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ORIGINAL PAPER

Meso- and bathypelagic distribution and abundance of chaetognaths in the Atlantic sector of the Southern Ocean

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Abstract We conducted multinet sampling during winter and summer in the Southern Ocean (Atlantic sector) to investigate the effect of water mass, season and water depth on abundance and species composition of meso- and bathypelagic chaetognaths. *Eukrohnia hamata* (mean 115 ind. 1,000 m⁻³) and *Sagitta marri* (mean 51 ind. 1,000 m⁻³) were dominant, complemented by *E. bathypelagica* (mean 19 ind. 1,000 m⁻³) and *E. bathyantartica* (mean 19 ind. 1,000 m⁻³) below 1,000 m. A further six species were identified, among them the rare bathypelagic species *Heterokrohnia fragilis* and the subtropical *Eukrohnia macroneura* that is new to the Antarctic. Water depth and season were the principal determinants of abundance and species composition patterns, indicating vertical seasonal migration and vertical segregation of species. The life cycles of *E. hamata* and *S. marri* were studied additionally. Their maturity stages were vertically segregated and prolonged reproductive periods are suggested for both species.

Keywords Chaetognatha · Antarctica · Bathypelagial · Distribution · Abundance · Life cycle

Introduction

Chaetognaths represent a major component of the world's marine zooplankton. In the Southern Ocean they contribute

significantly to the total zooplankton stock, at times reaching up to 30% of the total zooplankton abundance (Piatkowski 1985; Froneman and Pakhomov 1998; Pakhomov et al. 1999, 2000). As main predators of copepods (Øresland 1990, 1995) chaetognaths may consume up to 5.2% of the standing stock per day (Froneman and Pakhomov 1998). Hence, they are of great importance for the energy transfer from copepods to higher trophic levels (Bone et al. 1991) and may contribute considerably to the vertical carbon flux (Dilling and Alldredge 1993).

Detailed studies on the Antarctic chaetognath fauna started at the beginning of the twentieth century (e.g. by Ritter-Záhony 1911), already more than 100 years after the first publication concerning a chaetognath (Slabber 1775, reviewed by Bone et al. 1991). So far, investigations on Antarctic chaetognath ecology focused on the austral summer and on the upper 500 m (e.g. Timonin 1968; Terazaki 1989; Bielecka and Zmijewska 1993; Blachowiak-Samolyk et al. 1995) to 1,000 m (Thiel 1938; Duró et al. 1999; Duró and Gili 2001; Johnson and Terazaki 2004) of the water column. Despite the extensive data on Antarctic chaetognath distribution and abundance below 1,000 m of David (1958a, 1965) and Alvaríño et al. (1983a, b), our knowledge of the deep water chaetognath ecology is still fragmentary. There is a general lack of deep samples, and, quite often, unsuitable large mesh sizes were used (Hagen 1985; Duró and Gili 2001). Consequently, reliable quantitative data are rare, and hitherto a number of bathypelagic species are known from very few specimens only (Terazaki 1991).

One major objective of our study was to evaluate the effects of water mass (Polar Frontal Zone, Weddell Gyre, Coastal Current), of season (summer–winter) and of water depth (4 depth strata) on abundance and species composition of meso- and bathypelagic chaetognaths in the Atlantic sector of the Southern Ocean. Furthermore, the two expeditions

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provided a unique opportunity for seasonal deep sampling with small mesh sizes (100 μm) in the same area, thus allowing an investigation of the complete community composition covering the entire size range and all maturity stages of the predominant chaetognath species. Detailed life cycle analyses were possible, and contribute to our knowledge on chaetognath biology in the Southern Ocean.

Materials and methods

Field sampling

Chaetognaths were sampled during two expeditions in the Lazarev Sea with the RV Polarstern, expedition ANT 23-6 in Antarctic winter 2006 (17 June–21. August 2006), and expedition ANT 24-2 in Antarctic summer 2007/2008 (28 November 2007–04 February 2008). Stratified sampling with a multinet was performed at 28 stations in winter (between 60° and 68°30'S) and at 15 stations in summer (at 52°S and between 62° and 70°S) along three transects (3°W, 3°E and 0°E). This multiple opening/closing net (opening size: 0.25 m²) was equipped with five nets with 100- μm mesh size and sampled the following standard depth intervals: 2,000–1,500, 1,500–1,000, 1,000–750, 750–500, 500–0 m. Exceptions from the standard depths were made at three stations during ANT 23-6 (at 61°30'S and 62°S 3°E to 3,000 m, at 65°S 3°E to 1,250 m depth) and at one during ANT 24-2 (at 70°S 3°W to 1,500 m depth). The winter station around 66°S 0°E was a 5-days station, located at a drifting ice camp.

As the abundance of chaetognaths in the epipelagial is already well known and as we are particularly interested in meso- and bathypelagic chaetognaths, we neglected the 500–0 m depth layer in the present study.

Our sampling scheme covered three different water masses, the Polar Frontal Zone (PFZ) with two stations at 52°S in summer, the Weddell Gyre (WG), water mass between 60°S and 68°S, and the Coastal Current (CC) at and south of 68°S. The different pelagic zones are defined as follows: epipelagic (0–500 m), mesopelagic (500–1,000 m) and bathypelagic (below 1,000 m).

Laboratory methods and data processing

Directly after sampling, chaetognaths were sorted. The specimens were counted, identified to species level and their body length (without tail fin) was measured under a stereomicroscope (Olympus SZX12) to the nearest 0.5 mm. During the winter expedition, a part of each sample was immediately preserved in formaldehyde (4% final concentration, buffered with hexamine) and measured later in the home laboratory. To compensate for preservation induced shrinkage, we computed shrinkage factors for the dominant species from repeated length measurements of fresh and subsequently formaldehyde preserved specimens collected during the summer expedition. This allowed the comparison of lengths between formaldehyde preserved and frozen chaetognaths.

Taxonomic identification was conducted to species level under a stereomicroscope (see above) and a microscope (Zeiss Axioskop 2 plus) using the relevant literature (Alvariño 1969; O'Sullivan 1982; Casanova 1986, 1999; Kapp 1991a). Damaged chaetognaths, that could not be identified to species level, or smaller *Eukrohnia* individuals (<10 mm) were pooled as *Sagitta* or *Eukrohnia* spp., respectively. The two most abundant species, *Eukrohnia hamata* Möbius 1875 and *Sagitta marri* David 1956, were classified into five maturity stages according to Kramp (1939) and David (1955) (Table 1).

Table 1 Maturity stage classification of *Eukrohnia hamata* and *Sagitta marri* according to Kramp (1939) and David (1955)

Stage	<i>Eukrohnia hamata</i> (from Kramp 1939)		<i>Sagitta marri</i> (from David 1955 for <i>Sagitta gazellae</i>)	
	Male gonads	Female gonads	Male gonads	Female gonads
I	Unripe	Unripe	Tail segment empty; rudiments of testes present	Ovaries not visible or rudimentary
II	Tail containing more or less sperm	All eggs small	Tail segment opaque; seminal vesicles may show as small protuberances	Ovaries short and thin; eggs small
III	Sperm evacuated	All eggs small, seminal receptacles filled with sperm	Seminal vesicles fully formed; tail segment empty	Ovaries thin, but variable in length
IV	Sperm evacuated	Ovaries filled with ripe eggs	Seminal vesicles usually discharged	Ovaries thick and long; eggs enlarged
V	Sperm evacuated	Eggs evacuated, receptacles still containing sperm	Sperm discharged	Eggs discharged; remnants of ovaries are irregular masses sometimes spread into the tail segment

In the genus *Eukrohnia*, we pooled all individuals smaller than 6 mm (and usually larger than 2.5 mm) belonging to stage 1 into the group “*Eukrohnia* juveniles”. The small individuals of *Eukrohnia bathyantartica* David 1958 could easily be identified, but the juveniles of *E. hamata* and of *E. bathypelagica* Alvarino 1962 were difficult to distinguish, owing to lack of characters and congruence of size. Specific characteristics of adults such as a flabby, translucent body or coiled immature ovaries and a proportionally longer tail (described by Alvarino 1962) are not yet developed in juveniles of 5 mm length and this results in problems of species identification. Because of the absence of stages 4 and 5 individuals of *E. hamata* in summer, we suggest that the remaining juveniles are *E. bathypelagica*, as stage 4 and 5 individuals of this species were observed (Kruse 2009). It is possible, however, that we just missed the mature *E. hamata* adults (as discussed below).

Numbers per sample are standardized to number of individuals per 1,000 m³. For the 5-days winter station the geographical and vertical abundance data are averaged over all eight sub-stations.

