Biomass, abundance and trophic position of Chaetognatha species in the Namibian Upwelling Region

Master Thesis

Karolina Bohatá

born 31st March 1982 in Prague

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1. Supervisor: Prof. Dr. Christian Möllmann

2. Supervisor: Dr. Rolf Koppelmann

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i. Abstract

The vertical distribution of Chaetognatha species and their maturity stages were investigated in October 2010 at four stations located off Walvis Bay, Namibia, using a multiple closing net (double $1m^2$ – MOCNESS). 17 species were found and classified as pelagic, shallow-mesopelagic, deep-mesopelagic and bathypelagic species based upon the weighted mean depth derived from their average vertical distribution. High densities of Chaetognatha were found in the upper 100 m at all stations of the Walvis Bay transect. A maximum abundance of the Chaetognatha was found at the outer shelf station near the surface. The community was dominated by species of *Serratodentata* group. No clear differentiation could be established for the ontogenetic distribution of Chaetognatha species. Only juveniles of *Sagitta macrocephala, Sagitta lyra, Sagitta enflata, Sagitta sibogae, Sagitta planctonis, Sagitta zetesiois* and *Eukrohnia hamata* were observed. The richness and diversity of Chaetognatha species increased from the shelf to the open ocean. The eveness of the distribution of individuals was highest within the different Chaetognatha species at the shelf break and offshore stations. The vertical distribution of Chaetognatha species was more influenced by prey densities than by water properties. Chaetognatha were very abundant at the investigated stations and could possibly affect the standing stock of the prey.

Stable isotope ratios of Chaetognatha were determined for seven different areas located on the shelf, at the shelf break and offshore northern Namibia. The values of $\delta^{15}N$ ranged from 6.05 to 11.39 ‰ and the $\delta^{13}C$ values varied between -23.89 and -17.03 ‰. The highest values of $\delta^{15}N$ were observed at the Walvis Bay shelf break station. The lowest $\delta^{13}C$ values were found at the Rocky Point offshore station, which was significantly different from all other areas. The reason for these low values may be the different environmental parameters like temperature, turbulence or water mixing. Stable isotopes of carbon and nitrogen were determined for four taxa (*Sagitta minima, Planctonis* group*, Sagitta enflata, Sagitta decipiens*). The values of $\delta^{15}N$ ranged from 6.17 to 10.38 ‰ and the $\delta^{13}C$ values ranged from -22.70 to -21.56 ‰. The lowest $\delta^{15}N$ values were found for S. minima, which may be influenced by the slender prey composition. The C- and N- content of these species (*S. minima, S. zetesiois/S. planctonis, S. enflata, S. decipiens*) were also investigated. The C:N ratio of Chaetognatha ranged between 5.25 and 6.20. This high values have an origin in the larger amount of fat which was saved to help to survive periods of poor food concentrations that is so typical for pulsed Upwelling. This study provides important data for the understanding of trophic relationships in the Benguela Upwelling System and can help to calculate material fluxes within the pelagic food web.

ii. Zusammenfassung

Die vertikale Verteilung und taxonomische Zusammensetzung der Chaetognatha (Pfeilwürmer) wurde in dieser Arbeit untersucht. Im Oktober 2010 wurde an vier Stationen auf einem Transekt vom Schelf bis in den offenen Ozean vor Walvis Bay, Namibia, Zooplankton mithilfe eine Multischließnetzes (1m² - Doppel-MOCNESS) gewonnen. Es wurden insgesamt 17 Arten gefunden und als epipelagisch, flach-mesopelagisch, tief-mesopelagisch und bathypelagisch klassifiziert. Diese Klassifizierung basierte auf den gewichteten mittleren Tiefen (weighted mean depth). Entlang des Walvis Bay Transektes wurden die höchsten Abundanzen in den oberen 100 m gefunden. Die höchste Häufigkeit wurde am äußeren Schelf beobachtet. Die Analyse der ontogenetischen Verteilung einzelner Chaetognatha Arten ergab keine klaren Unterschiede. Bei den Arten *Sagitta macrocephala, Sagitta lyra, Sagitta enflata, Sagitta sibogae, Sagitta planctonis, Sagitta zetesiois* und *Eukrohnia hamata* wurden nur juvenile Vertreter gefunden. Arten der *Serratodentata* Gruppe dominierten die Chaetognatha-Gemeinschaft. Die Artenzahl und die Diversität der Chaetognatha nahmen vom Schelf in den offenen Ozean zu. Auch der Index für die Artengleichheit war an der Schelfkante und im offenen Ozean am höchsten. Die vertikale Verteilung der Chaetognatha Arten wird anscheinend mehr von der Abundanz der Beute als von den Wassermassen beeinflusst. An den untersuchten Stationen waren Chaetognatha sehr abundant und haben höchstwahrscheinlich die Abundanz der Beute, hauptsächlich Copepoda, beeinflusst.

Die stabilen Kohlenstoff und Stickstoff Isotope der Chaetognatha wurden an sieben Stationen im nördlichen Teil des Benguelas Auftriebsgebiets bestimmt. Die $\delta^{15}N$ Werte reichten von 6,05 bis 11,39 ‰ und die $\delta^{13}C$ Werte von -23,89 bis -17,03 ‰. Die höchsten $\delta^{15}N$ Werte wurden an der Schelfkante des Walvis Bay Transektes gemessen. Die niedrigsten $\delta^{15}N$ Werte wurden an der Schelfkante des Rocky Point Transektes gefunden. Die $\delta^{13}C$ Werte waren im offenen Ozean auf dem Rocky Point Transekts am niedrigsten und unterschieden sich signifikant von allen anderen Stationen. Die Ursache für diese niedrigen Werte könnte in den unterschiedlichen Umweltbedingungen wie Temperatur, Turbulenz oder Wasserdurchmischung liegen. Außerdem wurden die stabilen Isotope für vier Taxa (*Sagitta minima, Planctonis* group*, Sagitta enflata, Sagitta decipiens*) bestimmt. Die $\delta^{15}N$ Werte lagen zwischen 6,17 und 10,38 ‰ und $\delta^{13}C$ Werte zwischen -22,70 und -21,56 ‰. Die niedrigsten $\delta^{15}N$ Werte wurden für *S. minima* bestimmt. Diese niedrigen Werte sind auf die unterschiedliche Beutezusammenstzung zurückzuführen. Da das Beutespektrum von *S. minima* im Vergleich zu den anderen untersuchten Arten am kleinsten ist. Zusätzlich wurden die C- und N-Gehalte von *S. minima, S. zetesiois/S. planctonis, S. enflata, S. decipiens* ermittelt. Das C:N Verhältnis war im Vergleich zu Literaturwerten relativ hoch und reichte von 5,25 bis 6,20. Die Ursache für diese hohen Werte kann in der Einlagerung von Fett im Körper liegen, um nahrungsarme Zeiten in einem pulsierenden Auftriebsgebiet zu überdauern. Diese Arbeit liefert wichtige Daten zu den trophischen Beziehungen in Benguela Auftriebsgebiet und dient der Abschätzung von Materialflüssen im marinen Nahrungsnetz.

1. Introduction

Chaetognatha are an important group of carnivorous zooplankton in pelagic food webs (Clark *et al.,* 2001) and have been studied since the eighteenth century (Jennings *et al*., 2010 and references therein). They were present in the Early Cambrian (Vannier *et al*., 2006) and in the Middle Cambrian Burgess Shale (Szaniawski, 2005) since 542 million years ago. Chaetognatha are transparent marine metazoans living in all marine habitats (Vannier *et al*., 2007). Some Chaetognatha species act as indicators of water masses, since they are related to specific environmental variables (Casanova, 1999).

The phylum Chaetognatha comprised over 120 species (Jennings *et al*., 2010; Harzsch & Wanninger, 2010 and references therein). The position of Chaetognatha within the bilaterians still remains unclear. The molecular phylogeny of these organisms has been proven to be problematic, making their placement in the animal systematics difficult (Papillon *at al*., 2004; Marlétaz & Le Parco, 2008 and references therein). Morphological features such as the secondary mouth formation, a mesoderm derived directly from the archenteron and a trimeric coelom have been inferred to place Chaetognatha within the Deuterostomia (Helfenbein *et al*., 2004 and references therein). Some other studies speculate that Chaetognatha diverged from the triploblast lineage before the deuterostome/protostome split (see Helfenbein *et al*., 2004).

The body length of Chaetognatha ranges from 2 to 120 mm. Chaetognatha have a relatively simple body structure supplemented by some complex internal structures (Jennings *et al*., 2010). Their body is transparent to semi-opaque and sometimes partially pigmented. It consists of the head, trunk and tail (Figure 1). One or two pairs of lateral fins and a tail fin make Chaetognatha fast and very good swimmers. The head provides hooks, a vestibular organ and one or two rows of teeth (Casanova, 1999). Chaetognatha perform hermaphroditic reproduction (Jennings *et al.,* 2010 and references therein). Eggs of pelagic species are generally laid free in the water. Despite their small size, these marine predators play an important role in the food web (Casanova, 1999) and in the planctonic ecosystem (Marlétaz & Le Parco, 2008 and references therein).

Chaetognatha can be found at all depths from the surface to several thousands meters deep. The main parameters which influence the vertical distribution are temperature, age of specimens and light intensity (Casanova, 1999). Marazzo & Nogueira (1996) suggested that also copepod density could play an important role for the spatial and temporal distribution of Chaetognatha. Another studies assumed that low oxygen contents also reduce the abundance of Chaetognatha (Giesecke & Gonzáles, 2004; Kusum *et al*., 2011). This could be connected to the lower copepod density in these layers (Giesecke & Gonzáles, 2004). Many Chaetognatha species undertake ontogenetic migrations (Kehayias *et al*., 1994 and references therein) moving to deeper layers for spawning (Banse, 1964).

Chaetognatha are active predators grasping prey with rigid hooks (Casanova, 1999 and references therein). The typical and numerically dominant prey of Chaetognatha are copepods, but larger organisms such as fish larvae (Pearre, 1982), polychaeta (Giesecke & Gonzáles, 2004) or euphausiids are also captured. Chaetognatha prey even on their own. This behaviour of Chaetognatha is influenced by prey abundance and predator size (Pearre, 1982).

Some authors have recently reported on the distribution, feeding and diel migration of Chaetognatha species in the Benguela Upwelling Region (Clark *et al*., 2001; Duró *et al*., 1994; Gibbons, 1994). However, only one study from Duró and Gili (1996) described the influence of different water masses in the upwelling area on the horizontal and vertical distribution of Chaetognatha along an onshore-offshore transect off Walvis Bay, Namibia. Several studies were undertaken on the trophic position of Chaetognatha in the food web, but little is known about this topic in the Benguela Upwelling System. This study will investigate the vertical and horizontal distribution of the Chaetognatha with emphasis on the ontogenetic development and the trophic position of selected species in the Benguela upwelling system.

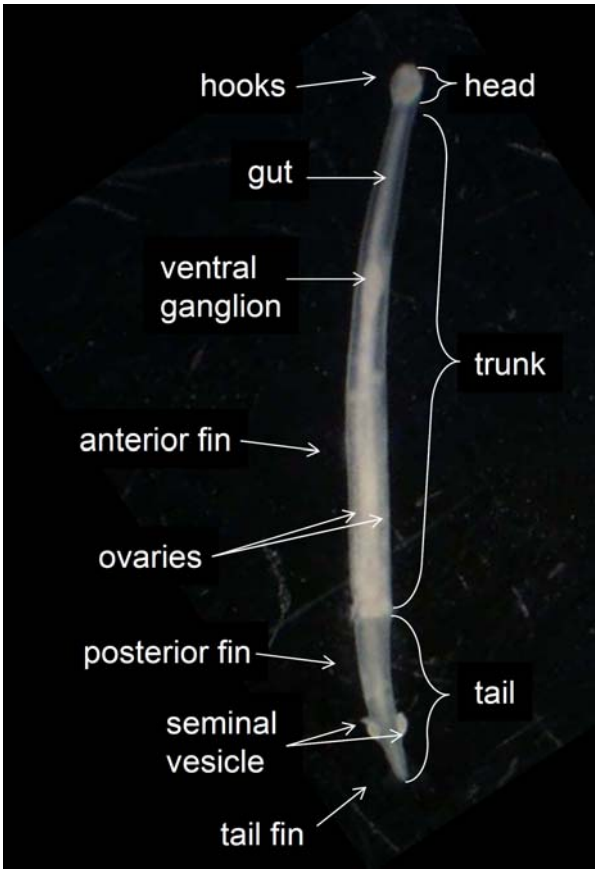

Fig. 1 *Body structure of Chaetognatha (S. serratodentata) showing main body features*

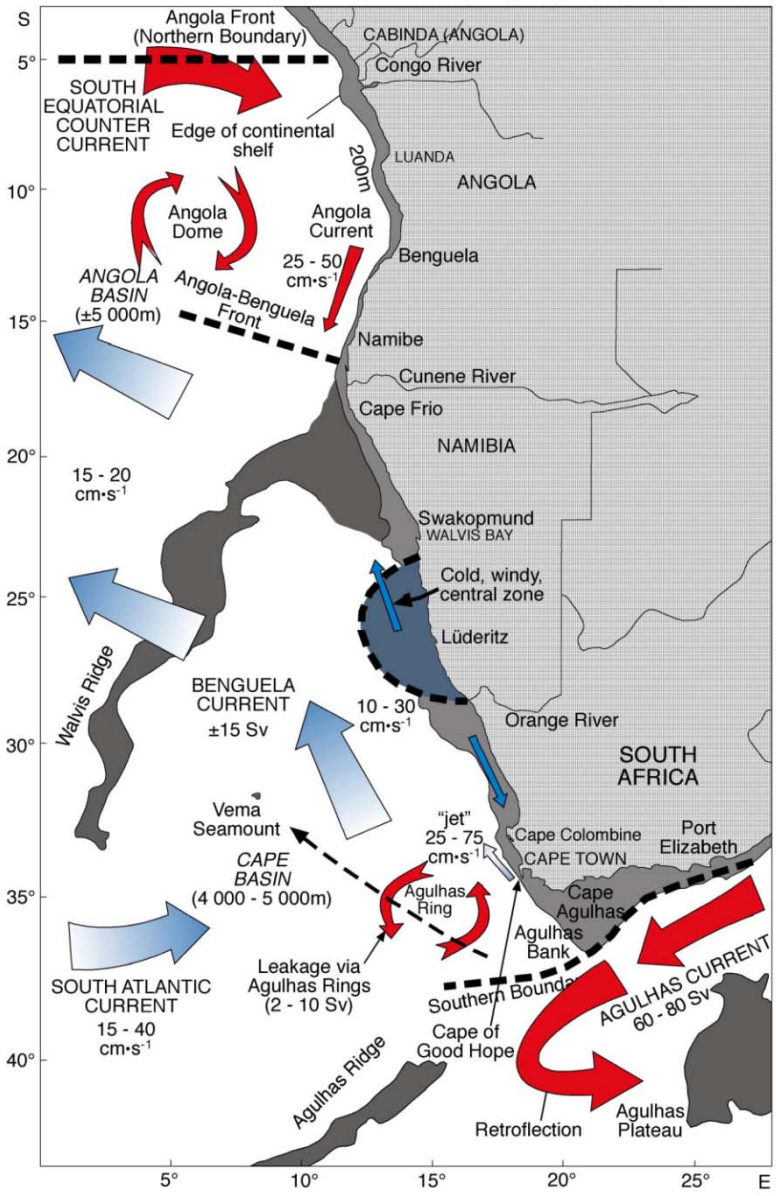

Fig. 2 *External and internal boundaries of the Benguela Current Large Marine Ecosystem, bathymetric features and surface currents (Shannon & O`Toole, 2003).*

2. Material and methods

2.1. Study area

Upwelling systems are special features within the world's coastal regions due to their high content of biomass and energy (Duró and Gili, 1996 and references therein). In the southern hemisphere, upwelling occurs when trade winds persistently blow northwards along the coast and the surface ocean water is transported offshore by the Coriolis deflection (Figure 2; Abel & McConnell, 2010). The resulting Ekman transport has a component perpendicular to the coastline. The current direction of the surface layer is 45° and the net water transport (Ekman transport) is 90° to the left of the wind direction (Denny & Gaines, 2007). The water deficit is replaced by deep water with a high concentration of nutrients, fostering the primary production in the euphotic zone and resulting in a productive food web (Cole & McGlade, 1998 and references therein).

The Benguela Upwelling System (BUS) is one of the major eastern boundary upwelling systems of the world (Hutchings *et al*., 2009). It is situated off the west coast of Africa between 15-37°S and 0-20°E. The BUS spans from Cape of Good Hope, in the south, along the southern coast of South Africa into Angolan waters (Shannon & O`Toole, 2003) and is influenced by along-shore winds (Nelson & Hutchings, 1983). The southern Benguela system is impacted by oceanographic processes, happening in the North Atlantic and the Indo-Pacific Oceans. From the Indo-Pacific, warm surface water moves into the Atlantic Ocean mostly in ring-formations, shed from the reflection of the Agulhas current (Shannon & O`Toole, 2003). The northern Benguela system is affected by the Angola-Benguela Front, resulting in seasonal and inter-annual changes of the intensity of upwelling cells at Cape Frio and Lüderitz and the occurrence of low-oxygen waters (Hutchings *et al*., 2009).

2.2. Sample collection

Zooplankton samples were taken on the British research vessel Discovery, cruise 356, at several locations off Namibia in September and October 2010 (Figure 3). Different types of nets were used at various depths and in different ways to collect the zooplankton (see below). The material for the determination of the Chaetognatha distribution was collected at 4 stations on the Walvis Bay transect (Figure 3, Table 1). Stations were located on the inner (WB1) and outer shelf (WB2), on the shelf break (WB3) and offshore (WB4). The samples were taken with a double 1m²-MOCNESS (Multiple Opening and Closing Net and Environmental Sensing System). It consists of 18 nets of 333 µm mesh size, which can be sequentially opened and closed at different water depths. The towing speed was 2 knots by a heaving speed of 0.5 $m.s^{-2}$. The double 1m²-MOCNESS is equipped with a flow meter. The volume filtered through each net was determined by the MOCNESS program, taking the towing angle

into account. Temperature, salinity and oxygen related to the depth of the water column were measured with a CTD (Seabird 911+) at all sampled stations.

After rinsing the nets with seawater, the zooplankton material was concentrated and fixed in a 4% formaldehyde-seawater solution buffered with sodium-tetraborate.

Samples for the determination of stable isotopes were taken with different nets (double 1m²-MOCNESS, WP-2, Ring Trawl, Driftnet) at 9 stations (SI1 – SI9) located on the shelf, on the shelf break and offshore north of Walvis Bay (Figure 3; Table 2). The WP-2 net has a mesh size of 300 µm and was towed vertically from 50 m depth to the surface. The Ring Trawl has a mesh size of 1000 µm and was towed horizontally over the stern. The driftnet, mesh size 30 µm, was released into the water and then dislodged by the current. The samples were rinsed in fresh water and deep frozen at - 80°C.

