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Biology of meso- and bathypelagic chaetognaths  
in the Southern Ocean

Biologie meso- und bathypelagischer Chaetognathen  
im Südlichen Ozean

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Svenja Kruse

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 HELMHOLTZ  
| GEMEINSCHAFT

ALFRED-WEGENER-INSTITUT FÜR  
POLAR- UND MEERESFORSCHUNG  
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Alfred-Wegener-Institut  
für Polar- und Meeresforschung  
D-27570 Bremerhaven  
Germany  
[www.awi.de](http://www.awi.de)

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**Biology of meso- and bathypelagic chaetognaths  
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**Svenja Kruse**

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Svenja Kruse  
Alfred-Wegener-Institut für Polar- und Meeresforschung  
Am Handelshafen 12  
D-27570 Bremerhaven

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## SUMMARY

Chaetognaths contribute significantly to the zooplankton abundance and biomass in the ocean. Numerous studies have focused on the epipelagic chaetognath community, whereas little attention has been paid to the meso- and bathypelagic realm in the Southern Ocean. Therefore stratified deep sampling between 500 and 2000 m depth with low mesh sizes combined with laboratory studies on board ship and at the home institute has provided a unique opportunity for a detailed investigation of Antarctic chaetognaths. Their distribution patterns, abundance and composition were studied in conjunction with their biology during summer and winter. Special attention was given to the examination of reproduction, feeding, respiration and lipid metabolism of selected species.

The Antarctic meso- and bathypelagic chaetognath community consisted of ten species from three genera. *Eukrohnia hamata* and *Sagitta marri* showed highest numbers and decreased with increasing depth. *E. bathypelagica* and *E. bathyantartica* were less abundant, but had their distribution maxima in the 1000 to 2000 m range. Rare species such as *Heterokrohnia fragilis* and *H. mirabilis* were only caught in few numbers below 1500 m depth. *S. gazellae* and *S. maxima*, the two largest species in this community, had also a low abundance, possibly due to escape reactions from the net and/or to a different vertical and horizontal distribution pattern. However, each species appears to have its own spatial niche within this ecosystem.

Total abundance and distribution of chaetognaths were determined by water depth and season. Water mass seems to have only little influence on the meso- and bathypelagic chaetognath community. Highest chaetognath numbers and biomass occurred in the 500 to 1000 m depth range. Seasonal vertical migrations were identified between summer and winter, generally from shallower to greater depth in winter. Chaetognaths probably follow migrating copepods. A vertical segregation of maturity stages occurred with mature specimens usually found at greatest depth, although young specimens could be found throughout the water column.

The population structures of the four dominating species were studied to obtain information on their life and maturity cycle. The populations of *E. hamata* and *S. marri* consisted mainly of young, developing specimens during both seasons. Adult specimens were only found in very low numbers. In *E. bathypelagica* and *E. bathyantartica* all maturity stages were present. Both deep-living species were characterized by carrying their young in marsupial sacs, which is typical for *Eukrohnia* species. *E. bathypelagica* carried up to 128 eggs and *E. bathyantartica* up to 13 eggs together in both brood sacs. Reproduction in these species seems not only to be continuous throughout the year, but a succession of at least two maturity cycles can also be assumed. Although a biennial life cycle is probably expressed in *E. hamata*, the life cycles of all four chaetognath species are difficult to understand on the basis of only two sampling seasons.

Meso- and bathypelagic chaetognaths fed in summer and winter. Feeding in *E. hamata*, *E. bathypelagica* and *E. bathyantartica* was studied in detail. Only few food items were found in *E. hamata* and *E. bathypelagica* which indicate a primarily copepod based diet. The fatty acid compositions of *E. bathypelagica* and *E. bathyantartica* were distinctly different. High amounts of the

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biomembrane fatty acids 22:6(n-3) and 20:5(n-3) were found in *E. bathypelagica*, whereas *E. bathyantartica* contained high relative amounts of the fatty acid 18:1(n-9) and the fatty alcohols 16:0 and 22:1(n-9), indicating a high degree of carnivory and calanid copepods as potential prey. Neither species store high amounts of lipids which can probably be explained by year-round feeding in chaetognaths. However, energy storage appears to be more important in *E. bathyantartica*. Although the lipid content increased with higher maturity in *E. bathypelagica*, *E. bathyantartica* had a higher average lipid content with a large portion of fatty alcohols and therefore wax esters.

Metabolism in Antarctic chaetognaths is at a low level. Lower metabolic losses in terms of body carbon were observed in *E. hamata* and *E. bathypelagica* especially compared to other Antarctic zooplankton. Nevertheless, the impact of meso- and bathypelagic chaetognaths on the copepod community in the Southern Ocean is probably significant and they may hold a central position channelling energy from lower to higher trophic levels. Therefore it is necessary to focus future investigations on the meso- and bathypelagic realm to elucidate zooplankton abundance and composition as well as to understand the role of deep-living zooplankton in carbon flux.



## ZUSAMMENFASSUNG

Chaetognathen tragen wesentlich zur Abundanz und Biomasse des marinen Zooplanktons bei. Viele der bisherigen Untersuchungen beschränkten sich auf die epipelagische Chaetognathengemeinschaft, während dem Meso- und Bathypelagial im Südlichen Ozean nur wenig Beachtung geschenkt wurde. Stratifizierte tiefe Probenahmen zwischen 500 und 2000 m Wassertiefe mit geringer Maschenweite lieferten eine einzigartige Gelegenheit der detaillierten Untersuchung antarktischer Chaetognathen. Ihre Verteilungsmuster, Abundanz sowie Artenzusammensetzung wurde im Zusammenhang mit ihrer Biologie im Sommer und Winter analysiert. Das Hauptaugenmerk lag auf der Reproduktion, dem Fraß, der Respiration und dem Lipidmetabolismus ausgewählter Arten.

Die antarktische meso- und bathypelagische Chaetognathengemeinschaft setzte sich aus zehn Arten dreier Gattungen zusammen. *Eukrohnia hamata* und *Sagitta marri* waren am häufigsten, wobei ihre Abundanz mit zunehmender Tiefe abnahm. *E. bathypelagica* und *E. bathyantartica* wiesen geringere Abundanzen auf, zeigten jedoch Maxima zwischen 1000 und 2000 m. Seltene Arten wie *Heterokrohnia fragilis* und *H. mirabilis* wurden nur in geringer Anzahl unterhalb von 1500 m gefangen. *S. gazellae* und *S. maxima*, die beiden größten Arten in dieser Gemeinschaft, waren ebenfalls seltener vorzufinden, was möglicherweise auf ein Fluchtverhalten vor dem Netz und/oder ein anderes vertikales sowie horizontales Verteilungsmuster schließen lässt. Jede Art scheint jedoch ihre eigene Nische im Ökosystem zu besitzen.

Wassertiefe und Jahreszeit bestimmten die Gesamtabundanz und Verteilung der Chaetognathen. Die Wassermassen scheinen hingegen nur wenig Einfluss auf die meso- und bathypelagische Gemeinschaft zu haben. Chaetognathen wiesen zwischen 500 und 1000 m Tiefe die größte Anzahl und Biomasse auf. Saisonale Vertikalwanderungen zeigten sich vom Sommer zum Winter durch Verlagerung in größere Tiefen. Chaetognathen folgten wahrscheinlich vertikal wandernden Copepoden. Darüber hinaus konnte eine vertikale Auftrennung der Entwicklungsstadien beobachtet werden. Adulte Tiere sind vor allem in den tiefsten Schichten anzutreffen, während junge Individuen über die gesamte Wassersäule verteilt vorliegen.

Die Populationszusammensetzung der vier dominanten Arten wurde untersucht, um Rückschlüsse auf den Lebens- und Reifezyklus ziehen zu können. Sowohl im Sommer wie auch im Winter setzten sich die Populationen von *E. hamata* und *S. marri* im Wesentlichen aus jungen, sich entwickelnden Individuen zusammen. Adulte Tiere wurden nur in geringer Anzahl gefangen. Bei *E. bathypelagica* und *E. bathyantartica* waren alle Entwicklungsstadien vorzufinden. Diese beiden tief lebenden Arten trugen ihre Jungtiere in Brutsäcken, die charakteristisch für die Gattung *Eukrohnia* sind. *E. bathypelagica* hatte insgesamt bis zu 128 Eier und *E. bathyantartica* bis zu 13 Eier in beiden Brutsäcken. Die Reproduktion in diesen beiden Arten scheint nicht nur kontinuierlich während des ganzen Jahres statt zu finden, darüber hinaus kann eine Aufeinanderfolge von mindestens zwei Reifezyklen vermutet werden. Die Lebenszyklen der vier Chaetognathenarten sind jedoch nur schwer auf der Basis von Proben aus zwei Jahreszeiten zu verstehen, obwohl ein zweijähriger Lebenszyklus für *E. hamata* wahrscheinlich ist.

Meso- und bathypelagische Chaetognathen fraßen im Sommer und im Winter. Fraß bei *E. hamata*, *E. bathypelagica* und *E. bathyantartica* wurde im

## ZUSAMMENFASSUNG

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Detail untersucht. In den Darmen von *E. hamata* und *E. bathypelagica* wurden nur wenige Nahrungsbestandteile gefunden, die jedoch insgesamt auf eine auf Copepoden basierende Nahrung schließen lassen. Die Fettsaurezusammensetzungen von *E. bathypelagica* und *E. bathyantartica* unterschieden sich deutlich. *E. bathypelagica* enthielt einen groen Anteil von den Biomembran-bildenden Fettsauren 22:6(n-3) and 20:5(n-3). *E. bathyantartica* hatte groere relative Mengen der Fettsaure 18:1(n-9) und der Fettalkohole 16:0 und 22:1(n-9) angereichert, die auf einen hohen Grad an Karnivorie sowie auf calanide Copepoden als Beute hinweisen. Beide Chaetognathen speichern keine groen Lipidmengen, was wahrscheinlich im kontinuierlichen Fressen begrundet liegt. Dennoch scheinen Energiespeicher eine groere Rolle bei *E. bathyantartica* zu spielen. Obwohl der Lipidgehalt bei *E. bathypelagica* mit der Reife zuzunehmen scheint, ist er bei *E. bathyantartica* insgesamt hoher, zu einem groen Anteil bestehend aus Fettalkoholen und somit Wachsestern.

Der Metabolismus antarktischer Chaetognathen ist auf einem niedrigen Niveau. Der metabolische Verlust in Form von Korperkohlenstoff ist sowohl bei *E. hamata* wie auch bei *E. bathypelagica* gering, insbesondere auch im Vergleich zu anderem antarktischen Zooplankton. Trotzdem kann der Einfluss meso- und bathypelagischer Chaetognathen auf die Copepodengemeinschaft im Sudlichen Ozean signifikant sein. Daruber hinaus konnen sie im Energietransfer von niedrigeren zu hoheren trophischen Ebenen eine zentrale Rolle spielen. Folglich ist es notwendig, den Fokus zukunftiger Untersuchungen auf das Meso- und Bathypelagial zu legen, um sowohl die Abundanz und Zusammensetzung des Zooplanktons zu analysieren, sowie auch die Bedeutung des tief lebenden Zooplanktons im Kohlenstofffluss zu verstehen.

# 1. GENERAL INTRODUCTION

The deep-sea pelagic environment is a vast habitat, still largely unexplored. A substantial contribution to the knowledge on Antarctic mesopelagic zooplankton was provided by studies undertaken with the research vessel “Discovery” in the first half of the last century (e.g. Mackintosh 1937; Hardy and Gunther 1935; Foxton 1956; David 1958). In recent decades numerous investigations were related to taxonomy, distribution and species composition of Antarctic zooplankton (e.g. Hagen 1985; Hopkins 1985a; Piatkowski 1987; Forster 1989; Lancraft et al. 1989; Boysen-Ennen et al. 1991; Ward et al. 2005, 2006). However, most of these studies concentrated more on copepods and euphausiids from the uppermost water layers, and only very little sampling has been carried out in mesopelagic and bathypelagic layers. Lately krill (*Euphausia superba*), which is usually found in the top 150 m of the water column, was observed at abyssal depths (Clarke and Tyler 2008; Sanderson 2008). But observations on distribution, abundance and composition of the “midwater”-animals are based on very few observations only. Therefore our knowledge on their biology and role in the food web as well as their contribution to the carbon cycle is in its infancy.

Chaetognaths were chosen for this study because they comprise a significant proportion of the zooplankton standing stock and are considered as one of the most important predators in the Southern Ocean (Øresland 1990; Hosie and Cochran 1994; Froneman et al. 2002). The transfer of energy from copepods to higher trophic levels may therefore be channelled through this zooplankton group (Reeve 1970a). Moreover, their fecal pellets may contribute significantly to the vertical carbon flux (Dilling and Alldredge 1993; Giesecke et al. 2009).

To provide more scientific background to this open field of investigation, I will focus in the following chapters on the Southern Ocean as marine habitat, on the present knowledge on general distribution patterns of chaetognaths and on important aspects of their biology.

## 1.1 The Southern Ocean

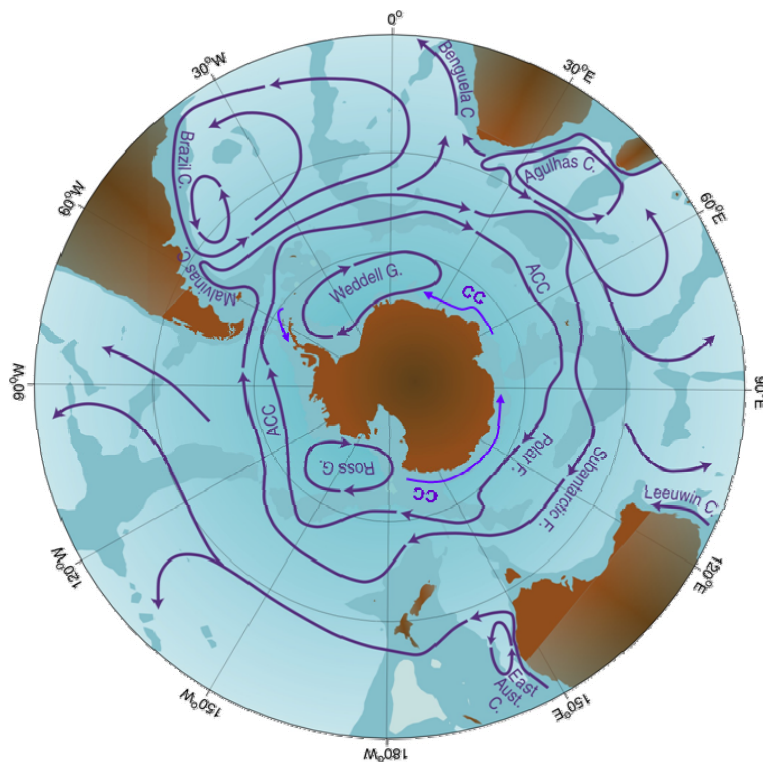
Southern Ocean ecosystems have been described by many authors (e.g. Karsten 1899; Peters 1929; Currie 1964; Holdgate 1967; Knox 1970, 1983; Hempel 1985, 2007). In the following I will mainly refer to Knox (2007) who provided a detailed review on the biology of the Southern Ocean. To understand zooplankton biology in the Southern Ocean, we have also to consider its geological evolution and the actual biogeography influenced by the main water masses of the current Southern Ocean.

The Southern Ocean or Antarctic Ocean is a large semi-enclosed system with a long evolutionary history. It covers the southern areas of the Atlantic, Indian and Pacific Ocean and encircles the Antarctic continent. In the Cretaceous period Antarctica together with South America, Africa, Arabia, New Zealand, Australia, India and Madagascar was part of the supercontinent Gondwana which was already located close to the South Pole. About 20 to 35 million years ago the circumpolar Southern Ocean evolved when Antarctica and South America separated, opening the Drake Passage. The separation of the continents finally allowed the formation of the Antarctic Circumpolar Current

# 1. GENERAL INTRODUCTION

(ACC) and the climatic and oceanographic isolation of Antarctica. During this period climate changed and caused an intense cooling of the southern hemisphere and the glaciation of Antarctica.

The main current of the Southern Ocean is the Antarctic Circumpolar Current (Fig. 1). This water mass flows continuously around the Antarctic continent in a clockwise direction driven by westerly winds. A westward surface current, known as the Antarctic Coastal Current (CC), is located in the vicinity of the Antarctic continent south of about 65°S (~68°-70°S at the prime meridian; Klatt et al. 2005). Both currents are characterized by eddies of variable size and duration, and are additionally shaped by large permanent cyclonic flowing gyres, the Ross Gyre and the Weddell Gyre. Due to the prevailing current system, most of the major taxonomic zooplankton groups occur circumpolar.



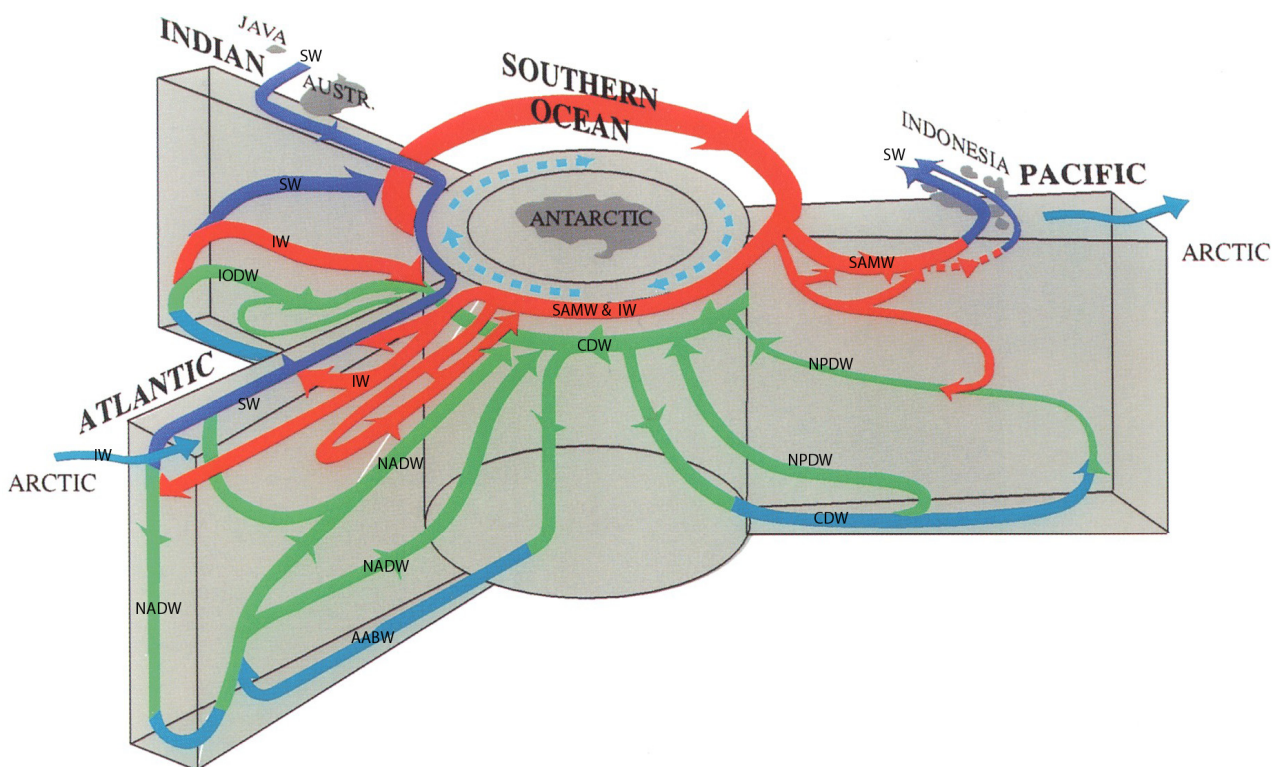
**Fig. 1:** The current system in the Southern Ocean (modified after Rintoul et al. 2001). ACC - Antarctic Circumpolar Current; C. - Current; F. - Front; G. - Gyre

The northern boundary of the Southern Ocean can be defined in different ways. The Antarctic treaty covers the area south of 60°S. The circumpolar frontal systems, however, constitute the natural boundaries to the adjacent oceans. The northernmost border is marked by the Subtropical Front (STF), followed by the Subantarctic Front (SAF) and the Antarctic Polar Front (APF, or Antarctic Convergence) to the south (Rintoul et al. 2001). The APF is the most significant of these fronts, as it is characterized by strong gradients in sea-surface temperature and distinct changes in salinity, phytoplankton abundance and zooplankton distribution. Cold, northward flowing waters from the Antarctic converge with warmer Subantarctic waters forming a hydrographical barrier. Considering the APF as the northern border, the Southern Ocean covers an

# 1. GENERAL INTRODUCTION

area of 38 million km<sup>2</sup> and fills a volume of 139 million km<sup>3</sup>. Consequently it represents 10.6% of the world oceans (Fahrbach 1995).

The formation of deep water masses in the Southern Ocean plays a key role in the water transport through the world's ocean. Cold water of high salinity originating from ice-shelf water forms the Antarctic Bottom Water (AABW) by sinking and moving northwards in all ocean basins (Fig. 2). As a countermove, warm Antarctic Circumpolar Deep Water (ACDW) flows southward where it upwells at the Antarctic Divergence. This high salinity water mass dominates the Southern Ocean in terms of volume. The somewhat less saline, cold Antarctic surface water (ASW) moves north to the APF, where it subducts under warmer Subantarctic Surface Water (SSW), and hence forms the Subantarctic Intermediate Water (SIW) (e.g. Olbers 2002).