Statistical analyses

To evaluate differences in species composition, we applied a cluster analysis (e.g. Everitt et al. 2001) to the species \times abundance matrix (9 species \times 170 samples, see Sect. “Results”). The resulting cluster identities were taken as representative for distinct species assemblages. Nominal logistic regression (e.g. Agresti 2002) was used to identify relationships between cluster identity and water mass, season and depth layer. Abundance values were square-root transformed prior to analysis to reduce the influence of outliers. We applied hierarchical clustering and compared several linkage methods (average, centroid, complete, Ward’s minimum variance) to check for consistency of results.

We analysed abundance data at the family level (Sagittoidea, i.e. all species present), at the genus level (*Eukrohnia* and *Sagitta*) and at the species level (abundant species only, see below). Maturity stages (mean stage per sample) were analysed for *E. hamata* and *S. marri*. Data were Box-Cox transformed to achieve normality and homogeneity of variances and subjected to a full factorial three-way ANOVA (abundance/mean stage versus water mass and season and depth and water mass \times depth and season \times depth) with subsequent post hoc test on differences between means ($\alpha = 0.05$, Sokal and Rohlf 1981). The interaction term water mass \times season was not tested, as there are no winter samples from the PFZ.

Additionally, a full factorial two-way ANOVA (length versus maturity stage and season and maturity

stage \times season) was applied to analyse differences in length in *E. hamata* and *S. marri* (data were treated as mentioned for the previous ANOVA). Seasonal differences between the length–frequency distributions were analysed by means of a Kolmogorov–Smirnow test in both species.

All statistical analyses were performed with the software package JMP (SAS Inc).

Results

Influence of formaldehyde on chaetognath body length

Due to the preservation of the samples with formaldehyde (4% final concentration, buffered with hexamine, 4 months exposure) the chaetognath body length shrunk up to 21%. Shrinkage amounted to 3.67% (SD \pm 2.51, $n = 104$) in *Eukrohnia hamata*, to 5.37% (\pm 3.38, $n = 93$) in *E. bathyantartica*, and to 6.23% (\pm 3.84, $n = 79$) in *E. bathypelagica* irrespective of length and maturity stage. Highest reduction of 7.17% (\pm 3.97, $n = 87$) in length was measured for *S. marri*. The chaetognaths shrunk particularly in the first days and weeks. However, they kept shrinking very slowly even after 4 months of formaldehyde preservation (personal observation).

Geographical and vertical chaetognath distribution

We were able to identify ten different species from three genera in our samples: *E. hamata*, *E. bathypelagica*, *E. bathyantartica*, *E. macroneura* Casanova 1986, *Heterokrohnia fragilis* Kapp and Hagen 1985, *H. mirabilis* Ritter-Záhony 1911, *S. marri*, *S. macrocephala* Fowler 1905, *S. maxima* Conant 1896 and *S. gazellae* Ritter-Záhony 1909. *E. hamata* and *S. marri* were the two most abundant of these species, independent of the water masses (Tables 2, 3, 4).

Eukrohnia juveniles were very frequent in summer, and for a better comparison of seasons they were excluded from the Figs. 1b, 2b, 3b, 4b that display summer data but are presented separately (Fig. 1c). During winter *Eukrohnia* juveniles were extremely rare and thus are not presented separately. Juveniles of other species, e.g. *Sagitta marri*, were readily identified and not treated separately.

The mean chaetognath abundance of the 500 to 2,000 m depth stratum ranged from 58 ind. 1,000 m⁻³ (61°30’S 3°E) to 443 ind. 1,000 m⁻³ (65°S 3°E; Fig. 1a) in winter, and from 91 ind. 1,000 m⁻³ (64°30’S 0°E) to 508 ind. 1,000 m⁻³ (70°S 3°W) in summer (without *Eukrohnia* juveniles; Fig. 1b). Juvenile *Eukrohnia* ranged from 2 ind. 1,000 m⁻³ (69°S 0°E) to 880 ind. 1,000 m⁻³ (66°S 3°E, 62°S 0°E, Fig. 1c) in summer.

Table 2 Chaetognath species abundance (individuals $1,000\text{ m}^{-3}$) and relative composition for each depth interval, presented for the summer and winter situation in CC (Coastal Current)

CC	Summer ($n = 4$)				Winter ($n = 4$)																				
	500–750 m		750–1,000 m		1,000–1,500 m		1,500–2,000 m		500–750 m		750–1,000 m		1,000–1,500 m		1,500–2,000 m										
	Mean	\pm SD	%	Mean	\pm SD	%	Mean	\pm SD	%	Mean	\pm SD	%	Mean	\pm SD	%	Mean	\pm SD	%							
<i>Eukrohnia bathyantarctica</i>	0	0	0	4	7	1.0	41	17	22.7	49	24	46.6	28	38	5.2	8	9	3.1	30	14	11.7	56	35	27.2	
<i>Eukrohnia bathypelagica</i>	21	27	1.8	8	16	2.4	13	4	7.5	27	17	25.2	12	24	2.2	4	8	1.6	30	14	11.7	24	11	11.6	
<i>Eukrohnia hamata</i>	425	258	35.2	78	22	23.1	10	13	5.8	15	13	14.4	340	24	62.5	148	98	57.8	120	63	46.9	84	73	40.8	
<i>Eukrohnia macroneura</i>	0	0	0	19	15	5.8	16	12	9.1	0	0	0	0	0	0	12	24	4.7	4	8	1.6	0	0	0	
<i>Eukrohnia</i> spp.	48	26	4.0	8	17	2.5	9	11	5.1	10	19	9.0	4	8	0.7	36	62	14.0	42	43	16.4	2	4	1.0	
Juvenile <i>Eukrohnia</i>	539	599	44.7	168	308	49.7	33	15	18.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heterokrohnia fragilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heterokrohnia mirabilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sagitta gazellae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	8	1.6	0	0	0	4	5	1.9	
<i>Sagitta macrocephala</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sagitta marri</i>	172	123	14.3	52	65	15.5	54	93	30.1	0	0	0	160	41	29.4	40	31	15.6	26	20	10.1	36	30	17.5	
<i>Sagitta maxima</i>	0	0	0	0	0	0	0	0	3	4	2.4	0	0	0	0	4	8	1.6	4	5	1.6	0	0	0	
<i>Sagitta</i> spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Juvenile chaetognaths	0	0	0	0	0	0	2	4	1.1	3	4	2.4	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

 n the number of investigated stations

Table 3 Chaetognath species abundance (individuals 1,000 m⁻³) and relative composition for each depth interval, presented for the summer and winter situation in WG (Weddell Gyre)

WG	Summer (n = 9)									Winter (n = 24)																		
	500–750 m			750–1,000 m			1,000–1,500 m			1,500–2,000 m			500–750 m			750–1,000 m			1,000–1,500 m			1,500–2,000 m			2,000–3,000 m			
	Mean	±SD	%	Mean	±SD	%	Mean	±SD	%	Mean	±SD	%	Mean	±SD	%	Mean	±SD	%	Mean	±SD	%	Mean	±SD	%	Mean	±SD	%	
<i>E. bathyantartica</i>	12	30	0.5	9	18	0.8	47	24	33.7	40	19	34.0	2	7	0.5	4	14	1.3	12	14	5.6	46	34	31.3	18	8	56.25	
<i>E. bathypelagica</i>	42	31	1.9	18	20	1.5	16	12	11.4	33	17	27.9	11	31	2.6	8	16	2.5	26	19	12.0	29	23	19.7	6	3	18.75	
<i>E. hamata</i>	474	242	21.2	95	61	8.0	17	19	11.9	13	15	11.3	278	162	67.1	146	118	46.1	87	62	39.9	48	40	32.5	2	3	6.25	
<i>E. macroneura</i>	0	0	0	15	22	1.2	4	6	2.6	0	0	0	0	0	0	3	11	1.1	2	3	0.8	0.3	2	0.2	0	0	0	
<i>Eukrohnia</i> spp.	125	103	5.6	7	12	0.6	15	15	10.7	10	11	8.9	17	30	4.2	23	30	7.2	10	11	4.4	3	7	2.3	2	3	6.25	
Juvenile <i>Eukrohnia</i>	1,330	1,363	59.3	920	923	77.7	25	32	17.4	1	3	0.8	0	0	0	0.7	3	0.2	5	12	2.1	3	15	2.4	0	0	0	
<i>H. fragilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>H. mirabilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	6.25
<i>S. gazellae</i>	7	11	0.3	2	5	0.1	2	6	1.3	4	6	3.0	9	15	2.2	1	5	0.4	2	4	0.8	1	5	0.9	0	0	0	
<i>S. macrocephala</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>S. marri</i>	252	116	11.2	107	70	9.0	9	14	6.4	3	6	3.0	96	88	23.2	130	89	41.0	74	71	33.8	15	23	10.0	2	3	6.25	
<i>S. maxima</i>	0	0	0	0	0	0	0	0	0	0	0	0	0.7	3	0.2	0.7	3	0.2	0.3	2	0.1	0.3	0.2	0.2	0	0	0	
<i>Sagitta</i> spp.	0	0	0	2	5	0.2	1	3	0.6	2	4	1.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Juvenile chaetognaths	0	0	0	7	16	0.6	6	12	4.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Unidentified	0	0	0	4	11	0.3	0	0	0	5	16	4.4	0	0	0	0	0	0	1	4	0.5	1	3	0.5	0	0	0	

n the number of investigated stations

Table 4 Chaetognath species abundance (individuals 1,000 m⁻³) and relative composition for each depth interval, presented for the summer and winter situation in PFZ (Polar Frontal Zone)