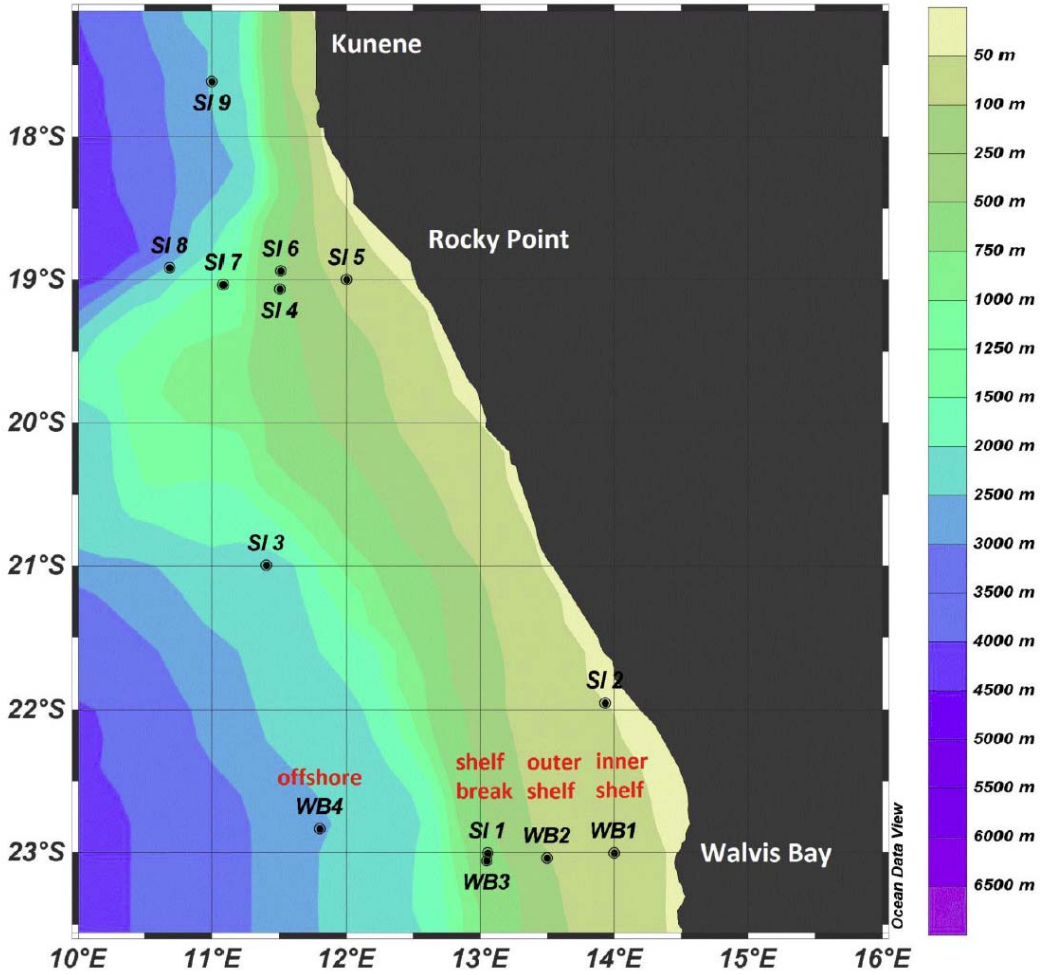

Fig. 3 *Research area with all sampled stations (SI = stable isotope samples; WB = samples for taxonomy and distribution)*

Tab. 1 *Sampling data for the analysis of the vertical and horizontal distribution of Chaetognatha species. Local time = UTC + 2h; n = night, d = day*

Ship station	Station name	Date	UTC	Latitude (Start)	Longitude (Start)	Water depth [m]	Haul intervals [m]
18	WB1 inner shelf	22.09.2011	21:43 (n)	23°32'S	14°03'N	132	100-50-25-0
17	WB2 outer shelf	22.09.2011	00:02 (n)	23°00'S	13°30'N	231	150-100-50-25-0
15	WB3 shelf break	19.09.2011	22:20 (n)	23°01'S	13°03'N	437	350-300-250-200-150-100-50-25-0
16	WB4 offshore	20.09.2011	17:16 (n)	22°50'S	11°47'N	2998	2620-2500-2250-2000-1750-1500-1250-1000-800-600-400-200-100-50-25-0

Tab.2 *Sampling data for the stable isotopes analysis of the areas (a) and species (b); n = night, d = day*

(a)

Ship station	Station name	Date	UTC	Latitude (Start)	Longitude (Start)	Number of subsamples	Water depth [m]	Net	Sampling depth [m]
43	SI1	08.10.2011	08:47 (d)	22°59'S	13°02'E	5	391	MOCNESS	300 - 0
19	SI2	24.09.2011	16:40 (d)	21°57'S	13°55'E	4	56	WP-2	50 - 0
22	SI3	27.09.2011	07:20 (d)	19°02'S	10°23 'E	9	2151	Driftnet	0 - 2
28	SI4	30.09.2011	01:02 (n)	19°04'S	11°30'E	1	200	MOCNESS	25 - 0
28	SI4	30.09.2011	01:02 (n)	19°04'S	11°30'E	6	200	MOCNESS	50 - 25
28	SI4	30.09.2011	01:02 (n)	19°04'S	11°30'E	4	200	MOCNESS	100 - 50
26	SI5	29.09.2011	12:04 (d)	19°00'S	12°00'E	2	198	MOCNESS	100 - 0
25	SI6	29.09.2011	00:26 (n)	18°56'S	11°30'E	8	285	MOCNESS	250 - 0
24	SI7	28.09.2011	22:30 (n)	19°02'S	11°04'E	13	1050	Ring Trawl	50 - 0
32	SI8	02.10.2011	14:20 (d)	18°14'S	10°50'E	3	3173	MOCNESS	50 - 25
32	SI8	02.10.2011	14:20 (d)	18°14'S	10°50'E	2	3173	MOCNESS	100 - 50
32	SI8	02.10.2011	14:20 (d)	18°14'S	10°50'E	3	3173	MOCNESS	200 - 100
32	SI8	02.10.2011	14:20 (d)	18°14'S	10°50'E	2	3173	MOCNESS	400 - 200
32	SI8	02.10.2011	14:20 (d)	18°14'S	10°50'E	3	3173	MOCNESS	600 - 400
32	SI8	02.10.2011	14:20 (d)	18°14'S	10°50'E	3	3173	MOCNESS	800 - 600
29	SI9	01.10.2011	23:15 (n)	17°36'S	11°00'E	1	112	Ring Trawl	50 - 0

(b)

Species	Ship station	Station name	Date	UTC	Latitude (Start)	Longitude (Start)	Number of sub-samples	Water depth [m]	Net
S. minima	26	SI5	29.09.2011	12:04 (d)	19°00'S	12°00'E	6	198	MOCNESS
S. enflata	19	SI2	24.09.2011	16:40 (d)	21°57'S	13°55'E	5	56	WP-2
S. enflata	22	SI3	27.09.2011	07:20 (d)	19°02'S	10°23 'E	2	2151	Driftnet
S. enflata	29	SI9	01.10.2011	23:15 (n)	17°36'S	11°00'E	4	112	Ring Trawl
S. decipiens	22	SI3	27.09.2011	07:20 (d)	19°02'S	10°23 'E	3	2151	Driftnet
S. zetesiois/ S. planctonis	22	SI3	27.09.2011	07:20 (d)	19°02'S	10°23 'E	3	2151	Driftnet

2.3. Sample processing

2.3.1. Distribution and abundance

In the home laboratory, the samples collected with the double 1m²-MOCNESS were transferred into a sorting fluid composed of 94.5% fresh water, 5.0% propylene glycol and 0.5% propylene-phenoxetol for the analysis of taxonomic composition and vertical and horizontal distribution. The samples were separated into different size classes for further analysis using a band-pass filter. Afterwards, Chaetognatha species were extracted from these subsamples, measured and sorted into size intervals of < 5.0, 5.0 – 7.5, 7.5 – 10.0, 10.0 – 12.5, 12.5 – 15.0, 15.0 – 20.0, 20.0 – 25.0, 25.0-30.0 and > 30.0 mm. The body length was measured from the top of the head to the end of the tail, excluding the tail fin. All Chaetognatha species were classified into three maturity stages following Zo (1973; Table 3). The species were counted and standardized to the number of individuals per 1000 m^3, using the filtered volume measured for each net.

Tab.3 *The somatic characteristics of Chaetognatha stages following Zo (1973)*

Stage	Somatic characteristics
I	young individuals without visible ovaries
II	individuals with visible ovaries and immature ova that varied in size and with well developed gonads
III	individuals with some mature ova in the ovaries

To determine the mean vertical distribution of the species, the weighted mean depth (WMD) was calculated as follows:

$$WMD = \frac{\sum (N_{Ti} \times T_i)}{\sum N_{Ti}}$$

where N_{Ti} is the abundance in the depth layer i and T_i the mean depth of the sampling interval in meter.

Individual components of diversity were calculated by different indices. Richness was represented by number of species per station. The Shannon-Weaver diversity index (H) was calculated as follows (Shannon & Weaver, 1949):

$$\overline{H} = -\sum (n_i / N) \ln(n_i / N)$$

where N is the total abundance of all species, n_i represents the abundance of the species. The index usually assumes values between 0 and 5, where 0 represent only one species in the community.
To examine, how the abundances of species differ in a community, the evenness (J) at each station was calculated using Pielou's (1975) formula with the Shannon-Weaver index (H):

$$J = \overline{H} / \ln N$$

The values of this index vary from 0 to 1, where 0 represents species in equal abundance and 1 a community with perfect evenness (= all abundance in one species).

The dominance index was calculated according the Simpson index (1949):

$$D = \sum_{i=1}^{S} (n_i / N)^2$$

where S is the total number of species at the station, n is the number of individuals of the i species and N the total number of individuals of the Chaetognatha community. The values of the dominance index range from 0 to 1, where 1 represents complete dominance (only one species present in the community).

2.4. Stable isotopes

A stable isotope analysis is a reliable method to characterize the structure of the food web and to investigate the nutrient dynamics and pathways of energy flow within ecosystems (McConnaughey & McRoy, 1979; Saupe *et al*., 1989). All samples were wet weighed with an analytical balance with an accuracy of 0.1 mg and then dried in a freeze-dryer at -40°C for 24 h. The dried samples were pulverised using mortar and pistil. Afterwards, the dry weight was determined.

The carbon and nitrogen content and stable isotopes values of the different samples were determined using a Thermo Finnigan Delta V Isotope ratio mass spectrometer (EA-1112 CHN-Analyser) at the stable isotope laboratory of the Museum für Naturkunde - Leibniz-Institut für Evolutions- und Biodiversitätsforschung of Humboldt-Universität in Berlin. Results are related to standard atmospheric nitrogen or Peedee Belemnite and expressed as deviations from the standard in parts per thousand as follows:

$$\delta^{13}C \text{ or } \delta^{15}N\,(‰) = \left[\frac{\left(R_{sample} - R_{st.}\right)}{R_{st.}}\right] \times 10^{3}$$

where $R_{st.}$ is the standard ($^{13}C/^{12}C$) or ($^{15}N/^{14}N$).

Nitrogen isotopic compositions reflect important dietary relationships within the food web (Michener & Lajtha, 2007). Nitrogen isotope ratios become enriched by 3 – 4 ‰ per trophic level (Minigawa & Wada, 1984; Schoeniger & DeNiro, 1984; DeNiro & Epstein, 1978). Stable carbon isotope ratios are useful for identifying the source of the diet (DeNiro & Epstein,1978) because these exhibit only a small enrichment of about 0.5 – 1.0 ‰ (Michener & Lajtha, 2007; DeNiro & Epstein,1978).

The stable nitrogen and carbon data of the four taxa (*S. enflata, S. minima, S. zetesiois/S. planctonis, S. decipiens*) and the different stations (SI1 – SI9) were statistically analysed using one-way ANOVA with Tukey-HSD Post-Hoc-Test. In all cases, a 95% significance level was adapted.

Additionally, the relative amount of dry weight (DW) as a function of wet weight (WW), dry weight and wet weight per individual, relative amount of carbon and nitrogen and the C:N ration were calculated. Data were tested statistically using Kruskal-Wallis-test and Mann-Whitney-U-test.

3. Results

3.1. Oceanography

The oceanographic data reveal a typical upwelling situation in the Central Benguela Region with lower temperatures around 14°C and low oxygen concentrations near the bottom. The low dissolved oxygen was a result of high oxygen demands during the destruction of high amounts of sunken organic material produced in the productive surface layer (Figure 4).

On the inner shelf (133 m water depth; Table 1), the temperature decreased slightly from ~15.0°C near the surface (0 – 25 m) to ~11.0°C at 132 m. The salinity was almost constant over the depth (~35.1). Near the bottom, oxygen concentrations were at very low level, but above zero. The oxygen concentration in the surface layer reached almost 6 mL/L (Figure 4_a).

The outer shelf station (231 m water depth; Table 1) was characterised by a temperature of ~14°C in the surface layer which slightly decreased to ~12°C at 200 m. The salinity and dissolved oxygen showed similar patterns compared to the inner shelf station. The salinity was more or less stable over the depth (~35.2). At this station, dissolved oxygen values reached a relative maximum in the surface layer (~6 mL/L). There was a sharp decrease between 50 m and 150 m and the oxygen concentration was less than 1.0 mL/L at 150 to 200 m (Figure 4_b)

At the shelf break station (437 m water depth; Table 1), the temperature was slightly higher than 14°C near the surface and decreased below 12°C near the bottom. The salinity maximum was located at a depth of around 75 m (~35.3). The salinity decreased to ~34.8 near the bottom. High dissolved oxygen concentrations were found in the surface layer which reached ~ 5.9 mL/L. Below 150 m, a dissolved oxygen minimum was found with values around 1.0 mL/L (Figure 4_c).

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At the offshore station (2998 m water depth; Table 1) a thermocline was detected at 50 m depth. The surface temperature was around 16.0°C and decreased continuously to 4.0°C at ~1000m. The salinity ranged between 35.2 and 35.3 in the upper 100 m and decreased with increasing depth to a 34.4 at 750 m. Between 750 and 2000 m the values increased again to 34.9. The maximum oxygen concentration (~8.0 mL/L) was found in the surface layer. The lowest dissolved oxygen value (~2.0 mL/L) was determined at a depth of 400 m. Below 2000 m depth, the temperature, salinity and oxygen were almost constant with values of ~2.0°C, 34.9 and 5.4 mL/L (Figure 4_{d1} and 4_{d2}).

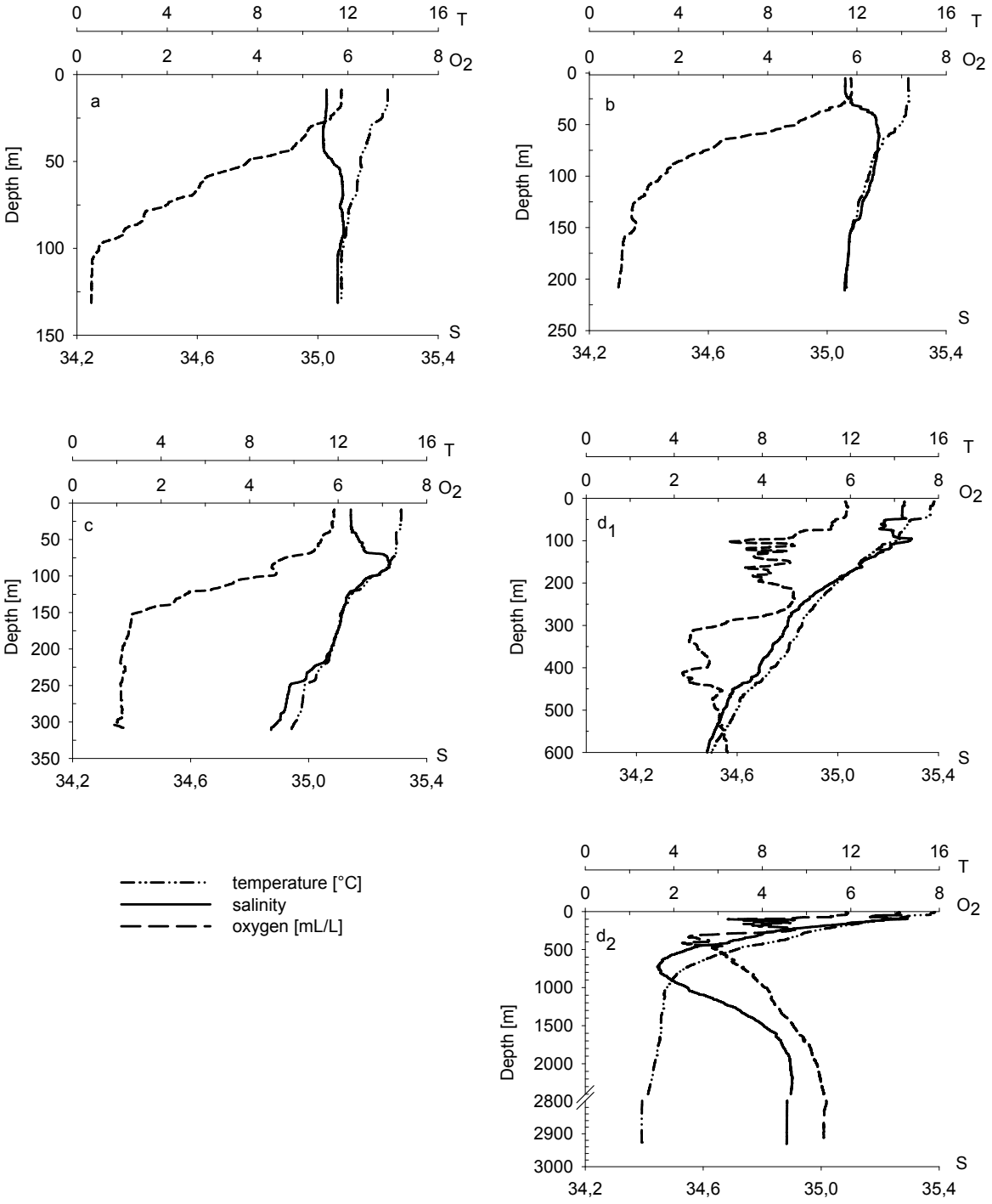

Fig. 4 *Temperature, salinity and oxygen values of the four stations located on the Walvis Bay transect at the start of the sampling; (a) inner shelf station WB 1, (b) outer shelf station WB 2, (c) shelf break station WB 3, (d_1) offshore station WB4 – detail of upper 600 m, (d_2), offshore station WB4.*

3.2. Abundance and distribution

3.2.1. Abundance

At the inner shelf station, the maximum abundance of Chaetognatha was found between 25 and 50 m (5606 ind. 1000 m^{-3}). The abundance in the surface layer (0 – 25 m) and at 50 to 100 m reached values of 4194 and 3902 ind. 1000 m^{-3}, respectively (Figure 5_a).

The highest density of Chaetognatha at the Walvis Bay transect was found in the surface layer at the outer shelf station (32403 ind. 1000 m^{-3}). The abundance decreased with depth to 2376 ind. 1000 m^{-3} at 100 – 150 m (Figure 5_b).

The shelf break station showed a similar pattern as the inner shelf station. However, with lower densities of 1017 ind. 1000 m^{-3} in the 25 to 50 m layer (Figure 5_c). The abundance at the surface layer (0 – 25 m) reached 6485 ind. 1000 m^{-3}. Below 50 m to 150 m, a decrease of Chaetognatha abundance was found with lowest value at 100 to 150 m depth (724 ind. 1000 m^{-3}). Between 200 and 350 m, the densities were more or less constant with values below 5000 ind. 1000 m^{-3}.

Relatively low concentrations of Chaetognatha were found at the offshore station. The maximum density was found in the layer between 25 and 50 m depth (5232 ind. 1000 m^{-3}). Between 50 and 400 m depth, the abundance was relatively constant with values up to ~ 1400 ind. 1000 m^{-3}. Below 400 m depth, the abundances decreased rapidly and reached a minimum at 1250 to 1500 m, where only 9 ind. 1000 m^{-3} were found.

3.2.2. Species composition and ontogenetic distribution

The Chaetognatha community on the Walvis Bay transect comprised of seventeen species. The species were assigned to seven groups and one ungrouped species following Casanova (1999; Table 4). Not all three maturity stages were always found for all species. Adults for *Sagitta macrocephala, Sagitta lyra, Sagitta enflata, Sagitta sibogae, Sagitta planctonis* and *Sagitta zetesiois* were not found. It was not possible to differentiate juveniles of the species of the *Serratodentata* group, because the main diagnostic features for identification of stage I and II were not conspicuously discernible in the investigated material. Adults of *Sagitta tasmanica* and *Sagitta serratodentata* were identified on the basis of the development of the gonads and ovaries and the shape of the fins. Hence, all stages I and II were pooled in the results as *Serratodentata* group (see Table 5 and Figure 7). At all stations, only adults of *S. tasmanica* and *S. serratodentata* were found, for this reason, I assume that the juveniles identified belonged to this two species.