**Fig. 2:** Schematic drawing of the global thermohaline circulation and the water masses (modified after Schmitz 1996). AABW, Antarctic Bottom Water; CDW, Circumpolar Deep Water; IODW, Indian Ocean Deep Water; IW, Intermediate Water; NADW, North Atlantic Deep Water; NPDW, North Pacific Deep Water; SAMW, Subantarctic Mediate Water; SW, Surface Water

Although the Southern Ocean has such a uniform current pattern, it can be divided into large-scale regions on the basis of a) physical parameters (Orsi et al. 1995; Longhurst 1998), b) ice and nutrient dynamics (Tréguer and Jacques 1992) or c) distribution of species (Ekman 1953; Dell 1972; Linse et al. 2006), especially of the benthic fauna. Recently, a new concept for the bioregionalisation of the Southern Ocean has been developed, including depth, sea surface temperature, silicate and nitrate as primary properties, sea ice

## 1. GENERAL INTRODUCTION

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concentration and chlorophyll *a* values as secondary datasets (Grant et al. 2006). The water masses defined on the basis of temperature and salinity data in the South Atlantic are in line with four zooplankton community groupings identified across the ACC to the northwest of South Georgia (Grant et al. 2006). This close physical and biological coupling consequently supports the conclusion that zooplankton community changes occur across frontal zones and in particular at the APF. However, the APF does not seem to represent a major biogeographic boundary for small copepods (Grant et al. 2006). The pattern of clusters in primary production and sea ice cover shown by the second order regionalisation seems to be consistent with the clusters in krill length distribution from the area between the Antarctic Peninsula to the South Sandwich Island. This approach of the bioregionalisation of the Southern Ocean is in its infancy. Additional datasets, particularly biological data, will be incorporated in future to produce a more profound concept of bioregionalisation for the Southern Ocean (Grant et al. 2006).

### 1.2 Geographical and vertical distribution of chaetognaths

Chaetognatha are assumed to be oceanic in origin (Pierrot-Bults and Van der Spoel 1979; Kapp 1993). Their dispersion possibly emanated from the shallow Pacific into the Indian and Atlantic Oceans, from tropical regions to higher latitudes and from epipelagic to mesopelagic layers with the bathypelagic realm the latest to be populated. Hence, bathypelagic plankton is believed to have originated from cold water organisms (Pierrot-Bults and Nair 1991). The oldest chaetognaths in terms of evolution would consequently be located in the tropical Pacific. Chaetognaths, however, may be older than present day oceans, so that this dispersion might be quite different (Kapp 1993).

Chaetognaths are common animals in all world oceans, inhabiting areas from surface water layers down to the deep-sea floor. More than 120 species are known and they are mainly pelagic. More than 39 species have been reported for the South Atlantic (0° to 60°S) and the number will probably still increase (Casanova 1999). *Bathyspadella*, *Heterokrohnia*, *Eukrohnia*, *Krohnitta*, *Pterosagitta* and *Sagitta* are the six pelagic chaetognath genera, the two first generally inhabiting depths below 1000 m (Alvariño 1964). The genus *Eukrohnia* is meso- and bathyplanktonic, except for *E. hamata* which is ubiquitous (see below), whereas *Pterosagitta* and *Krohnitta* occur in the upper ocean layers (Alvariño 1965). *Sagitta* is the most successful chaetognath genus. It is a genus rich in species and inhabits the greatest variety of environments. The genus *Spadella* is a benthic genus occurring in the world ocean. In the past 30 years further deep-living genera like *Archeterokrohnia*, *Xenokrohnia*, *Paraspadella* and *Hemispadella* were described (Casanova 1999).

Some species are restricted to one geographical region, whereas others have a wide range of distribution covering several oceanic regions. The latter species inhabit more or less the same depth range throughout all oceans (Alvariño 1964). Nevertheless, their distribution may be affected by local conditions. The chaetognath distribution patterns are influenced by water circulation, physiochemical and ecological factors (Pierrot-Bults and Nair 1991). The first parameter basically refers to the water masses described in the previous section. Further influencing factors are historical events like past water

## 1. GENERAL INTRODUCTION

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circulation patterns, the morphology of ocean basins and the evolutionary history of this animal group (Pierrot-Bults and Nair 1991).

The horizontal chaetognath distribution in the Southern Ocean is often related to water masses. The STF is considered as the surface hydrographic north-south boundary for the distribution of chaetognaths, followed in importance by the APF (David 1965). However, there is no evidence that the APF represents a major biogeographical boundary for the distribution of mesopelagic organisms (Atkinson and Sinclair 2000), as mentioned above. Species typically found in the Antarctic-Subantarctic region are *Eukrohnia bathyantartica*, *Sagitta gazellae*, *S. marri*, *S. planctonis* and *S. tasmanica* (Alvariño et al. 1983b). Moreover, the cosmopolitan species, *E. bathypelagica*, *E. fowleri*, *E. hamata*, *S. macrocephala* and *S. maxima* are usually observed in Antarctic-Subantarctic areas.

Water masses also affect the vertical distribution of chaetognaths. The water columns in the tropics and subtropics are usually strongly stratified in the upper regions in contrast to higher latitudes where a permanent surface stratification is missing (Pierrot-Bults and Nair 1991). Therefore there is often a weak division of epipelagic and mesopelagic fauna at higher latitudes and polar species have a wider vertical range in distribution. The cosmopolitan *E. hamata* is unique in this respect. *E. hamata* exhibits the tropical submergence, i.e. this species lives at meso- to bathypelagic depths in the tropics and prefers epipelagic layers in the polar regions (Thiel 1938; Alvariño 1964).

Physiochemical and ecological parameters may also play an important role for the vertical distribution of chaetognaths. These animals perform vertical migrations that may be triggered by, for example, light intensity conditions, prey availability, predator occurrence, breeding or seasonal migration patterns (e.g. Alvariño 1964; Pearre 1973, 1979). Competition between species may also influence vertical distribution patterns (David 1965). The species diversity of chaetognaths generally decreases from the epipelagic to the bathypelagic zone, with the epipelagic generally defined as the depth range between 0 and 200 m, the mesopelagic between 200 and 1000 m and the bathypelagic deeper than 1000 m (Pierrot-Bults and Nair 1991). Bathypelagic chaetognaths are suggested to have a wide distribution, but proof for this hypothesis is missing due to the scarcity of deep ocean samples. *E. bathyantartica*, *E. bathypelagica* and *Heterokrohnia mirabilis* are considered bathypelagic species with a global distribution, whereas other deep-living *Heterokrohnia* species, which were described from the North Atlantic and in the Antarctic during the recent decades, might represent provincialism (Pierrot-Bults and Nair 1991). However, Vinogradov (1970) reported that chaetognaths seem to be very rare below 4000 to 5000 m depth. Only isolated specimens were found down to 7000 m in the Kurile-Kamchatka Trench for example (Vinogradov 1970).

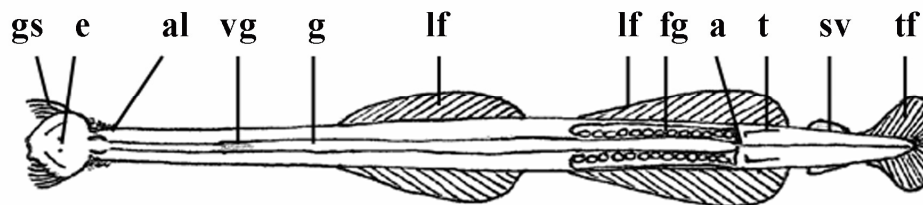
### 1.3 The biology of chaetognaths

The biology of chaetognaths has been intensively studied and described by several authors (see e.g. Alvariño 1965; Ghirardelli 1968; Bone et al. 1991). Here I will provide a general overview and refer to the relevant literature especially when describing the morphology and reproduction of chaetognaths.

## 1. GENERAL INTRODUCTION

### *Phylogeny*

The phylogenetic position of the chaetognaths within the Metazoa has remained obscure since its discovery. Chaetognatha have been linked to Nematoda, Annelida, Mollusca, Crustacea, Arachnoidea, Protocoelomata, Oligomera and Chordata in the past (Bone et al. 1991). Embryology and morphology, including the enterocoely and the posterior position of the blastopore for example, have traditionally allied them with deuterostomes. However, molecular analyses (e.g. Telford and Holland 1993; Wada and Satoh 1994; Halanych 1996) and genomic studies (e.g. Helfenbein et al. 2004; Papillon et al. 2004) did not support the inclusion of the chaetognaths within the deuterostomes. More recent molecular phylogenomic studies suggest them to be either sister to the Lophotrochozoa (Matus et al. 2006) or to all protostomes (Marlétaz et al. 2006), but final proof of their phylogenetic position is still missing.



**Fig. 3:** Schematic drawing of a chaetognath (*Sagitta*, modified after Kapp 1991a). a, anus; al, alveolar tissue; e, eye; fg, female gonad; g, gut; gs, grasping spines; lf, lateral fin; sv, seminal vesicle; t, testis; tf, tail fin; vg, ventral ganglion

### *Morphology*

Chaetognaths are commonly known as arrow worms due to their elongated body shape and high swimming velocity. The name chaetognath, however, refers to their large cephalic grasping spines (Fig. 3). Generally chaetognath lengths range between 2 and 120 mm. Most of these animals are transparent, some are translucent or have pigmented parts (blue, orange or red). Depending on the genus they possess one or two pairs of lateral fins and a tail fin, all more or less provided with rays. Their body can be divided into three parts: the head, the trunk and the tail. The head bears the grasping spines or hooks, one or two rows of teeth (anterior and posterior), the vestibular organs and a ventral mouth. Eyes are located on the dorsal side of the head, in most species consisting of a central pigment cell surrounded by photoreceptive cells. In a few species the eyes are ommatidia-like structures or completely missing, as is the case in some deep-living species. The head and the long muscular trunk are separated by a transverse septum. The gut, which is sometimes provided with a pair of anterior intestinal diverticula, extends through the trunk to the anus. The ventral anus lies anterior to a second transverse septum, which divides the trunk into an anterior part containing the female organs (ovary and seminal receptacle) and a posterior part with the male organs (testes and a pair of seminal vesicles). This posterior part of the trunk is usually called the tail. In many species an alveolar tissue (formerly called collarette), i.e. the epidermis is thickened and formed by vesicular cells, occupies the neck or occurs along the complete trunk or is concentrated in the region of the ventral ganglion for example. The ventral



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nervous ganglion lies under the epidermis in the anterior part of the trunk. Sensitive receptors can be located on the head, trunk, tail and even on fins of chaetognaths. The *corona ciliata*, a ciliary loop, occurs on the dorsal surface of the posterior part of the head and the anterior part of the trunk in many species (or only on the head or in the neck region).

### *Reproduction*

Chaetognaths are hermaphrodite with female and male reproductive organs spatially separated. The development of ovaries and testes starts at the same time, but ovaries mature later. The status of ontogenetic development, both of female and male gonads in an organism, is important for the classification of maturity stages for each species.

Although self-fertilization seems to be possible when protandry is not strongly developed, it is suggested that cross-fertilization is more common. However, this is a topic which has been widely discussed in the past (reviewed by Pearre 1991).

The testes are located posterior to the trunk-tail septum. These release clusters of spermatogonia which mature to spermatocytes and spermatozoa while floating in the tail cavity. Mature sperm exit via a ciliated *vas deferens* into seminal vesicles which protrude from the body wall in the caudal region. The seminal vesicles, especially when filled with mature sperm, have a species-specific size, shape and position, all of which are used for species' maturity stage identification.

The ovaries lie in the posterior part of the trunk between the intestine and the body wall. The size of the ovaries is species-specific and depends on the maturity stage. Oocytes fill the largest part of the ovaries. The seminal receptacles (or ovispermatiduct) run along the entire length of the ovaries (except in *Spadella*), opening dorsolaterally in external gonopores. They are probably linked to the oocytes by two suspension or accessory fertilization cells.

Once in contact with the body surface of another individual (in the case of cross-fertilization), the sperm move rapidly towards the opening of the ovary and into the seminal receptacle. The ova are probably fertilized via the accessory fertilization cells while they are still in the ovary. Alvarino (1990) stated however, that fecundation by the spermatozoa takes place during egg release, when the ova reach the vagina where the duct of the seminal receptacle opens. *Eukrohnia* species lay their eggs into incubatory pouches (= brood sacs or marsupial sacs; Alvarino 1990). In the benthic *Spadella*, clusters of 4 to 12 eggs are attached by an "elastic peduncle" to the grasses or seaweeds of the substratum (Ghirardelli 1968). Most of the *Sagitta* species release their eggs freely into the water column. Spawning as one single deposition of eggs is very unlikely (Pearre 1991). Species like *S. setosa* (Dallot 1968), *S. hispidata* (Reeve 1970a) and *S. crassa* (Nagasawa 1984) lay several batches of eggs; *Eukrohnia* species like *E. bathypelagica* may lay only a single batch (Terazaki and Miller 1982).

Chaetognaths have generally been considered to die after spawning (McLaren 1969). However, there are indications of at least two spawning cycles for several species, such as *S. enflata* (reviewed by Furnestin 1957) and *S. bedoti* (Nair 1974). Moreover, alive specimens of the genus *Eukrohnia* were found after egg release (Alvarino 1992).

## 1. GENERAL INTRODUCTION

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Chaetognaths' life cycles and generation lengths have been studied since years. Generation length is thought to be a function of temperature (Pearre 1991) and is decreasing from the poles towards the equator (e.g. Owre 1960; Alvarino 1965). The extent of breeding seasons, however, seems to increase from high to low latitudes (Alvarino 1990). Breeding seasons are affected by temperature, illumination and nutrition (Alvarino 1990). *S. elegans* (Kramp 1939) and *S. gazellae* (David 1955) are reported to breed once a year in the Arctic-Subarctic, and in Antarctic-Subantarctic waters respectively. Towards its southernmost distribution boundary in the temperate region, *S. elegans* has two to five broods per year, as supposed by Alvarino (1965). In tropical regions reproduction is continuous throughout the year (Alvarino 1990).

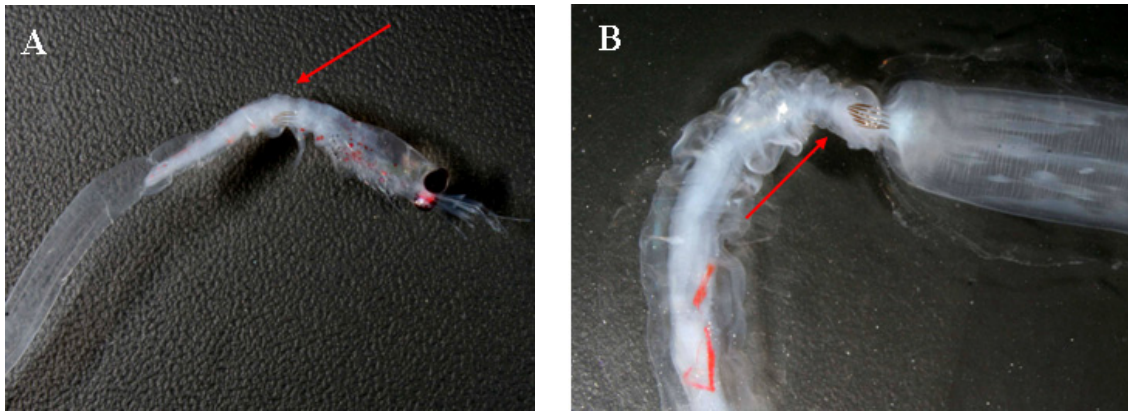
### *Food and feeding behavior*

Chaetognaths are carnivores, feeding on zooplankton of several trophic levels. They recognize prey by their distinctive locomotion (Feigenbaum and Reeve 1977). Sensing the very special turbulence field, chaetognaths can easily detect their preferred prey, copepods. When planktonic chaetognaths sense prey, they attack by flex and flick their tail (Feigenbaum 1991). They swim only short distances to capture and do not pursue their prey if it escapes (Feigenbaum 1991).

The chitinous hooks at the tip of the chaetognaths seize the prey while the mouth is projecting forward. Each hook helps pass the food into the mouth and down into the gut by individual movements. The injection of tetrodotoxin, a venom produced by bacteria within the chaetognaths that immobilizes the prey (Parry 1944; Feigenbaum and Maris 1984; Nagasawa 1985), eases the process of ingestion and enhances their feeding capabilities. The toxic and sticky secretions are produced in the upper part of the oesophagus and in the vestibular organs and pits (Parry 1944; Bieri et al. 1983; Thuesen and Bieri 1987; Thuesen et al. 1988; Kapp and Mathey 1989). The prey is probably paralyzed when the papillae of the vestibular ridge are pressed against the wounds caused by the grasping spines and teeth (Bieri et al. 1983). Neither the teeth nor the grasping spines directly inject the tetrodotoxin into the victim.

Rigid prey is usually eaten endwise (Feigenbaum 1991), as shown in Fig. 4A, whereas soft-bodied prey like chaetognaths may even be folded (Kuhlmann 1977). Chaetognaths feed on prey of various sizes, large enough to be captured with the hooks and small enough to pass through the mouth (Feigenbaum 1991). When ingested, the prey is covered by a peritrophic membrane which is secreted by the oesophagus' wall (Reeve et al. 1975). This membrane might protect the gut wall from potentially damaging prey fragments as it is also suggested for crustaceans (Shedder and Evans 1975). By peristaltic movements of the gut wall the prey passes to the posterior part of the gut (Parry 1944) and is defecated as a soft pellet.

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**Fig. 4:** Feeding by the chaetognath *Sagitta*. The red arrow points to the head of the feeding chaetognath. A: *Sagitta gazellae* feeding on *Thysanoessa* (Euphausiacea). B: Cannibalism within the genus *Sagitta*

The diet depends on the chaetognath size, as mentioned above, and therefore also on the age of the specimen and prey density in the guts may reflect the relative frequency of prey abundance (e.g. Pearre 1976; Sullivan 1980). Juvenile chaetognaths usually start to feed a few days after hatching (Feigenbaum 1991). Their diet probably consists mainly of copepod nauplii, complemented by tintinnids and small meroplankters when available (Reeve 1970b; Pearre 1981). In general chaetognaths eat copepodites and adult copepods, which are very abundant in the ecosystem. Appendicularians, cladocerans and euphausiids contribute to their diet too (Feigenbaum 1991). Cannibalism also occurs (Fig. 4B), but other chaetognaths represent a smaller part of their diet. However, their contribution in terms of weight may be significant (Feigenbaum 1991). They prey on both, their own and on other species. For large species, cannibalism may be necessary for covering their energetic demands (Pearre 1982), but at the same time it may be responsible for the high mortality observed in some populations (Szyper 1978; Øresland 1987).

## 2. AIMS AND OUTLINE OF THE THESIS

The importance of chaetognaths in the ecosystem of the Southern Ocean has been particularly studied in the last decades (e.g. Dilling and Alldrege 1993; Froneman and Pakhomov 1998; Giesecke et al. 2009) with special attention given to the abundant epipelagic species. Therefore the focus of this thesis is to study the distribution patterns and the biology of meso- and bathypelagic chaetognaths. The main emphasis concerns the deep-living species *Eukrohnia bathyantartica* and *E. bathypelagica* in the Southern Ocean.

The special aims of this thesis are:

- To examine species composition, density, distribution patterns (temporal and spatial) and population structure of meso- and bathypelagic chaetognaths in the Atlantic sector of the Southern Ocean.
- To investigate the biology of the deep-living chaetognaths especially in terms of reproduction, feeding, respiration and lipid metabolism during summer and winter.
- To estimate the role of the chaetognaths as predators on the mesopelagic zooplankton/copepod community and to evaluate their role in cycling of organic matter in the deep pelagic waters of the Southern Ocean.

The results of these investigations are presented and discussed in the following papers which are already published (publication I and II) or submitted (publication III and IV).

- I. Kruse S, Bathmann U, Brey T (2009) Meso- and bathypelagic distribution and abundance of chaetognaths in the Atlantic sector of the Southern Ocean. *Polar Biology* 32:1359-1376. doi:10.1007/s00300-009-0632-3
- II. Kruse S (2009) Population structure and reproduction of *Eukrohnia bathypelagica* and *Eukrohnia bathyantartica* in the Lazarev Sea, Southern Ocean. *Polar Biology* 32:1377-1387. doi:10.1007/s00300-009-0633-2
- III. Kruse S, Hagen W, Bathmann U (submitted to *Marine Biology*) Feeding ecology and energetics of the Antarctic chaetognaths *Eukrohnia hamata*, *E. bathypelagica* and *E. bathyantartica*
- IV. Kruse S, Brey T, Bathmann U (submitted to *Marine Ecology Progress Series*) The role of midwater chaetognaths in Southern Ocean pelagic energy flow

## 2. AIMS AND OUTLINE OF THE THESIS

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The basis of these studies are the results of two expeditions with RV “Polarstern” in the Atlantic sector of the Southern Ocean. In a first step, deep sampling in different water masses in summer and winter were performed to focus on identification of species composition and distribution patterns of the meso- and bathypelagic chaetognaths (**Publication I**). I investigated species abundance for different depth strata between 500 and 2000 m. To include juvenile and small chaetognaths, often disregarded in previous studies due to coarse mesh sizes, we used a fine meshed multinet (100 µm) in this study. The Polar Frontal Zone (PFZ), the Weddell Gyre (WG) and the Coastal Current (CC) were considered as different water masses where differences in distribution patterns were expected. The seasonal aspect was included to prove or disprove vertical migrations and to study the maturity stage composition. **Publication I** examines additionally the maturity stage and length frequency distribution of the two abundant species *Eukrohnia hamata* and *Sagitta marri*. **Publication II** is directly connected to this topic, but focuses on the maturity stage distribution and on reproduction details in the two deep-living species *E. bathypelagica* and *E. bathyantartica*. As these two species intensively reproduce during summer and winter, shown by the presence of marsupial sacs, they were treated in a separate publication. Studies on their life cycle in the Antarctic Ocean are especially scarce (Alvariño et al. 1983b).