PFZ	Summer (n = 2)											
	500–750 m			750–1,000 m			1,000–1,500 m			1,500–2,000 m		
	Mean	±SD	%	Mean	±SD	%	Mean	±SD	%	Mean	±SD	%
<i>Eukrohnia bathyantartica</i>	0	0	0	32	22	8.2	16	11	9.1	48	35	35.7
<i>Eukrohnia bathypelagica</i>	47	20	16.3	40	34	10.2	89	11	50.0	32	22	23.4
<i>Eukrohnia hamata</i>	147	92	51.4	79	22	20.4	32	0	18.2	16	0	11.8
<i>Eukrohnia macroneura</i>	0	0	0	8	11	2.0	28	6	15.9	0	0	0
<i>Eukrohnia</i> spp.	15	21	5.3	32	0	8.2	0	0	0	4	6	2.9
Juvenile <i>Eukrohnia</i>	23	32	8.0	143	202	36.8	0	0	0	24	33	17.4
<i>Heterokrohnia fragilis</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heterokrohnia mirabilis</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sagitta gazellae</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sagitta macrocephala</i>	0	0	0	8	11	2.0	0	0	0	4	6	2.9
<i>Sagitta marri</i>	46	42	16.1	32	22	8.2	4	6	2.2	0	0	0
<i>Sagitta maxima</i>	8	12	2.9	8	11	2.0	8	11	4.6	4	6	2.9
<i>Sagitta</i> spp.	0	0	0	8	11	2.0	0	0	0	0	0	0
Juvenile chaetognaths	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified	0	0	0	0	0	0	0	0	0	4	6	3.0

n the number of investigated stations

Regarding water depth, highest abundances were encountered between 500 and 1,000 m in winter (Figs. 2a, 3a, 4a), attaining values up to 1,248 ind. 1,000 m⁻³ (500–750 m, 64°S 0°E, Fig. 3a), and between 500 to 750 m in summer (Figs. 2b, 3b, 4b), with a maximum of 1,470 ind. 1,000 m⁻³ (63°S 3°E, Fig. 4b). *Eukrohnia* juveniles did rarely occur deeper than 1,500 m and distinctly preferred the 500–1,000 m depth range in summer (Tables 2, 3, 4).

Chaetognath species composition

The cluster analysis of the 9 species × 170 samples matrix (we excluded *Heterokrohnia mirabilis*, because it occurred in one of the two exceptional samples collected below 2,000 m only) produced a rather consistent sample grouping pattern, irrespective of the linkage method applied. Species composition was significantly affected by water depth ($P < 0.001$, $\chi^2 = 144.78$), season ($P < 0.001$, $\chi^2 = 45.65$) and water mass ($P = 0.001$, $\chi^2 = 32.98$; effect likelihood ratio test of the nominal logistic regression). The effect of water depth was mainly related to *E. bathyantartica* and *E. bathypelagica* which dominated the deeper community but were almost absent in the upper layers, and to *E. hamata* that showed the opposite pattern (Tables 2, 3, 4). The seasonal effect was related to the less frequent species. *E. bathyantartica*, *E. bathypelagica*, *E. macroneura* and *H. fragilis* were more frequent in summer, whereas *S. gazellae* was more frequent in winter. The water mass

effect was most likely caused by the (non-) occurrence of species in just one water mass, such as *Sagitta macrocephala* and *H. fragilis* that occurred exclusively in the PFZ and the WG, respectively.

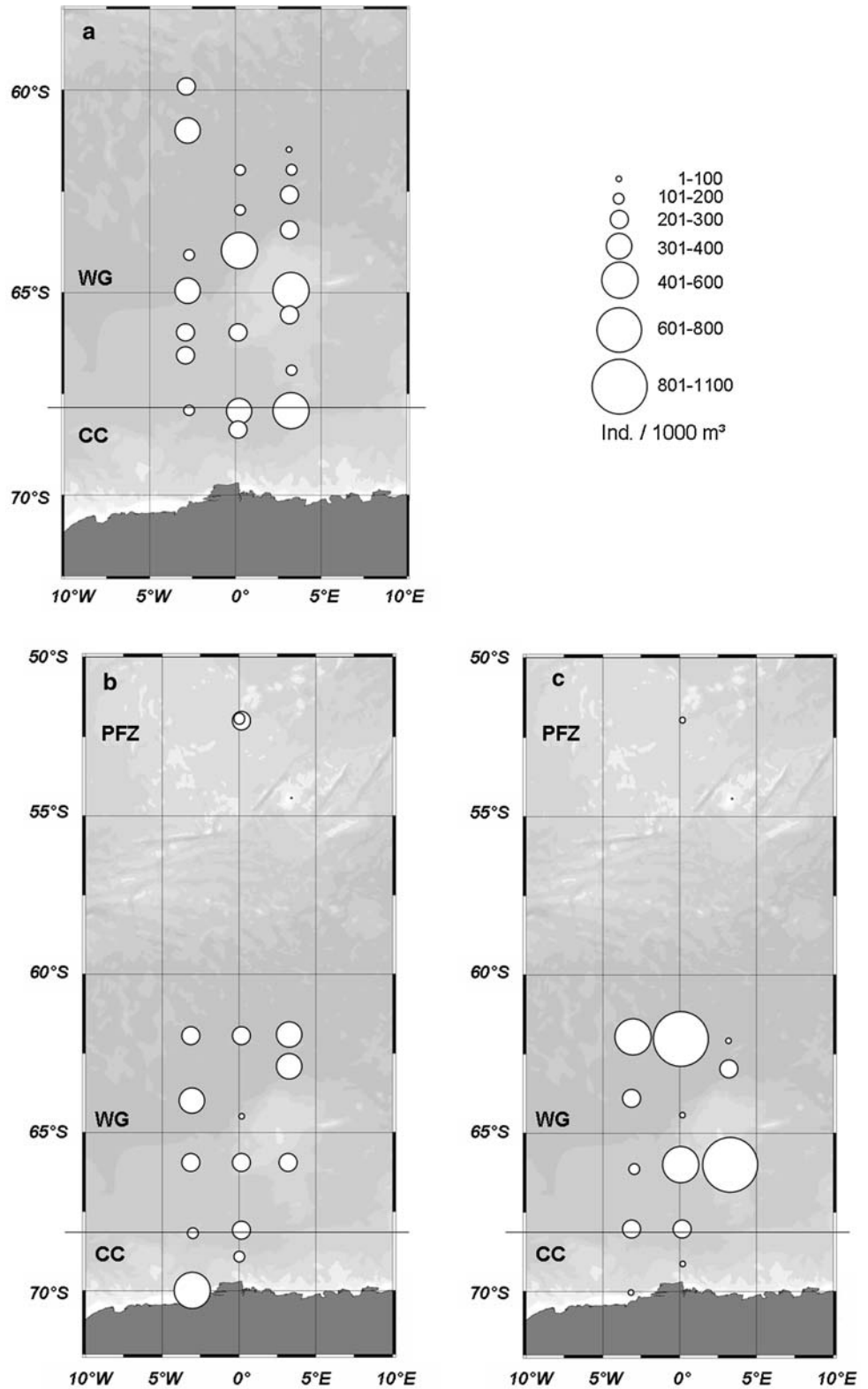
Chaetognath abundance

ANOVA of abundance data at the genus and the species level indicated that water mass had barely any effect, only the abundance of *E. bathypelagica* was significantly higher in Polar Frontal Zone (PFZ) than in Weddell Gyre (WG) and Coastal Current (CC, Table 5). The same holds true for the interaction of water mass and depth. Here, we found a significant effect on all species pooled (class Sagittoidea), where abundance decreased with depth within the WG and CC, and in the genus *Eukrohnia*, where it decreased only within the WG.

Significant seasonal differences were detected in the genera *Eukrohnia* and *Sagitta* (Table 5). *Sagitta* was more abundant in winter than in summer and *Eukrohnia* vice versa. Within the genus *Sagitta*, *S. marri* was 8 times more abundant in the 1,000–1,500 m stratum in winter (74 ind. 1,000 m⁻³ in WG, Table 3) than in summer. The higher abundance of *Eukrohnia* in summer, however, can be attributed to the high number of juveniles, as the dominant *E. hamata* was again significantly more abundant in winter.