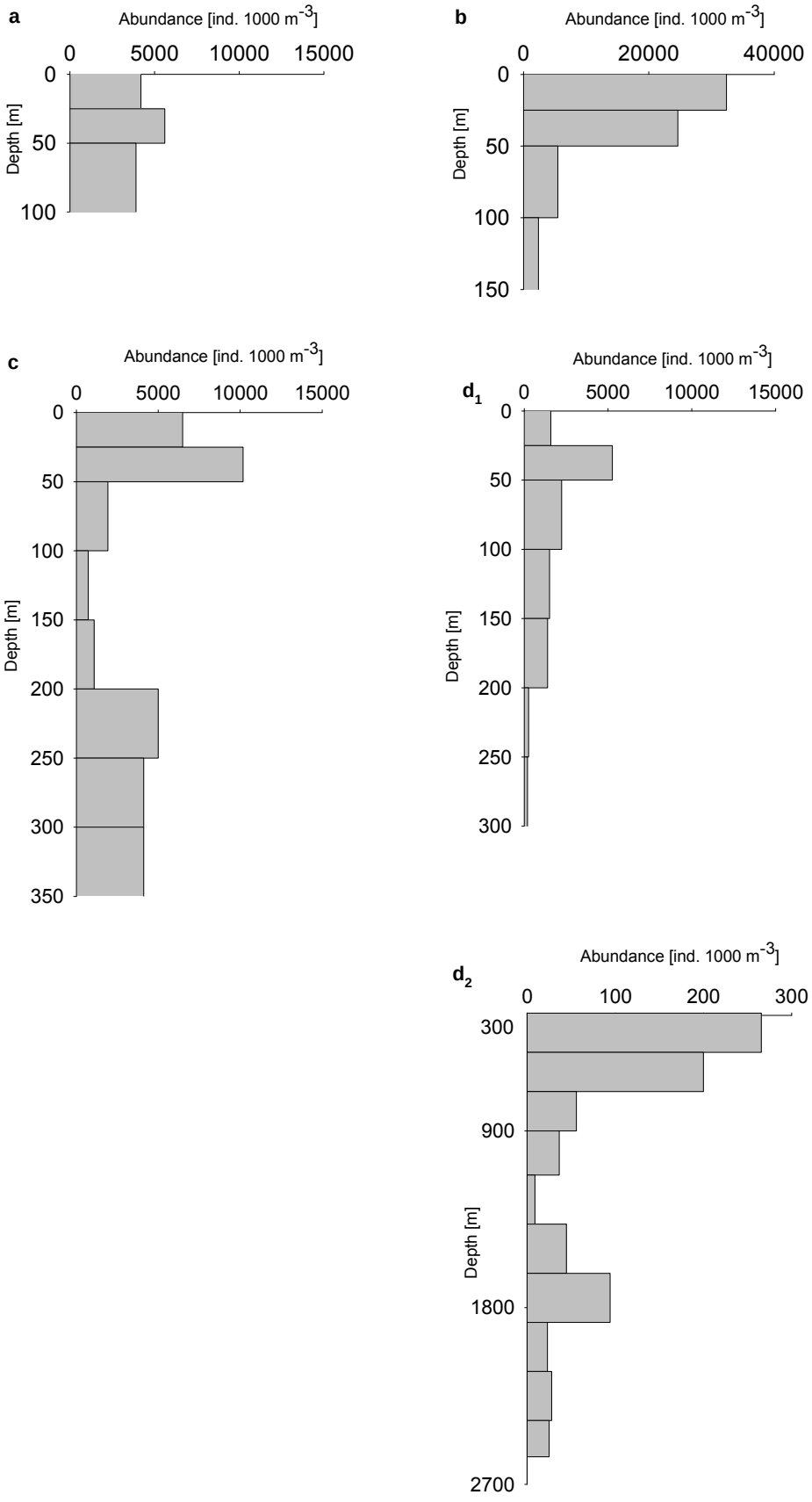

Fig. 5 *Abundance and vertical distribution of Chaetognatha on the Walsvis Bay transect; (a) WB 1 inner shelf, (b) WB 2 outer shelf, (c) WB 3 shelf break, (d_1) WB4 offshore – upper 300 m (d_2) WB 4 offshore – from 300 m to 2620 m depth; note the different scales*

Table 4 *Chaetognatha groups and species detected on the Walvis Bay transect; asigned following Casanova (1999)*

	Group	**Species**
Pterosagittidae	*Pterosagitta*	*Pterosagitta draco* (Krohn, 1853)
Eukrohniidae	*Hamata*	*Eukrohina flaccicoeca* (Casanova, 1986)
		Eukrohina hamata (Möbius, 1875)
	Fowleri	*Eukrohina bathyantarctica* (David, 1958)
		Eukrohina fowleri (Ritter-Záhony, 1909)
Sagittidae	*Lyra*	*Sagitta lyra* (Krohn, 1853)
		Sagitta maxima (Conant, 1896)
	Serratodentata	*Sagitta serratodentata* (Tokioka, 1940)
		Sagitta tasmanica (Thomson, 1947)
	Hexaptera	*Sagitta enflata* (Grassi, 1881)
		Sagitta hexaptera (d'Orbigny, 1843)
	Minima	*Sagitta decipiens* (Fowler, 1905)
		Sagitta minima (Grassi, 1881)
		Sagitta sibogae (Fowler, 1906)
	Planctonis	*Sagitta zetesiois* (Fowler, 1905)
		Sagitta planctonis (Steinhaus, 1896)
	ungrouped	*Sagitta macrocephala* (Fowler, 1905)

At the inner shelf station, only three Chaetognatha groups were found: the *Serratodentata* group, the *Minima* group and the *Hamata* group (Figure 6). Five Chaetognatha groups were found at the outer shelf station: the *Serratodentata* group, the *Hamata* group, the *Minima* group, the *Hexaptera* group and the *Lyra* group. Two more groups were identified at the shelf break and offshore stations: the *Planctonis* group and the *Pterosagitta* group, which consisted of only one species *Pterosagitta draco*.

On the Walvis Bay transect, 17 species were found (Table 4). Based on the weighted mean (WMD) depths calculated from the average vertical distribution (Table 5), the 17 species were classified as pelagic, shallow- or deep-mesopelagic or bathypelagic (Table 6). Epipelagic species were defined as possessing a WMD within the upper 200 m, shallow mesopelagic species between 200 and 600 m, deep mesopelagic species between 600 and 1000 m and bathypelagic species below 1000 m. Seven species were characterized as epipelagic species, three species as epipelagic to shallow mesopelagic species, one species as shallow-mesopelagic, two species as shallow- to deep-mesopelagic species and four species were attributed to the bathypelagic species (Table 6).

Tab. 5 *Weighted mean depths (WMD) in meter of Chaetognatha species and their maturity stages on the Walvis Bay transect.*

	WB1 inner shelf			WB2 outer shelf			WB3 shelf break			WB4 offshore		
	Stage I	Stage II	Stage III	Stage I	Stage II	Stage III	Stage I	Stage II	Stage III	Stage I	Stage II	Stage III
P. draco							37	75	75	42	43	59
E. flaccicoeca												1445
E. hamata	75			117			267			344	700	
E. bathyantarctica												2020
E. fowleri												880
S. lyra							176			70	43	355
S. maxima							287			418	307	356
Serratodentata gr.	34	34		48	30		103	71		94	37	
S. tasmanica			19			31						
S. serratodentata						19			31			46
S. enflata										105		
S. hexaptera							199			67	46	87
S. decipiens	38	14	15	65	37		214	252	253	92	85	75
S. minima				12	19	41	34	42	47	36	72	46
S. sibogae	58	73										
S. zetesiois							320	325		673	988	
S. planctonis							29			69		
S macrocephala										1240		

The *Serratodentata* group dominated all four investigated stations and belongs to the epipelagic and shallow-mesopelagic community. It constituted 60% of the standing stock at the inner shelf station, 89% at the outer shelf station, 36% at the shelf break station and 40% at the offshore station (Figure 6). In the surface layer (0 – 50 m depth), the *Serratodentata* group accounted for over 80% of the standing stock at the inner and outer shelf station, over 60% at the shelf break station and over 43% at the offshore station (Figure 7). The highest abundance of this group was found at the outer shelf station accounting for 25118 ind.1000 m^{-3} at the surface layer (0 – 25 m) and 18282 ind. 1000 m^{-3} at the depth from 25 to 50 m (Figure 8). The distribution pattern for the stages I and II showed similarities at all four stations with high abundances at a depth between 25 and 50 m. The adults of *S. tasmanica* and *S. serratodentata* preferred the upper layers between 0 and 50 m.

Dominant epipelagic and shallow-mesopelagic species were *Sagitta minima, Sagitta decipiens* and *Sagitta sibogae* from the *Minima* group. The *Minima* group was the second dominant group at the inner shelf station with a relative amount of 20% of the standing stock (Figure 6). The proportion of the *Minima* group was relatively high at the shelf break station and at the offshore station, where this group made up 5% and 11% of the standing stock, respectively. Only *S. decipiens* was found at all stations. The abundance of this species was high at the shelf break and offshore stations. *S. sibogae* was only formed by the developmental stage I and occurred at the inner shelf station between 50 to 100 m depth. *S. minima* preferred the upper layers between 0 to 150 m depth of the shelf break and the offshore stations (Figures 7 and 8) with peak density values of 172 ind. 1000 m^{-3} in the upper 25 m at the outer shelf station, 661 ind. 1000 m^{-3} at the shelf break station and 412 ind. 1000 m^{-3} at the offshore station between 25 and 50 m.

The *Hamata* group was found at all four investigated stations of the Walvis Bay transect. The relative densities at the inner and outer shelf stations were low (Figure 6). This group contributed with less than 1% to the standing stock at the inner and outer shelf stations. At the shelf break station and the offshore station respective densities of 14% and 10% were recorded. At the inner and outer shelf and shelf break stations, only stage I of *Eukrohnia hamata* was found and preferred layers near the bottom or deeper than 200 m with densities over 1400 ind. 1000 m^{-3} at the shelf break station and 350 ind. 1000 m^{-3} at the offshore station (~30% of the total at each depth layer). Some stage II of *E. hamata* and adults of *Eukrohnia flaccicoeca* were found at the offshore station between 600 and 1000 m depth. *E. flaccicoeca* reached a maximum density of 33 ind. 1000 m^{-3} in the depth layer between 600 and 800 m (Figure 8). Because of the low abundances of species belonging to the *Hamata* group (*E. hamata, E. flaccicoeca*), these species were pooled in Figures 7 and 8.

Individuals of *P. draco* were mainly found in oceanic waters of the Walvis Bay transect and occurred at depths between 50 to 200 m. The abundances at the shelf break station were very low (Figures 8). The maximum density was found in the depth layer between 25 to 50 m at the offshore station, consisting of 444 ind. 1000 m^{-3}. The immature stage I dominated the population, it consisted of 141 ind. 1000 m^{-3} in the upper 100 m at the offshore station.

Tab. 6 *The occurrence of the species in different depths of the study area*

Species / Area of occurence	*P. draco*	*S. tasmanica*	*S. serratodentata*	*S. enflata*	*S. minima*	*S. sibogae*	*S. planctonis*	*S. hexaptera*	*S. lyra*	*S. decipiens*	*S. maxima*	*E. hamata*	*S. zetesiois*	*S macrocephala*	*E. flaccicoeca*	*E. fowleri*	*E. bathyantarctica*
Epipelagic 0 - 200 m	■	■	■	■	■	■	■	■	■	■							
Shallow-mesopelagic 200 - 600 m								■	■	■	■	■	■				
Deep-mesopelagic 600 - 1000 m												■	■				
Bathypelagic > 1000 m														■	■	■	■

Sagitta hexaptera and *Sagitta enflata* belong to the *H*exaptera group and were mainly found at the offshore station (Figure 6). Horizontal differences in the ontogenetic distribution of *S. hexaptera* were detected (Figure 8). Only maturity stage I was found at the shelf break station and occurred in depth layers between 150 and 300 m whereas all three stages were found at the offshore station. At this station, *S. hexaptera* was found in the upper 200 m, reaching a maximum density of 301 ind. 1000 m^{-3} at 25 to 50 m (Figure 8).

The *Lyra* group was found at the shelf break stations and offshore station (Figure 6). *Sagitta lyra* showed similar distribution pattern as *S. hexaptera* with a deeper occurrence of stage I at the shelf break station and a lower occurrence at the offshore station. No adults of *S. lyra* were found at the shelf break station. At the offshore station, the density of stage I reached a maximum value of 207 ind.1000 m^{-3} at 50 to 100 m. Stage II preferred the upper layers with a peak density of 95 ind. 1000 m^{-3} at the depth of 25 to 50 m. *S. maxima* was mainly found at the offshore station between 100 and 2500 m depth (Figure 8).

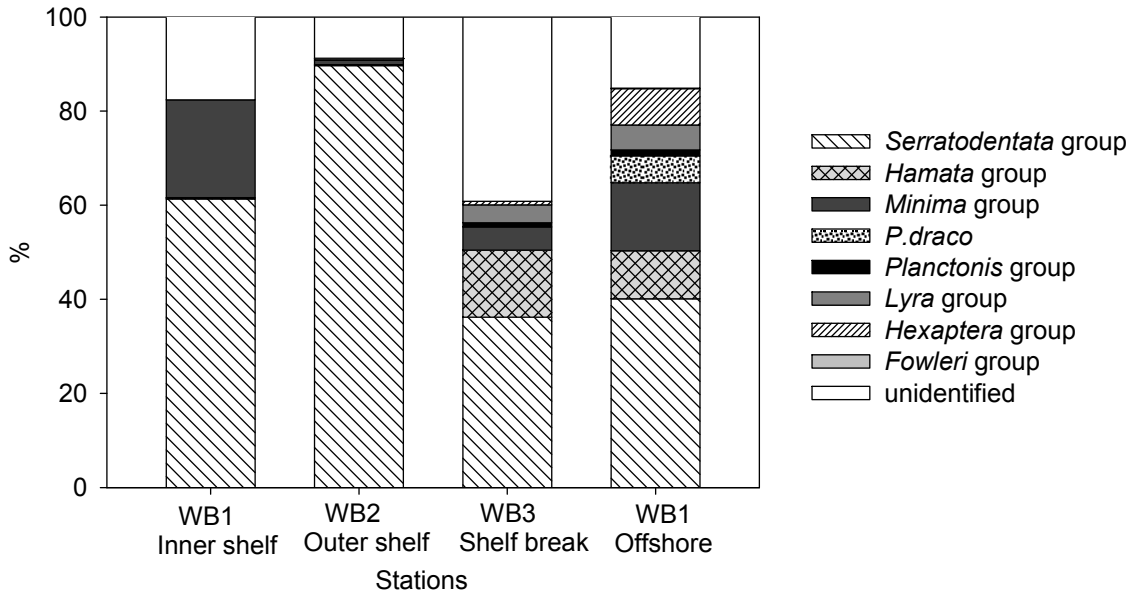

Fig. 6 *Relative composition of Chaetognatha groups at the four investigated stations of the Walvis Bay transect.*

The *Planctonis* group was found at the shelf break and offshore station (Figure 6). It consists of two species, *Sagitta planctonis* and *Sagitta zetesiois*. *S. planctonis* is an epipelagic and shallow-mesopelagic species, which was found sporadically in the upper 400 m. *S. zetesiois* is a deep-mesopelagic to bathypelagic species and preferred deeper water layers below 250 m at the shelf break station and below 400 m at the offshore station (Figure 7 and 8).

Sagitta macrocephala belongs to the deep-mesopelagic and bathypelagic species (Figure 7 and 8). Only stage I was found at the offshore station with a peak density of 26 ind. 1000 m^{-3} between 600 and 800 m. The abundances in the deeper layers were relatively low with up to 8 ind. 1000 m^{-3} (Figure 8).

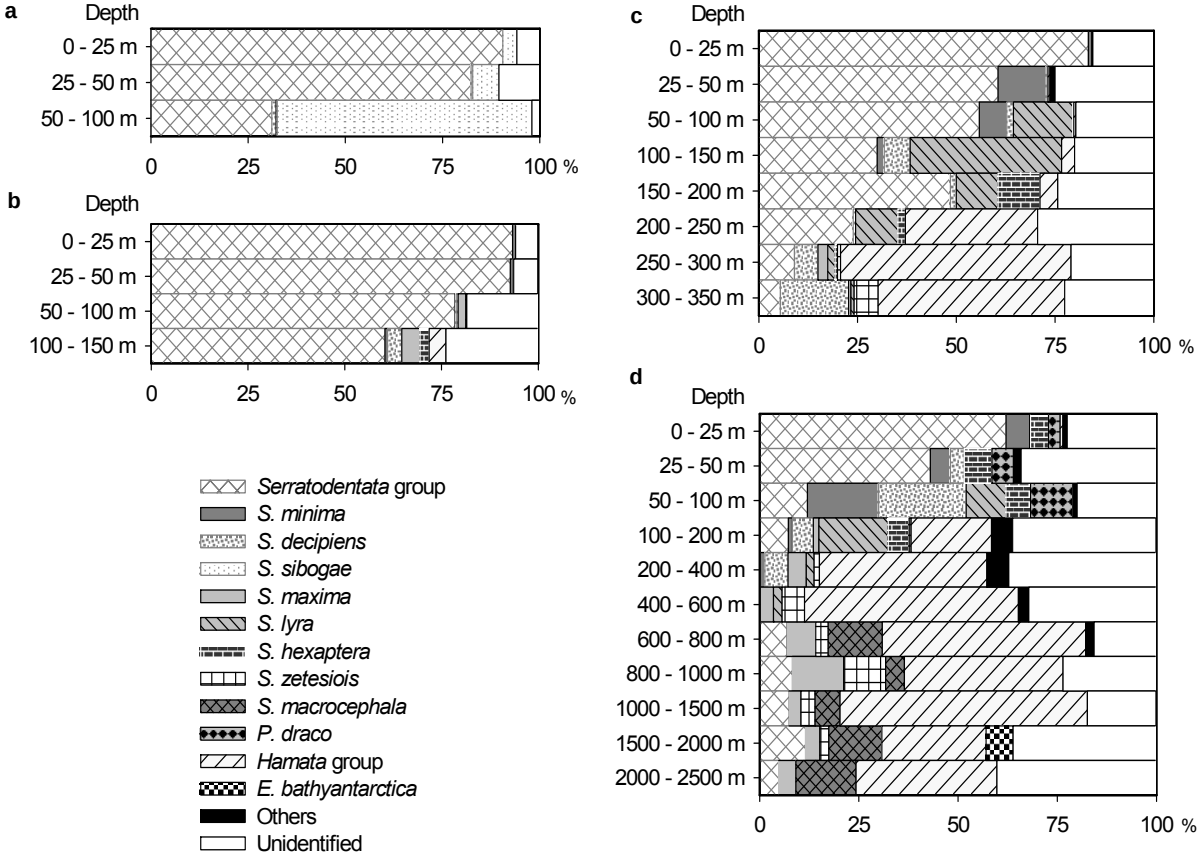

Fig. 7 *Relative abundance of the Chaetognatha species at the four investigated stations of the Walvis Bay transect; (a) WB 1 inner shelf station, (b) WB 2 outer shelf station, (c) WB 3 shelf break station, (d) WB 4 offshore station; the Serratodentata group = stages I and II of Serratodentata group and adults of S. serratodentata and S. tasmanica; Hamata group = E. hamata, E. flaccicoeca; Others = E. fowleri, S. enflata and S. planctonis.*