**Publication III** is based on a combination of respiration experiments, conducted on board ship, with gut content and biochemical parameters of chaetognaths such as carbon and nitrogen, lipid as well as fatty acid composition, with all analyses performed later in the home laboratory. This publication closely examines the chaetognath species *E. hamata*, *E. bathypelagica* and *E. bathyantartica*. As gut content analyses generally give little information on the chaetognath diet and feeding history, due to few findings of prey remains in the guts (Hopkins 1985b, 1987; Øresland 1995), we additionally applied fatty acid analyses to investigate this aspect. Both methods gave indications of the diet composition. Measurements of species respiration rates replenished these results and species-specific lipid contents provided additional information on chaetognath energetics.

A more extensive step constitutes **publication IV**. Here we estimate the energy flow through meso- and bathypelagic chaetognaths. Based on the abundance data from **publication I** and carbon data (partially in **publication III**) we calculated the average chaetognath biomass. We further combine gathered respiration data with corresponding literature information for chaetognaths from different marine environments to formulate a new chaetognath respiration model. Thereafter we calculated respiration rates in a second step for the different depth intervals and the two main seasons (summer, winter) in the Southern Ocean. From these results and from published relationships between respiration, production and consumption in chaetognaths we estimated chaetognath carbon consumption and the primary production required to fuel this carbon uptake via copepods. These calculations provided first rough estimates of the predation impact of meso- and bathypelagic chaetognaths. We compared these estimates to existing assumptions on predation pressure on the copepod community.

All four publications combined contribute to the overall picture of the “midwater” chaetognath community in the Southern Ocean. These publications are summarized in the final synoptic discussion. Here I synthesize the main

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results to discuss future aspects of chaetognath and mesopelagic plankton research.

### **3. PUBLICATION I**

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

Svenja Kruse\*<sup>1)</sup>, Ulrich Bathmann\*, Thomas Brey\*

\*

Alfred Wegener Institute for Polar and Marine Research,  
Am Handelshafen 12,  
D-27570 Bremerhaven, Germany

1) Contact information:

E-mail: [Svenja.Kruse@awi.de](mailto:Svenja.Kruse@awi.de)

Phone: + 49-471-48311688

Fax: + 49-471-48311149

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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. 1000 m<sup>-3</sup>) and *Sagitta marri* (mean 51 ind. 1000 m<sup>-3</sup>) were dominant, complemented by *E. bathypelagica* (mean 19 ind. 1000 m<sup>-3</sup>) and *E. bathyantartica* (mean 19 ind. 1000 m<sup>-3</sup>) below 1000 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 and particularly the dominating *Eukrohnia hamata* Möbius, 1875 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 20<sup>th</sup> century (e.g. by Ritter-Záhony 1911), already more than one hundred 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 1000 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 1000 m of David (1958a, 1965) and Alvariño 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 (four depth strata) on abundance and species composition of meso- and bathypelagic chaetognaths in the Atlantic sector of the Southern Ocean. Furthermore, the two expeditions 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 m<sup>2</sup>) was equipped with five nets with 100 µm mesh size and sampled the following standard depth intervals: 2000-1500 m, 1500-1000 m, 1000-750 m, 750-500 m, 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 3000 m, at 65°S 3°E to 1250 m depth) and at one during ANT 24-2 (at 70°S 3°W to 1500 m depth). The winter station around 66°S 0°E was a five 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 (500-1000 m) and bathypelagic (below 1000 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*

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*hamata* and *Sagitta marri* David, 1956, were classified into five maturity stages according to Kramp (1939) and David (1955) (Table 1).

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* Alvariño, 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 Alvariño 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 1000 m<sup>3</sup>. For the five days winter station the geographical and vertical abundance data are averaged over all eight sub-stations.

**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

#### Statistical analyses

To evaluate differences in species composition, we applied a cluster analysis (e.g. Everitt et al. 2001) to the species x abundance matrix (9 species x 170 samples, see results). The resulting cluster identities were taken as representative for distinct species assemblages. Nominal logistic regression

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(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 analyzed abundance data at the class 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 analyzed 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 & season & depth & water mass x depth & season x depth) with subsequent *post-hoc* test on differences between means ( $\alpha = 0.05$ , Sokal and Rohlf 1981). The interaction term water mass x season was not tested, as there are no winter samples from the PFZ.

Additionally, a full factorial two-way ANOVA (length versus maturity stage & season & maturity stage x season) was applied to analyze 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 analyzed by means of a Kolmogorow-Smirnow test in both species.

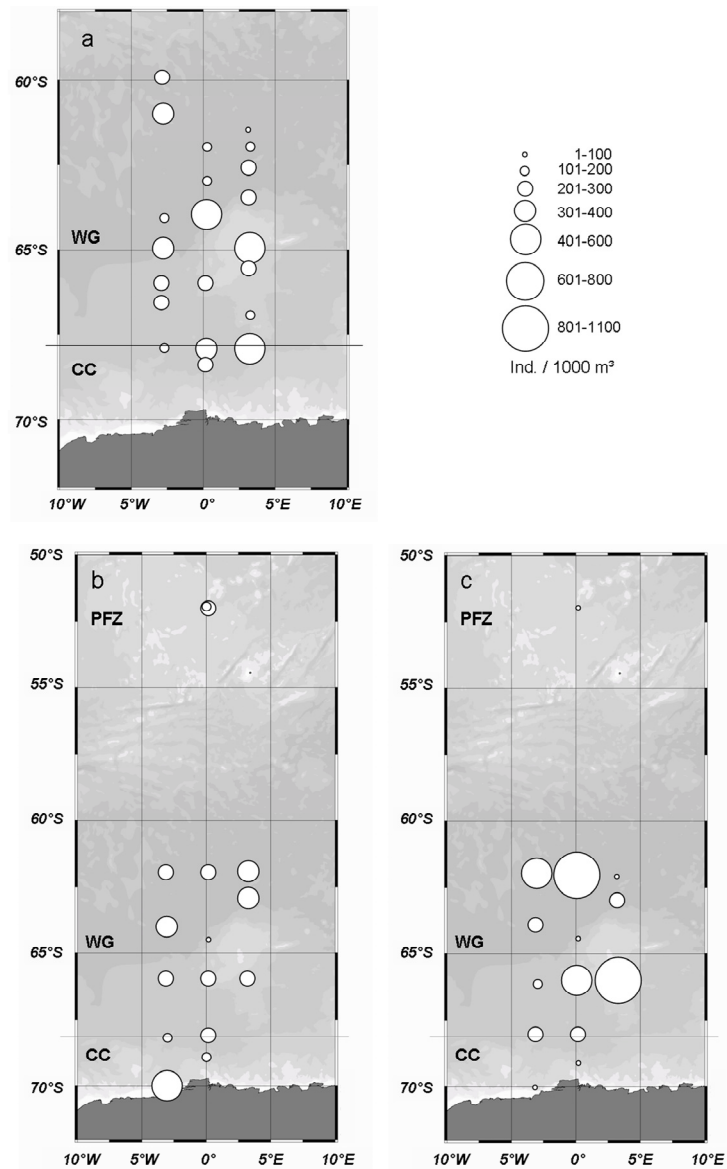
All statistical analyses were performed with the software package JMP (SAS Inc).

## Results

### **Influence of formaldehyde on chaetognath body length**

Due to the preservation of the samples with formaldehyde (4% final concentration, buffered with hexamine, four 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 *Eukrohnia 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 *Sagitta marri*. The chaetognaths shrunk particularly in the first days and weeks. However, they kept shrinking very slowly even after four months of formaldehyde preservation (personal observation).

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**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)

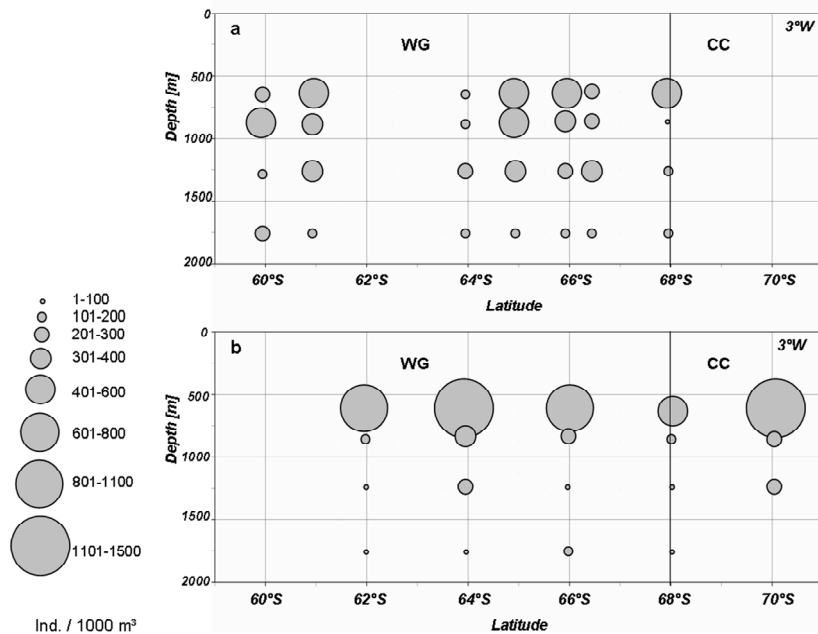
### Geographical and vertical chaetognath distribution

We were able to identify ten different species from three genera in our samples: *Eukrohnia hamata*, *E. bathypelagica*, *E. bathyantartica*, *E. macroneura* Casanova, 1986, *Heterokrohnia fragilis* Kapp and Hagen, 1985, *H. mirabilis* Ritter-Záhony, 1911, *Sagitta 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 2a, b, c).

*Eukrohnia* juveniles were very frequent in summer, and for a better comparison of seasons they were excluded from the Figures 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.

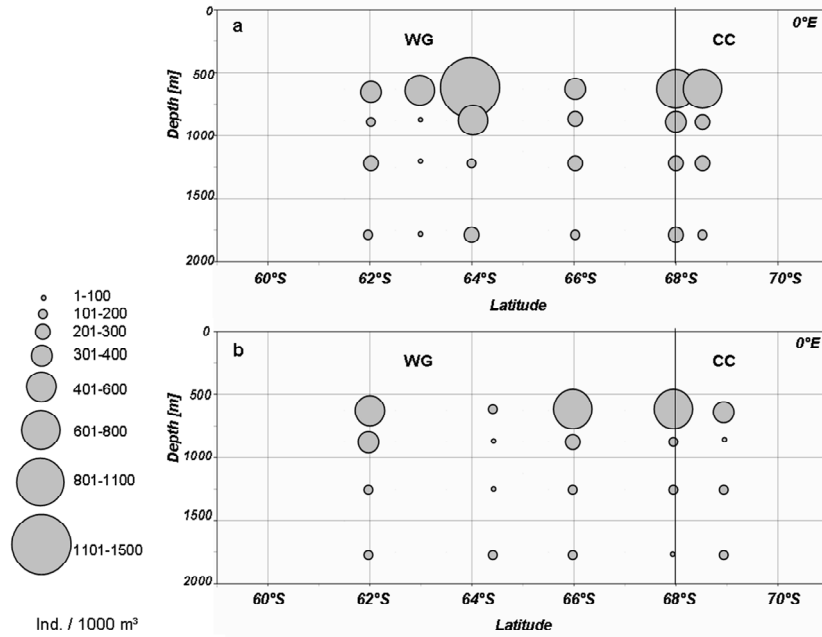
The mean chaetognath abundance of the 500 to 2000 m depth stratum ranged from 58 ind. 1000 m<sup>-3</sup> (61°30'S 3°E) to 443 ind. 1000 m<sup>-3</sup> (65°S 3°E, Fig. 1a) in winter, and from 91 ind. 1000 m<sup>-3</sup> (64°30'S 0°E) to 508 ind. 1000 m<sup>-3</sup> (70°S 3°W) in summer (without *Eukrohnia* juveniles; Fig. 1b). Juvenile *Eukrohnia* ranged from 2 ind. 1000 m<sup>-3</sup> (69°S 0°E) to 880 ind. 1000 m<sup>-3</sup> (66°S 3°E, 62°S 0°E, Fig. 1c) in summer.

Regarding water depth, highest abundances were encountered between 500 and 1000 m in winter (Figs. 2a, 3a, 4a), attaining values up to 1248 ind. 1000 m<sup>-3</sup> (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 1470 ind. 1000 m<sup>-3</sup> (63°S 3°E, Fig. 4b). *Eukrohnia* juveniles did rarely occur deeper than 1500 m and distinctly preferred the 500 to 1000 m depth range in summer (Table 2).

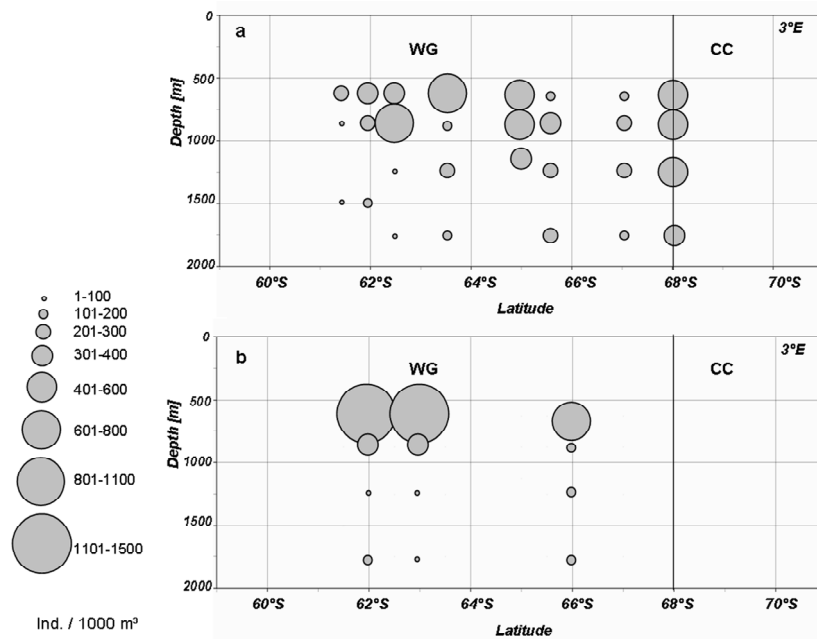


**Fig. 2:** Vertical distribution and abundance of chaetognaths (without juveniles) along the 3°W transect during winter (a) and summer (b). WG: Weddell Gyre, CC: Coastal Current. Stations at and south of 68°S are considered within the CC (vertical line)

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**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)



**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)

#### **Chaetognath species composition**

The cluster analysis of the 9 species x 170 samples matrix (we excluded *Heterokrohnia mirabilis*, because it occurred in one of the two exceptional samples collected below 2000 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 *Eukrohnia 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 (Table 2). 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.

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**Table 2:** Chaetognath species abundance (individuals 1000 m<sup>-3</sup>) and relative composition for each depth interval, presented for the summer and winter situation in the three water masses (a: CC: Coastal Current, b: WG: Weddell Gyre, c: PFZ: Polar Frontal Zone). *n* = number of investigated stations

**a**

CC	Summer n=4											
	500-750 m			750-1000 m			1000-1500 m			1500-2000 m		
	mean	± sd	%	mean	± sd	%	mean	± sd	%	mean	± sd	%
<i>Eukrohnia bathyantartica</i>	0	0	0	4	7	1.0	41	17	22.7	49	24	46.6
<i>Eukrohnia bathypelagica</i>	21	27	1.8	8	16	2.4	13	4	7.5	27	17	25.2
<i>Eukrohnia hamata</i>	425	258	35.2	78	22	23.1	10	13	5.8	15	13	14.4
<i>Eukrohnia macroneura</i>	0	0	0	19	15	5.8	16	12	9.1	0	0	0
<i>Eukrohnia</i> spp.	48	26	4.0	8	17	2.5	9	11	5.1	10	19	9.0
juvenile <i>Eukrohnia</i>	539	599	44.7	168	308	49.7	33	15	18.6	0	0	0
<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	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
<i>Sagitta maxima</i>	0	0	0	0	0	0	0	0	0	3	4	2.4
<i>Sagitta</i> spp.	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
unidentified	0	0	0	0	0	0	0	0	0	0	0	0

CC	Winter n=4											
	500-750 m			750-1000 m			1000-1500 m			1500-2000 m		
	mean	± sd	%	mean	± sd	%	mean	± sd	%	mean	± sd	%
<i>Eukrohnia bathyantartica</i>	28	38	5.2	8	9	3.1	30	14	11.7	56	35	27.2
<i>Eukrohnia bathypelagica</i>	12	24	2.2	4	8	1.6	30	14	11.7	24	11	11.6
<i>Eukrohnia hamata</i>	340	24	62.5	148	98	57.8	120	63	46.9	84	73	40.8
<i>Eukrohnia macroneura</i>	0	0	0	12	24	4.7	4	8	1.6	0	0	0
<i>Eukrohnia</i> spp.	4	8	0.7	36	62	14.0	42	43	16.4	2	4	1.0
juvenile <i>Eukrohnia</i>	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
<i>Heterokrohnia mirabilis</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sagitta gazellae</i>	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
<i>Sagitta marri</i>	160	41	29.4	40	31	15.6	26	20	10.1	36	30	17.5
<i>Sagitta maxima</i>	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
juvenile chaetognaths	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



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**Table 2** (continued)

**b**

WG	Summer n=9											
	500-750 m			750-1000 m			1000-1500 m			1500-2000 m		
	mean	± sd	%	mean	± sd	%	mean	± sd	%	mean	± sd	%
<i>E. bathyantarctica</i>	12	30	0.5	9	18	0.8	47	24	33.7	40	19	34.0
<i>E. bathypelagica</i>	42	31	1.9	18	20	1.5	16	12	11.4	33	17	27.9
<i>E. hamata</i>	474	242	21.2	95	61	8.0	17	19	11.9	13	15	11.3
<i>E. macroneura</i>	0	0	0	15	22	1.2	4	6	2.6	0	0	0
<i>Eukrohnia</i> spp.	125	103	5.6	7	12	0.6	15	15	10.7	10	11	8.9
juvenile <i>Eukrohnia</i>	1330	1363	59.3	920	923	77.7	25	32	17.4	1	3	0.8
<i>H. fragilis</i>	0	0	0	0	0	0	0	0	0	6	8	5.2
<i>H. mirabilis</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. gazellae</i>	7	11	0.3	2	5	0.1	2	6	1.3	4	6	3.0
<i>S. macrocephala</i>	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
<i>S. maxima</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sagitta</i> spp.	0	0	0	2	5	0.2	1	3	0.6	2	4	1.5
juvenile chaetognaths	0	0	0	7	16	0.6	6	12	4.0	0	0	0
unidentified	0	0	0	4	11	0.3	0	0	0	5	16	4.4

WG	Winter n=24											
	500-750 m			750-1000 m			1000-1500 m			1500-2000 m		
	mean	± sd	%	mean	± sd	%	mean	± sd	%	mean	± sd	%
<i>E. bathyantarctica</i>	2	7	0.5	4	14	1.3	12	14	5.6	46	34	31.3
<i>E. bathypelagica</i>	11	31	2.6	8	16	2.5	26	19	12.0	29	23	19.7
<i>E. hamata</i>	278	162	67.1	146	118	46.1	87	62	39.9	48	40	32.5
<i>E. macroneura</i>	0	0	0	3	11	1.1	2	3	0.8	0.3	2	0.2
<i>Eukrohnia</i> spp.	17	30	4.2	23	30	7.2	10	11	4.4	3	7	2.3
juvenile <i>Eukrohnia</i>	0	0	0	0.7	3	0.2	5	12	2.1	3	15	2.4
<i>H. fragilis</i>	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
<i>S. gazellae</i>	9	15	2.2	1	5	0.4	2	4	0.8	1	5	0.9
<i>S. macrocephala</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. marri</i>	96	88	23.2	130	89	41.0	74	71	33.8	15	23	10.0
<i>S. maxima</i>	0.7	3	0.2	0.7	3	0.2	0.3	2	0.1	0.3	0.2	0.2
<i>Sagitta</i> spp.	0	0	0	0	0	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	1	4	0.5	1	3	0.5

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**Table 2** (continued)

**b** (continued)

WG	Winter n=2		
	2000-3000 m		
	mean	± sd	%
<i>E. bathyantartica</i>	18	8	56.25
<i>E. bathypelagica</i>	6	3	18.75
<i>E. hamata</i>	2	3	6.25
<i>E. macroneura</i>	0	0	0
<i>Eukrohnia</i> spp.	2	3	6.25
juvenile <i>Eukrohnia</i>	0	0	0
<i>H. fragilis</i>	0	0	0
<i>H. mirabilis</i>	2	3	6.25
<i>S. gazellae</i>	0	0	0
<i>S. macrocephala</i>	0	0	0
<i>S. marri</i>	2	3	6.25
<i>S. maxima</i>	0	0	0
<i>Sagitta</i> spp.	0	0	0
juvenile chaetognaths	0	0	0
unidentified	0	0	0

**C**

PFZ	Summer n=2											
	500-750 m			750-1000 m			1000-1500 m			1500-2000 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

#### **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 *Eukrohnia bathypelagica* was significantly higher in PFZ (Polar Frontal Zone) than in WG (Weddell Gyre) and CC (Coastal Current, Table 3a). 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 3a). *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 1000-1500 m stratum in winter (74 ind. 1000 m<sup>-3</sup> in WG, Table 2b) 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. *Eukrohnia hamata*, the dominant species, was significantly more abundant in the 500 to 750 m depth range than at greater depths (Table 3a), attaining maximum summer abundances of 425 and 474 ind. 1000 m<sup>-3</sup> in the CC and WG respectively. *Sagitta marri*, which was second in abundance, preferred a wider depth range, 500 and 1000 m, with a maximum of 252 ind. 1000 m<sup>-3</sup> in the WG in summer (500-750 m, Table 2b). *Eukrohnia bathypelagica* and *E. bathyantartica* showed the opposite abundance pattern, as they preferred layers below 1000 m (Table 3a). They reached highest numbers of 89 ind. 1000 m<sup>-3</sup> (summer, PFZ, 1000-1500 m, Table 2c) and 56 ind. 1000 m<sup>-3</sup> (winter, CC, 1500-2000 m, Table 2a), respectively. *Eukrohnia macroneura* differed from all other species, as it was most abundant between 750 and 1500 m depth (maximum of 28 ind. 1000 m<sup>-3</sup>, summer, PFZ, Table 2c). Although juveniles of the genus *Eukrohnia* could not be subjected to sound statistical analyses, their centre of abundance was observed between 500 and 1000 m, with values up to 1330 ind. 1000 m<sup>-3</sup> in the WG (500-750 m, Table 2a), then representing 59.3% of total chaetognath abundance.