Depth had the most distinct effect on chaetognath abundance. *E. hamata*, the dominant species, was significantly more abundant in the 500–750 m depth range than at

Fig. 1 Geographical distribution and mean abundance of chaetognaths along the three sampling transects during winter (a) and summer (b) without juveniles. The juveniles from the summer expedition are presented separately (c). *PFZ* Polar Frontal Zone, *WG* Weddell Gyre, *CC* Coastal Current. Stations at and south of 68°S are considered within the *CC* (horizontal line)



greater depths (Table 5), attaining maximum summer abundances of 425 and 474 ind. 1,000 m⁻³ in the CC and WG, respectively. *Sagitta marri*, which was second in abundance, preferred a wider depth range, 500 and

1,000 m, with a maximum of 252 ind. 1,000 m⁻³ in the WG in summer (500–750 m, Table 3). *Eukrohnia bathypelagica* and *E. bathyantartica* showed the opposite abundance pattern, as they preferred layers below 1,000 m

Fig. 2 Vertical distribution and abundance of chaetognaths (without juveniles) along the 3°W transect during winter (a) and summer (b). WG Weddell Gyre, CC Coastal Current. Stations at and south of 68°S are considered within the CC (vertical line)

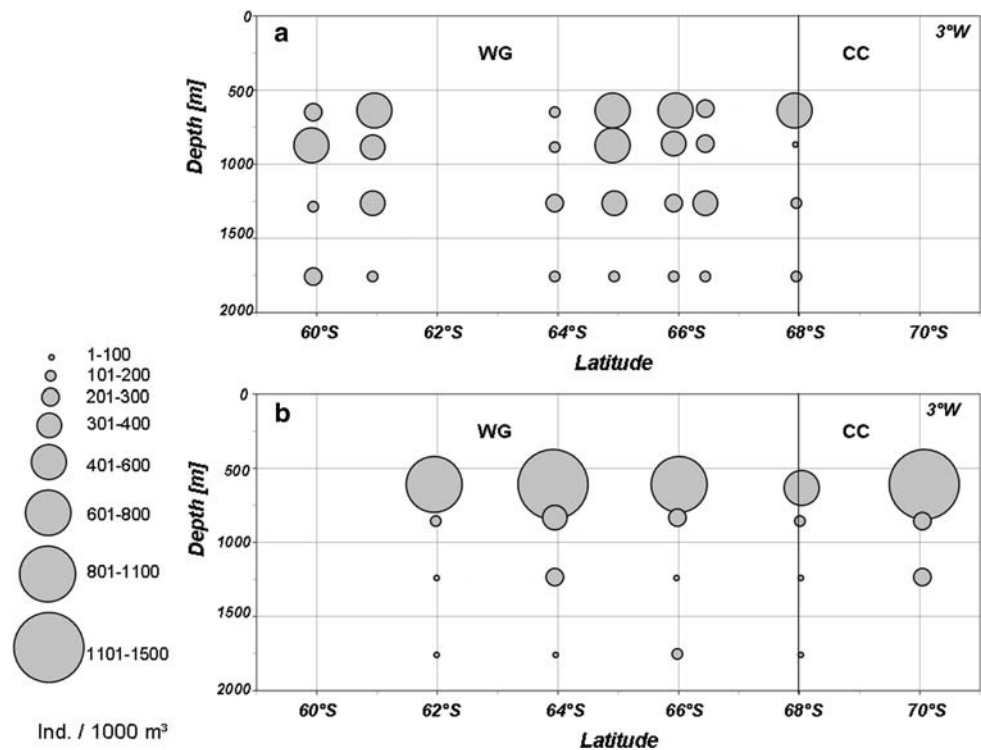
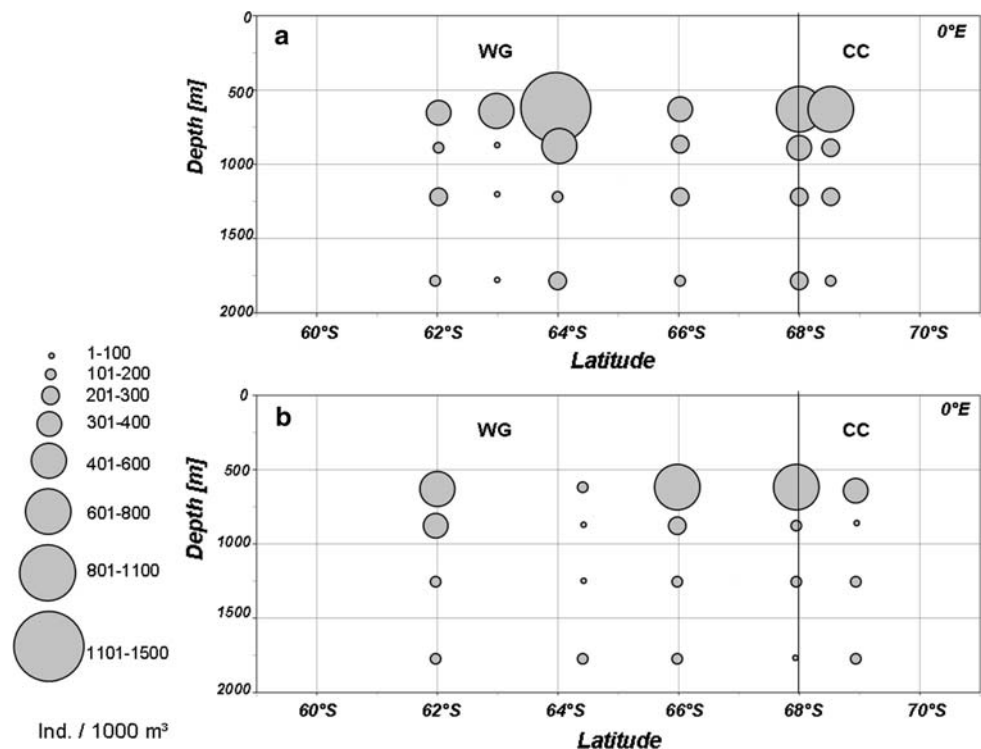


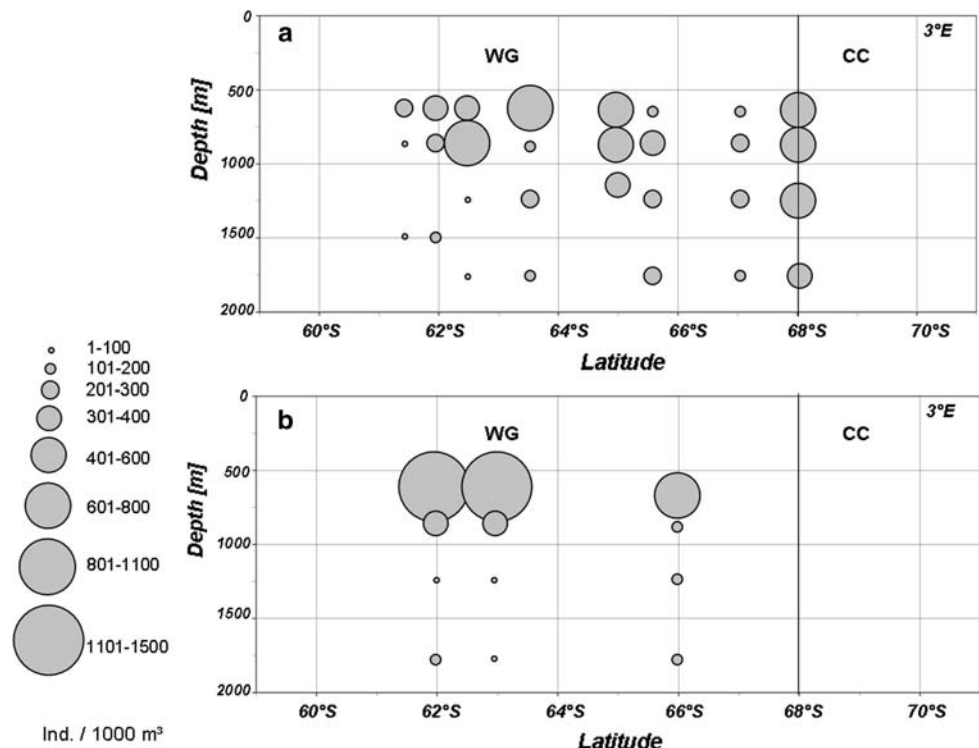
Fig. 3 Vertical distribution and abundance of chaetognaths (without juveniles) along the prime meridian during winter (a) and summer (b). WG Weddell Gyre, CC Coastal Current. Stations at and south of 68°S are considered within the CC (vertical line)



(Table 5). They reached highest numbers of 89 ind. $1,000\text{ m}^{-3}$ (summer, PFZ, 1,000–1,500 m, Table 4) and 56 ind. $1,000\text{ m}^{-3}$ (winter, CC, 1,500–2,000 m, Table 2), respectively. *Eukrohnia macroneura* differed from all other species, as it was most abundant between 750 and 1,500 m depth (maximum of 28 ind. $1,000\text{ m}^{-3}$, summer, PFZ,

Table 4). Although juveniles of the genus *Eukrohnia* could not be subjected to sound statistical analyses, their centre of abundance was observed between 500 and 1,000 m, with values up to 1,330 ind. $1,000\text{ m}^{-3}$ in the WG (500–750 m, Table 3), then representing 59.3% of total chaetognath abundance.