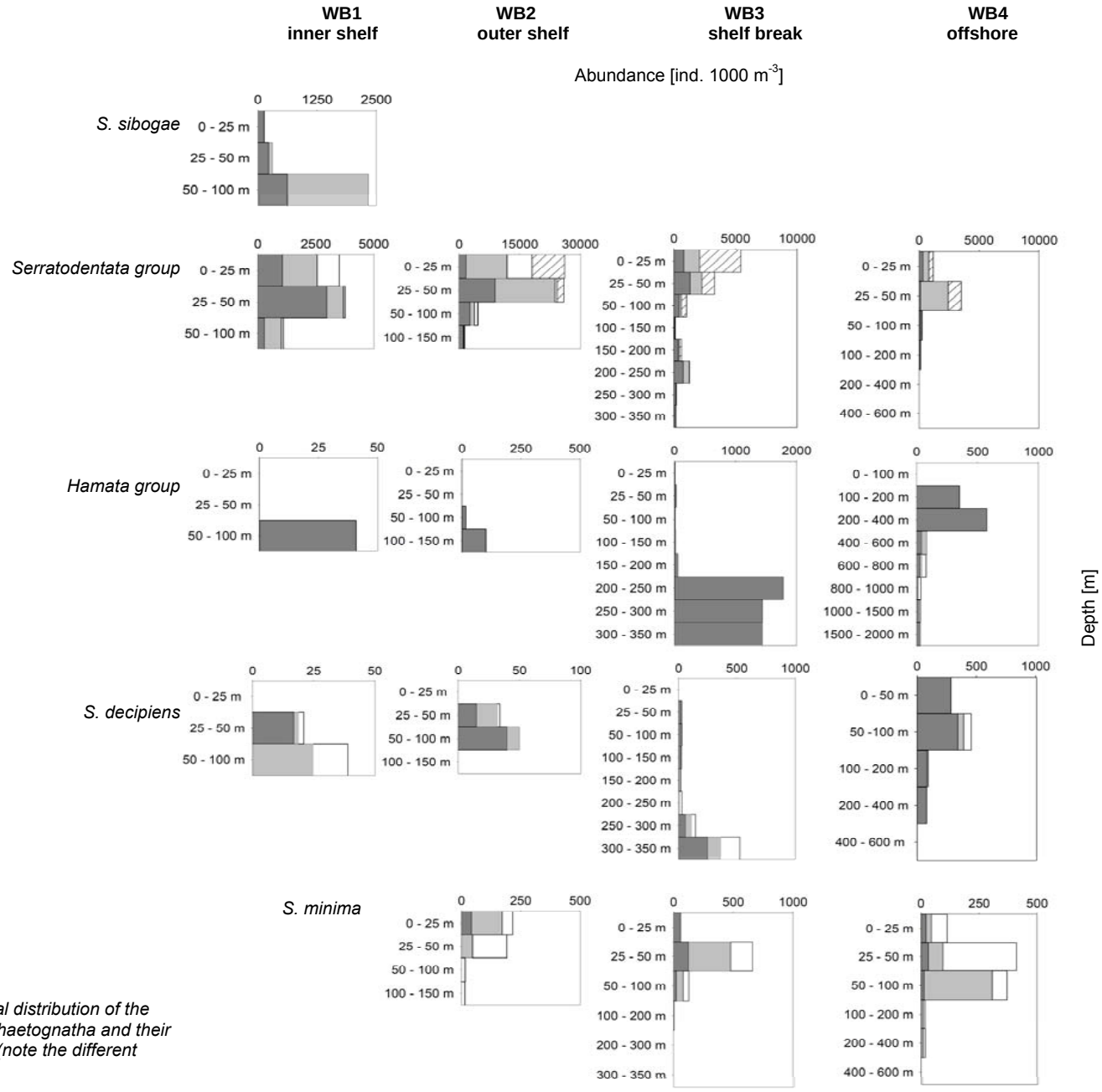

Fig. 8 *Abundance and vertical distribution of the most numerous species of Chaetognatha and their life stages at all four station. (note the different scales)*

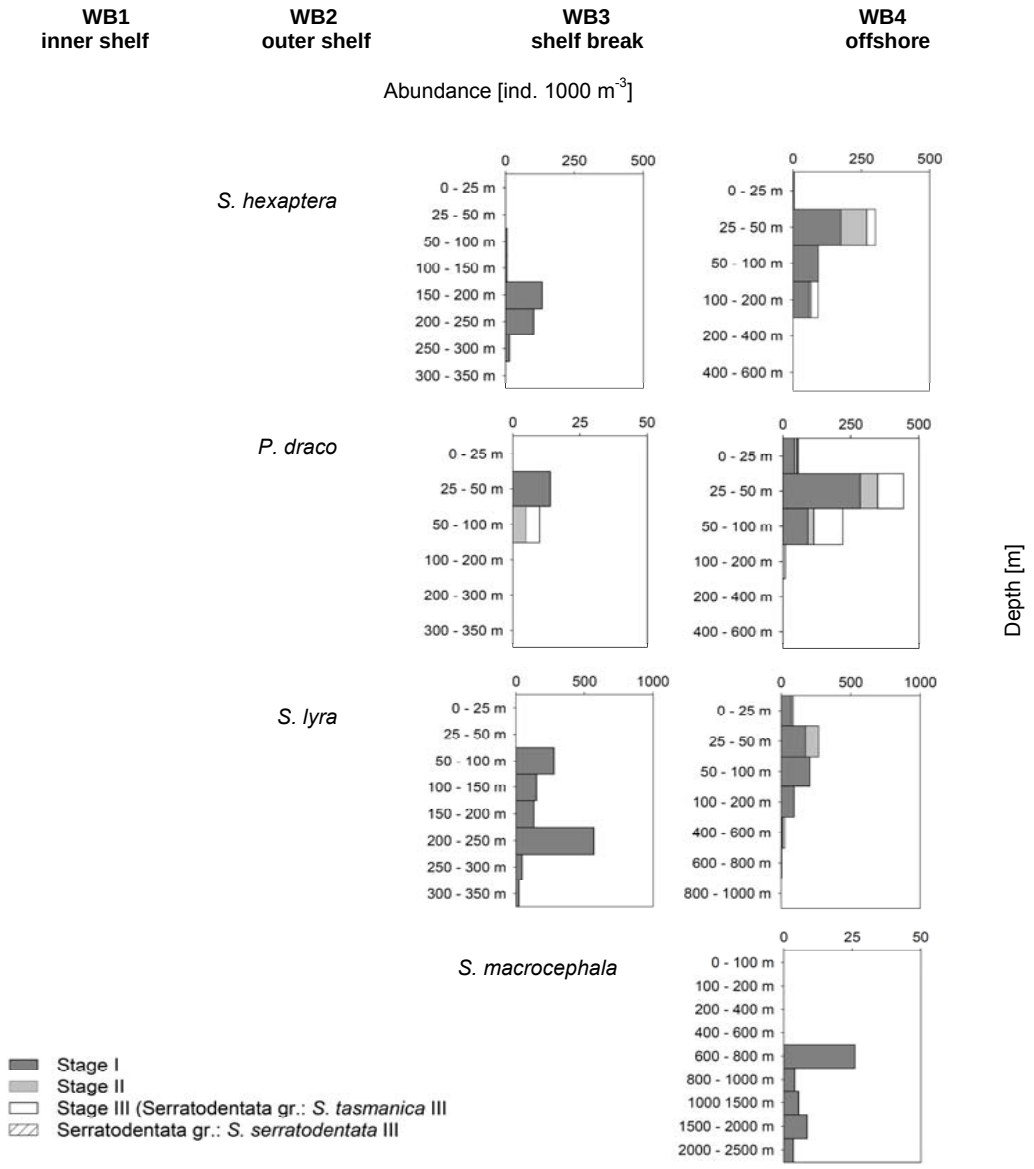
WB1
inner shelf
WB2
outer shelf
WB3
shelf break
WB4
offshore
Abundance [ind. 1000 m-3]
S. hexaptera
P. draco
S. lyra
S. macrocephala
Depth [m]
0 - 25 m
25 - 50 m
50 - 100 m
100 - 150 m
150 - 200 m
200 - 250 m
250 - 300 m
300 - 350 m
100 - 200 m
200 - 300 m
200 - 400 m
400 - 600 m
600 - 800 m
800 - 1000 m
1000 1500 m
1500 - 2000 m
2000 - 2500 m
Stage I
Stage II
Stage III (Serratodentata gr.: S. tasmanica III
Serratodentata gr.: S. serratodentata III

***Fig. 8** cont.*

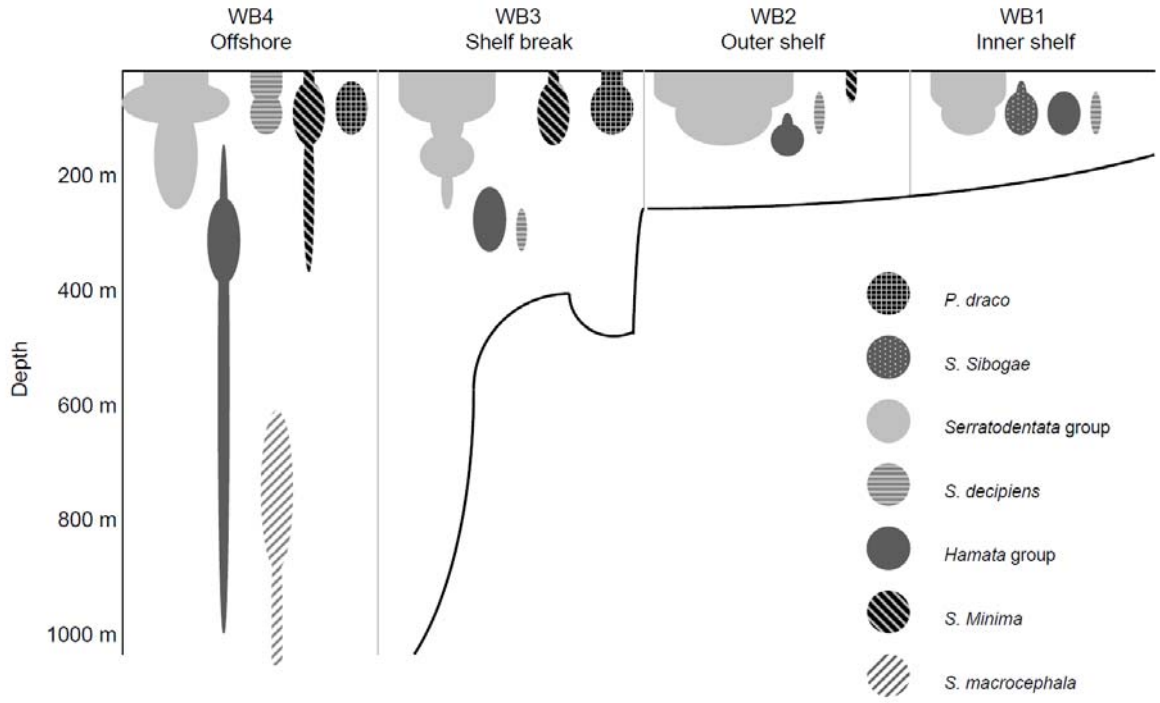

***Fig. 9**: A conceptional picture of the vertical (upper 1000 m) and horisontal distribution of the major species/groups of the Walvis Bay transect; distances and the dimension of the bubbles are not scaled.*

3.2.3. Abundance and distribution - short summary

The horizontal distribution of Chaetognatha species along the Walvis Bay transect differed (Figure 9). The community of Chaetognatha was dominated by epipelagic and shallow-mesopelagic species. With increasing distance from the shelf to the open ocean, the number of mesopelagic (*S. maxima, E. hamata, S. zetesiois*) and bathypelagic species (*S. macrocephala*, and species of *Fowleri* group) as well as the number of oceanic species (*P. draco*, *S. minima*) increased. The most abundant group in the Chaetogntha community of the Walvis Bay transect was the *Serratodentata* group which reached a maximum abundance at the outer shelf station. Within the vertical distribution of Chaetognatha species a segregation of maturity stages on the Walvis Bay transect was not clearly detected.

3.3. Diversity, dominance and evenness

The richness and diversity of Chaetognatha species showed a tendency to increase from the shelf towards the open ocean (Table 7). The diversity of the Chaetognatha community (Shannon-Weaver index H) was much lower at the inner shelf station (H = 0.3) compared to the offshore station (H = 1.38). The evenness (J) of the distribution of the individuals between the different Chaetognatha species was lowest at the inner shelf station (J = 0.21) and highest at the shelf break and offshore station (J > 0.50). The values of Simpson Dominance Index (D) at the shelf and shelf break stations (D = 0.31 – 0.55) showed a higher dominance of one group (*Serratodentata* group) compared to the offshore station (D = 0.03).

Tab. 7 *Number of species, values of the Shannon –Weaver index H, the Evenness J and the Simpson index D at the four sampling stations*

	WB1 inner shelf	WB2 outer shelf	WB3 shelf break	WB4 offshore
Nummber of species	4	7	10	15
Shannon-Weaver index H	0.3	0.63	1.21	1.38
Evenness J	0.21	0.33	0.52	0.51
Simpson index D	0.55	0.31	0.42	0.03

3.4. Length frequency and maturity stage

Since not all three stages were found for all Chaetognatha species and for some species just a few adult individuals were observed, it was not possible to determine the size frequency distribution according to maturity stage for all species described above. Figure 10 shows the size frequency distribution for S*. minima, S. decipiens, S. hexaptera, P. draco* and the *Serratodentata* group. *S.minima* was the smallest species with a maximal length of adult individuals between 7.5 and 10.0 mm. Stage I mainly formed the population of *S. decipiens* and *P. draco*. The adults of these two species reached a maximum body length of 7.5 to 10.0 mm. *S. hexpatera* was a species with a body length between 30.0 and 40.0 mm of the adults.

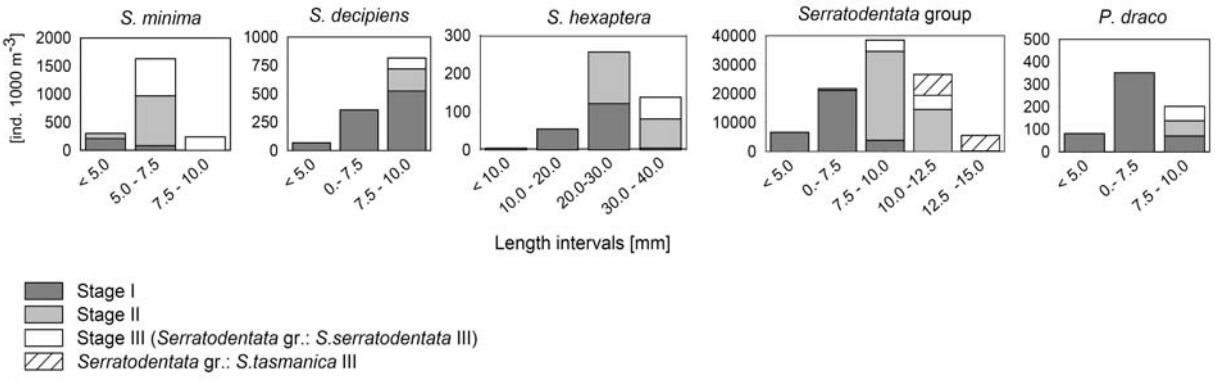

Fig. 10 *Length-frequency distribution of five Chaetognatha taxa according to maturity stage. Stage I and II of species from the Serratodentata group could not be differentiated, hence, stage I and II of the Serratodentata group and adults of S. tasmanica and S. serratodentata are shown together in one figure.*

3.5. Stable Isotopes

Carbon and nitrogen stable isotope ratios of Chaetognatha were determined for seven different areas (9 stations SI1 – SI9) located on the shelf, on the shelf break and offshore off northern Namibia (Figure 3). All sampled individuals were pooled according to the stations. Additionally, carbon and nitrogen stable isotopes were estimated for four taxa*: S. minima, Planctonis* group (*S. planctonis* and *S. zetesiois*)*, S. enflata, S. decipiens.* For the determination of stable isotopes of the four taxa, samples from different areas were pooled. It was not possible to differentiate between two species from the *Planctonis* group (*S. zetesiois* and *S. planctonis)* on the vessel*,* these two species were pooled (Figure 12).

3.5.1. Differences between areas

Significant differences in $\delta^{13}C$ were found between the areas (One-way ANOVA: $F = 4.904$; $P < 0.001$; $\alpha < 0.050$). The values for $\delta^{13}C$ ranged from -23.89 to -17.03 ‰. The lowest values determined were found at the Rocky Point offshore station (-23.89 to -21.87 ‰) which were significantly different from all other stations ($P < 0.023$; Tab. 8_a). No significant differences were found between the other combinations ($P > 0.050$).

A one-way ANOVA showed significant differences for $\delta^{15}N$ values between the areas (one-way ANOVA: $F = 7.05$; $P < 0.001$; $\alpha < 0.050$). The values varied from 6.05 to 11.39 ‰ (Figure 11). The highest $\delta^{15}N$ values were found at the Walvis Bay shelf break station and ranged between 9.93 and 11.39 ‰. The lowest values for $\delta^{15}N$ were measured at the Rocky Point shelf break station (6.05 to 11.07 ‰), which was significantly different from Walvis Bay shelf break, SI2 and Rocky Point offshore station ($P < 0.001$; Table 8_b). No significant differences in $\delta^{15}N$ existed between SI2 shelf station, SI3 offshore and Kunene station and between Rocky point shelf break and offshore station ($P > 0.050$).

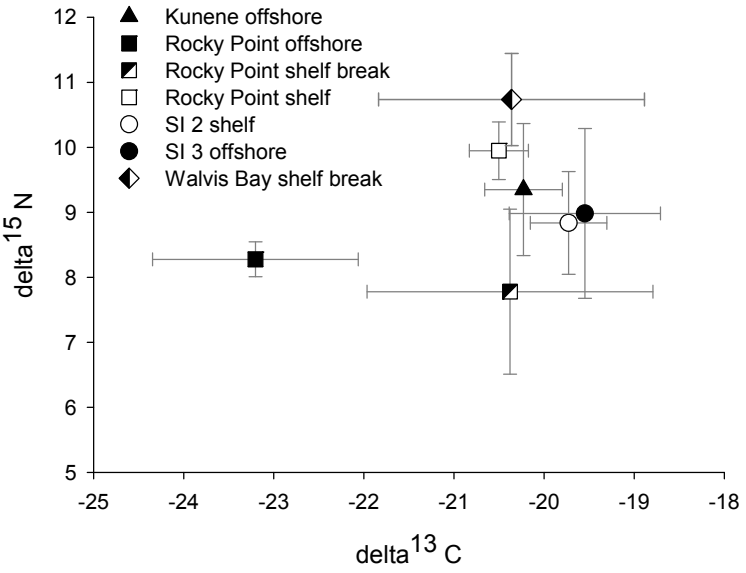

Fig.11 *Relationship between δ13C and $\delta^{15}N$ for various areas of northern Namibia. Mean values and standard deviations are shown.*

Tab. 8 *Summary of One-way ANOVA with Tukey-HSD Post-Hoc-Test investigating differences in the $\delta^{13}C$ (a) and $\delta^{15}N$ values for different locations in the northern Namibian Upwelling System; n.s. = no significant differences (P > 0.050)*

(a)	Walvis Bay shelf break	Sl2 shelf	Sl3 offshore	Rocky Point shelf	Rocky Point shelf break	Rocky Point offshore
Kunene offshore	n.s.	n.s.	n.s.	n.s.	n.s.	P = 0.019
Walvis Bay shelfbreak		n.s.	n.s.	n.s.	n.s.	P = 0.019
Sl 2 shelf			n.s.	n.s.	n.s.	P < 0.001
Sl 3 offshore				n.s.	n.s.	P < 0.001
Rocky Point shelf					n.s.	P = 0.023
Rocky Point shelfbreak						P = 0.004

(b)	Walvis Bay shelf break	Sl2 shelf	Sl3 offshore	Rocky Point shelf	Rocky Point shelf break	Rocky Point offshore
Kunene offshore	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Walvis Bay shelfbreak		P = 0.046	P = 0.040	n.s.	P < 0.001	P = 0.036
Sl 2 shelf			n.s.	n.s.	n.s.	n.s.
Sl 3 offshore				n.s.	P = 0.021	n.s.
Rocky Point shelf					P = 0.002	P = 0.024
Rocky Point shelfbreak						n.s.

3.5.2. Differences between species

Significant differences in $\delta^{13}C$ were found comparing the four taxa (one-way ANOVA: F = 5.63; P = 0.004; α < 0.050); the $\delta^{13}C$ values ranged between -22.70 and -19.00 ‰. Statistical differences were found between *S. enflata* and the other three species (P < 0.001; Table 9_a). The $\delta^{13}C$ values of *S.enflata* ranged from -22.70 to -21.56 ‰. The highest $\delta^{13}C$ values were found for *S. minima* (-20.29 to -19.39 ‰) and *S. decipiens* (-20.84 to -20.37 ‰).

A one-way ANOVA showed significant differences for $\delta^{15}N$ values between the four investigated species (F= 7.05; P < 0.001; α < 0.050). The values for $\delta^{15}N$ ranged between 6.17 and 10.38 ‰ (Figure 12). The $\delta^{15}N$ values from *S. decipiens* were consistently higher (9.16 to 10.05 ‰) than those of *S. minima* and *S. enflata* with a significant difference of P < 0.001 and P =0.038, respectively (Table 9_b). Significant differences were also found between *S minma* and *S. zetesiois/S. planctonis* (P = 0.001). No significant differences in $\delta^{15}N$ were found between the other combinations (*S. enflata* and *S. minima*, *S. zetesiois/S. planctonis* and *S. enflata*, *S. zetesiois/S. planctonis* and *S. decipiens;* P > 0.050).