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**Table 3:** Effects of water mass WM (PFZ: Polar Frontal Zone, WG: Weddell Gyre, CC: Coastal Current), season (S: summer, W: winter) and depth (1: 2000-1500 m, 2: 1500-1000 m, 3: 1000-750 m, 4: 750-500 m) on chaetognath abundance (a) and maturity stage distribution (mean maturity stage per station and depth interval; b see following page). Full factorial (except WM x season) ANOVA with subsequent Tukey HSD *post-hoc* test on differences between means ( $\alpha = 0.05$ ).

ns: no significant effect, letters (A, B...) indicate groups that differ significantly, the alphabetical order indicates decreasing abundance/mean maturity stage. The interaction term WM x 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

**a**

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

Abundance	Season x depth							
	W 1	W 2	W 3	W 4	S 1	S 2	S 3	S 4
Class Sagittoidea	B	B	C	B	C	C	A	A
Genus <i>Eukrohnia</i>	C	C	C	C	C	C	B	A
Genus <i>Sagitta</i>	B	B	A	B	C	B	A	A
<i>E. bathyantartica</i>	C	C	B	B	C	C	B	A
<i>E. bathypelagica</i>	A	A	C	C	A	A	C	A
<i>E. hamata</i>	C	B	B	A	D	D	B	A
<i>E. macroneura</i>	C	C					C	
<i>S. marri</i>	B	B	B	B	B	A	A	B
	C	B	A	A	C	C	B	A

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**Table 3** (continued)

**b**

Mean stage	Water mass			Season		Depth			
	PFZ	WG	CC	W	S	1	2	3	4
<i>E. hamata</i>	A	B	A B	A	B	A	A	A	B
<i>S. marri</i>	A	B	B	B	A	A	A B	C	B C

Mean stage	Season x depth							
	W 1	W 2	W 3	W 4	S 1	S 2	S 3	S 4
<i>E. hamata</i>	A	A B	B	B	B C	A B	A B	C
<i>S. marri</i>	B	B	B	B	A	A B	B	B

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 x depth interaction term of the ANOVA (Table 3a). In contrast, *E. bathypelagica* exhibited a more distinct depth gradient in winter, with a clear preference for the 1000 to 2000 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. *Sagitta macrocephala* was only captured in summer in the PFZ (8 ind. 1000 m<sup>-3</sup> in 750-1000 m, Table 2c). *Sagitta maxima* was primarily found in the PFZ as well, where this species was encountered between 500 and 1500 m in summer (8 ind. 1000 m<sup>-3</sup>, Table 2c). Two species of *Heterokrohnia* were found below 1500 m in the WG (Table 2b). A total number of 7 individuals of *H. fragilis* (7 to 10 mm length) were caught in summer, *H. mirabilis* occurred exclusively between 2000 and 3000 m in winter and with 2 ind. 1000 m<sup>-3</sup> (= 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 *Eukrohnia hamata* and *Sagitta marri***

ANOVA of mean maturity stage showed a significant effect of all parameters investigated (Table 3b). In both species mean maturity stage was higher in the PFZ than in the WG. Season affected *Eukrohnia hamata* and *Sagitta 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 1500-2000 m stratum compared to the 750-1000 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 *Eukrohnia hamata* and *Sagitta 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 stage 1 and 2 individuals (Fig. 5). *E. hamata* had a maximum length of 29 mm in summer and 32 mm in winter, respectively (Table 4). 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.

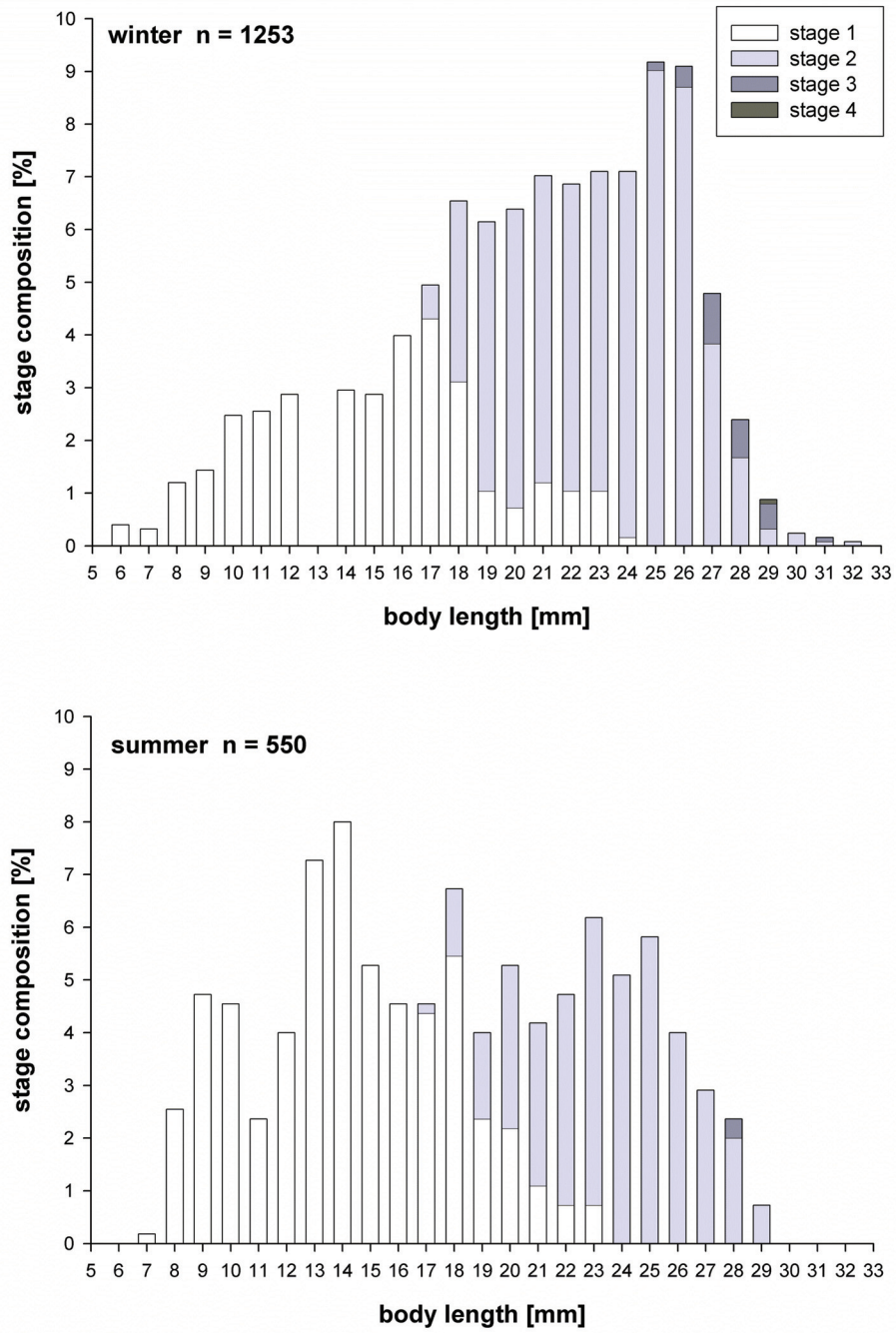
The shape of the length-frequency distribution differed significantly between summer and winter (Kolmogorow-Smirnow test,  $P < 0.005$ ). Apparently there was a higher proportion of large animals (>20 mm) present in winter. This coincides with a significantly higher mean maturity stage in winter (see above). Including the unidentified *Eukrohnia* individuals would slightly increase the stage 1 individuals (especially below 10 mm length).

##### *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 5). The stage-specific mean lengths differed seasonally only between stage 1 specimens. In the 500 to 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:  $r = 0.801$ ,  $P < 0.001$ ).

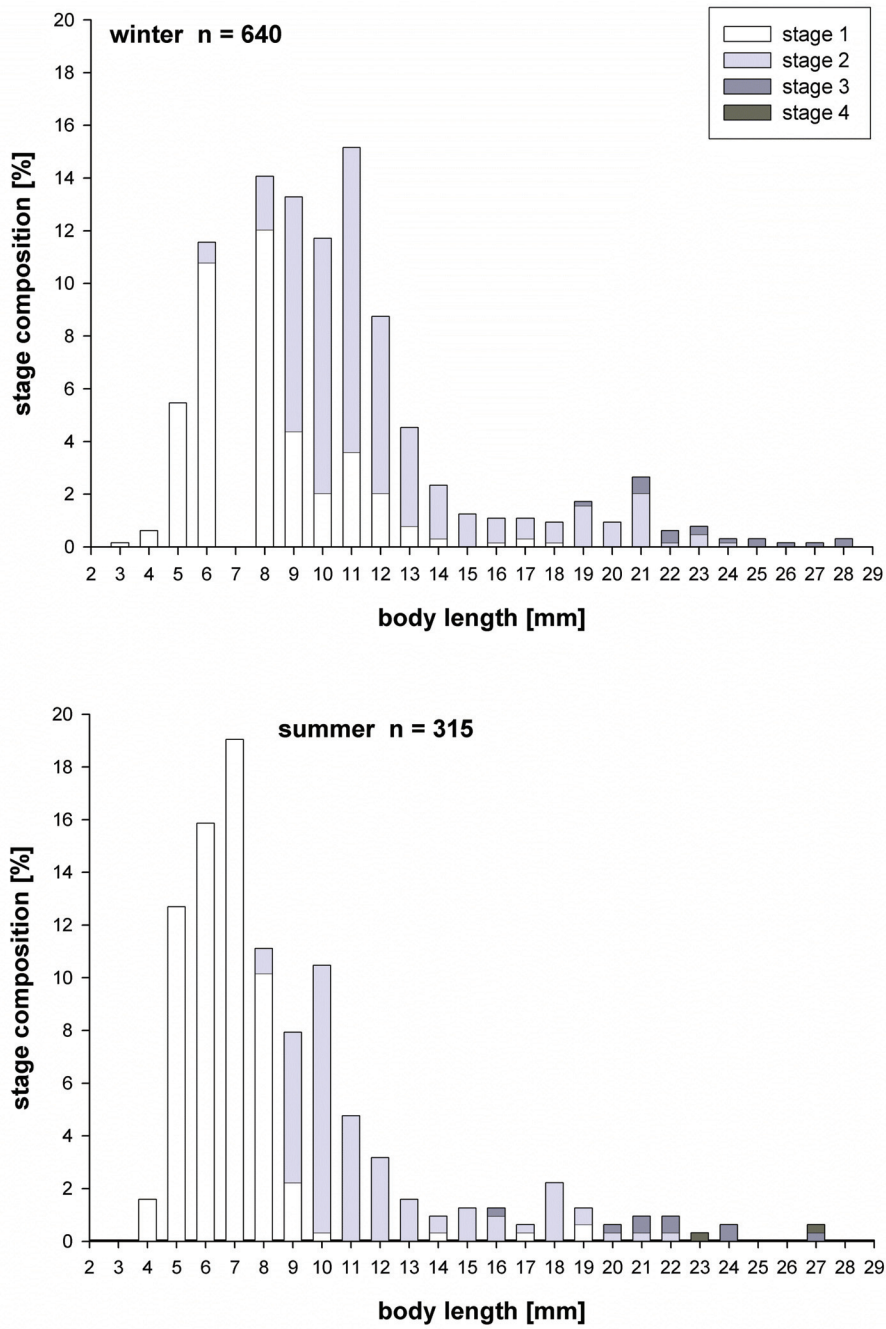
The population size-frequency structure (Fig. 6) did not differ significantly between winter and summer (Kolmogorow-Smirnow test,  $P > 0.1$ ). As a result of longer specimens (see above) the structure for the winter situation was slightly shifted towards greater lengths with highest values between 8 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.

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

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**Fig. 6:** Length-frequency and corresponding maturity stage distribution of *Sagitta marri* in winter and summer.  $n$  = number of investigated individuals



**Table 4:** Length-frequency distribution for *Eukrohnia hamata* in the different depth intervals for winter and summer. *n* = number of investigated individuals

<b>Winter</b>		
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	
500-750	490	5 4 5 5 8 14 11 15 14 14 24 28 44 32 42 38 38 32 23 35 36 17 8 2 1
750-1000	257	7 7 8 8 11 4 7 9 14 9 15 13 20 18 23 18 26 24 11 4 1
1000-1500	335	2 2 9 10 6 13 11 12 13 19 14 14 22 17 26 37 37 35 21 9 4 2
1500-2000	171	1 1 1 3 4 6 4 5 7 10 16 11 8 13 8 11 17 19 11 9 5 1 1
<b>Summer</b>		
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	
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
750-1000	83	3 3 3 3 4 6 3 3 7 8 7 14 9 3 6 1
1000-1500	32	1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 5 4 6 5 1
1500-2000	25	1 1 3 1 1 3 1 1 1 1 1 1 1 1 1 1 1 1 3 2 1 2

**Table 5:** Length-frequency distribution for *Sagitta marri* in the different depth intervals for winter and summer. *n* = number of investigated individuals

<b>Winter</b>																												
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	
500-750	167	1	4	4	8	12	24	16	34	20	12	1	5	5	3	2	6	2	6	1	3							
750-1000	183	1	17	15	29	29	18	30	17	8	1	1	1	1	1	1	2	2	6	2	2							
1000-1500	232	2	12	46	40	27	32	24	16	7	11	1	1	1	1	2	1	3	1	1	1	1	1	1	1	1	2	
1500-2000	58	2	5	9	5	9	9	3	2	2	2	2	2	3	2	1	1	2	1	2	1							
<b>Summer</b>																												
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	
500-750	201	5	29	31	34	23	17	22	9	5	4	2	3	4	2	3	4	1	2	1								
750-1000	75	9	15	18	7	6	6	5	2	1		1			1	1	1	1	1	1	1	1	1					
1000-1500	35	2	4	8	5	2	5	1	3	1			1		1	1	1										1	
1500-2000	4																2										1	

## Discussion

Of the ten species found during this investigation, *Eukrohnia hamata*, *Sagitta 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  $\mu\text{m}$  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 five 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 solely 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 (Table 2). At this depth a tongue of warm (about 2°C) and saline (>34.7) water stretches from Subantarctic into polar regions (Schröder and Fahrback 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 *Eukrohnia 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 bathypelagial of the Antarctic Convergence, however, these differences in zooplankton density are probably not detectable any more.

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#### *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 1000 m. It showed a significant decrease in abundance with depth, a pattern already found in previous studies (e.g. Alvariño et al. 1983a,b). *Eukrohnia bathypelagica* and *E. bathyantartica* coexist 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 1000 m in Antarctic waters.

*Eukrohnia bathypelagica* preferred the 1000 to 2000 m depth range and reached average numbers of up to 33 ind. 1000 m<sup>-3</sup> in summer in the WG (1500-2000 m) and 89 ind. 1000 m<sup>-3</sup> in the PFZ (1000-1500 m). So far, only Alvariño 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* ( $\leq 10$  ind. 1000 m<sup>-3</sup>) in the meso- and bathypelagic 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 Alvariño et al. (1983a) excluded the Weddell Sea, but data for the South Pacific showed abundances of more than 100 ind. 1000 m<sup>-3</sup> below 1000 m north of 60°S. To the south this species always occurred with less than 100, in some areas dropped even below 10 ind. 1000 m<sup>-3</sup> in the meso- and bathypelagic zone. We note that Alvariño et al. (1983a) included the 200-500 m range in 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 (>1000 m, Table 3a), in the CC and PFZ it was even completely absent above 750 m during summer (Table 2). Maximum abundance of maturing specimens was <60 ind. 1000 m<sup>-3</sup>, but total abundance below 1000 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 1500 m and 1000 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

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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. *Eukrohnia macroneura* preferred the depth range between 750 and 1500 m. Its vertical distribution overlapped with the one of *E. bathyantartica*, but it was distinctly less abundant.

*Sagitta marri* and *S. gazellae* are the only endemics from the Antarctic (Pierrot-Bults and Nair 1991). *Sagitta marri* was the second most abundant chaetognath species in our study (Table 2). It occurred preferentially between 500 and 1000 m (Table 3a), with a maximum of 252 ind. 1000 m<sup>-3</sup> (500-750 m) in the WG in summer. Both Hagen (1985) and Alvarino et al. (1983a) reported similar vertical patterns with maxima within the 250 to 735 m and the 200 to 1000 m depth range, respectively. In the mesopelagic layer, Alvarino et al. (1983a) found summer abundances of mostly up to 100, occasionally up to 1000 ind. 1000 m<sup>-3</sup>. Interestingly, they observed comparable numbers in the bathypelagic realm, which, however, declined sharply towards south to numbers <10 ind. 1000 m<sup>-3</sup>.

*Sagitta gazellae* was only found in very low numbers (<10 ind. 1000 m<sup>-3</sup>) 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 *Eukrohnia hamata*, although, it may occur down to 3000 m, particularly stages of higher maturity (David 1955). Our abundance data are even below those reported by Alvarino et al. (1983a), below 10 ind. 1000 m<sup>-3</sup> compared to up to 100 ind. 1000 m<sup>-3</sup> 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 ind. 1000 m<sup>-3</sup>) 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 2000 m) and the very rare *H. mirabilis* (below 2000 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 (Alvarino 1964). Highest numbers are found in

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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 *Eukrohnia hamata*, *Sagitta 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 *Eukrohnia hamata* and suggested for *Sagitta 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, Alvarino et al. 1983a). For *E. hamata*, Alvarino et al. (1983a) reported high numbers during summer and fall in the epipelagic layer, whereas large numbers between 200 and 1000 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 Alvarino 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 1000 – 1500 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 *Eukrohnia 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; Alvarino 1964; Sullivan 1980; Hagen 1985; Øresland 1995; Timofeev 1998). Juveniles of *Eukrohnia* were concentrated between 500 and 1000 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

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maturity stage in *Eukrohnia hamata* and *Sagitta marri*) and seem to invest less in growth and more in the development of the reproductive organs (observed for *Sagitta gazellae* by David 1955). The migration of adult specimens to greater depth might be common in chaetognaths. Alvaríño (1964) hypothesized that this is a 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 *Eukrohnia 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 *Eukrohnia 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 2000 m. This is the case in the Arctic Basin, where Dawson (1968) reported mature *E. hamata* descending deeper than 3000 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 to 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 *Eukrohnia hamata* during both seasons indicates a rather complex life cycle. It might be longer than one year and include several reproductive periods. Thus, our observations seem to support the hypothesis of a two-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 *Sagitta marri* are lacking so far. Nothing is known except that this species matures in the 750 to 1000 m depth range (David 1965). Vertical segregation of maturity stages in this species was not as pronounced as in *Eukrohnia hamata*. Stage 1 and 2 individuals inhabited almost the complete sampling range. More stage 1 individuals occurred at depth in

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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 1500 and 2000 m depth, this is only based on few stage 3 and 4 individuals.

From the two seasons studied it can be suggested that *Sagitta 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 also 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 *Eukrohnia 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 1500 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 *Sagitta 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 with 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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##### **Population structure and reproduction of *Eukrohnia bathypelagica* and *Eukrohnia bathyantartica* in the Lazarev Sea, Southern Ocean**

Svenja Kruse\*

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Alfred Wegener Institute for Polar and Marine Research,  
Am Handelshafen 12,  
D-27570 Bremerhaven, Germany  
E-mail: [Svenja.Kruse@awi.de](mailto:Svenja.Kruse@awi.de)  
Phone: + 49-471-48311688  
Fax: + 49-471-48311149

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### Abstract

In the Lazarev Sea, Southern Ocean, I studied the population structure and reproduction of *Eukrohnia bathypelagica* and *E. bathyantartica* during winter and summer. A lack of unimodality in their population structures indicated at least two generations building one population and a life cycle longer than one year. During both seasons all maturity stages were present, therefore continuous reproduction is very probable. Extensive breeding seasons with several releases of eggs by one generation are assumed, as adults with empty marsupial sacs continue to build new ova. *E. bathypelagica* carried between 86 and 128 eggs in both marsupial sacs. *E. bathyantartica* had only between 8 and 13 eggs. Although self-fertilization seemed at least to be possible in *E. bathyantartica*, cross-fertilization appears to be more common in both species, as most individuals developed testes and ovaries consecutively.