Fig. 4 Vertical distribution and abundance of chaetognaths (without juveniles) along the 3°E transect during winter (a) and summer (b). WG Weddell Gyre, CC Coastal Current. Stations at and south of 68°S are considered within the CC (vertical line)



In species that showed decreasing abundance with depth (*E. hamata*, *S. marri*), this vertical gradient became significantly more distinct in summer, as indicated by the season \times depth interaction term of the ANOVA (Table 5). In contrast, *E. bathypelagica* exhibited a more distinct depth gradient in winter, with a clear preference for the 1,000–2,000 m layer which, however, was caused mainly by a decrease in abundance in shallower layers from summer to winter.

In *Sagitta gazellae* we could not detect any effects of water mass, season or depth. All other species were too rare for reliable analysis. *S. macrocephala* was only captured in summer in the PFZ (8 ind. $1,000\text{ m}^{-3}$ in 750–1,000 m, Table 4). *S. maxima* was primarily found in the PFZ as well, where this species was encountered between 500 and 1,500 m in summer (8 ind. $1,000\text{ m}^{-3}$, Table 4). Two species of *Heterokrohnia* were found below 1,500 m in the WG (Table 3). A total number of 7 individuals of *H. fragilis* (7–10 mm length) were caught in summer, *H. mirabilis* occurred exclusively between 2,000 and 3,000 m in winter and with 2 ind. $1,000\text{ m}^{-3}$ (6.3%) was even rarer than *H. fragilis*. Only one *H. mirabilis* specimen of 19 mm length was caught in the WG.

Distribution of maturity stages in *E. hamata* and *S. marri*

ANOVA of mean maturity stage showed a significant effect of all parameters investigated (Table 5). In both species, mean maturity stage was higher in the PFZ than in the WG.

Season affected *E. hamata* and *S. marri* differently; the former species showed higher mean maturity in winter, the latter in summer. Generally, mean maturity stage increased with depth. However, in *E. hamata* no significant differences were detected below 750 m. In *S. marri* mean maturity stage was significantly higher in the 1,500–2,000 m stratum compared to the 750–1,000 m stratum. The interaction of season and depth indicated that in *E. hamata* the vertical gradient was more distinct in winter, in *S. marri* however, in summer, as in this species depth had no effect at all in winter.

Population structure of *E. hamata* and *S. marri*

Eukrohnia hamata

Of all *Eukrohnia hamata* caught, 99.6% (summer) and 99.9% (winter) were complete and could be measured. The population of *E. hamata* consisted essentially of stages 1 and 2 individuals (Fig. 5). *E. hamata* had a maximum length of 29 mm in summer and 32 mm in winter, respectively (Table 6). During both seasons their length increased slightly with increasing depth, as maturity stage and body length are positively correlated (winter: $r = 0.764$, $P < 0.001$; summer: $r = 0.813$, $P < 0.001$), albeit with much overlap in length between subsequent stages (Fig. 5). Comparing both seasons the mean body length per stage did not differ significantly between seasons: stage 1:14.6 mm, stage 2:23.3 mm, and stage 3:27.7 mm.

Table 5 Effects of water mass WM, season and depth on chaetognath abundance and maturity stage distribution (mean maturity stage per station and depth interval)

		Water mass			Season		Depth				Season × depth							
		PFZ	WG	CC	W	S	1	2	3	4	W 1	W 2	W 3	W 4	S 1	S 2	S 3	S 4
Abundance																		
Class Sagittoidea	ns					A		A	A								A	A
					B		B	B	B		B	B		B			B	
										C	C	C	C	C	C			
Genus <i>Eukrohnia</i>	ns					A		A	A								A	A
					B		B	B	B		B	B		B		B	B	
										C	C	C	C	C	C			
Genus <i>Sagitta</i>	ns				A			A	A				A	A			A	A
						B		B			B	B	B			B		
							C			C					C	C		
<i>E. bathyantartica</i>	ns					A	A	A		A					A	A		
					B				B	B		B					B	
												C	C				C	C
<i>E. bathypelagica</i>	A					A	A	A		A	A				A	A	A	A
		B	B	B					B	B		B	B				B	
<i>E. hamata</i>	ns				A				A				A					A
						B			B		B	B					B	
							C	C		C	C						C	
														D	D			
<i>E. macroneura</i>	ns					A		A	A							A	A	
					B		B		B	B	B	B	B	B	B			B
<i>S. marri</i>	ns				A				A	A			A	A			A	A
						B		B			B	B	B			B		
							C			C				C	C			
Mean stage																		
<i>E. hamata</i>	A		A	A		A	A	A		A	A					A	A	
		B	B		B				B		B	B	B	B	B	B	B	
														C				C
<i>S. marri</i>	A				A	A	A								A	A		
		B	B	B		B		B	B	B	B	B	B		B	B	B	B
							C	C										

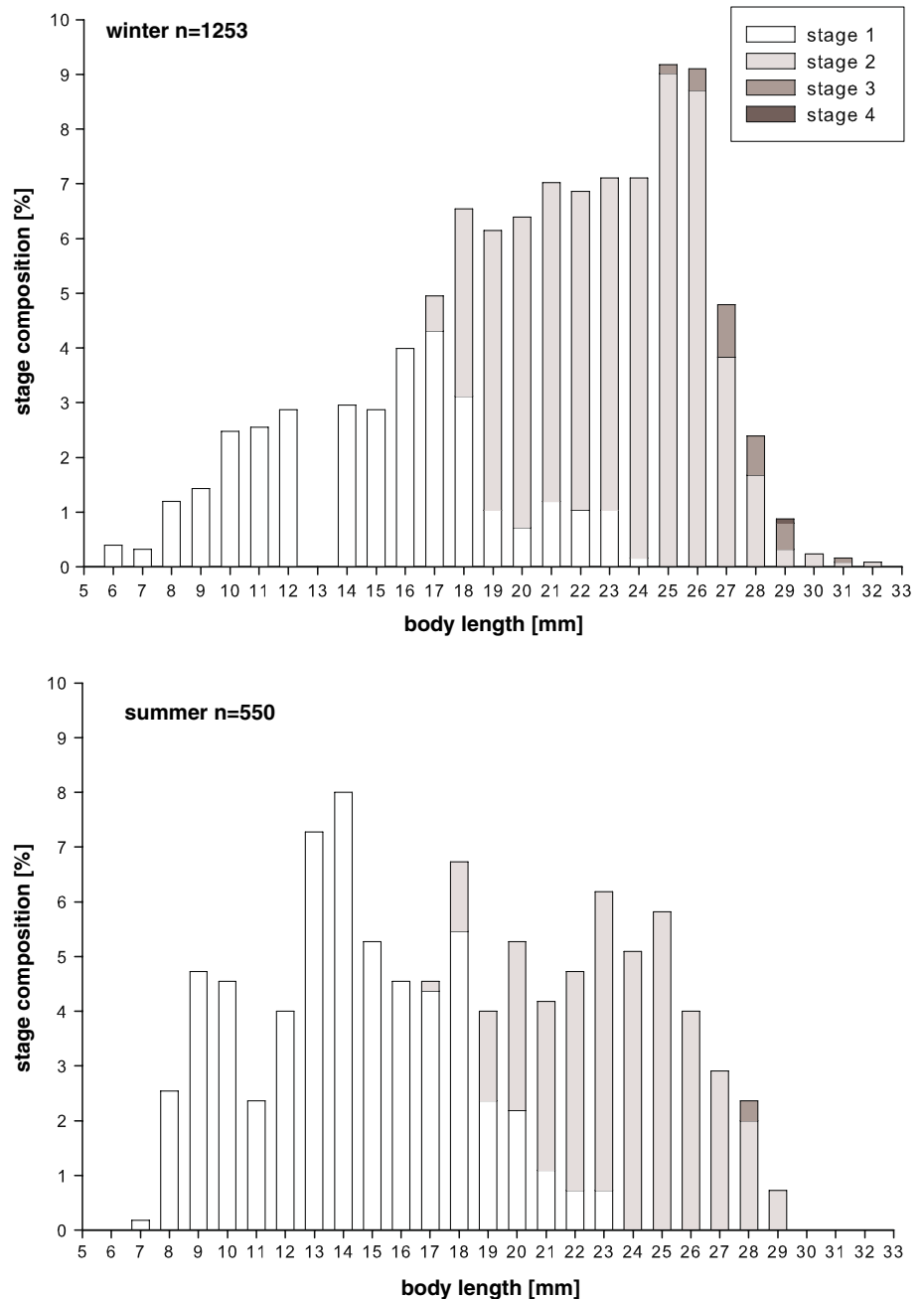
Full factorial (except WM × season) ANOVA with subsequent Tukey HSD post hoc test on differences between means ($\alpha = 0.05$), letters (A, B...) indicate groups that differ significantly, the alphabetical order indicates decreasing abundance/mean maturity stage. The interaction term WM × depth is not shown here, because it was significant only for the class Sagittoidea where abundance decreased with depth in WG and CC, but not in PFZ, and for the genus *Eukrohnia* where abundance decreased with depth within WG. *Sagitta gazellae* is not mentioned in this table, because all tests were not significant