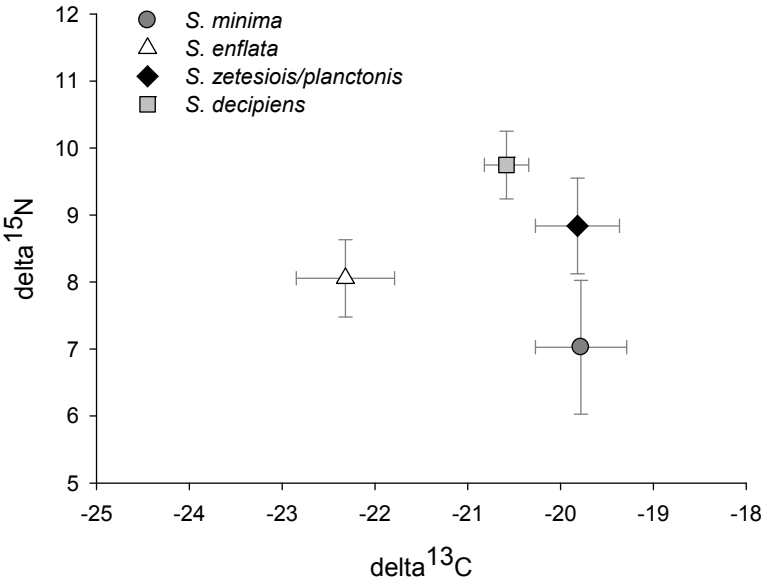

Fig.12 *Relationship between δ13C and $\delta^{15}N$ for various species. Mean value and standard deviation are shown.*

Tab. 9 *Summary of One-way ANOVA with Tukey-HSD Post-Hoc-Test investigating differences in the $\delta^{13}C$ (a) and $\delta^{15}N$ (b) values of different species; n.s. = no significant differences (P > 0.050)*

(a)	*S. enflata*	*S. planctonis/ S. zetesiois*	*S. decipiens*
S. minima	P < 0.001	n.s.	n.s.
S. enflata		P < 0.001	P < 0.001
S. planctonis/ S. zetesiois			n.s.

(b)	*S. enflata*	*S. planctonis/ S. zetesiois*	*S. decipiens*
S.minima	n.s.	P = 0.001	P < 0.001
S.enflata		n.s.	P = 0.038
S. planctonis/ S. zetesiois			n.s.

3.6. Carbon and nitrogen content

The relative N content of different Chaetognatha species varied from 7.1 to 10.1% of the dry weight (Table 9). The highest value was found in the *Planctonis* group (= *S. planctonis/S. zetesiois*) and the lowest was found in *S. minima.* The relative C content varied from 32.0 to 51.8%. The highest value was determined for *S. decipiens* and the lowest for *S. minima*. The mean C:N ratio (mol/mol) ranged from 5.25 for *S. minima* to 6.20 for *S. decipiens.* The relative dry weight (DW) varied between 1.9 and 5.2% in *S. enflata* and *S. zetesiois/S. planctonis*, respectively. Kruskal –Wallis-Test showed significant differences in relative C and N content and C:N ratio between the four species (χ^2 = 10.68, P = 0.014 for C; χ^2 = 9.28, P=0.026 for N; χ^2 = 8.67, P = 0.003 for C:N). The combinations were statistically tested with Mann-Whitney-U-test. Significant differences were detected between *S. minima* and the other species in relative C and N content (P < 0.038). *S. minima* was significant different form *S. enflata, S. zetesiois/S. planctonis* in C:N ratio (P < 0.033). No significant differences were found between the other combinations (P > 0.071).

Tab. 9 *The percentage of carbon and nitrogen of different species (n_s = number of samples; n_i = number of individuals; DW = dry weight; WW = wet weight)*

Species	n_s	n_i	Size interval [mm]	WW [mg/ind.] mean ± SD	DW [mg/ind.] mean ± SD	DW [% of WW] mean ± SD	Carbon [% DW] mean ± SD	Nitrogen [% DW] mean ± SD	C:N mean ± SD
S. minima	6	390	0-10	1.88 ± 0.28	0.06 ± 0.01	3.2 ± 0.8	32.0± 9.6	7.1 ± 1.6	5.25 ± 0.42
S. enflata	5	24	0 - 20	23.31 ± 5.84	0.57 ± 0.31	2.5 ± 0.8	40.7± 8.2	8.8 ± 1.1	5.44 ± 0.44
S. enflata	4	8	20 - 30	95.46 ± 16.31	1.85 ± 0.84	1.9 ± 0.6	47.4 ± 7.0	9.6 ± 1.1	5.79 ± 0.36
S. zetesiois/ S. planctonis	3	18	10 - 20	49.59 ± 13.28	2.56 ± 1.34	5.2 ± 1.2	49.9 ± 3.0	10.1± 0.1	6.20 ± 0.76
S. decipiens	3	180	-	2.26 ± 0.54	0.05 ± 0.02	2.2 ± 1.6	51.8 ± 4.0	9.8 ± 0.6	5.83 ± 0.31

4. Discussion

The aim of this study was to investigate the vertical and horizontal distribution of the Chaetognatha species with an emphasis on the ontogenetic development and to determine the trophic position of selected Chaetognatha species in the Benguela Upwelling System (BUS).

Some procedures during sampling and processing of the material made the subsequent identification of Chaetognatha species difficult. Due to the destroyed diagnostic features like fins and head, it could not be identified 17.6% at the inner shelf station, 8.76% at the outer shelf station and even 38.6% at the shelf break station and 29.7% at the offshore station (Figure 6). The reason for these results was the utilising a band-pass filter and the rinsing of the samples. The longer duration of net towing at the deep offshore and shelf break stations as source of destroyed diagnostic features can be excluded, since, Chaetognatha occurred mainly in the upper 100 m. A further obstacle was the sampling using a net with 330 µm mesh size. The net probably failed to catch small species because of their elongated and slender constitution. Other authors already discussed that plankton nets with 200 µm mesh size could have under-sampled the smaller Chaetognatha species such as *S.minima* (Kehayias & Ntakou, 2008). It is well known that the mesh size in plankton nets is a trade-off between the gain in larger species and loss of the smaller ones (McGowan & Fraundorf, 1966; Kehayias & Kourouvakalis, 2010).

4.1. Abundance and distribution

In general, the vertical distribution of Chaetognatha on the Walvis Bay transect determined in this study is in concordance with results obtained in other studies (Duró & Gili, 1996; Gibbons, 1994). Most of the species (juveniles of the *Serratodentata* group and S*. tasmanica, S. serratodentata*, *E. hamata, S. decipiens, S. minima, S. hexaptera, P. draco, S. maxima, S. lyra*) preferred the warmer water between 8 and 16°C in the upper 400 m. The bathypelagic species, except *S. macrocephala*, mainly occurred in depth between 1500 and 2620 m (the maximal sampling depth at the offshore station), where temperature, oxygen and salinity were almost constant at around 3°C, 5 mL/L and 34.9, respectively. Grant (1991) suggested that some Chaetognatha species depend strictly on specific water masses and are influenced by hydrological factors. Cheney (1985) assumed that temperature, salinity, oxygen concentration and pressure affect not only the distribution but also the reproduction and mortality rates of Chaetognatha and other zooplankton species. The thermocline has an important effect as a physical barrier to migration and limits the distribution patterns of some Chaetognatha species (Conway & Williams, 1986). In September 2010 (southern spring), small temperature differences in water column (< 3.0°C) were found on the shelf and at the shelf break station. At the offshore station, a continuous decrease of temperature from 16°C in the surface layer (0 – 25 m) to 4°C below 750 m was observed. Salinity was relatively stable at the shelf and shelf break stations varying between 34.8 and 35.4. The highest variability in salinity was found at the offshore station

(<1.0). Salinity differences as small as those have probably no measurable effect on the physiology and distribution of the Chaetognatha (Cheney, 1985; McLaren *et al.*, 1968). Some authors (Escribano *et al.*, 2000; Pearre, 1979; Giesecke & Gonzáles, 2004) assumed that low oxygen contents may reduce the abundance of several species. An explicit impact of the low oxygen concentrations in the BUS on the Chaetognatha distribution was not detected. Low oxygen values were found in the bottom layer at the shelf (< 0.5 mL/L) and shelf break (< 1.0 mL/L) stations below 100 and 150 m, respectively. At the first view, it seems like the low oxygen concentrations has an effect on the vertical distribution of the Chaetognatha because a high number of Chaetognatha were found above these low oxygen layers. However, the standing stock was mainly composed of species belonging to *Serratodentata* group (61.3% at the inner shelf station, 89.7% at the outer shelf station, 36.2% at the shelf break station), which was characterized as an epipelagic group having a WMD between 34 and 105 m. Another species, such as *E. hamata*, *S. decipiens, S. hexaptera* and *S. lyra*, were found in this low dissolved oxygen layers (Figure 13) and showed that these species are not influenced by low oxygen concentrations.

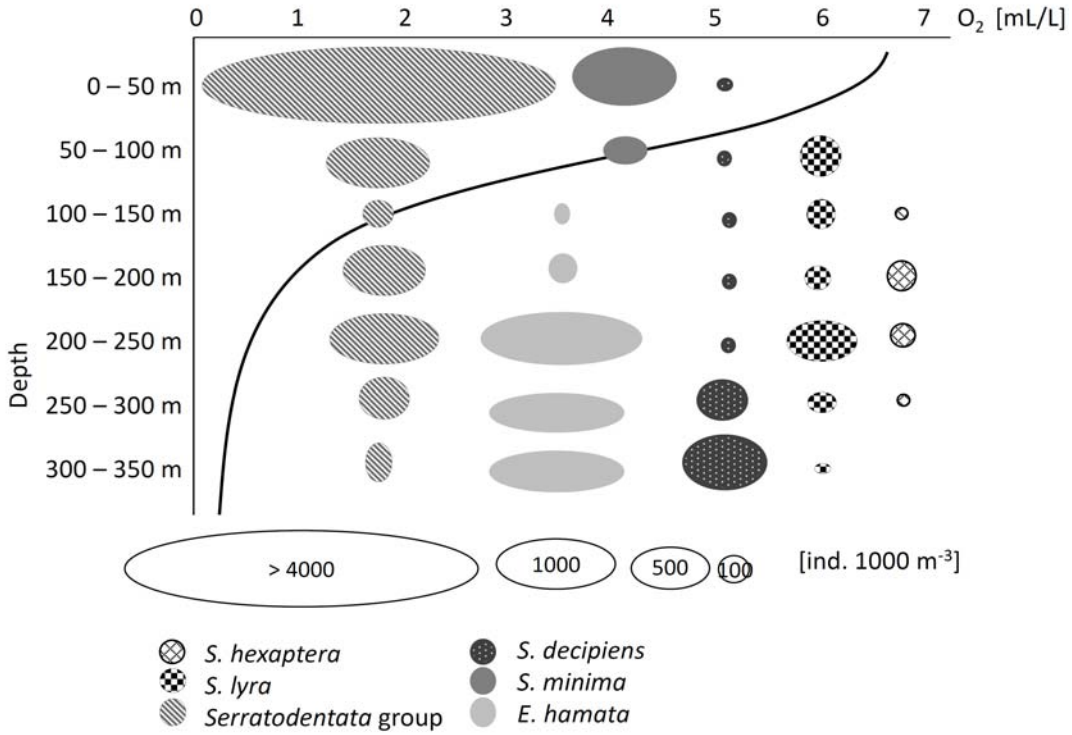

Fig. 13 *A conceptional picture of the vertical distribution of Chaetognatha species depending on oxygen concentrations (station WB3 as example); the line demonstrate the oxygen concentration; the dimension of the bubbles are not scaled.*

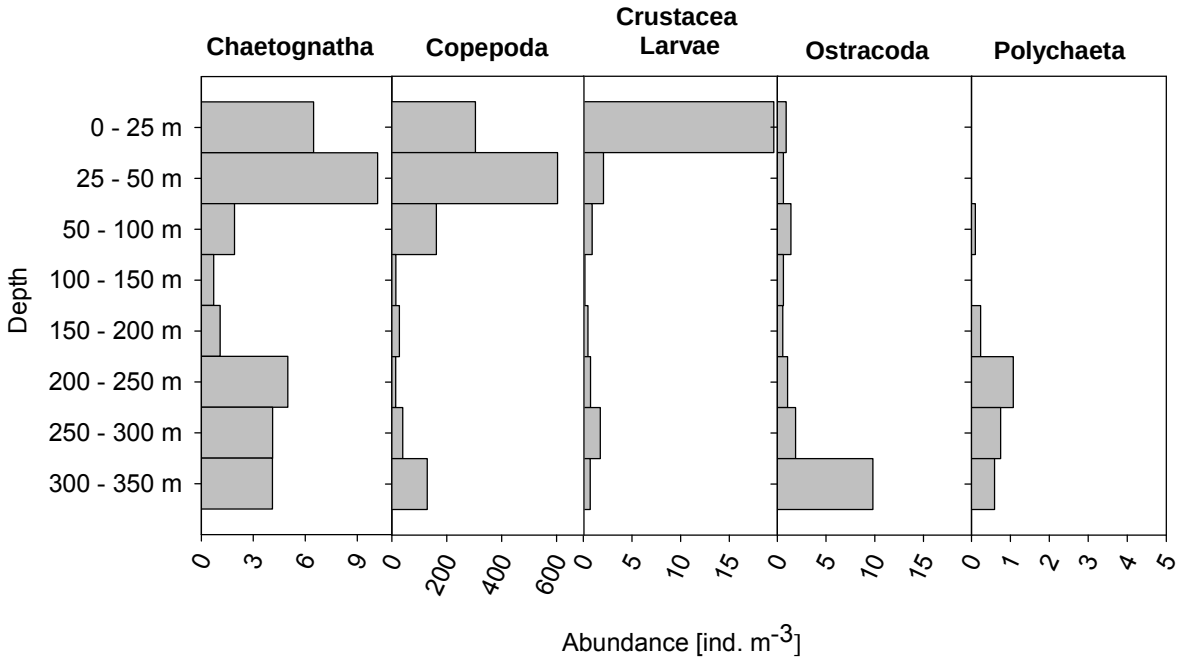

Fig. 14 *The vertical distribution of Chaetognatha (this study), Copepoda, Crustacea Larvae, Ostracoda and Polychaeta (Martin & Koppelmann, in progress) at the shelf break station WB3; note the different scales of the X-axis*

Many authors (Duró *et al*., 1994; Marazzo & Nogueira, 1996; Gibbons, 1992) investigated the effect of food availability as a determining factor, responsible for the vertical distribution and migration of Chaetognatha. The major food item recovered from Chaetognatha guts are copepods (Feigenbaum & Maris, 1984; Shannon & Pillar, 1986; Gibbons, 1992; Table 11). But also other organisms such as Polychaeta, Cladocera, Euphausiacea, Hydromedusae, Pteropoda, Appendicularia and Ostracoda were detected (Table 10; Kehayas, 2003; Terazaki, 1996; Batistic *et al.,* 2010; Giesecke & Gonzáles, 2004). Chaetognatha often prey even on its own. Giesecke and Gonzáles (2004) assumed that this may be an adaptive behaviour when food is limited. This behaviour was already described in many studies (Pearre, 1976; Feigenbaum and Maris, 1984; Giesecke and Gonzáles, 2004). Several authors call this behaviour (Chaetognatha prey on Chaetognatha) cannibalism which is not correct. Cannibalism is characterised as preying on individuals of the same species. Until now, cannibalism has been proven only for two species: *S. setosa* (Mironov, 1960) and *S. maxima* (Pearre, 1974).

Copepoda are very abundant within the zooplankton community in the BUS (Gibbons, 1992; Peterson *et al*., 1990). In spring 2010, high abundances of Copepoda were found at the shelf break station on the Walvis Bay transect (Figure 14; Martin & Koppelamnn, in progress). The densities of Copepoda show similar vertical distribution patterns as those of the Chaetognatha. It has been proven that Chaetognatha feed at the copepod maximum (Gibbons, 1994), which was in the samples from Martin & Koppelmann (in progress) near the surface between 25 and 50 m (603 ind. m^{-3}). The copepod

densities decreased below 100 m and increased again at depth greater 250 m to more than 39 ind. m^{-3} (Martin & Koppelmann, in progress). Chaetognatha generally cannot cope with starvation (Feigenbau & Maris, 1984). The vertical distribution of Chaetognatha and their potential prey like Copepoeda, Polyachaeta or Ostracoda suggests that Chaetognatha found in upper 100 m and below 250 m were not limited by lacks of food.

Tab. 10 *Composition of the gut contents of the Chaetognatha species.*

Author		Kehayas (2003)	Terazaki (1996)	Batistic *et al.* (2003)	Kehayias & Kourouvakalis (2010)	Giesecke & Gonzáles (2004)
Area		Eastern Meditteranean	Central Equatorial Pacific	South Adriatic	Eastern meditteranean	Northern Chile
Species	**Gut contents**					
S. enflata	Copepoda	40 - 96%	52%	52 - 94%	12 - 31%	81 - 93%
	Ostracoda		2%			
	Cladocera	17%		4 - 11%	39 - 77%	
	Euphausiacea			4%		
	Crus. larvae	20%	4%			
	Chaetognatha	4%	3%	7 - 20%		1%
	Hydromedusae			2 - 4%		2%
	Polychaeta					5%
	Pteropoda		2%			
	Appendicularia			4%		
S. minima	Copepoda	33 - 50%		65 - 95%	14 - 50%	
	Cladocera				40 - 73%	
	Crus. larvae			3%		
	Chaetognatha			9 - 18%		
S. lyra	Copepoda	50 - 100%		64 - 96%		
	Cladocera			1 - 2%		
	Chaetognatha	25%		6 - 22%		
	Hydromedusae			1 - 5%		
	Appendicularia			1%		
S. hexaptera	Copepoda	100%				
S. decipiens	Copepoda	50 - 100%		70 -84%		
	Ostracoda			10%		
	Chaetognatha			3 - 4%		
S. serratodentata	Copepodsa				32 - 100%	
	Cladocera				0 - 33%	

Within the vertical distribution of Chaetognatha species a segregation of maturity stages on the Walvis Bay transect was not clearly detected. Kehayias *et al.* (1994) determined that epipelagic species do not exhibit ontogenetic vertical distribution, which could be caused by the relatively small depth range which characterizes these species (0 – 200 m). The community was dominated by epipelagic to shallow-mesopelagic species. Seven epipelagic and three epipelagic to shallow-mesopelagic species were found on the Walvis Bay transect (Table 5). Some adults of these species such as *P. draco* or *S.decipiens* showed a tendency to occur in deeper layers than the juveniles (Figure 8 and Table 6) but these differences were not evident enough to make a clear statement about the ontogenetic distribution of these species. It was difficult to determine the ontogenetic vertical distribution of the deep-mesoplegic and bathypelagic species because the community of these species was dominated by juveniles which may be associated with the winter spawning (Gibbons *et al.*, 1992 and references therein). Cheney (1985) assumed that Chaetognatha stage structure coupled with an ontogenetic distribution can influence the vertical distribution of the total population. This may have had an influence on the classification of the species as deep-mesopelagic or bathypelagic in this study.

The richness and diversity of Chaetognatha species along the Walvis Bay transect showed a tendency to increase from the shelf towards the open ocean (Table 7). The most obvious reason for these findings is the water depth of the area. At the inner and outer shelf stations, the water depth was 132 and 231 m, respectively. These two stations were dominated by epipelagic species such as *S. tasmanica, S. decipiens, S. sibogae* and *S. minima,* but also some mesopelagic species were found (*E. hamata, S. hexaptera*). At the shelf break station, one deep-mesopelagic species had already been found (*S. zetesiois*). At the offshore station, all categories were represented. The other reason for the increase of richness and diversity from the shelf towards the open ocean is the occurrence of oceanic species like *S. minima, S. lyra* and *P. draco* at the shelf break and offshore stations.