**Keywords:** Chaetognatha, Antarctica, Bathypelagial, Reproduction, Life cycle, Breeding

### Introduction

Chaetognaths have a world-wide distribution and inhabit a great variety of bathymetric levels. These carnivorous animals are hermaphroditic with male and female gonads spatially separated in the body. The testes are located in the tail and the seminal vesicles on the tail. The ovaries are situated on each side in the posterior part of the trunk. Protandry is common among chaetognaths, as male gonads usually mature earlier than female gonads. Instead of releasing the fertilized eggs directly into the water column, as reported for most *Sagitta* species (Pearre 1991), *Eukrohnia* species keep them in marsupial or brood sacs until they hatch and develop to juveniles (reviewed by Alvariño 1968).

Although reproduction and egg deposition have been studied quite intensively (e.g. reviewed by Alvariño 1983a,b and by Pearre 1991), our knowledge of reproduction and breeding of the genus *Eukrohnia* and especially of deep living species of this genus is based on only a few detailed descriptions (David 1958; Alvariño 1968; Dawson 1968). More recent and comprehensive data were presented by Terazaki and Miller (1982) for *Eukrohnia bathypelagica* Alvariño, 1962 and *E. fowleri* Ritter-Záhony, 1909 in the North Pacific and by Timofeev (1998) for *E. hamata* Möbius, 1875 in the Arctic Ocean. Studies on the life cycle of the meso- and bathypelagic *Eukrohnia* species are extremely rare. Except for a first attempt by Alvariño et al. (1983), data on the life cycle of *E. bathypelagica* and *E. bathyantartica* David, 1958 for the Antarctic Ocean are lacking.

The use of a multinet during the present investigation allowed a gentle sampling which brought animals from 2000 m depth to the surface in a very good condition. Due to a very fine mesh size (100 µm), juvenile chaetognaths, which are not collected with wide-meshed nets, were also sampled. By means of this sampling method the study of the maturity stage composition and breeding of *Eukrohnia bathypelagica* and *E. bathyantartica* in the Southern Ocean was possible. Winter and summer sampling provided additional information on the life cycle of these two chaetognath species.

### Materials and methods

#### Field sampling

Chaetognaths were sampled during two expeditions in the Lazarev Sea with the RV "Polarstern". Seasonal sampling was conducted in Antarctic winter 2006 (ANT 23-6, 17 June - 21 August 2006) and in Antarctic summer 2007/2008 (ANT 24-2, 28 November 2007 - 04 February 2008). The samples were taken with a multinet 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 had a mesh size of 100 µm and an opening size of 0.25 m<sup>2</sup>. It was deployed to 2000 m depth and sampled the following standard depth intervals: 2000-1500 m, 1500-1000 m, 1000-750 m, 750-500 m, 500-0 m. The samples from the four greater depth intervals were chosen for detailed analysis.

The sampling scheme covered three different water masses, the Polar Frontal Zone (PFZ, at 52°S), the Weddell Gyre (WG, between 60° and 68°S) and the Coastal Current (CC, at and south of 68°S). For further sampling details see Kruse et al. (2009).

#### Laboratory methods and data processing

After picking the chaetognaths out of the multinet samples on board ship, the specimens were sorted on species level, counted and measured for body length (without tail fin) to the nearest 0.5 mm under a stereomicroscope (Olympus SZX12). A microscope (Zeiss Axioskop 2 plus) was used for the identification of smaller individuals. To distinguish *Eukrohnia bathypelagica* from *E. hamata* the tail length was measured additionally and given in percentage of total length. From all newly hatched *Eukrohnia* juveniles (<6 mm length) only those of *E. bathyantartica* could clearly be identified (see Kruse et al. 2009).

As not all chaetognaths of ANT 23-6 were measured on board ship, but after four months' preservation in formaldehyde (4% final concentration, buffered with hexamine), these lengths were corrected by a shrinkage factor of 6.23% for *Eukrohnia bathypelagica* and 5.37% for *E. bathyantartica* (see Kruse et al. 2009).

The measurements of brood sac and egg size have been carried out on the preserved chaetognaths in the home laboratory, as accurate measurements were not possible on board ship. Images were taken using the stereomicroscope with an Olympus camera and the appropriate imaging software (cell<sup>P</sup> program), which allowed measurements to the nearest 0.01 µm.

The chaetognaths *Eukrohnia bathypelagica* and *E. bathyantartica* of both expeditions were classified in four maturity stages according to Alvariño (1967, 1969). A fifth stage was additionally defined. This stage includes those specimens which released their fertilized eggs into the marsupial sacs. These specimens of the fifth stage carry either filled or already emptied brood sacs.

The stage of egg development within the marsupial sacs was additionally categorized into five phases. The definition of these brood phases was modified after Alvariño (1968): phase 1: brood sac developing; phase 2: brood sac filled with mature eggs; phase 3: brood sac with embryos in a single coil; phase 4: brood sac with eggs containing double coiled embryos or hatched juveniles; phase 5: brood sac ruptured after the release of the larvae. Special attention

has been given to the chaetognaths containing eggs or juveniles in their marsupial sacs (phases 2 to 4).

To evaluate the parameters which affect maturity stage distribution, I computed the mean stage of *E. bathypelagica* and *E. bathyantartica* per sample. Data were Box-Cox transformed to achieve normality and homogeneity of variances and subjected to a full factorial three-way ANOVA (mean stage versus water mass & season & depth & water mass x depth & season x depth) with subsequent *post-hoc* test on differences between means ( $\alpha = 0.05$ , Sokal and Rohlf 1981). The interaction term water mass x season was not tested, as there are no winter samples from the PFZ.

Additionally, a full factorial two-way ANOVA (length versus maturity stage & season & maturity stage x season) was applied to analyze differences in length in *E. bathypelagica* and *E. bathyantartica* (data were treated as mentioned for the previous ANOVA). Furthermore, seasonal differences between the length-frequency distributions were analyzed by means of a Kolmogorow-Smirnow test in both species.

## Results

### Maturity stage and length-frequency distribution

#### *Eukrohnia bathypelagica*

Of all *Eukrohnia bathypelagica* caught, 97.3% (winter) and 98.7% (summer) could be assigned to maturity stages and be readily measured. All five maturity stages of this species were found. The population was dominated by stage 2 individuals during both seasons. Stage 1 and 2 were present over the total depth range, whereas older stages, especially stage 4 and 5, were found with increasing depth. Nevertheless, some individuals of stage 5 occurred in the 500-750 m layer in winter. The segregation of maturity stages was also observed by an increase of the mean maturity stage with depth (Table 1). It was highest between 1500 and 2000 m and more distinct in summer than in winter. The water mass had no effect on the maturity stage distribution.

The maximum body length of *Eukrohnia bathypelagica* was measured at 26 mm during both seasons (Table 2), most individuals being larger than 16 mm. Generally only a slight increase in length could be observed with descending depth as maturity stage and length were positively but not highly correlated (summer:  $r = 0.571$ ,  $P < 0.001$ , winter:  $r = 0.493$ ,  $P < 0.001$ ). This was due to a strong overlap in length between subsequent maturity stages. Stage-specific length was only significantly different between winter and summer in stage 3 individuals (mean lengths: 23 mm in winter, 21.5 mm in summer).

The population structures between the two seasons were not significantly different (Kolmogorow-Smirnow:  $P > 0.1$ ). In summer compared to winter, there were fewer individuals of stage 3 and more of stage 4 present (Fig. 1). Most individuals reached 19 to 23 mm length independent of season. The dashed bars added in both graphs (Fig. 1) show the *Eukrohnia* individuals which could not be assigned to either *E. bathypelagica* or *E. hamata*. The individuals were difficult to identify either because of their small size or because they were damaged. These data are presented to indicate that high numbers of young and small individuals of *E. bathypelagica* might be present during both seasons. A second maximum around 7 and 8 mm body length for individuals of stage 1

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should therefore be considered as possible offspring of *E. bathypelagica*, even if a portion of these *Eukrohnia* young might belong to *E. hamata*.

**Table 1:** Effects of season (S: summer, W: winter) and depth (1: 2000-1500 m, 2: 1500-1000 m, 3: 1000- 750 m, 4: 750-500 m) on maturity stage distribution (mean maturity stage per station and depth interval) of *Eukrohnia bathypelagica* and *E. bathyantartica*

Mean stage	Depth				Season x depth							
	1	2	3	4	W 1	W 2	W 3	W 4	S 1	S 2	S 3	S 4
<i>E. bathypelagica</i>	A	B	C	B	A	B	B	B	A	A	A	
				C		C	C	C		B		C
							D	D			D	D
<i>E. bathyantartica</i>	A	A	B	A	ns							
		B	B	B								

Full factorial (except WM x season) ANOVA with subsequent Tukey HSD *post-hoc* test on differences between means ( $\alpha = 0.05$ ). ns: no significant effect, letters (A, B...) indicate groups that differ significantly, the alphabetical order indicates decreasing mean maturity stage. The parameters season, waters mass WM and the interaction term WM x depth are not shown here, because they were not significant

**Table 2:** Length-frequency distribution of *Eukrohnia bathypelagica* in the different depth intervals for winter and summer (without young *Eukrohnia* spp. individuals).  
n = number of investigated individuals

##### Winter

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
500-750	20													1			6	6	4	2	1	
750-1000	12											1	1	1	1	3	3	1				1
1000-1500	96		1							2		3	8	6	13	13	15	13	12	5	4	1
1500-2000	91				1		1	1			1	1	1	3	11	8	15	14	10	11	5	8

##### 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
500-750	35	1		1			1	2						1	1	4	5	1	4	4	9	1
750-1000	17			1		1									2	3	1	3	1	1	3	1
1000-1500	46									1					5	4	6	10	10		8	2
1500-2000	56										1					1	4	6	3	11	20	7



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##### *Eukrohnia bathyantarctica*

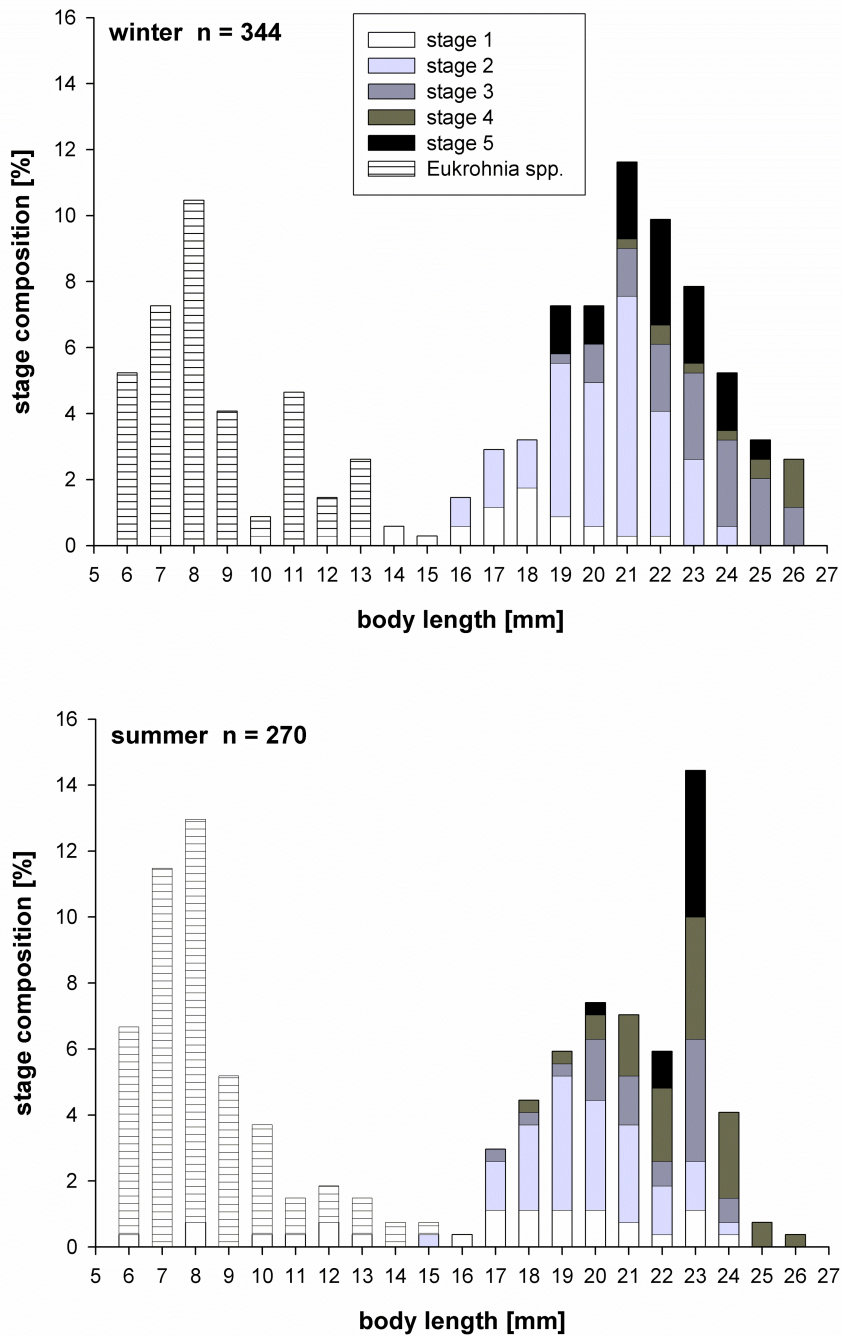
For *Eukrohnia bathyantarctica*, 95.8% and 100% of all individuals were complete and could be assigned to length-frequency distribution in winter and in summer. All maturity stages of *E. bathyantarctica* were sampled. The vertical maturity distribution of *E. bathyantarctica* was similar in both winter and summer and was again not influenced by water mass (Table 1). The largest proportion of the population belonged to stage 1 over the complete depth range sampled, followed by stage 2 individuals in number. Juveniles (newly hatched young, <6 mm length, Table 3) occurred below 1000 m, but also between 500 and 750 m in summer. Older individuals (stages 3-5) were comparatively rare and only caught in the two deepest strata, which is shown by highest mean stages between 1500 and 2000 m depth (Table 1).

A maximum body length of 30 and 29 mm was reached in winter and summer, but only by a few specimens (Table 3). A higher degree of maturity coincided with larger individuals (positive correlation: summer:  $r = 0.775$ ,  $P < 0.001$ , winter:  $r = 0.709$ ,  $P < 0.001$ ) and occurred with increasing depth. The average body length per stage was similar in both seasons. The shape of the length-frequency distribution did not differ significantly between summer and winter (Kolmogorow-Smirnow:  $P > 0.1$ ). The population structure in both seasons was formed by a high maximum of stage 1 individuals (between 8 and 17 mm length) and a second but smaller maximum compiled stage 2 to 5 individuals (between 24 and 28 mm; Fig. 2).

**Table 3:** Length-frequency distribution of *Eukrohnia bathyantarctica* in the different depth intervals for winter and summer (including newly hatched young <6 mm length). *n* = number of investigated individuals

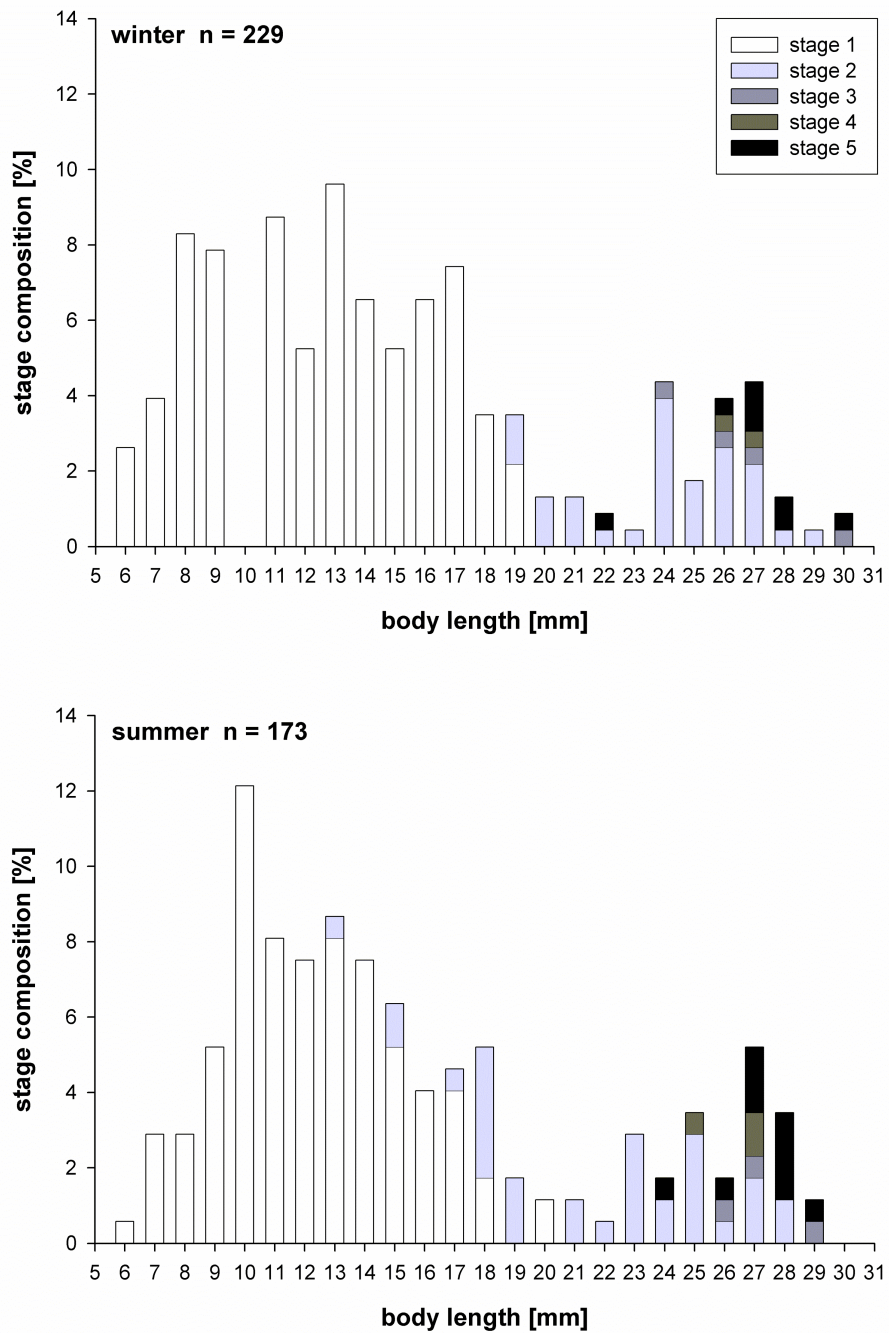
<b>Winter</b>																															
Depth (m)	n	Length (mm)																													
		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
500-750	10						1	2	2	1	1	1														1	1				
750-1000	7							3	1	1						1							1								
1000-1500	61					1	5	10	6	5	2	5	2	1	1	2	2	1	2	2	1	1	1	1	2	1	2	1	3	1	
1500-2000	169					5	3	4	9	13	10	16	13	11	14	15	6	6	3	2	1	1	1	8	1	7	7	3	2		
<b>Summer</b>																															
Depth (m)	n																														
		2	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	29	30	
500-750	5						1			2																					
750-1000	11								1	3	2	1	3																		
1000-1500	93						2	5	7	12	9	8	9	6	5	3	2	4	1	1			1	1	1	1	2	2			
1500-2000	79					1			1	4	3	4	6	4	6	4	6	5	2	1	2	1	5	2	5	2	7	4	2		

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**Fig. 1:** Length-frequency distribution of maturity stages of all *Eukrohnia bathypelagica* investigated during winter and summer given in %. Dashed marked bars indicate *Eukrohnia* specimens that could not be assigned to *E. bathypelagica* or *E. hamata*.  $n$  = number of investigated individuals

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**Fig. 2:** Length-frequency distribution of maturity stages of all *Eukrohnia bathyantarctica* investigated during winter and summer (without newly hatched young <6mm).  $n$  = number of investigated individuals

### **Breeding**

During both seasons *Eukrohnia bathypelagica* and *E. bathyantartica* were reproducing and carried fertilized eggs or juveniles in their marsupial sacs primarily in more than 1000 m water depth (Figs. 3a-d, 4a-d). These chaetognaths had no eggs in their ovaries (Figs. 3c, 4b, c). The eggs were either all released through the oviduct into the marsupial sac (Fig. 3b) or had already escaped as juveniles from the sac (Figs. 3d, 4d).

#### *Eukrohnia bathypelagica*

In winter, 19.8% of all *Eukrohnia bathypelagica* individuals (unidentified young *Eukrohnia* not included) carried marsupial sacs. The lateral fins were bent to the dorsal side, protecting the eggs and young in its sacs. Within these individuals (stage 5) 18.2% had full brood sacs. Empty sacs were found for the remaining 81.8% (brood phase 5). The mature chaetognaths still carrying their brood measured between 18.5 and 21 mm in length (Table 4). A brood sac was in average 3068  $\mu\text{m}$  long and 1689  $\mu\text{m}$  wide, filled with 43 to 63 eggs. The offspring was in brood phase 2 to 4. The eggs measured an average of 531  $\mu\text{m}$  in the major axis and 476  $\mu\text{m}$  in the minor axis for phase 2. During brood phase 3 the eggs were longer, but more slender (610  $\mu\text{m}$  x 448  $\mu\text{m}$ ). The uncurled offspring in the phase 3 eggs already had an average length of 951  $\mu\text{m}$  (Table 4). Only one brood at phase 4 was found in the marsupial sacs, and measured 945 and 1212  $\mu\text{m}$ . One empty marsupial sac was observed from which all but four juveniles (average length of 1687  $\mu\text{m}$ ) had already escaped.