PFZ Polar Frontal Zone, WG Weddell Gyre, CC Coastal Current, S summer, W winter, 1: 2,000–1,500 m, 2: 1,500–1,000 m, 3: 1,000–750 m, 4: 750–500 m), ns no significant effect

The shape of the length–frequency distribution differed significantly between summer and winter (Kolmogorow–Smirnow test, $P < 0.005$). Apparently there was a higher proportion of large animals (>20 mm) present in winter. This coincides with a significantly higher mean maturity

stage in winter (see above). Including the unidentified *Eukrohnia* individuals would slightly increase the stage 1 individuals (especially below 10 mm length), but not significantly change the size–frequency structure (Kolmogorow–Smirnow test, $P > 0.1$).

Fig. 5 Length–frequency and corresponding maturity stage distribution of *Eukrohnia hamata* in winter and summer. *n* the number of investigated individuals



Sagitta marri

All specimens of *Sagitta marri* could be measured in summer, during winter the measuring success rate was 93.3%. This population was dominated by maturity stages 1 and 2 (Fig. 6). Maximum body length was 27 mm in summer and 28 mm in winter, respectively (Table 7). The stage-specific mean lengths differed seasonally only between stage 1 specimens. In the 500–750 m layer *S. marri* had, e.g. a mean length of 6.8 mm in summer compared to 9.4 mm in winter. Maturity stage and length were positively correlated

in this species, too (winter: $r = 0.636$, $P < 0.001$; summer: $r = 0.801$, $P < 0.001$).

The population size–frequency structure (Fig. 6) did not differ significantly between winter and summer (Kolmogorow–Smirnow test, $P > 0.1$). As a result of longer specimens (see above), the structure for the winter situation was shifted towards greater lengths with highest values between 8 and 11 mm body length dominated by stage 2 individuals. Highest values in summer were shown at 6 and 7 mm body length represented by stage 1 individuals.

Table 6 Length–frequency distribution for *Eukrohnia hamata* in the different depth intervals for winter and summer

Depth (m)	n	Length (mm)																															
		6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32					
<i>Winter</i>																																	
500–750	490	5	4	5	8	14	11	15		14	14	24	28	44	32	42	38	38	32	23	35	36	17	8	2			1					
750–1,000	257			7	7	8	8	11		4	7	9	14	9	15	13	20	18	23	18	26	24	11	4				1					
1,000–1,500	335			2	2	9	10	6		13	11	12	13	19	14	14	22	17	26	37	37	35	21	9	4	2							
1,500–2,000	171			1	1			3	4		6	4	5	7	10	16	11	8	13	8	11	17	19	11	9	5	1	1					
<i>Summer</i>																																	
500–750	410		1	14	24	25	9	20	36	38	24	24	21	31	15	24	19	17	24	19	10	9	5	1									
750–1,000	83						3		3	3	3			4	6	3	3	7	8	7	14	9	3	6	1								
1,000–1,500	32				1		1	1	1		1		1	1		1		1	1	1	5	4	6	5	1								
1,500–2,000	25				1			1		3	1	1	3	1	1	1	1	1	1	1	3		2	1	2								

n the number of investigated individuals

Discussion

Of the ten species found during this investigation, *E. hamata*, *S. gazellae*, *S. marri* and *S. maxima* were most frequently recorded in the past 50 years of Antarctic research (David 1958a; Alvarino 1969; Dinofrio 1973; Alvarino et al. 1983a, b; Hagen 1985; Johnson and Terazaki 2004). Different nets of varying and rather coarse mesh sizes were used in previous studies compared to our multinet with 100- μ m mesh size. Thus, abundance data are difficult to compare, as we have caught smaller (younger) animals with higher efficiency, but larger chaetognaths (e.g. *S. gazellae*, Hagen 1985) may be underrepresented to some extent due to active escape reactions.

Parameters influencing chaetognath abundance and species composition

Water mass

Spatial variability of chaetognath abundance is enormous (Fig. 1), even on small scales, as observed during all hauls at the station located at the ice camp (WG) within 5 days and 32 nm total drift distance (start to end distance, 7 nm). This patchiness, that is typical for zooplankton, might have obscured to a large extent differences in chaetognath abundance and composition between the three different water masses PFZ, WG and CC.

The sole finding of *Sagitta macrocephala* in the PFZ supports previous reports, as this species was described to be more frequent in the deep mesopelagic layers of the Subantarctic than in those of the Antarctic waters (David 1958a, 1965). We found just one significant effect of water mass: *Eukrohnia bathypelagica* was more abundant in the PFZ than in the other two water masses, particularly below 750 m (Tables 2, 3, 4). At this depth a tongue of warm

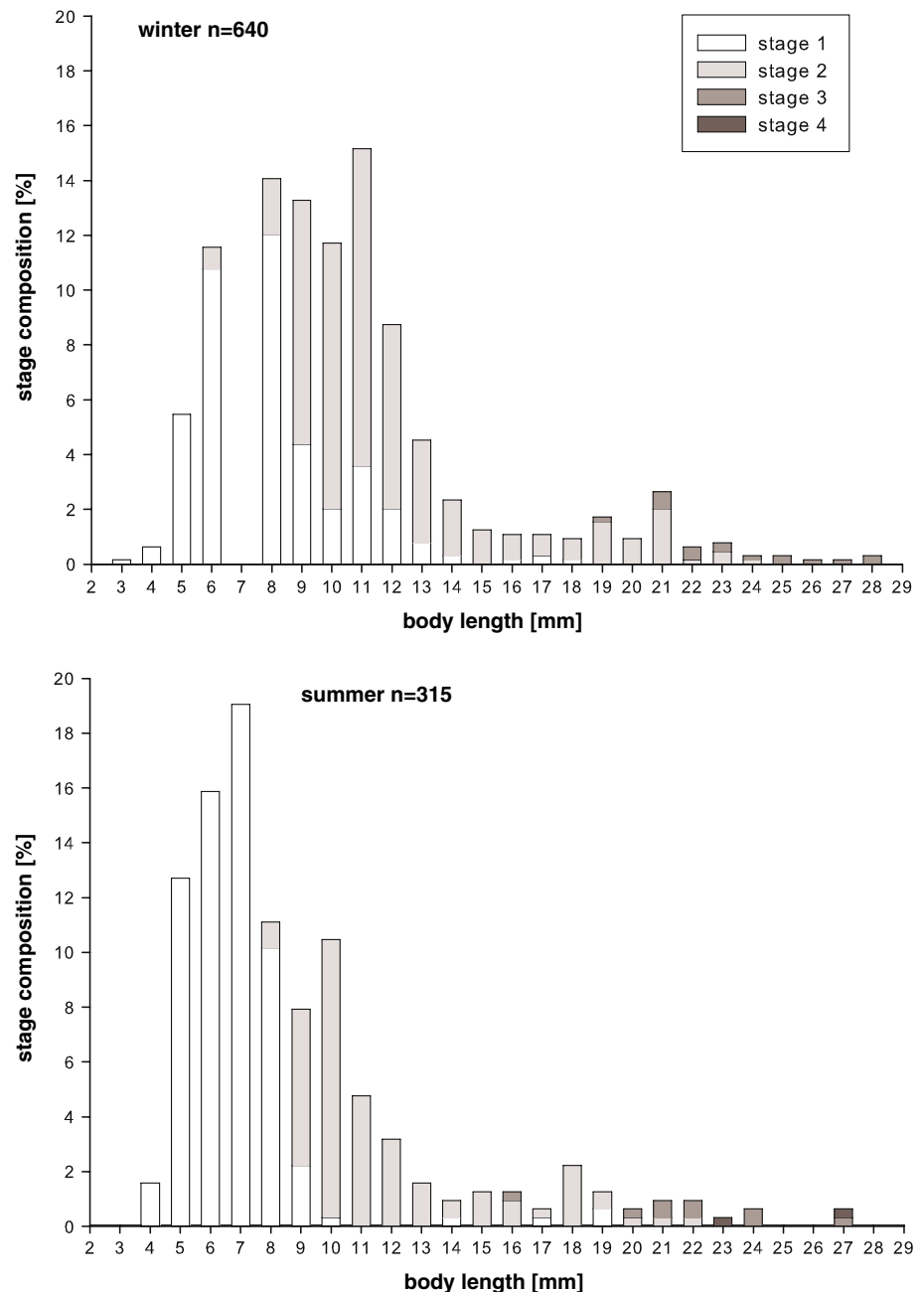
(about 2°C) and saline (>34.7) water stretches from Subantarctic into polar regions (Schröder and Fahrbach 1999). One should keep in mind that our stations were situated at the southernmost edge of the PFZ or Antarctic Convergence. Thus, our data might not have caught the full impact of the particular PFZ hydrodynamics on chaetognath distribution. This might also explain to some extent that we did not see higher abundance of *E. hamata* in PFZ waters. *E. hamata*, a cosmopolitan species (Alvarino 1969), is considered to be the most abundant species in Subantarctic and Antarctic waters, showing maximum abundance in the vicinity of the Antarctic convergence where higher densities have been reported even deeper in the water column (David 1958a). In the top 500 m *E. hamata* is known to reach maximum concentrations (David 1958a, 1965; Johnson and Terazaki 2004); hence, generally higher densities of *E. hamata* may occur around the Antarctic Convergence in the epipelagic realm. In general, the upper layer of this water body reveals higher plankton concentrations than adjacent areas (Voronina 1968). Between 49° and 50°S, highest downward velocity is observed at 20°E which results in an increased zooplankton abundance especially in the upper 100 m (Voronina 1968). In the meso- and bathypelagic of the Antarctic Convergence, however, these differences in zooplankton density are probably not detectable any more.