The *Serratodentata* group dominated the Chaetognatha community at the shelf and shelf break stations ($D > 0.31$). The high abundances of the species belonging to this group are in concordance with other study from Duró and Gili (1996). As a consequence of the high abundance of the *Serratodentata* group at the shelf stations and the high diversity at the shelf break and offshore stations, higher variations in community evenness between species was found on the shelf ($J < 0.33$).

4.2. Stable isotopes

Nitrogen isotopic composition reflects important dietary relationships within the food web (Michener & Lajtha, 2007). The trophic position of Chaetognatha could be determined using the enrichment factor of 3,4 ‰ per trophic level (Post, 2002). The phytoplankton $\delta^{15}N$ values were not available for this area. Hence, seston values were used as baseline. Unfortunately, the seston data have only been analysed for the shelf break and offshore stations yet (Figure 15_a). The values ranged between 1.24 and 7.03 ‰ with mean a value of 4.55 ± 1.99 ‰ at the shelf break station and between 2.59 and 5.92 ‰ at the offshore station with a mean value of 4.90 ± 2.26 ‰ (Lahajnar, unpublished data). The lowest $\delta^{15}N$ values were found near the surface in upper 30 m, which reflected a higher productivity (Holmes *et al.,* 2000).

In addition, Kullmann (2011) examined the $\delta^{15}N$ and $\delta^{13}C$ values of Thecostomata (formally known as Pteropoda) in the Northern Benguela (Figure 15_b). Thecostomata are considered to be predominantly herbivorous, capturing food with a mucous web (Hunt *et al*., 2008). It is expected that Thecostomata as primary consumers (Gilmer & Harbison, 1986) occupy a trophic level between primary producers (phytoplankton) and carnivorous organisms like Chaetognatha in the food web. The $\delta^{15}N$ values of Thecostomata and seston are relatively close to each other. For the stable isotopes analysis, the guts of the Thecostomata were not removed. The guts probably contained a high amount of phytoplankton which may had an influence on the stable isotopes values. The Chaetognatha $\delta^{15}N$ values (8.96 ± 1.19 ‰ at the offshore station, 8.33 ± 1.62 ‰ at the shelf break station, 9.28 ± 0.86 ‰ at the shelf station) were 3 - 4 ‰ higher than those of Thecostomata (4.56 ± 0.45 ‰ at the offshore station, 5.50 ± 0.70 ‰ at the shelf break station, 5.39 ± 0.50 ‰ at the shelf station) and met the expectation that Chaetognatha as secondary consumers form a higher trophic level.

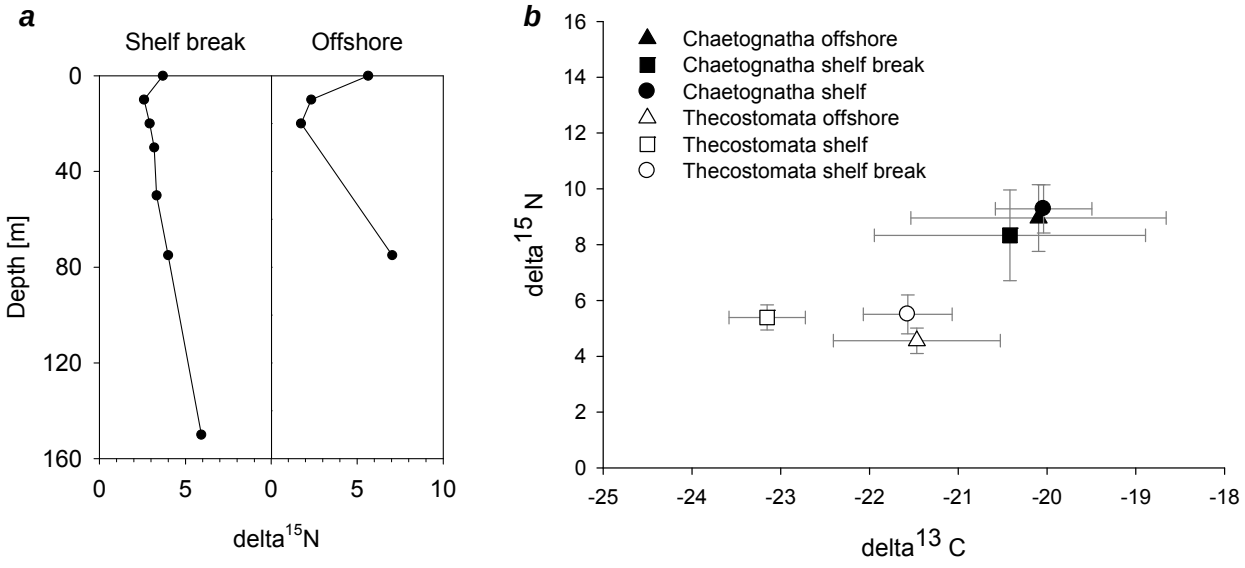

Fig. 15 *The $\delta^{15}N$ values of seston (a; Lahajnar, unpublished data) and he trophic position of Thecostomata (Kullmann, 2011) and Chaetognatha (b) in southern spring 2010.*

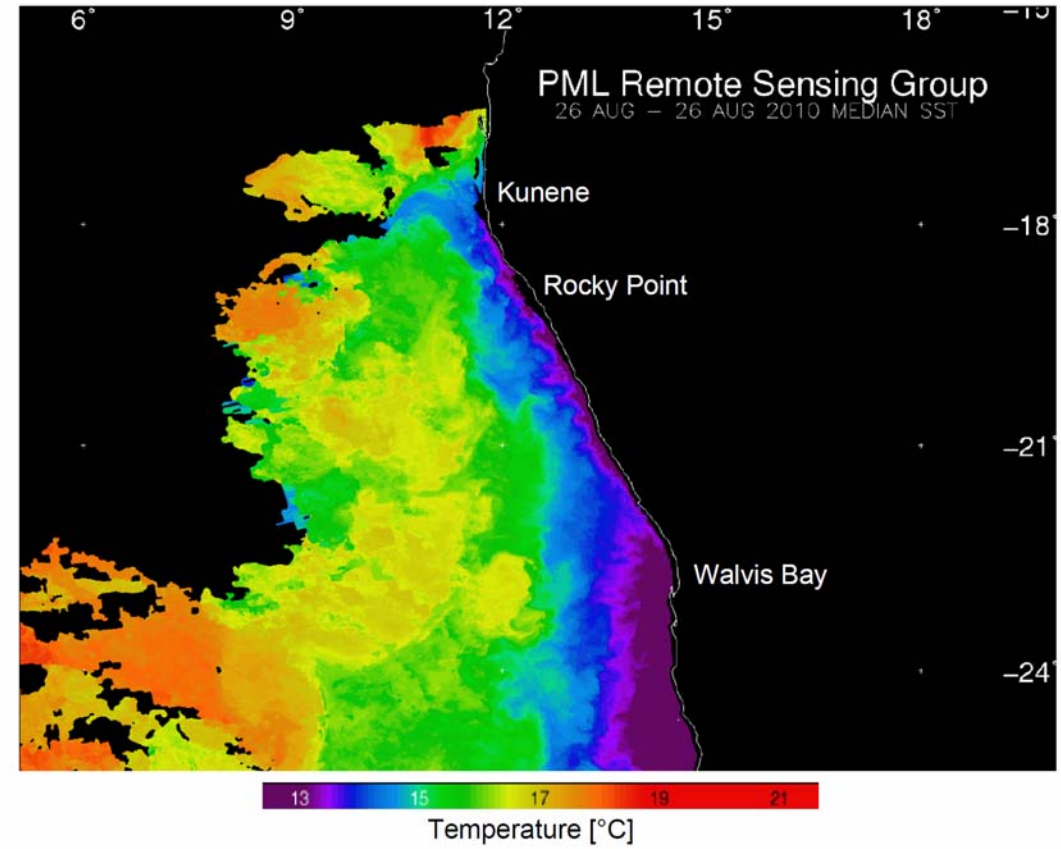

Fig. 16 *The surface temperature measured in August 2010 off the west coast of Africa (on-line source: NODC)*

In this study, differences in the isotopic carbon composition of Chaetognatha between the Rocky Point offshore station and other stations were detected. Stanly (2010) observed that the values of $\delta^{13}C$ for phytoplankton are positively correlated with the water temperature and indirectly affect the $\delta^{13}C$ of zooplankton. Not only the temperature, also strong turbulent mixing and upwelling influence the $\delta^{13}C$ values (Stanly, 2010). Under conditions of high nutrient availability, the productivity of phytoplankton increases and discrimination against the heavier carbon isotope decreases which caused enriched $\delta^{13}C$ signal in phytoplankton (Farquhar *et al*., 1989; O'Reilly *et al*., 2011). The extension of the upwelling can be determined by analysing sea surface temperature (Figure 16). The Rocky Point offshore station is located more oceanic than the other stations, hence mixing and turbulence are lower than at the more dynamic shelf stations. This may explain the low $\delta^{13}C$ values detected at the Rocky Point offshore station.

The differences in $\delta^{13}C$ and $\delta^{15}N$ may also be influenced by different species composition at the sampling stations. Duró and Gili (1996) investigated that the species of the BUS can be grouped into 4 main categories according to their latitudinal conditions: (1) species with broad distributions over the entire area; (2) species concentrated in the northernmost part of the BUS; (3) species concentrated in the central part of the BUS; (4) species present only in the southernmost part of the BUS.

The stable isotope ratios of four taxa (*S. minima, Planctonis* group*, S. enflata, S. decipiens*) were determined. The $\delta^{15}N$ values from *S. decipiens* were higher (9.16 to 10.05 ‰) than those found in other species. The lowest $\delta^{15}N$ values were found for *S. minima.* These differences could be a result of the body size of the species and hence of a different food composition i.e. body size correlates with prey size. *S. minima* is the smallest species found on the Walvis Bay transect, reaching a maximal body length between 7 - 10 mm (Casanova, 1999). The potential preys of this species in the Northern Benguela are Copepoda, Chaetognatha and Crutacea larvae (Table 11). The small body size of *S. minima* lets assume that this species prey over smaller Copepoda species. In comparison to *S. minima*, *S. enflata* and *S. decipiens* reached a body length up to 25 (Pierrot-Bults & Chidgey, 1988) and 14 mm (Casanova, 1999), respectively. These larger species have a wider range of potential prey items. As the *S. decipiens, S. enflata* contain animals of higher trophic level, the nitrogen isotope content of these species may reach higher values. The prey composition of *S. zetesiois* and *S. planctonis* has not been closely investigated yet.

As discussed above, the results of stable isotope analyses varied between the areas. For the determination of the stable isotopes of the four taxa, samples taken on different stations were pooled. However, the values of the four taxa did not range greatly. No significant differences were found between the areas, where the samples for the determination of stable isotopes of the taxa were taken.

4.3. Body composition

Body composition can vary with seasons (Reeve *et al.*, 1970) and locations (Ikeda, 1974). The body composition is possibly influenced by dissimilar life cycles and nutritional conditions of animals (Ikeda & Kirkwood, 1989). Ikeda (1974) found that the nitrogen content of zooplankton changes greatly from species to species and no consistent relation to body size and habitat temperature exists. Differences between the relative nitrogen content of the species were found. The relative nitrogen values of *S. enflata* (from 8.77 ± 1.08% to 9.93 ± 0.78%) are in concordance with those found by Gorsky *et al.* (9.1 ± 2.8%; 1988) and Batistić (9.58 ± 2.04%; 2003). The relative nitrogen amount of *S. minima* was 7.14 ± 1.55%. Batistić (2003) and Gorsky *et al.* (1988) reported higher values of 11.88 ± 0.70% and 11.8 ± 0.2%, respectively. Differences of the nitrogen content may be caused by differences in the life history and in seasonal trends of zooplankton production at different localities (Omori, 1969).

The results of the relative carbon content of Chaetognatha species determined in this study are generally similar to those found in other studies (Gorsky *et al.,* 1988; Batistić, 2003). However, there are some differences. In this study, the relative carbon content of *S. enflata* varied from 40.70 ± 8.91% to 49.94 ± 2.96%. The percentage of carbon of *S. enflata* determined by Batistić (2003) ranged between 30.41 ± 2.53% and 40.39 ± 1.63%. Gorsky *et al.* (1988) reported carbon percentage of 43.7 ± 11%. The relative carbon content of S*. minima* determined in this study (31.98 ± 9.58%) is similar to those values found by Batistić (2003; between 27.73 ± 2.68 and 39.31 ± 1.99%). For *S. minima,*

Gorsky *et al*. (1988) reported higher relative carbon values (51.0 ± 2.1%). The higher relative C values investigated for *S. minima* and *S. enflata* in this study may originate in the different developmental stage composition of the samples. Carbon and nitrogen content of some species depends on the maturity stage and increase with age and thus with dry weight and length class (Batistić, 2003). Gorsky *et al.* (1988) did sampling during a spring-season in the north-western Mediterranean Sea. In this period more mature individuals occurred in higher numbers (Kehayas *et al*., 1994). Another possibility for these variations may be differences in the area and time of sampling. In spring in north-western Mediterranean Sea, the temperature can reach high values up to 25°C (Brasseur *et al*., 1996). Batistić, 2003 sampled in the Adriatic Sea at a different time of the year and temperatures ranged from 12°C in February to 22.5°C in August. The temperature measured in spring at the Benguela Upwelling Area was lower than 16°C.

The high carbon values reflect a high proportion of organic matter in the animal body, and low nitrogen values indicate low proportions of protein. The C:N ratio is a useful index to distinguish protein from fat. The ratio varied greatly from 4.5 for some Copepoda species to 45 for Leptomedusae (Ikeda, 1974). The C:N ratio of different Chaetognatha species described in this study ranged between 5.25 ± 0.42 and 6.20 ± 0.36. Kruse *et al.* (2010) found for species belonging to Eukrohniidae C:N ratios varying between 4.3 ± 0.6 and 5.1 ± 1.0. Also, the C:N ratio determined by Gorsky *et al.* (1988) was lower and varied between 4.0 ± 0.7 and 5.0 ± 1.4. The higher C:N ratio of Chaetognatha occuring the BUS suggested that larger amount of fat was saved in the animal body (Ikeda, 1974). The high lipid content may help to survive periods of poor food concentrations which are typical for pulsed upwelling (Gibbons *et al*., 1992). The C:N ratios of Chaetognatha determined in this study are close to C:N ratio of zooplankton determined by Redfield (6.24; 1934).

5. Conclusion

In this study, differences in the horizontal distribution of the Chaetognatha species along the Walvis Bay transect were observed. The community of Chaetognatha was dominated by epipelagic and shallow-mesopelagic species. With increasing distance from the shelf towards the open ocean, the number of mesopelagic and bathypelagic species increased. The vertical distribution of Chaetognatha species is more influenced by the prey densities than by the water properties. No effect of low oxygen concentrations on the vertical distribution of Chaetognatha was detected.

Findings in this study support the view that the Chaetognatha of the Benguela Upwelling System (BUS) play a significant role in the food web. Chaetognatha may exert a high predation impact on the copepod community and thereby influence the standing stock of copepods. This study can help to understand the trophic relationships between the different taxonomical groups in the BUS and can also help to calculate material fluxes within the pelagic food web.

Repeated observations in different seasons and at different locations will help to complete the view on the Chaetognatha community of the BUS.

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Appendix

Chaetognatha of the Benguela Upwelling System

Key for the identification of species

Karolina Bohatá
University of Hamburg
Institute for Hydrobiology und Fisheries Science
2011

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1. Introduction

Chaetognatha are transparent marine metazoans living in various marine habitats (Harzsch & Waninger, 2010 and references therein). Some Chaetognatha species can be used as a good indicator of the water masses, since they are related to specific environmental variables (Casanova, 1999). Chaetognatha have been already studied since the eighteenth century (Jennings *et al*., 2010 and references therein). They were present in the Early Cambrian (Vannier et al., 2006) and in the Middle Cambrian Burgess Shale (Szaniawski, 2002).

The phylum Chaetognatha is comprised of over 120 species (Jennings *et al*., 2010; Harzsch & Wanninger, 2010 and references therein). The position of Chaetognatha within the bilaterians still remains unclear. The molecular phylogeny of these organisms has been proven to be problematic, making their placement in the animal systematics difficult (Papillon *at al*., 2004; Marlétaz & Le Parco, 2008 and references therein). Morphological features such as the secondary mouth formation, a mesoderm derived directly from the archenteron and a trimeric coelom have been inferred to place Chaetognatha within the Deuterostomia (Helfenbein *et al*., 2004 and references therein). Some other studies speculate that Chaetognatha diverged from the triploblast lineage before the deuterostome/protostome split (see Helfenbein *et al*., 2004).

In the most recent studies, Chaetognatha have been placed as basal members of protostomes (Papillon *et al*., 2004). Papillon *et al.* (2004) compared the mitochondrial DNA genome of *Spadella cephaloptera* with other bilaterians. The author found that with 11,905 base pairs (bp) the mtDNA genom of this species is the smallest known metazoan genome and contains only 13 of the 37 genes usually found. Another study from Helfenbein *et al*. (2004) showed that the mtDNA of *Paraspadella gotoi* is also relatively small compared to the genomes of other triploblastic animals. The mtDNA of *P. gotoi* consist of only 11,423 bp and contains only 14 genes. In both species, protein-encording genes atp6 and atp8 are missing (Helfenbein *et al*., 2004; Papillon *et al*., 2004). Papillon *et al*. (2004) also tested the position of Chaetognatha statistically within the protostomes, deuterostomes and a third bilaterian branch. The authors revealed that Chaetognatha belong to protostomes but the exact position of Chaetognatha could not be accurately determined. Marlétaz *et al.* (2006) studied the position of Chaetognatha using a ribosomal protein dataset including hemichordate genomic data. The authors propose that Chaetognatha are a sister-group to all protostomes. However, Matus *et al.* (2006) suggest Chaetognatha as a sister group of Lophotrochozoa. They analysed the phylogenetic position of Chaetognatha using existing datasets e.g. small and large subunit nuclear ribosomal RNAs and complete mitochondrial genomes, and new dataset from the tropomyosin gene of many Metazoa. Alternative arrangements are still advanced.

Chaetognatha can be found at all depths from the surface to several thousands meters deep. The main parameters which influence the vertical distribution are temperature, age of specimen and light

intensity (Casanova, 1999). Marazzo & Nogueira (1996) suggest that also copepod density could play an important role for the spatial and temporal distribution of Chaetognatha. Another study from Giesecke and González (2004) assumed that low oxygen layers also reduce the abundance of Chaetognatha which could be connected to the lower copepod density in these layers.

The body length of Chaetognatha ranges from 2 to 120 mm. Despite of their small size these marine predators play an important role in the food web (Casanova, 1999) and in the planctonic ecosystem (Marlétaz & Le Parco, 2008 and references therein). The role of benthic species in the ecosystem is still unknown (Casanova, 1999 and references therein). Chaetognatha have a relatively simple body structure with some complex internal structures (Jennings *et al.,* 2010). Their body is transparent to semi-opaque and sometimes partially pigmented. It consists of the head, trunk and tail (Figure 1). One or two pairs of lateral fins and a tail fin makes Chaetognatha fast and very good swimmers. The head provides hooks, a vestibular organ and one or two rows of teeth (Casanova, 1999). Chaetognatha perform hermaphroditic reproduction (Casanova, 1999 and references therein; Jennings *et al*., 2010 and references therein). Eggs of pelagic species are generally laid free in the water. The benthic species laid their eggs to the substratum (Casanova, 1999).

Chaetognatha are active predators and their prey is grasped with rigid hooks (Casanova, 1999 and references therein). The typical and numerically dominant prey of Chaetognatha are copepods but also larger organisms such as fish larvae (Pearre, 1982), polyachaeta (Giesecke & Gonzáles, 2004) or euphausiids were found in field-preserved Chaetognatha. Chaetognatha prey even on their own. This behaviour in Chaetognatha is influenced by prey abundance and predator size. Larger species may primarily be predators on smaller ones. This behaviour can reduce the number of reproducing individuals in a population (Pearre, 1982).

Figures 2 – 3, 5 – 19, 21-22, 24 - 28: Casanova J. (1999): South Atlantic Zooplankton. Chaetognatha. Vol. 2. Backhuys Publishers, Leiden, p. 1353 - 1374.