During summer, 10.4% of *Eukrohnia bathypelagica* were breeding (unidentified young *Eukrohnia* not included). Only two chaetognaths or 12.5% of the individuals of stage 5 were found with filled marsupial sacs. These two fully mature specimens of 22 and 22.5 mm length were at least 1 mm longer than the individuals in winter. The average brood sac was 2978  $\mu\text{m}$  long and 1550  $\mu\text{m}$  wide, each containing large numbers of eggs in phase 2 (Table 4; 66 eggs). The egg size averaged 524  $\mu\text{m}$  in the major axis and 472  $\mu\text{m}$  in the minor axis. The offspring was tightly packed, covered by a thin and tender membrane, which could easily be ruptured with a needle.

**Table 4:** All individuals of the species *Eukrohnia bathypelagica* each carrying two filled brood sacs during the winter and the summer expedition

<b>Winter</b>										
Latitude	Longitude	Depth (m)	Ind. number	Body length (mm)	Tail length (% of body length)	Brood phase	Size of brood sac ( $\mu\text{m}$ )	Egg/Juvenile number	Average egg size ( $\mu\text{m}$ )	Average juvenile size "uncurled" ( $\mu\text{m}$ )
65°31'S	2°59'E	1500-2000	1	21	25.5	2	3350 x 1851	63	475 x 456	
66°59'S	3°4'E	1500-2000	1	20	27.1	2	3037 x 1687 3054 x 1843	no data no data	531 x 490 560 x 534	
68°29'S	0°7'E	1500-2000	2	21	30.0	3	3314 x 1922 3173 x 1805	no data no data	626 x 483 603 x 466	
66°5'S	0°1'W	1000-1500	1	19	28.0	2	damaged 3600 x 2098	63 65	579 x 457 577 x 507	
66°13'S	0°2'W	1500-2000	1	19	25.6	4	damaged	59		1212
62°59'S	0°E	1000-1500	1	18.5	30.6	3	3317 x 1807	no data	572 x 445	945
59°57'S	2°58'W	1500-2000	1	20	28.9	3	2762 x 1361 second missing	43	608 x 456	951
						2	2603 x 1471 2475 x 1178 damaged	no data no data	610 x 398 604 x 435	
						2	2689 x 1374	57	501 x 474	

Table 4 (continued)

## Summer

Latitude	Longitude	Depth (m)	Ind. number	Body length (mm)	Tail length (% of body length)	Brood phase	Size of brood sac ( $\mu\text{m}$ )	Egg/Juvenile number	Average egg size ( $\mu\text{m}$ )	Average juvenile size ( $\mu\text{m}$ )
62°1'S	2°58'W	1500-2000	1	22.5	30.6	2	damaged		521 x 463	
66°S	3°E	1500-2000	1	22	28.8	2	2306 x 1267 second	no data	526 x 480	

**Table 5:** All individuals of the species *Eukrohnia bathyantarctica* each carrying two filled brood sacs during the winter and the summer expedition

<b>Winter</b>									
Latitude	Longitude	Depth (m)	Ind. number	Body length (mm)	Brood phase	Size of brood sac ( $\mu\text{m}$ )	Egg/Juvenile number	Average egg size ( $\mu\text{m}$ )	Average juvenile size "uncurled" ( $\mu\text{m}$ )
66°10'S	0°7'E	1500-2000	1	30	2	2301 x 1229 2235 x 1214	6 6	1146 x 683 1163 x 755	
66°15'S	0°6'E	1500-2000	1	27	2	2269 x 1212 2473 x 1107	6 6	1092 x 751 1072 x 696	
62°59'S	0°E	1500-2000	2	27	4	2313 x 1339 2500 x 1305	6 7		1682 1608
				27	3	damaged 2233 x 1101			
66°34'S	3°6'W	1500-2000	1	28	2	2365 x 1129 second missing	6	1061 x 767 1029 x 545	1297



Table 5 (continued)

## Summer

Latitude	Longitude	Depth (m)	Ind. number	Body length (mm)	Brood phase	Size of brood sac ( $\mu\text{m}$ )	Egg/Juvenile number	Average egg size ( $\mu\text{m}$ )	Average juvenile size "uncurled" ( $\mu\text{m}$ )
67°56'S	2°56'W	1000-1500	1	23.5	4	2283 x 1078	6		2136
						second missing			
66°S	3°E	1500-2000	1	29	3	2374 x 1251	6		1449
						2361 x 1140	6		1872
66°S	0°E	1500-2000	1	27.5	4	2392 x 1216	4		3116
						second missing			

### *Eukrohnia bathyantartica*

Only 3.5% of all *Eukrohnia bathyantartica* investigated were fully mature and had brood sacs in winter. 62.5% of them still carried eggs or juveniles in marsupial sacs. Being between 27 and 30 mm long, they had brood sacs of 2336  $\mu\text{m}$  length and 1205  $\mu\text{m}$  width in average (Table 5). Each contained 6 or 7 eggs in phase 2 to 4. The eggs at stage 2 measured 1100  $\mu\text{m}$  x 686  $\mu\text{m}$  and at stage 3 1061  $\mu\text{m}$  x 767  $\mu\text{m}$ . The young at stage 4 were long and uncurled, reaching a length of more than 1600  $\mu\text{m}$ .

During the summer season 5.8% of all *Eukrohnia bathyantartica* individuals carried filled or empty marsupial sacs. 30%, three individuals, of 23.5 to 29 mm length had brood sacs containing juveniles. The brood sacs of 2353  $\mu\text{m}$  length and 1171  $\mu\text{m}$  width protected 4 to 6 eggs at phases 3 and 4 (Table 5). The membrane was even more resistant and firmer than that of *E. bathypelagica*. The offspring at brooding phase 4 was, with 2136 and 3116  $\mu\text{m}$ , already very large. The body of the young was completely covered with a broad and massive alveolar tissue.

## Discussion

In the Southern Ocean, the two chaetognath species *Eukrohnia bathypelagica* and *E. bathyantartica* have their highest abundances in the meso- and bathypelagic realm (David 1964; Alvarino et al. 1983; Kruse et al. 2009). During this study all maturity stages of both species were present in winter as well as in summer. Their body length and maturity stage generally tended to increase with increasing depth. Adult individuals carrying marsupial sacs were an indicator of ongoing reproduction. Differences in reproduction and life cycle in addition to fertilization, egg number and egg size of *E. bathypelagica* and *E. bathyantartica* will be discussed in the following.

### Body length and maturity stage

Within the vertical distribution of *Eukrohnia bathypelagica* and *E. bathyantartica* a segregation of size classes and especially maturity stages was observed. The vertical segregation of maturity stages, particularly in *E. bathyantartica*, was not as clear as seen for *E. hamata* or for other epi- and mesopelagic species (e.g. Kramp 1939; David 1965; Sullivan 1980; Øresland 1995; Kruse et al. 2009). Some stage 2 specimens of *E. bathyantartica* e.g. were found together with older stages below 1000 m in summer. It can be suggested, however, that a part of the *E. bathyantartica* population (including more mature individuals) occurs at depths greater than 2000 m (Kruse et al. 2009, 2000-3000 m) and is therefore missing in our study.

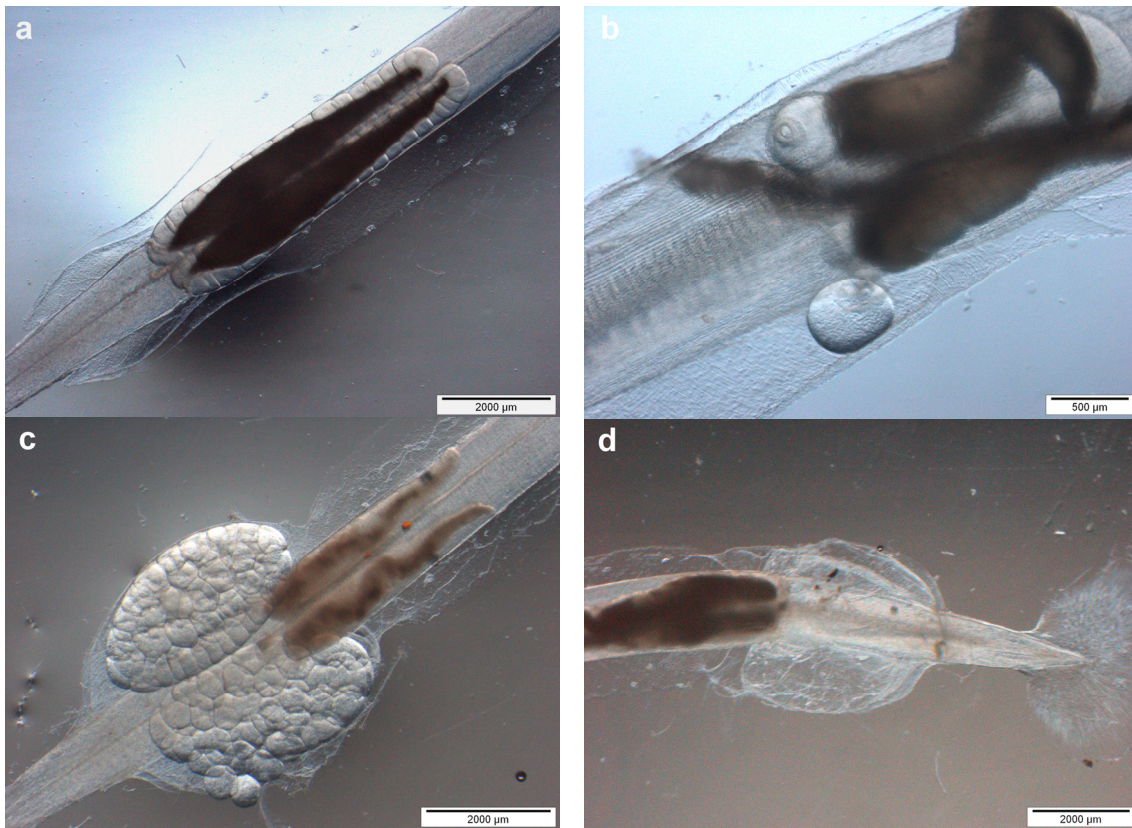
At the same time as the maturity increased with depth, the body lengths increased slightly. However, a seasonal difference in length, especially for stage 1, was not observed. The observations of greater lengths in winter due to the delay in gonad development (Alvarino et al. 1983) can therefore not be supported.

##### **Reproduction and life cycle**

Reproduction throughout the year can be suggested for *Eukrohnia bathypelagica* and *E. bathyantartica*. During winter and summer all developmental stages were present, from which it can be concluded that the populations of the two species consist of at least two generations. As growth is generally slower in polar regions, an alternating or two-phase breeding cycle is effective to ensure the occurrence of large specimen numbers of the species (Dunbar 1941). In this case, e.g. two generations, separated in age by one year, occur at the same time, as observed for *Sagitta elegans* in the Arctic (Dunbar 1941, 1962). Such generations may have long breeding seasons and could therefore cover a year-round reproduction. If mature individuals do not die after spawning and continue to build new ova, as Terazaki and Miller (1982) and personal observations indicate, several releases of eggs by one generation can be expected.

A bimodal length-frequency distribution supports the hypothesis of the presence of several generations, as mentioned before. This distribution was observed for *Eukrohnia bathyantartica* and for *E. bathypelagica*, even, accepting that the number of stage 1 individuals is underestimated for the latter species. As the advanced stages invest probably more in the development of the reproductive organs and less in growth (David 1955), more than one generation could be hidden within the second mode, shown in the present manuscript by a distinct overlap of body sizes for different maturity stages. Alvarino et al. (1983) suggested a life cycle longer than one year based on a lack of unimodality in the stage- and length-frequency distribution of *E. bathypelagica*. This is also indicated for both species under discussion. To verify the life cycle length for the two species, additional seasonal sampling involving spring and fall is required. Furthermore, food availability is suggested to be a key determinant for the reproduction cycle, for the duration of each maturity stage and for the reproduction success (i.e. number of offspring) (Terazaki and Miller 1986; Alvarino 1994). Studies on the diet of both species will shed a light on the importance of food supply triggering reproduction.

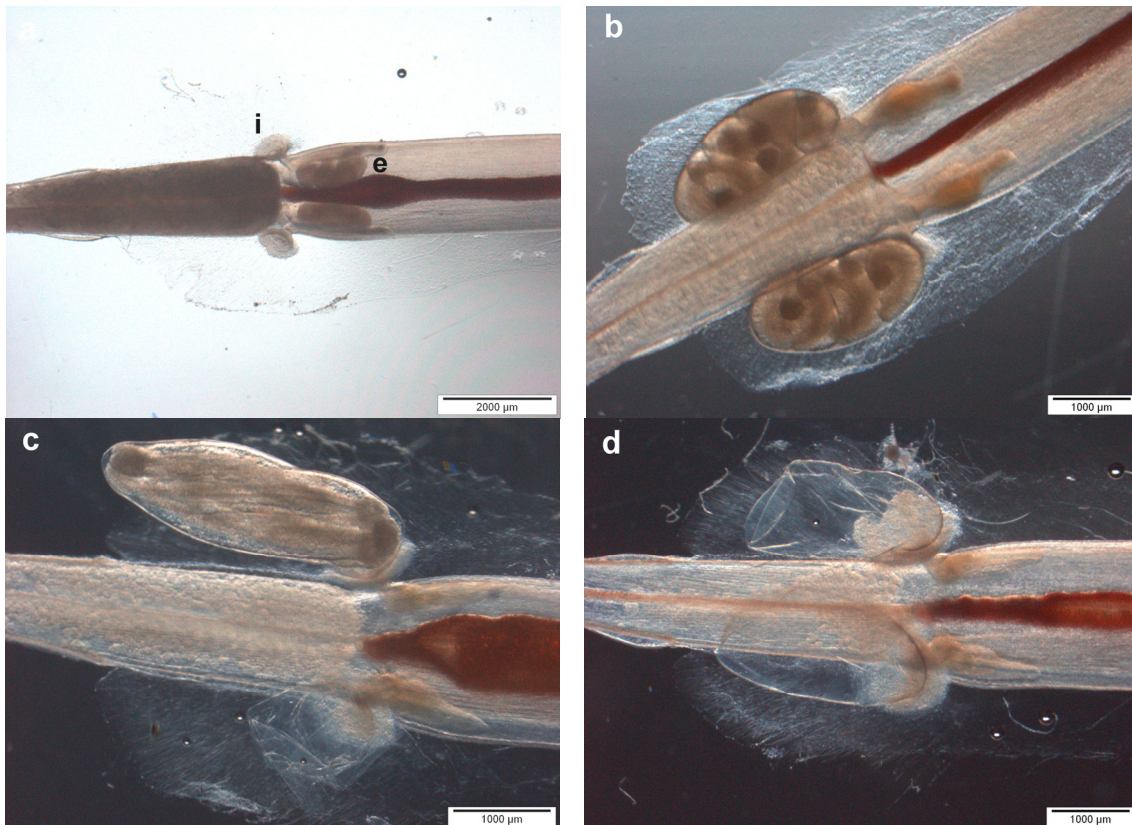
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**Fig. 3:** The posterior part of *Eukrohnia bathypelagica* is shown at different stages of development (maturity stage 4 for a, stage 5 for b-d). a: both ovaries with numerous large ova and receptaculum seminis filled with sperm. b: the release of fertilized eggs and shrinking ovaries (brood sacs lost). c: marsupial sacs filled with eggs. d: empty marsupial sacs

### Fertilization

Fertilization within chaetognaths has often been discussed (reviewed in Pearre 1991). As chaetognaths are hermaphroditic, both self- and cross-fertilization are possible. In the case of these deep living species with comparatively low abundances, self-fertilization has been considered to be likely (Terazaki and Miller 1982). Usually testes mature sooner than the ovaries, but personal observations during this investigation confirm that in some individuals of *Eukrohnia bathyantartica* ripe reproductive organs of males and females are well developed within the same specimen at the same time. This suggests self-fertilization among these species. However, most individuals of both species developed testes and ovaries consecutively, suggesting cross-fertilization to be more common. The observations in this study are therefore concordant with those of Terazaki and Miller (1982) from the North Pacific.



**Fig. 4:** The posterior part of *Eukrohnia bathyantartica* is shown at different stages of development (maturity stage 4 for a, stage 5 for b-d). a: ovaries with few large ova (e) and the external opening of the oviduct (i). b and c: developing juveniles in marsupial sacs. d: empty marsupial sacs

### Egg number

*Eukrohnia bathypelagica* and *E. bathyantartica* were both found carrying their young in brood sacs at greater depths. All eggs of both species were released in a single batch through the oviduct into the marsupial sacs, where they are protected (Figs. 3b,c, 4b,c).

Each *Eukrohnia bathypelagica* carried at least 86 eggs. This is equivalent to the number of ova carried by the adult chaetognath (Alvariño 1994). Alvariño (1983a) reported an average number of approximately 42 ova arranged in two (occasionally 3) lines per ovary of *E. bathypelagica*, resulting in 84 ova per individual. The ova number thus coincides with the lower range of the egg numbers found during this investigation. Because the ova or egg number is a function of animal size (Alvariño 1994), this relationship has also to be considered when comparing the data. *E. bathypelagica* of 19 mm length had approx. 86 eggs and the individual of 22.5 mm length approx. 132 eggs in its marsupial sacs, confirming very clearly the relationship between the egg/ova number and body length.

*Eukrohnia bathypelagica* from station P in the North Pacific (50°N 145°W) carried only 19 to 30 eggs in total per individual (Terazaki and Miller 1982). Geographical differences which are reflected in a stronger seasonality, for example, might cause this difference in egg number, although, variability within a species can have several reasons. Increased numbers of ova generally occur in 'poor' areas and in species living under stress (e.g. bathypelagic and cold water species; Alvariño 1994), as found in the Antarctic. Consequently egg

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numbers per brood sac might decrease from the poles to the tropics with tropical chaetognaths having small egg numbers. Even annual variations within species can exist because of the high dependence of egg production on food supply (Alvariño 1994). However, the averaged data from Terazaki and Miller (1982) and the data presented here fit very well to the ova number given by Alvariño (1983a).

*Eukrohnia bathyantartica* carried a comparatively low number of eggs with a maximum of 13 eggs in both brood sacs, although numbers of about 10 ova per ovary could also be observed in younger individuals. In this species, Alvariño (1983a) found 20 ova per ovary arranged in 2 lines which corresponds to 40 ova per individual. For the closely related species *E. fowleri*, that has a wider distribution than, but the same depth range as, *E. bathyantartica* (David 1958), comparable numbers of 5 to 8 eggs were found (Alvariño 1983a; Terazaki and Miller 1982). The differences in egg numbers may again be a result of geographical distribution or annual variability as previously mentioned. Above all it might also be advantageous for chaetognaths to produce larger eggs and in consequence larger juveniles to achieve higher survival rates via reduced predation or successful competition. Therefore, a clear variability within each species appears to depend highly on predation and the prevailing environmental conditions such as temperature and food supply.

Because fecundity is defined as 'the number of eggs produced per individual per species and geographic location' (Alvariño 1994), it can be concluded that *Eukrohnia bathypelagica* had a higher fecundity in the Southern Ocean than in the subarctic Pacific. However, the fecundity of *E. bathyantartica* during the present investigation was lower than the fecundity of the individuals analyzed by Alvariño (1983a) and lower than that of *E. bathypelagica* in general.

#### **Egg size**

The egg size in *Eukrohnia bathypelagica* varied between 398 and 534  $\mu\text{m}$  for the minor and between 475 and 626  $\mu\text{m}$  for the major axis, whereas the eggs increased in size with older brood phases. Compared to other species of *Sagitta* e.g. *S. elegans* with an egg size of 0.31 to 0.34 mm (Zo 1973), the eggs of *E. bathypelagica* are large. Terazaki and Miller (1982) measured a similar egg diameter of 480  $\mu\text{m}$  for *E. bathypelagica*, but a length of 2.5 mm for nearly hatched juveniles in the North Pacific (Terazaki and Miller 1986). As a few juveniles of *E. bathypelagica* were found in phase 4 and while hatching, it can only be suggested that a length of about 1.5 to 2 mm is reached when hatching.

In contrast, the eggs of *Eukrohnia bathyantartica* were with about 700 x 1000  $\mu\text{m}$  significantly larger. When hatching the young were at least 2 mm, sometimes even more than 3 mm long. Within one brood sac the juvenile body length was slightly variable, but a more obvious variability between individuals of the same species was observed.

The size of freshly hatched juveniles of both *Eukrohnia* species differs only slightly, although *E. bathyantartica* produced fewer eggs. However, its brood sac is smaller than that of *E. bathypelagica*. Furthermore, the young *E. bathypelagica* were more slender, whereas *E. bathyantartica* juveniles were broader having a thick alveolar tissue. Nevertheless, they are both relatively long when hatching especially when compared to epipelagic species such as *Sagitta elegans*, 1.2 to 1.4 mm long (Kotori 1975) or *S. nagae*, 0.5 to 0.6 mm long (Nagasawa and Marumo 1978). The production of large eggs and juveniles

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might therefore be a species-specific adaptation to be more successful in cold waters. Additionally, longer juveniles might be more successful in escaping from predators. Consequently, this adaptation is of great importance when living in deep meso- and bathypelagic zones of the Southern Ocean.