Water depth

Depth was found to be the major determinant of chaetognath abundance and distribution on all taxonomic levels.

Eukrohnia hamata was the dominant species in terms of abundance, especially between 500 and 1,000 m. It showed a significant decrease in abundance with depth, a pattern already found in previous studies (e.g. Alvarino et al. 1983a, b). *E. bathypelagica* and *E. bathyantartica* coexist

Fig. 6 Length–frequency and corresponding maturity stage distribution of *Sagitta marri* in winter and summer. *n* the number of investigated individuals



with, and partially displace, *E. hamata* in the deep meso- and bathypelagic oceanic strata. Whereas *E. bathypelagica*, a species with a worldwide distribution (e.g. Rottmann 1978, Gulf of Thailand; Terazaki 1996, Equatorial Pacific), inhabits the layers below 500 m, *E. bathyantartica* occurs mainly below 1,000 m in Antarctic waters.

Eukrohnia bathypelagica dominated the 1,000–2,000 m depth range and reached average numbers of up to 33 ind. $1,000\text{ m}^{-3}$ in summer in the WG (1,500–2,000 m) and 89 ind. $1,000\text{ m}^{-3}$ in the PFZ (1,000–1,500 m). So far, only Alvarino et al. (1983a, b) provided detailed information on the geographical and bathymetric distribution of

E. bathypelagica in the Southern Ocean. In summer, they observed low densities of *E. bathypelagica* (≤ 10 ind. $1,000\text{ m}^{-3}$) in the meso- and bathypelagial of the Scotia Sea, Weddell Sea and the Drake Passage, which is three times less than we observed in average. The winter data given by Alvarino et al. (1983a) excluded the Weddell Sea, but data for the South Pacific showed largest abundances of up to 1,000 ind. $1,000\text{ m}^{-3}$ below 1,000 m north of 60°S . To the south this species always occurred with less than 100, in some areas dropped even below 10 ind. $1,000\text{ m}^{-3}$ in the meso- and bathypelagic zone. We note that Alvarino et al. (1983a) included the 200–500 m range in

Table 7 Length–frequency distribution for *Sagitta marri* in the different depth intervals for winter and summer

Depth (m)	n	Length (mm)																											
		3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28		
<i>Winter</i>																													
500–750	167	1	1	4	8		12	24	16	34	20	12	1	5	5	3	2	6	2	6	1	3		1					
750–1,000	183		1	17	15		29	29	18	30	17	8	1	1	1	1	1	2	2	6	2		2						
1,000–1,500	232		2	12	46		40	27	32	24	16	7	11		1		1	2	1	3	1	1		1	1	1	2		
1,500–2,000	58			2	5		9	5	9	9	3	2	2	2		3	2	1	1	2		1							
<i>Summer</i>																													
500–750	201		5	29	31	34	23	17	22	9	5	4	2	3	4	2	3	4	1	2	1								
750–1,000	75			9	15	18	7	6	6	5	2		1				1		1	1	1	1	1	1					
1,000–1,500	35			2	4	8	5	2	5	1	3	1		1			1				1						1		
1,500–2,000	4																	2					1				1		

n the number of investigated individuals

the mesopelagic zone, thus making their and our numbers difficult to compare. Nevertheless, our observations on *E. bathypelagica*—wide distribution and rather similar abundance below 500 m in the Lazarev Sea—complement the data of Alvariño et al. (1983a).

Eukrohnia bathyantartica was considered to be an endemic circumpolar Antarctic species first (David 1958b), but later it was found in other regions, too, e.g. in the Gulf of Mexico, the Caribbean Sea and off the Chilean coast (Fagetti 1968, 1972). Observations on this species are few, primarily due to the low sampling depths chosen during most investigations, and secondly because most sampling used large mesh sizes. Particularly winter records of this species are very rare (e.g. Alvariño et al. 1983a, b), hence the data presented here (complemented by Kruse 2009) are unique and contribute to a better understanding of this deep-living species. Our samples indicate a significant preference for deeper layers (>1,000 m, Table 5), in the CC and PFZ it was even completely absent above 750 m during summer (Tables 2, 3, 4). Maximum abundance of adults was <60 ind. 1,000 m⁻³, but total abundance below 1,000 m was distinctly higher in the CC, as 83% of the *Eukrohnia* juveniles found there could be attributed to *E. bathyantartica*. Both David (1964) and Alvariño et al. (1983a) reported a similar vertical distribution for *E. bathyantartica*, highest numbers were found below 1,500 and 1,000 m, respectively, particularly in summer.

The blind chaetognath *Eukrohnia macroneura* was first described from the eastern Atlantic, between about 0° and 18°S. *E. macroneura* lives at greater depths than *E. hamata*, from which it has been evolved (Casanova 1986). Few records exist of this species (Pierrot-Bults and Nair 1991). Here, we present the first record of *E. macroneura* from the Antarctic Ocean that extends its geographical distribution distinctly into colder regions thus demonstrating a wider

tolerance of hydrographical factors. *E. macroneura* preferred the depth range between 750 and 1,500 m. Its vertical distribution overlapped with the one of *E. bathyantartica*, but it was distinctly less abundant.

Within the genus *Sagitta*, *S. marri* and *S. gazellae* are the only endemics from the Antarctic epi- and mesopelagic zone (Pierrot-Bults and Nair 1991). *S. marri* was the second most abundant chaetognath species in our study (Tables 2, 3, 4). It occurred preferentially between 500 and 1,000 m (Table 5), with a maximum of 252 ind. 1,000 m⁻³ (500–750 m) in the WG in summer. Both Hagen (1985) and Alvariño et al. (1983a) reported similar vertical patterns with maxima within the 250–735 m and the 200–1,000 m depth range, respectively. In the mesopelagic layer, Alvariño et al. (1983a) found summer abundances of mostly up to 100, occasionally up to 1,000 ind. 1,000 m⁻³. Interestingly, they observed comparable numbers at some locations in the bathypelagic realm, which, however, declined sharply towards south to numbers <10 ind. 1,000 m⁻³.

Sagitta gazellae was only found in very low numbers (<10 ind. 1,000 m⁻³) over the complete depth range, but in the WG only. This species is known to have highest abundances between 50 and 100 m (David 1964), where it coexists with *E. hamata*, although, it may occur down to 3,000 m, particularly stages of higher maturity (David 1955). Our abundance data are even below those reported by Alvariño et al. (1983a), below 10 ind. 1,000 m⁻³ compared to up to 100 ind. 1,000 m⁻³ in the mesopelagic zone of the South Atlantic, but owing to the overall low numbers it is difficult to say whether this discrepancy results from different sampling schedules/gears, or is just statistical noise. David (1958a) observed an extension of *S. gazellae* occurrence into deeper waters (ca. 700 m) in the region of the Antarctic Convergence which, however, we cannot confirm.

Sagitta maxima was rarely encountered, with highest abundances ($<10 \text{ ind. } 1,000 \text{ m}^{-3}$) in the PFZ and showed no distinct vertical distribution pattern. As this species is seen as the Subantarctic counterpart of *S. marri* with a main distribution between 150 and 500 m (David 1965), our few observations are not surprising.