Figure 7: Chaetognatha of the World. URL: http://nlbif.eti.uva.nl/bis/chaetognatha.php?set=4&menuentry=zoeken&selected=foto (last call: 29.3.2011)

Figure 21: Centro de biologia marinha universidade de sao Paulo. URL: http://200.144.190.194/cbm/index.php/component/rsgallery2/category/99/asInline.html (last call: 29.3.2011)

Figure 28 (left): B-NEAT Baltic and North East Atlantic Taxa. URL: http://test.b-neat.org/species_sheet/?id=1000061 (last call: 29.3.2011)

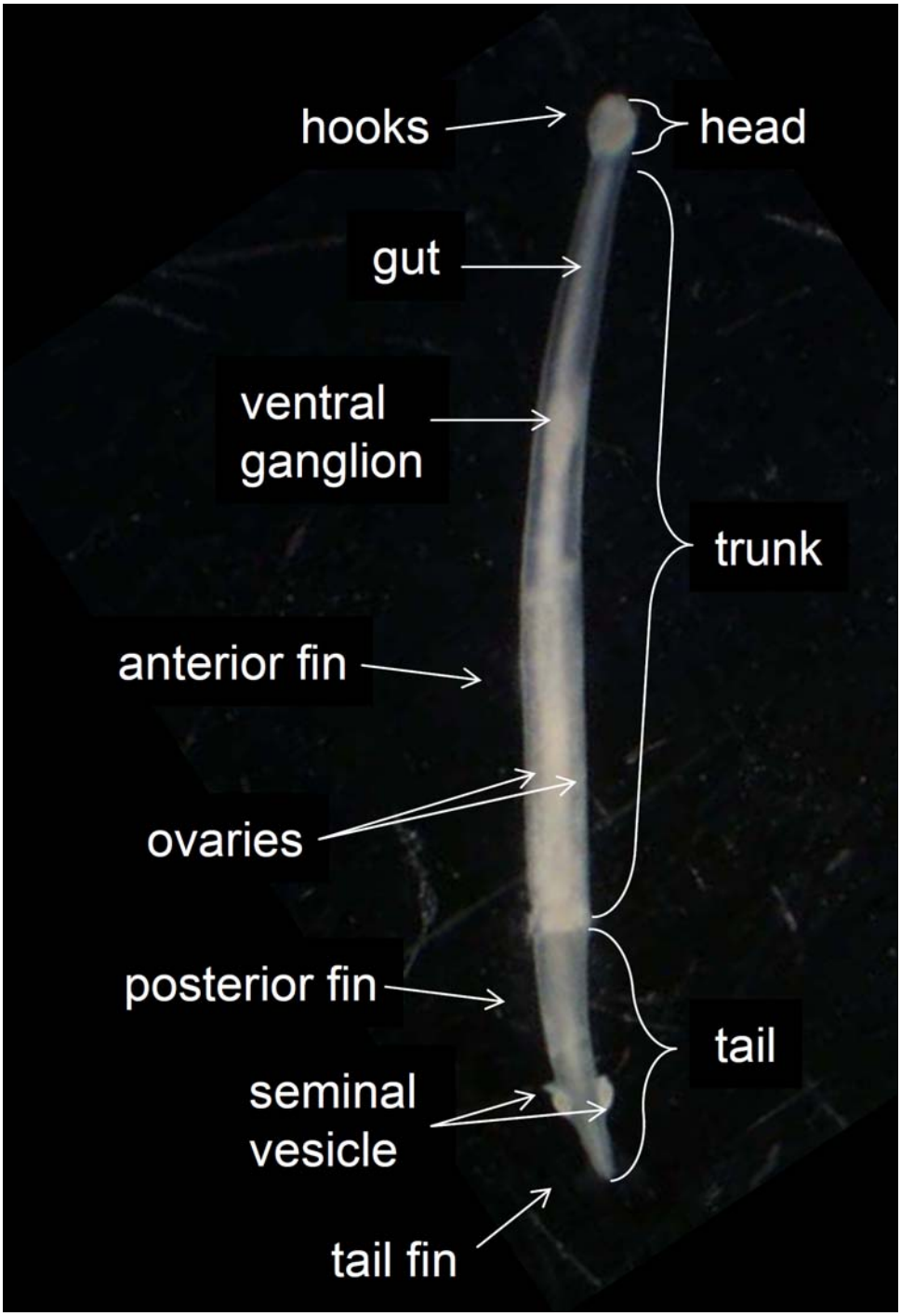
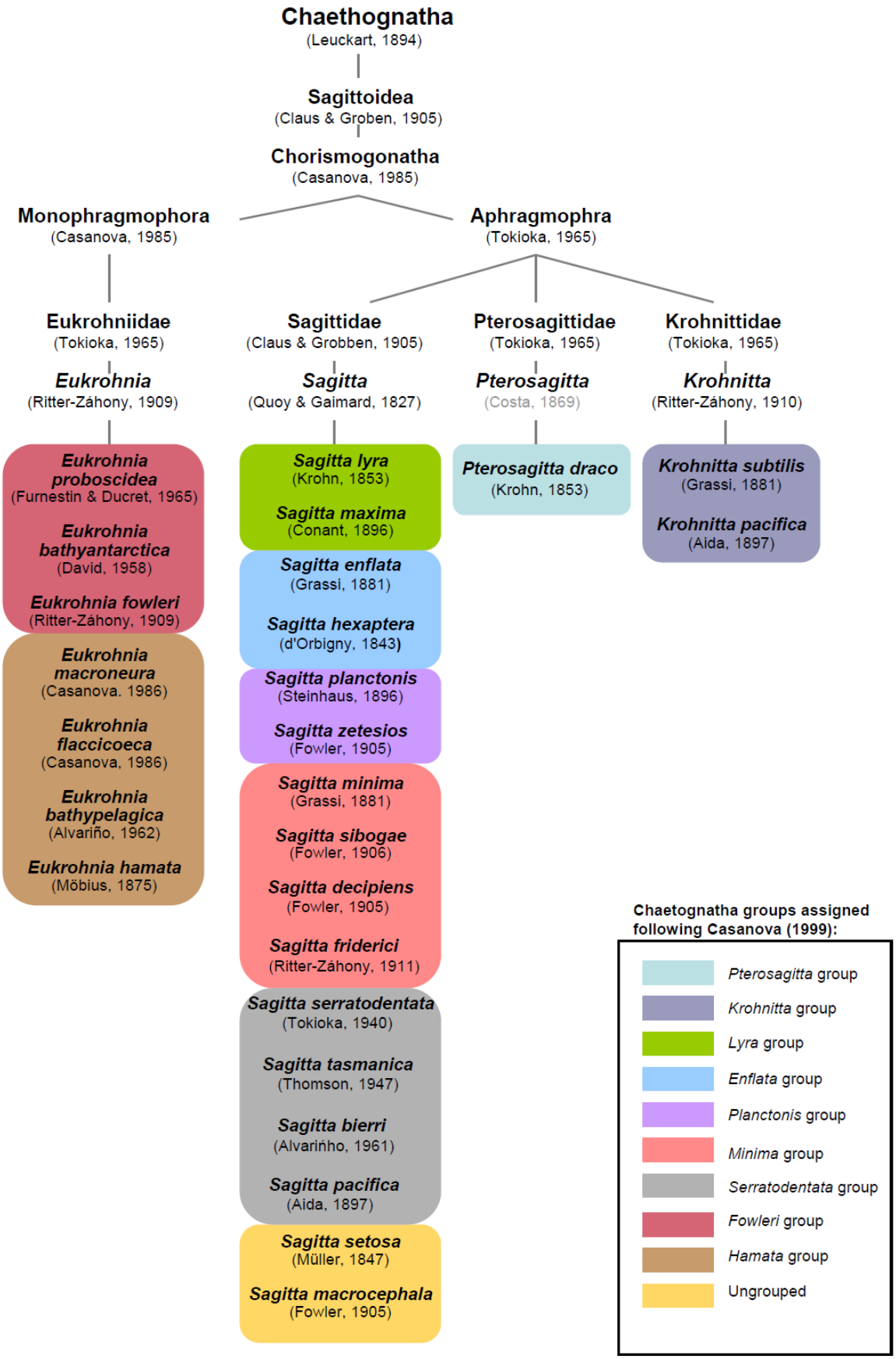


Figure 1: *Main diagnostic features of a Chaetognatha (S. serratodentata)*

2. Classification



3. Key for the identification of species

Modified from:

Casanova, J.-P. (1999): South Atlantic Zooplankton. Chaetognatha. Vol. 2. Backhuys Publishers, Leiden, p.1353-1374.

Pierrot-Bults, A.: Chaetognatha of the World. http://www.nlbif.nl/. Stand: 4.2.2011URL: http://nlbif.eti.uva.nl/bis/chaetognatha.php (last call: 29.3.2011)

Marine species identification Portal. http://species-identification.org Stand: 4.2.2011 URL: http://species-identification.org/species.php?species_group=zmns&id=8&menuentry=groepen (last call: 29.3.2011)

SERTC Southeastern Regional Taxonomic Center. http://www.dnr.sc.gov/marine/sertc/info.htm#. Stand: 4.2.2011 URL: http://www.dnr.sc.gov/marine/sertc/Chaetognath%20key/Chaetognath%20key.htm (last call: 29.3.2011)

1 a One pair of lateral fins **2**

b Two pairs of lateral fins **10**

2 a Transversal musculature absent **3**

b Transversal musculature present on trunk **7**

3 a Coralette very large; lateral and tail fins not connected; transversal musculature absent; 8-10 hooks; anterior teeth; hooks not serrated
→ ***Pterosagitta draco*** p.9

b Without collarette **4**

4 a Eyes present without pigment spot; hooks with claws **5**

b Eyes absent; hooks with slender nail **6**

5 a Lateral fins rayed only externally
→ ***Krohnitta subtilis*** p.13

b Lateral fins almost totally rayed; length up to 8 mm
→ ***Krohnitta pacifica*** p.13

6 a Ovaries straight
→ ***Eukrohnia macroneura*** p. 12

b Ovaries rounded; body expanded at the area of trunk-tail septum
→ ***Eukrohnia flaccicoeca*** p. 12

7 a Orange-colored gut, 13-14 dark brown hooks **9**

b Up to 11 clear amber hooks **8**

8 a 9-10 hooks; 23-25 posterior teeth; tail segment < 24% of body length; ovaries straight with small ova in 3 or 4 rows
→ ***Eukrohnia hamata*** p.11

b 7-10 hooks; 17-22 posterior teeth; tail segment > 27% of body length; ovaries distally curved, with large ova in 2 rows
→ ***Eukrohnia bathypelagica*** p.11

9 a Eyes without pigment cell
→ ***Eukrohnia bathyantarctica*** p. 10

b Eyes with pigment cell; foamy collarette around ventral ganglion; pigment spot triangular
→ ***Eukrohnia fowleri*** p. 10

c Eyes with pigment cell; No collarette; pigment spot elongated
→ ***Eukrohnia proboscidea*** p. 9

10 a With fin bridge **11**

b No fin bridge **12**

11 a Anterior fin begins a short distance from ventral ganglion; max. adult body length 42 mm; posterior fins angular; ovaries reaching till middle of anterior fins
→ ***Sagitta lyra*** p.16

b Anterior fin begins at level of ventral ganglion; max. adult body length 55 mm; posterior fins rounded; ovaries reaching till region of ventral ganglion
→ ***Sagitta maxima*** p.16

12 a Hooks serrated **13**

b Hooks smooth **14**

13 a Collarette small or absent; 5-8 anterior teeth; 8-16 posterior teeth
→ ***Sagitta bierii*** p.14

b Collarette small or absent; 10-11 anterior teeth; 3-19 posterior teeth
→ ***Sagitta serratodentata*** p.14

c Collarette conspicuous; 7-13 anterior teeth; 16-24 posterior teeth
→ ***Sagitta pacifica*** p.15

d Collarette conspicuous; 2-9 anterior teeth; 3-19 posterior teeth
→ ***Sagitta tasmanica*** p.15

14 a Body transparent **15**

b Body not transparent **17**

15 a Anterior fins begin at the end of ventral ganglion; posterior teeth 6-17; max. body length 15 mm; body firm; tail 25-28% of the body length
→ ***Sagitta friderici*** p.18

b Anterior fins begin close to ventral ganglion; posterior teeth 9-15; max. body length 30 mm; body slender; tail 20-30% of the body length
→ ***Sagitta sibogae*** p. 19

c Anterior fins begins far beyond ventral ganglion **16**

16 a Posterior teeth 4-13; max. body length 25 mm; body flaccid; anterior fins partially rayed; tail 14-17% of the body length
→ ***Sagitta enflata*** p.17

b Posterior teeth 2-6; max. body length 70 mm; body flaccid; tail 16-20% of the body length
→ ***Sagitta hexaptera*** p.17

c Posterior teeth 15-19; Anterior fins begins far beyond ventral ganglion; 5-8 hooks; 15-19 posterior teeth
→ ***Sagitta decipiens*** p.19

17 a Anterior fins entirely without rays
→ ***Sagitta minima*** p.18

b Fins completely rayed **18**

c Anterior fins with some rays **19**

d The rays are unidentifiable **20**

18 a Posterior teeth 12-16; tail 29-34% of the body length; head medium; posterior fins rounded; seminal vesicle separated from tail fin
→ ***Sagitta setosa*** p.21

b Posterior teeth 20-35; tail 29-34% of the body length; head very large; posterior fins angular; seminal vesicles neither touch the posterior fins nor the tail fin
→ ***Sagitta macrocephala*** p.21

19 a Anterior fins begins at the level of end of ventral ganglion; 8-11 hooks; 15-22 posterior teeth
→ ***Sagitta zetesiois*** p.20

b Anterior fin begins at the level of middle of ventral ganglion; 8-11 hooks; 10-14 posterior teeth
→ ***Sagitta planctonis*** p.20

20 a Eyes without pigment spot
→ ***Sagitta macrocephala*** p.21

b Eyes with pigment spot **21**

21 a Anterior fins begins far beyond of ventral ganglion **22**

b Anterior fins begins at the level of end of ventral ganglion; 8-11 hooks; 15-22 posterior teeth

→ ***Sagitta zetesiois*** p.20

c Anterior fin begins at the level of middle of ventral ganglion; 8-11 hooks; 10-14 posterior teeth

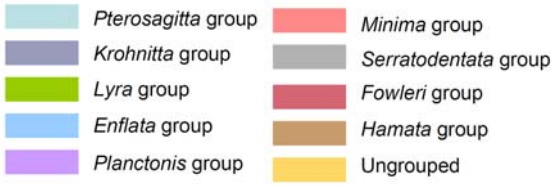
→ ***Sagitta planctonis*** p.20

22 a Eyes with T-shaped pigment spot; 8-10 anterior teeth; 15-19 posterior teeth; 5-8 hooks; 200-500 m depth
→ ***Sagitta decipiens*** p.19

b Eyes with star-shaped pigment spot; 6-8 anterior teeth; 12-16 posterior teeth; 8-9 hooks; 0-200 m depth
→ ***Sagitta setosa*** p. 21

7. Description of species

Chaetognatha groups assigned following Casanova (1999):



Pterosagitta draco

Main diagnostic features:
- 8 - 10 hooks
- 6 - 10 anterior teeth
- 8 - 18 posterior teeth
- max. body length 11 mm
- tail 38 - 45% of the body length
- one pair of lateral fins
- lateral fins fully rayed, rounded
- body firm and muscular
- collarette very large
- seminal vesicles touches posterior fins at some distance from tail fin
- ovaries very long, reaching to neck region

Distribution:
- epi- and mesopelagic
- circumglobal between 40°N and 40°S

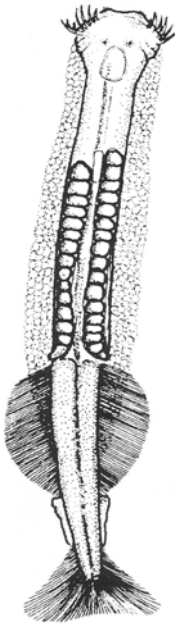


***Figure 2**: P. draco*

Eukrohnia proboscidea

Main diagnostic features:
- 10 - 13 hooks
- 23 - 25 posterior teeth
- max. body length 18-30 mm
- tail 20 - 31% of the body length
- eyes with pigment spot (elongate)
- no collarette
- ovaries short
- hooks sharply inward

Distribution:
- South Atlantic
- widespread species
- deep-mesopelagic to bathypelagic

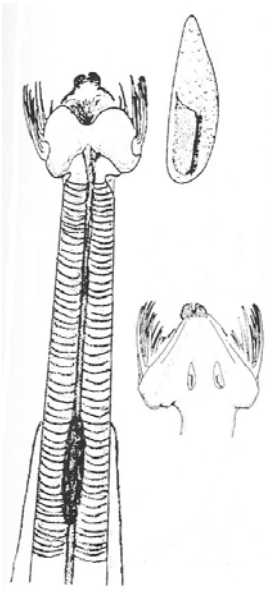


***Figure 3:** E. proboscidea with detail of the eyes*

Eukrohnia fowleri

Main diagnostic features:
- 10 - 14 hooks with straight tips
- 20 - 30 posterior teeth
- max. body legth 34 - 40 mm
- small eyes with pigment spot
- thick band of epidermal tissue encircles body at ventral ganglion
- ovaries short

Distribution:
- South Atlantic
- widespread species
- deep-mesopelagic to bathypelagic

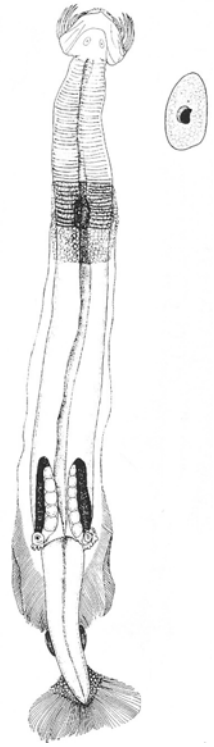


***Figure 4**: E. fowleri with detail of the eye*

Eukrohnia bathyantarctica

Main diagnostic features:
- 11 - 14 hooks
- no anterior teeth
- posterior teeth 11 - 16
- max. body length 31 mm
- Tail 19 - 25% of the body length
- transverse muscles on trunk
- eyes without pigment spot
- hooks serrated in juveniles
- body firm, broadest at region of tail septum
- ovaries very short
- lateral fins partially rayed

Distribution:
- deep-mesopelagic and bathypelagic

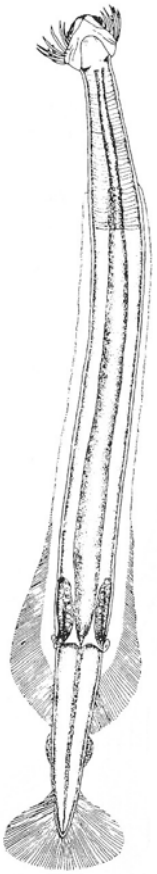


***Figure 5**: E. bathyantarctica*

Eukrohnia hamata

Main diagnostic features:
- 9 - 10 hooks (South Atlantic); 8 - 9 hooks (global)
- no anterior teeth
- 23 - 25 posterior teeth
- max. body length 19 - 32 mm (global: 43 mm)
- tail 19 - 24% of the body length
- transverse muscles in trunk only
- no anterior teeth
- eyes without pigment spot
- hooks thick with claws
- hooks serrated in juveniles
- body slender and rigid
- ovaries straight and short
- collarette absent

Distribution:
- eurybathyal
- North-east Pacific, Atlantic

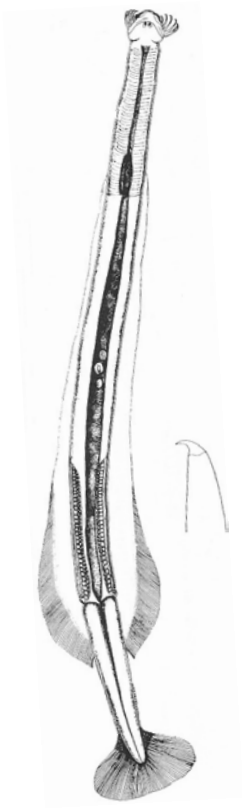


Figure 6: *E. hamata with detail of the hooks*

Eukrohnia bathypelagica

Main diagnostic features:
- 7 - 10 hooks (South Atlantic); 8-9 hooks (global)
- no anterior teeth
- 17 - 22 posterior teeth
- max. body length 23 mm
- tail 26 - 34% of the body length
- transverse muscles in trunk only
- large eyes without pigment spot
- hooks serrated in juveniles
- ovaries long, reaching to neck region
- lateral fins partially rayed