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## 5. PUBLICATION III

### **Feeding ecology and energetics of the Antarctic chaetognaths *Eukrohnia hamata*, *E. bathypelagica* and *E. bathyantartica***

Svenja Kruse<sup>1\*</sup>, Wilhelm Hagen<sup>2</sup>, Ulrich Bathmann<sup>1</sup>

<sup>1</sup> Alfred Wegener Institute for Polar and Marine Research,  
Am Handelshafen 12,  
D-27570 Bremerhaven, Germany

<sup>2</sup> Marine Zoology, P.O. Box 33 04 40, University of Bremen,  
D-28334, Germany

\* Corresponding author:  
Svenja.Kruse@awi.de  
Phone: + 49-471-48311688  
Fax: + 49-471-48311149

**Submitted to Marine Biology**

### Abstract

The chaetognaths *Eukrohnia hamata*, *E. bathypelagica* and *E. bathyantartica* were investigated from meso- to bathypelagic layers in the Weddell Sea, Antarctica, during summer and winter. Ecological and physiological studies focused on dietary preferences, lipid biochemistry and energetics (e.g. respiration rates). Chaetognath guts rarely contained food items, mostly copepods. Lipid compositions were dominated by fatty acids typical of biomembranes in *E. bathypelagica* and by the fatty acid 18:1(n-9) in *E. bathyantartica*. The latter species exhibited high amounts of fatty alcohols (23% versus 77% fatty acids) and hence deposited wax esters. Fatty alcohols were dominated by 16:0, 20:1(n-9) and 22:1(n-9), the latter two typical of calanid copepods. Lipid levels in *E. bathyantartica* and *E. bathypelagica* ranged below 26% of dry mass with no seasonal trends, suggesting year-round feeding. *E. hamata* and *E. bathypelagica* respired  $0.15 \mu\text{l O}_2 \text{ mg DM}^{-1} \text{ h}^{-1}$  on average (resting metabolism), which translates to a metabolic loss of <1.1% of body carbon.

**Key words:** Chaetognatha, Antarctica, Midwater, Seasonal, Lipids, Fatty acids and alcohols, Trophic marker, Respiration

### Introduction

Chaetognaths are known as important predators in all oceans, including the Southern Ocean (Pakhomov et al. 1999). They may contribute substantially to total zooplankton abundance and biomass (Hosie and Cochran 1994; Pakhomov et al. 1999, 2000). As main predators of copepods (Øresland 1990, 1995) and as food for a wide variety of larger organisms they hold a central position in planktonic food webs (Feigenbaum 1991).

Intensive studies especially on the taxonomy, abundance and distribution of Antarctic chaetognaths have been carried out in the past 100 years (e.g. Ritter-Záhony 1911; Thiel 1938; David 1955, 1958, 1965; Alvaríño et al. 1983a,b; Hagen 1985; Johnson and Terazaki 2004; Kruse et al. 2009). Originally, little information on food and feeding behavior of chaetognaths other than their diet composition was known, due to the difficulty to keep these delicate animals alive in the laboratory (reviews by Feigenbaum and Maris 1984 and Feigenbaum 1991). A first attempt to systematically analyze the gut content of chaetognaths was made by Wimpenny (1936) on *Sagitta setosa* and *S. elegans*. Twenty-five years later, the first report of controlled laboratory feeding was given by Reeve (1964) who worked with *Sagitta hispidata*. Since then, numerous studies followed (Feigenbaum 1991) that primarily focussed on the species-rich genus *Sagitta*. However, our knowledge on the feeding ecology of the genus *Eukrohnia*, except for the abundant *E. hamata* (e.g. Hopkins 1985, 1987; Øresland 1990, 1995; Froneman et al. 1998), is rudimentary.

To investigate the feeding preferences of *Eukrohnia hamata* and the two deep-living species *E. bathypelagica* and *E. bathyantartica*, we studied gut contents and analyzed fatty acids as trophic markers. The trophic marker concept is based on the observation that dietary fatty acids are incorporated in the body lipid of zooplankton largely unmodified (e.g. Lee et al. 1971; Lee 1974, 1975). In our study, this characteristic was used to obtain a good estimate of the chaetognath dietary composition. As information on the metabolism and energy

budget in this genus is rare (Båmstedt 1979; Thuesen and Childress 1993), we studied the lipid content and respiration of the three chaetognath species. Our aim was to elucidate the role of feeding and lipid storage for the life strategies of these predators at meso- and bathypelagic depths.

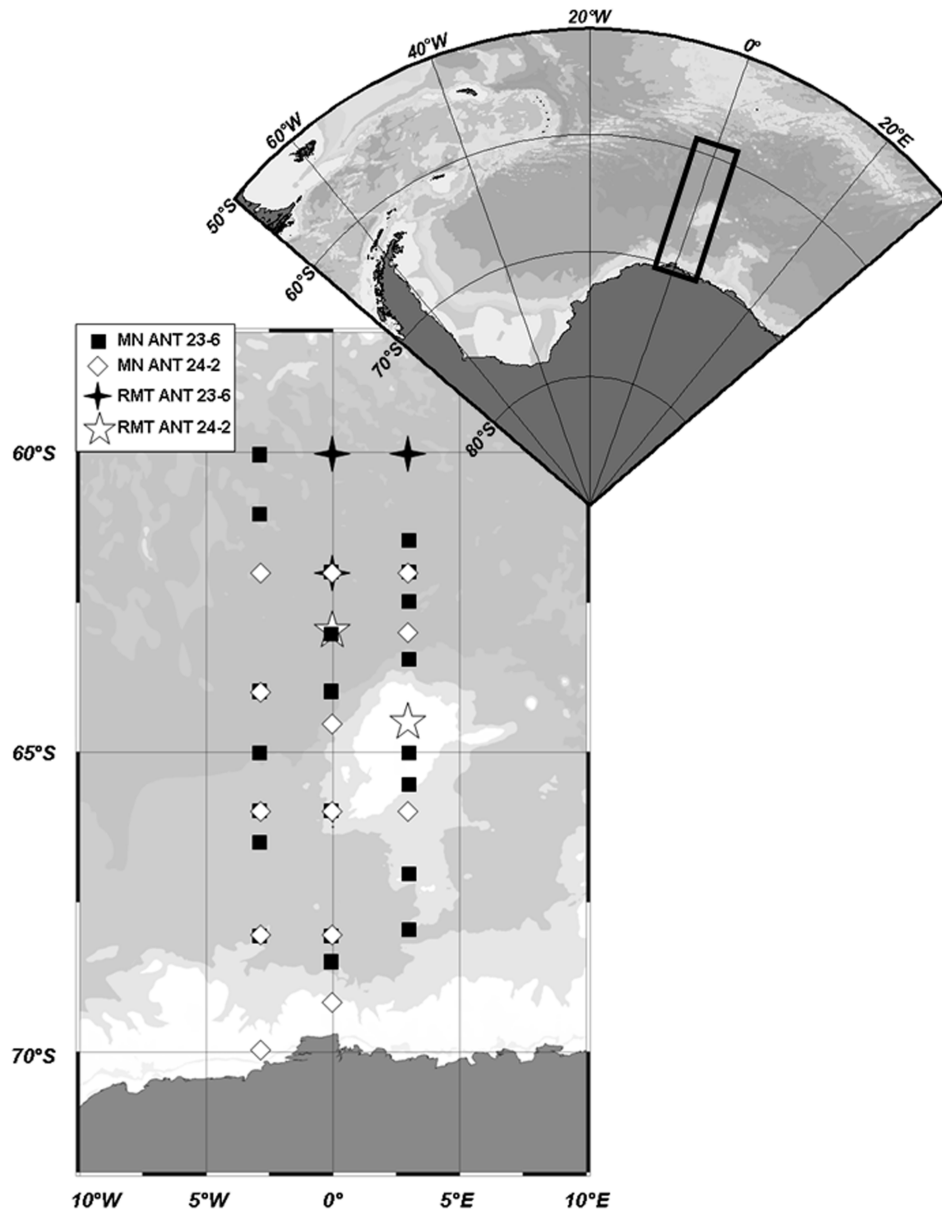
### Material and Methods

#### Sampling

Chaetognaths were sampled during the Antarctic winter 2006 (17 June - 21 August 2006, ANT 23-6) and the Antarctic summer 2007/2008 (28 November 2007 - 04 February 2008, ANT 24-2) with RV "Polarstern" in the Weddell Sea. The study area was located between 60°-70°S and 3°W-3°E (Fig. 1). During winter, samples were taken at 28 stations (with 8 repetitive stations at 66°S 0°E) with a multinet (MN, five nets, 100 µm mesh size; 0.25 m<sup>2</sup> mouth area) and at three stations with a rectangular midwater trawl (RMT 8: 4.5 mm mesh size, 8 m<sup>2</sup> mouth area; RMT 1: 320 µm mesh size, 1 m<sup>2</sup> mouth area). In summer, the MN was deployed at 15 stations (two at 52°S 0°E, not shown on Fig. 1) and a multiple RMT, consisting of three pairs of nets, at two stations. The MN sampled the following standard depth intervals during both seasons: 2000-1500-1000-750-500-0 m (four exceptions, see Kruse et al. 2009). The winter RMT hauls included the depth range from surface to approximately 3000 m and back to the surface, whereas the multiple RMT was deployed to an opening depth at 1900 and 2500 m, respectively (at 64°30'S 3°E: 1900–1500–750–500 m; at 63°S 0°E: 2500-2000-1000-500 m; Fig. 1). The RMT cod-end bucket comprised a volume of approx. 26 l of water, so the animals were in suspension that resulted in high survival rates and healthy specimens.

Chaetognaths of the species *Eukrohnia hamata*, *E. bathypelagica* and *E. bathyantartica* were observed alive and in good condition in the MN samples. Specimens were measured (head to tail, excluding tail fin) under a stereomicroscope (Olympus SZX12) to the nearest 0.5 mm, classified to maturity stage and then either quickly rinsed with Milli-Q water and stored in glass vials at -80°C for biochemical analysis or maintained alive in respiration experiments. Only few additional specimens of *E. bathypelagica* and *E. bathyantartica* were taken from the RMT for the lipid and fatty acid analyses. The remaining MN and RMT samples were either frozen or preserved in formaldehyde (4% final concentration, buffered with hexamine) for later investigations of the elemental composition and of the gut content.

Prior to the experiments and analyses, all chaetognaths were identified after Casanova (1999) and Alvariño (1969), staged and measured under a stereomicroscope and a microscope (Zeiss Axioskop 2 plus) either on board or later in the home laboratory. *Eukrohnia bathypelagica* and *E. bathyantartica* were classified to maturity stages according to Alvariño (1967, 1969) for lipid and fatty acid analyses. For the two latter species we assigned specimens which already released their eggs into the brood sacs to an additional fifth stage. The specimens analyzed in this study carried only empty brood sacs.



**Fig. 1:** Map of stations along three transects in the Weddell Sea, Southern Ocean. MN: multinet. RMT: rectangular midwater trawl. black: winter stations; white: summer stations

### Gut content analysis

Gut contents were analyzed in chaetognath specimens from formaldehyde-preserved MN and RMT samples. Only of *Eukrohnia hamata* also frozen specimens were taken in winter. Two hundred specimens of each species (*E. hamata*, *E. bathypelagica*, *E. bathyantartica*) were investigated from both, the summer and winter season. For this purpose each chaetognath was transferred to a few drops of glycerine on a microscope slide. Before and during preparation, the presence of lipid droplets in the gut was noted, the degree of gut fullness was measured (percentage of total gut length filled with content)

and differentiated into four categories (<10%, 10-20%, 25-50%, 50-100%). Especially when only little unidentifiable mass was in the gut or when ripe ovaries filled the body cavity in *E. bathypelagica*, the specimen and its gut had to be dissected before determining gut fullness. The gut was dissected with fine needles (0.15 mm) under a stereomicroscope, further analyzed under a microscope (400x magnification) and its content identified. The proportion of *Eukrohnia* specimens containing food (food containing ratio = FCR) and the number of prey per chaetognath (NPC) were noted for each species. The FCR is given as total FCR when the gut contained food, even if it was an unidentifiable mass, and separately as FCR for identifiable prey. Prey items found in the foregut were omitted from the analysis to avoid bias due to possible cod-end feeding.

### **Analyses of dry mass, elemental and biochemical composition**

For dry mass (DM), carbon (C) and nitrogen (N) analyses the chaetognaths of the three species *Eukrohnia hamata* (summer: n = 72, winter: n = 179), *E. bathypelagica* (summer: n = 40, winter: n = 43) and *E. bathyantartica* (summer: n = 42, winter: n = 35) were freeze-dried for about 24 h and weighed on a Sartorius microbalance (Sartorius Micro and Sartorius Supermicro 4504 MP8). The complete animal or subsamples of pestled animals were then analyzed in a Euro EA-CN Elemental Analyzer for C and N compositions with acetanilide as standard.

The lipid and fatty acid analyses focussed on the two meso- and bathypelagic species *Eukrohnia bathypelagica* and *E. bathyantartica*. *E. bathypelagica* individuals originated from 500 to 2000 m depth, *E. bathyantartica* individuals mostly from 1500 to 2000 m. To ensure sufficient biomass for lipid analysis, small individuals were pooled to obtain more than 1 mg DM. Total lipid was then extracted from single lyophilized individuals or pooled samples with dichloromethane/methanol (2:1 by volume), and the lipid content was determined gravimetrically according to Folch et al. (1957) as modified by Hagen (2000).

For gas-liquid chromatographic analysis of the fatty acid and alcohol compositions, aliquots of the extracted samples were taken. Lipids were hydrolysed and the fatty acids converted to their methyl ester derivatives in methanol containing 3% concentrated sulphuric acid at 80°C for 4 h (Kattner and Fricke 1986). Fatty acids and alcohols were separated and quantified using a Hewlett-Packard gas chromatograph (HP 6890A), equipped with a DB-FFAP column (30 m length, 0.25 mm inner diameter). Peaks were identified by comparing specific retention times with those from fish oil and copepod lipid standards of known composition.

The proportions of wax esters relative to total lipid were calculated for *Eukrohnia bathyantartica* on the basis of the fatty alcohol contents. We assumed equal masses for the fatty alcohol and fatty acid chains of each wax ester molecule.

Based on the fatty acid composition the biomarker ratio  $[18:1(n-9) + 20:1(n-9) + 22:1(n-9)] / [16:1(n-7) + 18:1(n-7)]$  was calculated as an indicator of carnivory. Fatty acids that occurred in more than 50% of all cases with a proportion of less than 2% were pooled and not presented separately. One exception was made for the fatty acid 18:1(n-7) in *Eukrohnia bathypelagica*, that is included, as its portion was used to calculate the biomarker ratio. Fatty

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alcohols generally amounting to less than 5% of the total fatty alcohol composition were also pooled in *E. bathyantartica*.

### Respiration rate measurements

Specimens from the 500 to 1000 m depth interval (multinet samples only) were chosen for the respiration experiments of *Eukrohnia hamata* and *E. bathypelagica* to ensure good physiological conditions of the chaetognaths and to minimize decompression damage. Additionally, in eight measurements on *E. hamata* in winter and in four measurements on *E. bathypelagica* in summer, individuals from the 1000 to 1500 m depth range were included. *E. bathyantartica* was not included in the respiration experiments, because it was difficult to collect enough specimens in good condition with similar properties.

Before the start of the experiment the chaetognaths were kept for up to about 24 h at constant temperature (0°C) in the dark for adaptation, because respiration rates may increase directly after the catch due to stress (Marshall et al. 1935, for *Calanus finmarchicus*). For respiration rate measurements specimens were incubated in sealed glass bottles of about 60 or 500 ml volume filled with filtered (0.7 µm pore size) and oxygen-saturated seawater for 19 to 24 h at the above mentioned temperature and light conditions. During the winter expedition always two specimens were incubated in a 60 ml bottle. In summer, experiments with four specimens per 500 ml bottle were conducted additionally to check the influence of bottle volume on respiration. The experiments showed that the volume (1 ind. per approx. 140 ml or 30 ml) had no significant influence on oxygen consumption of *E. hamata* (Mann-Whitney-U test,  $P > 0.05$ ;  $0.16 \pm 0.09 \mu\text{l O}_2 \text{ mg DM}^{-1} \text{ h}^{-1}$  for 140 ml and  $0.14 \pm 0.09 \mu\text{l O}_2 \text{ mg DM}^{-1} \text{ h}^{-1}$  for 30 ml). Therefore, the data were not treated separately. Individuals were chosen from the same depth range, maturity stage (primarily stage II) and similar size for one replicate. Each respiration experiment consisted of three to eight replicates with chaetognaths and two to four controls without chaetognaths. Overall, 52 and 51 replicates (including 34 in 500 ml bottles) were measured for *E. hamata* and five and nine replicates for *E. bathypelagica* during winter and summer, respectively. Dissolved oxygen was determined by the Winkler titration method (Grasshoff 1983) directly on the entire bottle or on subsamples carefully siphoned out of the 500 ml bottles. The decrease of oxygen concentration in the experiments compared to the controls was always less than 10%. All data was normalized per unit dry mass. Chaetognath dry mass and carbon content was measured of the specimens, which remained in the 500 ml experimental bottles and of specimens with similar qualities separately frozen from the net samples.

In order to estimate the metabolic loss in terms of the absolute and relative amount of carbon, which is respired by *E. hamata* and *E. bathypelagica* per day, the measured oxygen consumption rates in  $\mu\text{l O}_2 \text{ day}^{-1}$  per animal were converted to carbon units using a respiratory quotient (RQ) value of 0.97 in the following equation (Ikeda et al. 2000):

$$\text{mg carbon individual}^{-1} \text{ h}^{-1} = \text{ml O}_2 \text{ individual}^{-1} \text{ h}^{-1} \times \text{RQ} \times 12 / 22.4$$

where 12/22.4 is the carbon weight in 1 mol of CO<sub>2</sub>. For *E. bathyantartica*, we applied a comparable calculation on the basis of the general DM and carbon measurements using the average respiration rate of the two other *Eukrohnia* species.

### Statistical analyses

Differences in oxygen consumption ( $\mu\text{l mg DM}^{-1}$ ), carbon (C;  $\mu\text{g mg DM}^{-1}$ ), nitrogen (N;  $\mu\text{g mg DM}^{-1}$ ) and lipid content ( $\text{mg lipid mg DM}^{-1}$ ) were analyzed using a full factorial two-way ANOVA for each parameter (respiration/C/N/lipid versus species and season and species x season) with a subsequent *post-hoc* test on differences between means ( $\alpha = 0.05$ , Sokal and Rohlf 1981). A further ANOVA was used to examine the influence of depth on respiration (respiration versus season and depth and season x depth). Prior to the analyses the data were Box-Cox transformed when necessary to achieve normality and homogeneity of variances. Additionally, we applied a full factorial two-way ANOVA (lipid content versus maturity stage and season and maturity stage x season) to test for stage-specific differences in the lipid content of *Eukrohnia bathypelagica* and *E. bathyantartica*. For *E. bathypelagica* we had to exclude stage III from the analyses, for *E. bathyantartica* stages IV and V, as individuals of these stages were not available in very good condition during both seasons.

Furthermore, we applied a cluster analysis (hierarchical clustering, complete linkage method) on the fatty acid compositions to analyze differences between species, seasons, depths and maturity stages (no figure shown). All statistical analyses were performed with the software Statistica (StatSoft).

## Results

### Gut content

Less than half of all *Eukrohnia hamata* specimens analyzed had food in their guts, 39% during summer and 42% during winter (total FCR, Table 1). In *E. bathypelagica* 48% contained food during winter and 31% in summer. In both species the degree of gut fullness was rather low with mostly less than 25%. The content was located in the middle and posterior part of the gut. In contrast to these two species, the gut of *E. bathyantartica* is characterized by a brick-red color. Due to this pigmentation it was not possible to record the gut fullness precisely, but in general this species contained very little content in its guts. Even after careful dissection, no identifiable particles could be detected in *E. bathyantartica*.

In *Eukrohnia hamata* and *E. bathypelagica* we found some prey items. Rarely, prey occurred in identifiable condition, due to the advanced state of digestion. Copepods, protozoans (Acantharia, Radiolaria, tintinnids), jellyfish remains (especially nematocysts) and diatoms were the main food items identified in both species (Table 1). Only one complete copepod and few mandibles of copepods were found in comparatively good condition. Both could not be related to the respective species. They may be deep-sea copepods, because they do not seem to belong to species frequently encountered in the Southern Ocean. Excluding jellyfish remains and diatoms,  $\leq 0.12$  prey items were observed per specimen (NPC, Table 1).

Independent of the season, oil droplets were found in the guts of most *Eukrohnia hamata* specimens (>82%). In *E. bathypelagica*, 34% of all guts contained oil droplets in summer, and 57% in winter (Table 1). In *E. bathyantartica* oil droplets were difficult to identify, even after gut dissection, due to the intense gut pigmentation and the oil droplets therein.

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**Table 1:** Gut contents of *Eukrohnia hamata* and *E. bathypelagica* in the Weddell Sea during winter 2006 and summer 2007/2008. Data on guts containing oil drops, the degree of gut fullness, the food containing ratio (FCR) and the number of prey per specimen (NPC) are shown. Data are given in % of specimens investigated, except for the number of specimens and the NPC

Species Season Number of specimens (n)	<i>E. hamata</i>		<i>E. bathypelagica</i>	
	winter 200	summer 200	winter 200	summer 200
Guts with lipid droplets (%)	92.0	82.5	57.0	34.0
FCR (total, %)	42.0	39.0	48.0	31.0
Degree of gut fullness				
<10%	26.0	25.5	18.5	23.5
10-25%	10.0	12.5	20.0	7.0
25-50%	5.5	1.0	9.0	0.5
50-100%	0.5	-	0.5	-
FCR (identifiable content only)	8.0	25.0	4.0	16.0
FCR (without diatoms and jellyfish remains)	4.5	1.0	1.5	1.0
Diatoms ( <i>Fragilariopsis</i> , <i>Chaetoceros</i> )	2.0	0.5	-	-
Acantharia	1.0	-	-	-
Radiolaria	0.5	-	1.0	0.5
Tintinnids ( <i>Cymatocylis</i> )	1.0	0.5	-	-
Copepoda	3.5	0.5	1.0	0.5
Chaetognatha	0.5	-	-	-
Jellyfish remains	3.0	24.5	3.0	15.0
Fecal pellets	0.5	-	-	-
NPC (without diatoms and jellyfish remains)	0.12	0.01	0.03	0.01

### Carbon, nitrogen and total lipid content

The carbon and nitrogen contents depended significantly on the season and species ( $P < 0.001$ ). Carbon, nitrogen and C:N ratios were higher in winter than in summer (Table 2). In *Eukrohnia bathypelagica* we observed the lowest carbon (winter: 31.3% DM, summer: 24.6% DM) and nitrogen contents (winter: 6.9% DM, summer: 5.7% DM) of all three species. The C and N contents of *E. hamata* and *E. bathyantartica* were similar, but generally higher than those of *E. bathypelagica*. The same was true for the C:N ratio of *E. bathypelagica* (winter: 4.5, summer: 4.3), which was significantly lower than for the two other species ( $P < 0.001$ ).