Heterokrohnia species are rarely caught and most of them are found in the deep bathypelagial (Pierrot-Bults and Nair 1991). These authors presumed provincialism among the more recently described abyssal bathyplanktonic species of *Heterokrohnia* including *H. fragilis*, *H. longidentata* and *H. longicaudata* for the Antarctic region. Our few findings of the two species *H. fragilis* and *H. mirabilis* confirm the preference of this genus for the deep bathypelagial which coincides with earlier recordings (Tchindonova 1955; David 1958a; Bieri 1959; Pierrot-Bults and Nair 1991). Moreover, a vertical segregation between *H. fragilis* (above 2,000 m) and the very rare *H. mirabilis* (below 2,000 m) might exist.

Season

Seasonal differences in presence and vertical distribution of chaetognaths are linked to species life histories. These are associated with seasonal and breeding migrations (David 1965). Generally, the number of chaetognath species as well as of abundance, except within certain species (see above), decrease with increasing depth (Alvariño 1964). Highest numbers are found in the epipelagic zone, the best known part of the water column, however, is omitted from this study. This hampers the interpretation of seasonal effects to a certain extent. Our data confirm the general decline of chaetognath abundance with depth (Figs. 2, 3, 4), but indicate seasonal differences:

Chaetognaths in general and particularly *E. hamata*, *S. marri* and *E. bathypelagica*, occurred slightly deeper in the water column in winter. Furthermore, *E. hamata* and *S. marri* were more numerous in winter than in summer, whereas *E. bathypelagica* and *E. bathyantartica* showed the opposite trend.

A downward vertical migration towards winter was observed in *E. hamata* and suggested for *S. marri* (David 1958a). Higher abundances at greater depth in winter were also indicated in *E. hamata* in the South Pacific (130°W to 90°W, Alvariño et al. 1983a). For *E. hamata*, Alvariño et al. (1983a) reported high numbers during summer and fall in the epipelagic layer, whereas large numbers between 200 and 1,000 m depth were found in fall and winter. *S. marri* was described to occur at low densities in the epipelagic and at moderate numbers in the meso- and bathypelagic realm during winter, but the data of Alvariño et al. (1983a) give no indication of seasonal differences. Our data indicate a wintery downward migration in *E. hamata* and

in *S. marri*, and a corresponding upward migration in *Eukrohnia bathyantartica*. *E. bathypelagica* appears to accumulate in the 1,000–1,500 m layer by down as well as upward migration in winter.

The drivers of this seasonal migration are not yet clear. Johnson and Terazaki (2004) suggested that, while the chaetognath distribution in the subarctic Pacific is determined by temperature, the vertical distribution of Antarctic chaetognaths might rather be controlled by prey availability. If this would be true, chaetognaths might trace the migrating copepods to deeper layers in winter, or in case of *E. bathypelagica* and *E. bathyantartica*, to shallower layers in summer. Further studies on the gut contents should focus on this hypothesis.

Vertical segregation of developmental stages

Besides seasonality, ontogenesis has an important influence on vertical species distribution. A vertical segregation of size classes and corresponding maturity stages of *E. hamata* has been reported by several authors for the North Pacific (Sullivan 1980; Johnson and Terazaki 2003), the Arctic (Sameoto 1987; Timofeev 1998) and the Antarctic (Kramp 1939; David 1965; Øresland 1995). While the sexually mature chaetognaths aggregate at depth where they spawn, the eggs or juveniles rise up to the surface layer. During their development and maturation they start to migrate down to greater depth again (Kramp 1939; Alvariño 1964; Sullivan 1980; Hagen 1985; Øresland 1995; Timofeev 1998). Juveniles of *Eukrohnia* were concentrated between 500 and 1,000 m in summer, from where they may ascend to surface layers during their development. The small numbers of juveniles in winter may indicate either a reproduction break or a migration closer to the surface. Stages 1 and 2 dominated over a wide depth range in the present study and showed an increasing length with greater depth during both seasons. Most of the growth may take place during the first stages of development. This strategy facilitates the escape from the prey spectrum of small sized predators and increases the own prey size spectrum simultaneously (Øresland 1995). The advanced maturity stages occurred deeper (higher mean maturity stage in *E. hamata* and *S. marri*) and seem to invest less in growth and more in the development of the reproductive organs (observed for *S. gazellae* by David 1955). The migration of adult specimens to greater depth might be common in chaetognaths. Alvariño (1964) hypothesised that this is a purely physical process, owing to the increasing specific weight concurrent with the maturity of the gonads. However, some species, e.g. *Sagitta lyra* and *S. hexaptera*, have voluminous and gelatinous inner parts in the lateral fins which compensate the increased density (Kapp 1991b). Thus, alternative or

additional mechanisms are at work, the downward migration could, for instance, protect from large epipelagic predators.

Life cycles

The wide size range of *E. hamata* specimens encountered in winter and summer indicates an extended or even continuous period of reproduction, as presumed by Øresland (1995). Surprisingly, however, we found no stage 4 individuals in summer and just a few in winter, and no individuals carrying brood sacs (defined as stage 5). Øresland (1990, 1995) made the same observations in Gerlache Strait and concluded that these brood sacs are either easily damaged during sampling or extremely rare. However, Dawson (1968) and Timofeev (1998) found *E. hamata* with brood sacs. As we caught *E. bathypelagica* and *E. bathyantartica* with brood sacs, too, the sampling method is unlikely to be responsible for the absence in *E. hamata*. Moreover, large individuals of about 30 mm length but still far away from maturity were caught, as reported by Kramp (1939) from Greenland waters, too. So, how did we miss the mature *E. hamata*? There are two possibilities: on the one hand, mature *E. hamata* occur below our maximum sampling depth of 2,000 m. This is the case in the Arctic Basin, where Dawson (1968) reported mature *E. hamata* descending deeper than 3,000 m. On the other hand, our sampling schedule may have mis-matched the periods of high reproductive activity, or in contrast, continuous reproduction takes place on such a low level (Øresland 1990, 1995) that we did not catch mature individuals just by chance. Continuous but low breeding would explain the high number of 120–151 eggs per specimen (Arctic Ocean, Timofeev 1998) necessary to sustain the population of this species. Prospective seasonal and deep bathypelagic sampling should give an answer to this open question.

The lack of unimodality in the length–frequency distribution of *E. hamata* during both seasons indicates a rather complex life cycle. It might be longer than 1 year and include several reproductive periods. Thus, our observations seem to support the hypothesis of a 2-year life cycle (reviewed by Pearre 1991). However, the epipelagic layer was not included in the present study. Epipelagic data as presented by Hagen (1985) and Øresland (1990, 1995) from the Antarctic Peninsula show that there are great numbers of small and young chaetognaths. Moreover, the unidentified *Eukrohnia* individuals were not included in the length–frequency distribution, which might again slightly underestimate the number of smaller stage 1 individuals.

Observations on the life cycle of *S. marri* are lacking so far. Nothing is known except that this species matures in the 750 to 1,000 m depth range (David 1965). Vertical segregation of maturity stages in this species was not as

pronounced as in *E. hamata*. Stage 1 and 2 individuals inhabited almost the complete sampling range. More stage 1 individuals occurred at depth in winter and more stage 2 individuals in summer, resulting in higher mean maturity in summer than in winter. Although the mean maturity stage was highest between 1,500 and 2,000 m depth, this is only based on few stage 3 and 4 individuals.

From the two seasons studied it can be suggested that *S. marri* reproduces in spring or early summer and in fall. As small juveniles and large stage 3 individuals (maximum length 27 and 28 mm, respectively) occurred during both seasons, reproduction may be continuous. However, generation time of *S. marri* cannot be inferred from our data.

Conclusions

This investigation provides detailed information on the effect of water mass, season and water depth on the geographical and vertical distribution and abundance of chaetognaths in the Lazarev Sea. Compared to other regions of the world oceans and to other zones within the Antarctic such as the surroundings of the Antarctic Peninsula, the Lazarev Sea has rarely been sampled. Winter studies and investigations of the meso- and especially bathypelagic realm are very scarce. However, our observations are in accord with the worldwide distribution pattern of chaetognaths reviewed by Pierrot-Bults and Nair (1991). Additional extensive data are presented here on the abundance of *E. bathypelagica* and *E. bathyantartica*, the two species dominating the bathypelagic zone. In addition to current knowledge of diversity and prevailing species, *E. macroneura* was found for the first time in the Antarctic Ocean. Other rare species such as *Heterokrohnia fragilis* were observed occasionally below 1,500 m. A wide geographical distribution of these deep-living species can be suggested, albeit our knowledge on deep-living species is restricted by quite limited sampling from the bathypelagic in a few geographical locations. Beyond the insight in the deep water community of the Lazarev Sea, our data form the basis for further studies on the biology of chaetognaths. The observations on *E. hamata* and *S. marri* as well as on *E. bathypelagica* and *E. bathyantartica* (Kruse 2009) indicate that most Antarctic chaetognaths reproduce over an extended period of the year, either in several pulses or even continuously throughout the year. Therefore, more effort should be concentrated on the investigation of deep mesopelagic and bathypelagic species, focusing especially on their life cycles, activity and feeding.

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