Distribution:
- deep-mesopelagic to bathypelagic

Figure 7*: E. bathypelagica with detail of the hooks*

Eukrohnia macroneura

Main diagnostic features:
- 8 - 11 hooks
- no anterior teeth
- posterior teeth 5 - 11
- max. body length 16 mm
- Tail 25 - 29% of the body length
- transverse muscles on trunk
- eyes absent
- hooks serrated in juvenilles
- body firm, opaque, broadest at region of tail septum
- ovaries very short, ova large
- lateral fins partially rayed

Distribution:
- deep-mesopelagic

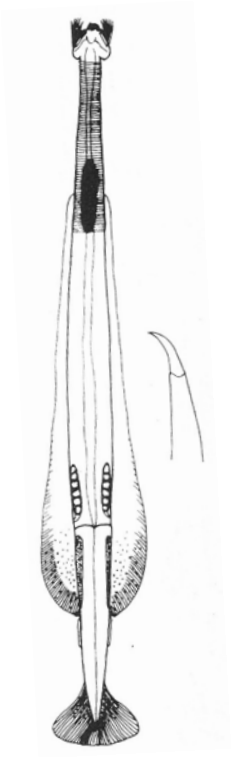


***Figure 8**: E. macroneura with detail of the hooks*

Eukrohnia flaccicoeca

Main diagnostic features:
- 8 - 11 hooks
- no anterior teeth
- posterior teeth 5 - 11
- max. body length 14 mm
- Tail 28 - 34% of the body length
- transverse muscles on trunk
- eyes without pigment spot
- hooks serrated in juveniles
- body flaccid, transparent, broadest at region of tail septum
- ovaries short, curved, ova large
- lateral fins partially rayed

Distribution:
- deep-mesopelagic to bathypelagic

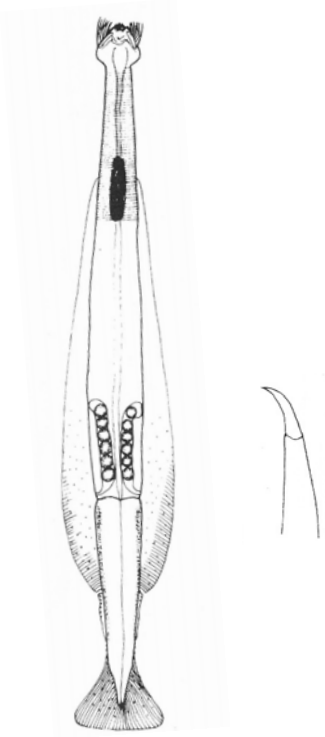


***Figure 9**: E. flaccicoeca with detail of the hooks*

Krohnitta subtilis

Main diagnostic features:
- 6 - 9 hooks
- anterior teeth 10 - 13
- no posterior teeth
- max. body length 16 mm
- Tail 30 - 40% of the body length
- no transverse muscles
- small eyes with pigment spot
- hooks not serrated
- body slender, transparent and thin
- ovaries short
- lateral fins partially rayed or no rays

Distribution:
- epipelagic to mesopelagic
- global between 40°N and 40°S

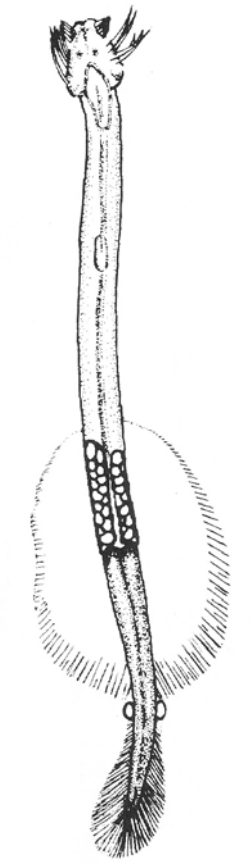


***Figure 10**: E. subtilis*

Krohnitta pacifica

Main diagnostic features:
- 8 - 11 hooks
- max. body length 8 mm
- tail 27 - 34% of the body length
- transverse muscles absent
- small eyes with star-shaped pigment spot
- hooks not serrated
- body slender
- ovaries of medium lengt, reaching top region of ventral ganglion
- collarette absent

Distribution:
- epi- and mesopelagic
- global between 30°N and 30°S
- tropical Atlantic and north-west Pacific

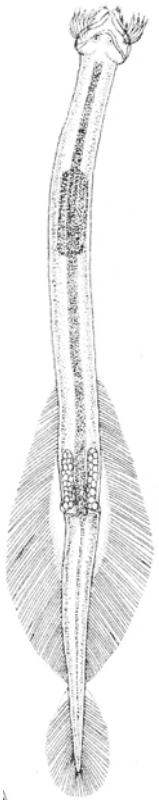


***Figure 11**: K. pacifica*

Sagitta bierri

Main diagnostic features:
- 5 - 7 hooks
- 5 - 8 anterior teeth
- 8 - 16 posterior teeth
- max. body length 19 mm
- tail 22 - 29% of the body length
- transverse muscles absent
- small eyes with T-shaped pigment spot
- hooks serrated in juveniles and adults
- body firm and opaque
- ovaries of medium length reaching to region of ventral ganglion
- collarette absent or very short

Distribution:
- epipelagic, distant neritic

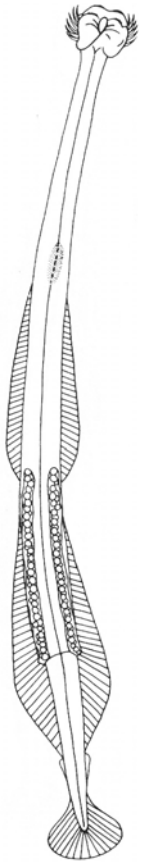


***Figure 12**: S. bierri*

Sagitta serratodentata

Main diagnostic features:
- hooks: 6 - 7 (South Atlantic); 5-9 (global)
- anterior teeth: 10 - 11 (South Atlantic); 6-10 (global)
- posterior teeth: 20 (South Atlantic); 12-20 (global)
- max. body length 10 - 13 mm
- tail 22 - 30% of the body length
- transverse muscles absent
- small eyes with T-shaped pigment spot
- hooks serrated in juveniles and adults
- body slender, needle-like and firm
- ovaries long reaching anterior end of ventral ganglion
- collarette absent or very small

Distribution:
- epipelagic
- Atlantic between 40°N and 40°S, tropical-subtropical

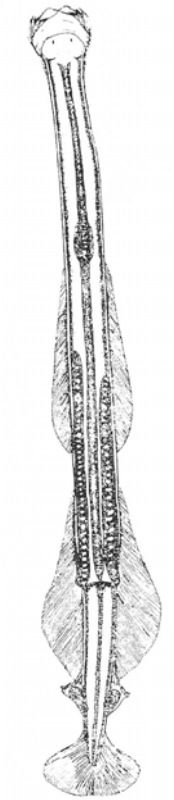


***Figure 13**: S. serratodentata*

Sagitta pacifica

Main diagnostic features:
- 5 - 8 hooks
- 7 - 13 anterior teeth
- 16 - 24 posterior teeth
- max. body length 14 mm
- tail 22 - 28% of the body length
- transverse muscles absent
- large eyes with T-shaped pigment spot
- hooks serrated in juveniles and adults
- body slender
- ovaries of medium length reaching to region of ventral ganglion
- collarette absent

Distribution:
- epipelagic
- tropical Atlantic, Indo-Pacific

***Figure 14**: S. pacifica*

Sagitta tasmanica

Main diagnostic features:
- 6 - 8 hooks (South Atlantic); 6 - 9 hooks (global)
- anterior teeth : 2 - 9 (South Atlantic); 6 - 9 (global)
- posterior teeth: 3 - 19 (South Atlantic); 9 - 15 (global)
- max. body length: 15 - 20 mm (South Atlantic); 30 mm (global)
- tail 20 - 30% of the body length
- transverse muscles absent
- small eyes with pigment spot
- hooks serrated in juveniles and adults
- body firm und needle-like
- ovaries long reaching anterior end of ventral ganglion
- collarette absent or very small

Distribution:
- epipelagic
- tropical Atlantic
- Indopacific

***Figure 15**: S. tasmanica*

Sagitta lyra

Main diagnostic features:
- hooks: 3 - 5 (South Atlantic); 3 - 10 (global)
- 2 - 8 anterior teeth
- posterior teeth: 3-5 (South Atlantic); 15 - 12 (global)
- max. body length 42 mm
- tail 15 - 17% of the body length
- transverse muscles absent
- small eyes with pigment spot
- hooks not serrated
- body flaccid and transparent
- ovaries of medium length
- collarette present

Distribution:
- epi- to shallow mesopelagic
- circumglobal, between 40°N and 40°S

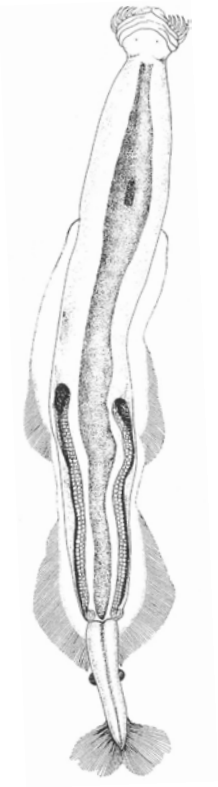


***Figure 16**: S. lyra*

Sagitta maxima

Main diagnostic features:
- hooks: 4 - 8 (South Atlantic); 5 - 11 (global)
- 4 - 6 anterior teeth
- 5 - 8 posterior teeth
- Max. body length: 55 mm (South Atlantic); 90 mm (global)
- tail 19 - 25% of the body length
- transverse muscles absent
- small eyes with pigment spot
- hooks not serrated
- body large and transparent
- lateral fins partially rayed
- fins connected with fin bridge
- ovaries long, extending to the ventral ganglion
- collarette absent

Distribution:
- deep meso- to bathypelagic
- cosmopolitan

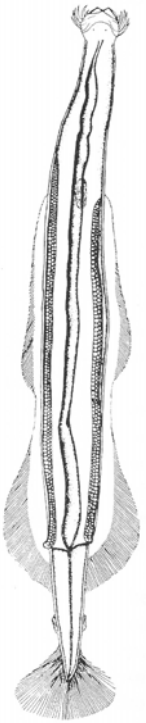


***Figure 17**: S. maxima*

Sagitta enflata

Main diagnostic features:
- 8-10 hooks
- 4-10 anterior teeth
- posterior teeth: 4-13 (South Atlantic); 4-15 (global)
- Max. body length 25 mm
- tail 14-17% of the body length
- transverse muscles absent
- small eyes with pigment spot
- hooks not serrated
- body flaccid and transparent
- ovaries short, rarely reaching posterior fins

Distribution:
- epipelagic
- circumglobal, between 40°N and 40°S

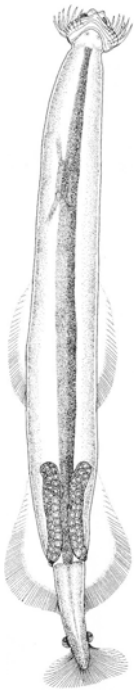


***Figure 18**: S. enflata*

Sagitta hexaptera

Main diagnostic features:
- 7-10 hooks
- posterior teeth: 2-6 (South Atlantic); 0-6 (global)
- 3-5 anterior teeth
- max. body length 70 mm
- tail 16-20% of the body length
- transverse muscles absent
- small eyes with round pigment spot
- hooks not serrated
- body flaccid, transparent
- fin bridge absent
- ovaries of medium length reaching to region of ventral ganglion
- collarette from neck to VG or absent

Distribution:
- epi- to shallow mesopelagic
- circumglobal, between 40°N and 40°S
- tropical and subtropical Atlantic

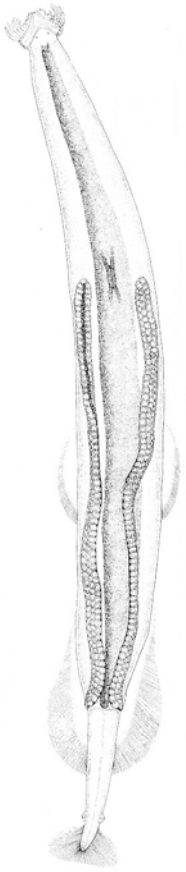
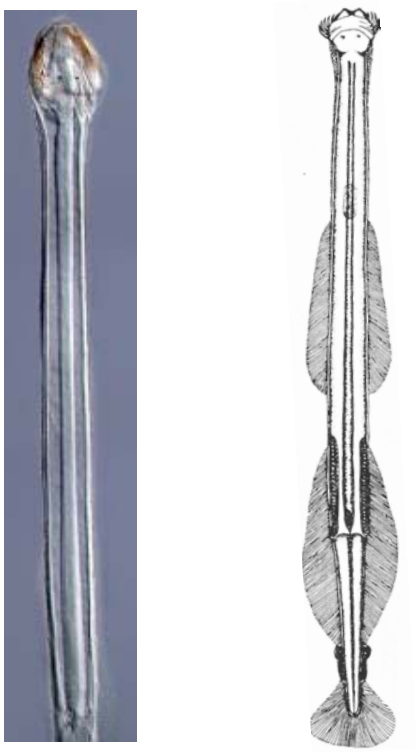


***Figure 19:** S. hexaptera*

Sagitta friderici

Main diagnostic features:
- 5-9 hooks
- anterior teeth: 3-8 (South Atlantic); 6-10 (global)
- posterior teeth: 6-17 (South Atlantic); 15-23 (global)
- max. body length 15 mm
- tail 15-28% of the body length
- transverse muscles absent
- small eyes with pigment spot
- hooks not serrated
- body firm und semi-transparent
- ovaries short
- short collarette

Distribution:
- epipelagic
- Atlantic, between 30°N and 30°S



***Figures 20** (left) **and 21** (right): S. friderici*

Sagitta minima

Main diagnostic features:
- 7-9 hooks
- 3-7 anterior teeth
- posterior teeth: 6-12 (South Atlantic); 6-16 (global)
- max. body length 7-10 mm
- tail 17-21% of the body length
- transverse muscles absent
- small eyes with pigment spot
- hooks not serrated
- body transparent and very small
- ovaries very short

Distribution:
- epipelagic
- circumglobal between 40°N and 40°S

***Figure 22**: S. minima*

Sagitta decipiens

Main diagnostic features:
- 5-8 hooks
- anterior teeth: 8-10 (South Atlantic); 4-10 (global)
- posterior teeth: 15-19 (South Atlantic); 6-18 (global)
- max. body length 12-14 mm
- tail 25-31% of the body length
- transversal muscles absent
- large eyes with T-shaped pigment spot
- hooks not serrated
- body slender
- ovaries short reaching to anterior end of posterior fins

Distribution:
- deep-mesopelagic
- circumglobal, between 40°N and 40°S

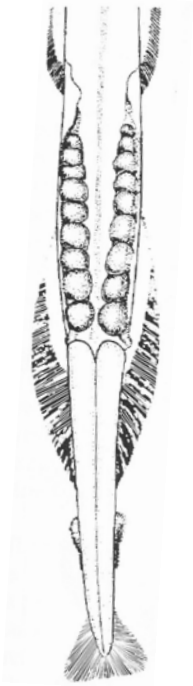


***Figure 23**: S. decipiens*

Sagitta sibogae

Main diagnostic features:
- 6-9 hooks
- anterior teeth: 6-9 (global)
- posterior teeth: 9-15 (global)
- max. body length 30 mm
- tail 20-30% of the body length
- transversal muscles absent
- eyes with T-shaped pigment spot
- hooks not serrated
- body slender
- ovaries short reaching to anterior end of posterior fins

Distribution:
- mesopelagic
- circumglobal, between 40°N and 40°S

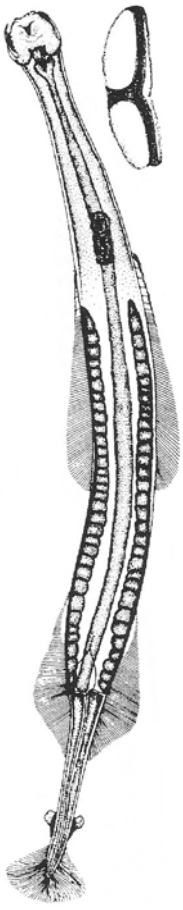


***Figure 24**: S. sibogae*

Sagitta zetesiois

Main diagnostic features:
- 8-11 hooks
- 8-12 anterior teeth
- 15-22 posterior teeth
- Max. body length45 mm
- tail 20-23% of the body length
- transverse muscles absent
- small eyes with T-shaped pigment spot
- hooks not serrated
- body large and firm
- ovaries very long reaching neck region
- collarette long
- collarette and ovaries as *S. planctonis*

Distribution:
- deep-mesopelagic
- cosmopolitan, between 60°N and 60°S

***Figure 25**: S. zetesios*

Sagitta planctonis

Main diagnostic features:
- hooks: 8-11 (South Atlantic); 10-14 (global)
- 6-9 anterior teeth
- 10-14 posterior teeth
- Max. body length 37 mm
- tail 19-21% of the body length
- transverse muscles absent
- small eyes with T-shaped pigment spot
- hooks not serrated
- body large and firm, opaque
- collarete long on entire body
- ovaries very long reaching neck region

Distribution:
- shallow-mesopelagic
- cosmopolitan circumglobal between 40°N and 40°S

***Figure 26**: S. planctonis*

Sagitta macrocephala

Main diagnostic features:
- 10-12 deep brown hooks
- 6-10 anterior teeth
- 20-35 posterior teeth
- Max. body length 22 mm
- tail 29-34% of the body length
- transverse muscles absent
- large eyes without pigment spot
- hooks not serrated
- body firm and opaque
- ovaries of medium length reaching to region of ventral ganglion

Distribution:
- deep meseopelagic to bathypelagic
- cosmopolitan

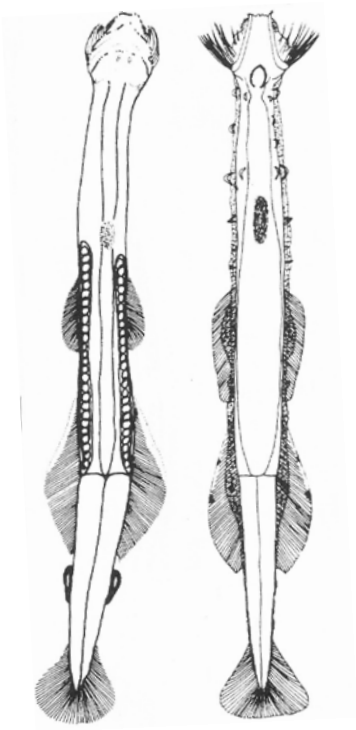


Figure 27: *S. macrocephala; species living upper water column (left) and species living near the bottom (right)*

Sagitta setosa

Main diagnostic features:
- hooks: 8-9 (South Atlantic);10-12 (global)
- anterior teeth: 6-8 (South Atlantic); 6-10 (global)
- posterior teeth: 12-16 (South Atlantic); 12-16 (global)
- max. body length: 10-14 mm (South Atlantic); 20 mm (global)
- tail 16-25% of the body length
- transverse muscles absent
- large eyes with star-shaped pigment spot
- hooks not serrated
- body firm and opaque
- ovaries of medium length
- collarette absent or small

Distribution:
- epipelagic
- East Atlantic

Figures 28 *(left) and* ***28*** *(right): S. setosa*

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Picture references:

Figures 1 – 3, 5 – 19, 21-22, 24 - 28: Casanova J. (1999): South Atlantic Zooplankton. Chaetognatha. Vol. 2. Backhuys Publishers, Leiden, p.1353-1374.

Figure 4: Chaetognatha of the World. URL: http://nlbif.eti.uva.nl/bis/chaetognatha.php?set=4&menuentry=zoeken&selected=foto (last call: 29.3.2011)

Figure 21: Centro de biologia marinha universidade de sao Paulo. URL: http://200.144.190.194/cbm/index.php/component/rsgallery2/category/99/asInline.html (last call: 29.3.2011)

Figure 23: B-NEAT Baltic and North East Atlantic Taxa. URL: http://test.b-neat.org/species_sheet/?id=1000061 (last call: 29.3.2011)

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Karolina Bohatá