Fro	0.091±0.22	0.010±0.025	0.026±0.04	0.066±0.09	0.014±0.02	E	E	-	E
<i>Krohnitta pacifica</i>	Kpa	0.472±0.35	0.043±0.056	0.014±0.021	0.012±0.02	0.003±0.008	E	E	E	E
<i>Krohnitta subtilis</i>	Ksu	0.089±0.079	0.040±0.06	0.116±0.15	0.053±0.08	0.023±0.03	E	E	E	-
<i>Pterosagitta draco</i>	Pdr	0.053±0.089	0	0.008±0.016	0.007±0.01	0	E	E	E	E
<i>Pseudosagitta maxima</i>	Pma	0	0	0.007±0.016	0.016±0.02	0.014±0.02	M	M	M	-
<i>Sagitta bipunctata</i>	Sbi	0.09±0.11	0.031±0.029	0.076±0.09	0.052±0.05	0.004±0.008	E	E	E	-
<i>Serratosagitta pacifica</i>	Spa	0.091±0.22	0.024±0.04	0.059±0.12	0.055±0.06	0.005±0.008	E	E	-	-
<i>Zonosagitta bedoti</i>	Zbe	0.082±0.13	0.008±0.019	0.017±0.04	0	0	E	E	-	E
<i>Zonosagitta pulchra</i>	Zpu	0.334±0.27	0.013±0.017	0.02±0.04	0.002±0.005	0	E	E	-	-

708 Table 2: Average dry weight (mg ind⁻¹) of the individuals and the elemental composition
709 (percentage of C and N) of Chaetognatha and different genus of Copepoda

	mg ind ⁻¹	C%	N%
<i>Chaetognatha</i>	0.334522	34.12	9.09
<i>Candacia</i>	0.077998	40.57	10.53
<i>Corycaeus</i>	0.004868	38.08	7.44
<i>Eucalanus</i>	0.091634	41.71	12.58
<i>Euchaeta</i>	0.115148	42.17	10.33
<i>Nannocalanus</i>	0.043338	40.98	9.57
<i>Pleuromamma</i>	0.065446	44.66	11.8
<i>Pontellina</i>	0.078694	37.83	7.96
<i>Macandrewella</i>	0.247665	42.48	11.33
<i>Macrosetella</i>	0.004401	50.75	7.09
<i>Rhincalanus</i>	0.158483	51.65	7.36
<i>Copilia</i>	0.034461	23.38	5.36
Oncaeidae	0.00684	42.02	8.96
<i>Oithona</i>	0.003708	18.07	4.23
<i>Sapphirina</i>	0.023054	41.99	11.11
<i>Undinula</i>	0.149606	42.9	11.3

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