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**Table 2:** Summarized results of body composition and daily metabolic loss (% body carbon; mean  $\pm$  sd and range) of *Eukrohnia hamata*, *E. bathypelagica* and *E. bathyantartica*. A lower number of nitrogen and thus C:N data were obtained for *E. hamata* and *E. bathyantartica* in summer (number of specimens given in brackets). DM: dry mass

Number of specimens	n	<i>Eukrohnia hamata</i>		<i>E. bathypelagica</i>		<i>E. bathyantartica</i>	
		summer	winter	summer	winter	summer	winter
		72 (70)	179	40	43	42 (41)	35
Length (mm)	Mean	21.3 $\pm$ 4.9	22.2 $\pm$ 3.2	21.1 $\pm$ 2.4	21.9 $\pm$ 2.2	22.0 $\pm$ 5.3	21.7 $\pm$ 4.3
	Range	11-29	12-28	15-25	16.5-26	12-30	11-27
Dry mass (mg)	Mean	2.8 $\pm$ 1.9	2.4 $\pm$ 1.2	2.6 $\pm$ 1.6	2.2 $\pm$ 1.2	3.4 $\pm$ 2.5	2.2 $\pm$ 1.0
	Range	0.3-8.8	0.5-6.1	0.5-6.4	0.8-6.7	0.3-9.5	0.4-4.1
Carbon (% DM)	Mean	30.4 $\pm$ 7.7	39.4 $\pm$ 6.1	24.6 $\pm$ 7.2	31.3 $\pm$ 8.9	32.4 $\pm$ 4.9	42.4 $\pm$ 7.1
	Range	12.1-52.8	16.4-65.3	14.3-39.2	19.2-51.5	21.8-42.6	29.2-56.9
Nitrogen (% DM)	Mean	6.8 $\pm$ 1.7	7.8 $\pm$ 1.2	5.7 $\pm$ 1.1	6.9 $\pm$ 1.2	6.9 $\pm$ 1.0	8.4 $\pm$ 1.4
	Range	2.4-13.1	3.7-11.6	3.6-8.0	5.0-9.3	3.9-8.2	5.9-11.8
C:N ratio	Mean	4.6 $\pm$ 0.7	5.1 $\pm$ 1.0	4.3 $\pm$ 0.6	4.5 $\pm$ 0.9	4.8 $\pm$ 0.8	5.1 $\pm$ 0.9
	Range	3.4-7.2	3.6-8.9	3.4-5.6	3.6-7.2	3.6-7.3	3.7-7.1
Body carbon respired (%)	n	51	52	9	5	43	35
	Mean	0.67 $\pm$ 0.45	0.49 $\pm$ 0.17	1.09 $\pm$ 0.97	0.45 $\pm$ 0.06	0.61 $\pm$ 0.10	0.47 $\pm$ 0.08
	Range	0.10-1.87	0.22-0.93	0.20-2.64	0.37-0.50	0.45-0.88	0.34-0.66

The total lipid contents of the two deep-living species *Eukrohnia bathypelagica* and *E. bathyantartica* were significantly different from each other ( $P < 0.05$ ; Tables 3 and 4). *E. bathyantartica* had an average lipid content of 15.4% DM ( $\pm 4.1$ ) and showed no significant changes among maturity stages and season ( $P > 0.05$ ; Table 4). In contrast, the lipid content in *E. bathypelagica* ranged between 1.4 and 25.4% DM and differed distinctly among maturity stages (Table 3). Stage IV (winter: 12.7% DM, summer: 20.0% DM) contained relatively more lipids than stages II and V. Seasonal fluctuations were represented by a higher lipid level in *E. bathypelagica* in summer (winter: 8.4% DM, summer: 13.9% DM;  $P < 0.05$ ).

### **Fatty acid and fatty alcohol compositions of *E. bathypelagica* and *E. bathyantartica***

Total lipids of *Eukrohnia bathypelagica* consisted mainly of fatty acids (mean 95.9% of TFA and TFAIc) with few fatty alcohols. *E. bathyantartica* had higher amounts of fatty alcohols (Table 4; mean 22.7%) compared to *E. bathypelagica*. This portion of fatty alcohols in *E. bathyantartica* indicates a higher wax ester content of up to 57.5% of total lipids.

The five fatty acids 16:0, 16:1(n-7), 18:1(n-9), 20:5(n-3) and 22:6(n-3) generally dominated within the two chaetognath species *Eukrohnia bathypelagica* and *E. bathyantartica* and comprised 59.5% and 69.0% of total

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fatty acids (TFA), respectively. However, there were significant differences between the fatty acid patterns of these two species (species-specific clustering, figure not shown).

The fatty acid composition of *Eukrohnia bathypelagica* was characterized by higher amounts of 16:0, 20:5(n-3) and 22:6(n-3). They contributed with average values of 9.4%, 10.7% and 22.1% respectively, to TFA (Table 3). Season, depth or maturity stage had only a marginal influence on the fatty acid compositions of *E. bathypelagica*. The cluster analysis on the fatty acids (11 FA shown in Table 3) revealed a grouping of stage IV individuals of *E. bathypelagica*, that originated from 1500 to 2000 m depth and contained lower amounts of 22:6(n-3) (winter: 15.0%, summer: 13.3%) compared to the other maturity stages. Few stage II specimens between 500 and 750 m had also a similar fatty acid composition in summer. Generally, moderate amounts of the monounsaturated fatty acids 16:1(n-7) (mean 7.5%) and 18:1(n-9) (mean 9.8%) were measured in *E. bathypelagica* (Table 3). 20:1(n-9) and 22:1(n-11) occurred with up to 14% (mean 4.8%) and 20.9% (mean 4.3%) in this species. The remaining fatty acids each accounted for less than 4% TFA in average.

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**Table 3:** *Eukrohnia bathypelagica*. Dry mass and total lipid content as well as fatty acid composition for different maturity stages during winter and summer (mean  $\pm$  sd). DM: dry mass, TL: total lipid, TFA: total fatty acids

<b>Winter</b>			
Maturity stage	II	IV	V
Number of samples	4	3	8
Number of individuals	5	4	10
Ind. dry mass [mg]	2.7 $\pm$ 1.5	4.5 $\pm$ 1.1	2.1 $\pm$ 0.3
Lipid [% DM]	8.4 $\pm$ 4.1	12.7 $\pm$ 3.0	6.8 $\pm$ 1.5
<b>Fatty acids [% TFA]</b>			
16:0	8.0 $\pm$ 0.7	9.7 $\pm$ 1.2	8.3 $\pm$ 2.1
16:1(n-7)	6.4 $\pm$ 2.5	11.1 $\pm$ 1.2	6.4 $\pm$ 1.7
18:0	4.0 $\pm$ 1.8	1.6 $\pm$ 0.1	4.1 $\pm$ 1.2
18:1(n-9)	8.7 $\pm$ 1.8	11.6 $\pm$ 4.0	9.6 $\pm$ 3.5
18:1(n-7)	1.7 $\pm$ 0.4	2.1 $\pm$ 0.5	1.6 $\pm$ 0.4
20:1(n-9)	3.7 $\pm$ 5.2	8.0 $\pm$ 0.7	2.2 $\pm$ 1.2
20:5(n-3)	10.5 $\pm$ 0.9	11.4 $\pm$ 1.1	11.7 $\pm$ 2.0
22:1(n-11)	3.6 $\pm$ 6.5	7.8 $\pm$ 5.3	1.4 $\pm$ 1.5
22:1(n-9)	3.7 $\pm$ 2.2	5.3 $\pm$ 2.5	2.7 $\pm$ 1.0
22:6(n-3)	27.8 $\pm$ 9.6	15.0 $\pm$ 3.0	28.3 $\pm$ 5.1
24:1(n-9)	5.0 $\pm$ 2.5	1.9 $\pm$ 0.2	5.0 $\pm$ 0.8
FA <2%	16.9 $\pm$ 2.8	14.4 $\pm$ 1.4	18.5 $\pm$ 2.1
<b>Ratio</b> [18:1(n-9) + 20:1(n-9) + 22:1(n-9)]/ [18:1(n-7) + 16:1(n-7)]	1.9 $\pm$ 0.5	1.9 $\pm$ 0.2	1.9 $\pm$ 0.7

<b>Summer</b>				
Maturity stage	II	III	IV	V
Number of samples	5	5	7	2
Number of individuals	6	13	14	2
Ind. dry mass [mg]	1.7 $\pm$ 0.4	2.5 $\pm$ 1.0	4.2 $\pm$ 0.9	2.7 $\pm$ 1.0
Lipid [% DM]	7.5 $\pm$ 3.9	13.1 $\pm$ 7.6	20.0 $\pm$ 4.6	10.8 $\pm$ 9.0
<b>Fatty acids [% TFA]</b>				
16:0	11.6 $\pm$ 2.4	7.8 $\pm$ 5.0	12.2 $\pm$ 0.9	3.7 $\pm$ 5.2
16:1(n-7)	6.6 $\pm$ 1.4	7.7 $\pm$ 1.8	9.1 $\pm$ 1.9	5.7 $\pm$ 0.5
18:0	5.7 $\pm$ 1.1	2.7 $\pm$ 1.7	1.9 $\pm$ 0.3	2.7 $\pm$ 1.8
18:1(n-9)	10.4 $\pm$ 2.1	8.5 $\pm$ 5.0	11.1 $\pm$ 3.8	7.3 $\pm$ 1.7
18:1(n-7)	1.6 $\pm$ 0.2	1.9 $\pm$ 0.9	2.5 $\pm$ 0.8	1.1 $\pm$ 0.5
20:1(n-9)	2.3 $\pm$ 0.7	5.4 $\pm$ 5.2	8.0 $\pm$ 4.1	6.7 $\pm$ 4.7
20:5(n-3)	9.6 $\pm$ 2.9	8.5 $\pm$ 4.6	10.8 $\pm$ 2.8	13.3 $\pm$ 0.9
22:1(n-11)	1.0 $\pm$ 0.7	6.5 $\pm$ 8.1	6.0 $\pm$ 2.6	8.9 $\pm$ 10.9
22:1(n-9)	2.2 $\pm$ 0.5	4.3 $\pm$ 3.7	5.1 $\pm$ 1.7	6.2 $\pm$ 5.2
22:6(n-3)	26.0 $\pm$ 4.1	20.9 $\pm$ 12.2	13.3 $\pm$ 2.1	20.7 $\pm$ 16.9
24:1(n-9)	4.4 $\pm$ 0.6	3.7 $\pm$ 1.6	2.2 $\pm$ 0.5	3.5 $\pm$ 2.7
FA <2%	18.8 $\pm$ 4.6	22.1 $\pm$ 7.3	17.7 $\pm$ 3.0	20.3 $\pm$ 6.6
<b>Ratio</b> [18:1(n-9) + 20:1(n-9) + 22:1(n-9)]/ [18:1(n-7) + 16:1(n-7)]	1.8 $\pm$ 0.3	1.8 $\pm$ 0.6	2.1 $\pm$ 0.3	3.0 $\pm$ 1.2

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**Table 4:** *Eukrohnia bathyantartica*. Dry mass, total lipid and wax ester content as well as fatty acid and fatty alcohol composition for different maturity stages during winter and summer (mean  $\pm$  sd). DM: dry mass. TL: total lipid. TFA: total fatty acids. TFAlc: total fatty alcohols

	Winter		
	I	II	III
Maturity stage			
Number of samples	1	6	3
Number of individuals	1	6	3
Ind. dry mass [mg]	2.1	3.4 $\pm$ 1.5	5.7 $\pm$ 0.3
Lipid [% DM]	17.7	16.9 $\pm$ 4.7	11.2 $\pm$ 4.0
Wax esters [% TL]	40.1	47.8 $\pm$ 7.6	42.4 $\pm$ 6.5
Fatty acids [% TFA]			
16:0	8.1	6.6 $\pm$ 0.6	7.1 $\pm$ 0.9
16:1(n-7)	10.0	12.0 $\pm$ 3.2	11.4 $\pm$ 1.2
18:1(n-9)	29.0	32.0 $\pm$ 3.5	35.1 $\pm$ 3.8
18:1(n-7)	5.7	6.4 $\pm$ 1.0	6.6 $\pm$ 1.0
20:1(n-9)	2.7	3.5 $\pm$ 1.9	3.2 $\pm$ 0.4
20:5(n-3)	8.3	6.0 $\pm$ 0.9	4.5 $\pm$ 1.0
22:1(n-9)	2.7	2.7 $\pm$ 1.4	1.6 $\pm$ 0.4
22:6(n-3)	12.1	11.6 $\pm$ 2.7	12.3 $\pm$ 3.8
24:1(n-9)	2.6	2.4 $\pm$ 0.7	2.8 $\pm$ 1.0
FA <2%	18.7	16.9 $\pm$ 3.7	15.5 $\pm$ 3.8
Ratio [18:1(n-9) + 20:1(n-9) + 22:1(n-9)]/ [18:1(n-7) + 16:1(n-7)]	2.2	2.1 $\pm$ 0.4	2.2 $\pm$ 0.4
Fatty alcohols [% TFAlc]			
14:0	11.6	8.4 $\pm$ 3.5	8.8 $\pm$ 2.9
16:0	28.1	26.3 $\pm$ 4.7	21.7 $\pm$ 1.4
18:1(n-9)	11.3	12.6 $\pm$ 4.7	13.3 $\pm$ 1.1
20:1(n-9)	13.4	13.6 $\pm$ 12.3	25.9 $\pm$ 7.2
22:1(n-11)	6.7	8.5 $\pm$ 5.1	6.5 $\pm$ 2.8
22:1(n-9)	20.4	22.1 $\pm$ 14.8	15.5 $\pm$ 4.3
FAlc <5%	8.5	8.5 $\pm$ 1.5	8.3 $\pm$ 1.5

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**Table 4** (continued)

	Summer				
	I	II	III	IV	V
Maturity stage					
Number of samples	2	9	4	1	1
Number of individuals	5	14	6	1	1
Ind. dry mass [mg]	0.6 ±0.2	3.2 ±1.6	5.5 ±0.6	5.9	4.3
Lipid [% DM]	14.2 ±0.7	16.5 ±4.4	15.3 ±3.0	15.3	10.1
Wax esters [% TL]	42.3 ±2.0	44.8 ±4.8	49.7 ±4.3	47.5	40.6
Fatty acids [% TFA]					
16:0	6.5 ±0.3	6.3 ±0.6	6.2 ±0.9	6.3	6.3
16:1(n-7)	10.5 ±0.8	13.1 ±2.5	13.1 ±2.6	12.6	10.1
18:1(n-9)	29.1 ±3.7	33.0 ±1.7	34.3 ±1.9	31.3	31.9
18:1(n-7)	6.5 ±0.9	6.5 ±0.7	6.2 ±0.3	7.3	6.5
20:1(n-9)	6.3 ±4.4	3.3 ±1.6	4.4 ±0.9	3.8	2.5
20:5(n-3)	5.9 ±2.3	6.2 ±1.3	5.6 ±1.3	6.7	7.1
22:1(n-9)	2.1 ±0.1	2.1 ±0.6	2.3 ±0.4	2.9	2.1
22:6(n-3)	13.0 ±1.4	11.4 ±3.0	10.4 ±1.1	11.0	14.3
24:1(n-9)	3.2 ±0.1	2.6 ±0.9	2.0 ±0.1	1.9	2.8
FA <2%	16.9 ±0.3	15.6 ±1.2	15.6 ±1.0	16.2	16.4
Ratio [18:1(n-9) + 20:1(n-9) + 22:1(n-9)]/ [18:1(n-7) + 16:1(n-7)]	2.2 ±0.3	2.0 ±0.2	2.1 ±0.2	1.9	2.2
Fatty alcohols [% TFAIc]					
14:0	9.0 ±3.0	9.7 ±3.1	7.7 ±3.8	4.7	9.0
16:0	25.7 ±1.5	25.9 ±4.0	26.2 ±3.0	16.1	25.9
18:1(n-9)	13.4 ±3.2	15.2 ±3.9	10.8 ±0.8	9.3	16.9
20:1(n-9)	18.6 ±9.7	14.8 ±6.4	23.2 ±4.1	23.8	14.0
22:1(n-11)	7.2 ±1.3	7.6 ±3.5	7.9 ±1.7	11.9	9.3
22:1(n-9)	17.1 ±4.1	17.5 ±6.5	16.3 ±1.8	25.4	15.5
FAlc <5%	9.1 ±0.4	9.2 ±1.2	7.9 ±1.0	8.8	9.3

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*Eukrohnia bathyantartica* contained high levels of 18:1(n-9), with a maximum of 39.0% of total fatty acids (Table 4; mean 32.6%  $\pm$  2.9). The fatty acids 16:0, 20:5(n-3) and 22:6(n-3) reached distinctly lower amounts in *E. bathyantartica* compared to *E. bathypelagica*, 22:6(n-3) accounted for 11.6% on average, which is about half of the portion determined for *E. bathypelagica* (Table 4). 16:0 and 20:5(n-3) contributed only 6.5% and 6.0% to total fatty acids. 16:1(n-7) and 18:1(n-7) were with 12.2% and 6.4% on average higher in this species, whereas similarly low levels of 20:1(n-9) were measured. There was no seasonal, depth or maturity stage related pattern identifiable.

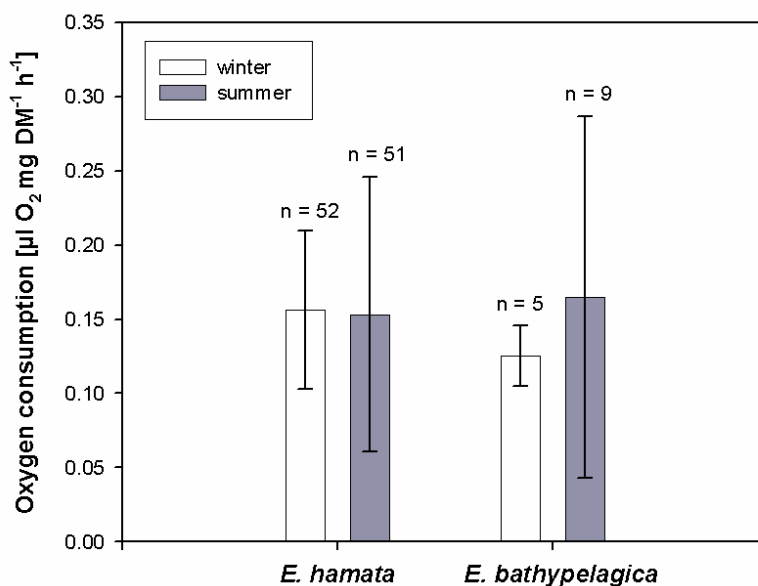
The fatty acid ratio  $[18:1(n-9) + 20:1(n-9) + 22:1(n-9)] / [16:1(n-7) + 18:1(n-7)]$  as indicator of carnivory was similar in *Eukrohnia bathypelagica* and *E. bathyantartica*, with mean values of 2.0 and 2.1, respectively (Tables 3 and 4).

The fatty alcohol contents were highly variable in *Eukrohnia bathypelagica* and ranged between 0 and 26.7% of TFA and TFAIc (mean 4.1%, not shown in the Table). *E. bathyantartica* contained with 22.7% of TFA and TFAIc more fatty alcohols compared to *E. bathypelagica*. These fatty alcohols mainly consisted of 16:0 (mean 25.3% TFAIc), 18:1(n-9) (13.3%), 20:1(n-9) (17.6%) and 22:1(n-9) (18.5%; Table 4).

### **Oxygen consumption**

An average respiration rate of 0.15  $\mu\text{l O}_2 \text{ mg DM}^{-1} \text{ h}^{-1}$  ( $\pm$  0.08) was measured for *Eukrohnia hamata* (0.155  $\mu\text{l O}_2 \text{ mg DM}^{-1} \text{ h}^{-1}$ ) and *E. bathypelagica* (0.151  $\mu\text{l O}_2 \text{ mg DM}^{-1} \text{ h}^{-1}$ ; Fig. 2). No significant differences were observed between species and seasons. Mass-specific oxygen consumption did not differ between specimens originating from different depths (500-750 m, 750-1000 m, 1000-1500 m).

The metabolic loss for all species during both seasons was very low with less than 1.1% of body carbon respired per day (Table 2). Due to higher carbon contents, but nearly constant respiration rates, the metabolic loss tended to be lower in winter (<0.5%).



**Fig. 2:** *Eukrohnia hamata* and *E. bathypelagica*. Oxygen consumption during winter and summer at 0°C. n: number of experiments

## Discussion

### Feeding ecology

Chaetognaths are carnivores, as indicated by a trophic level between 2.6 and 3.8 depending on the species (Hobson et al. 2002; Søreide et al. 2006). They locate their prey by sensing vibrations via sensory hairs. Fish larvae and other chaetognaths are sensed by the tail beat, although chaetognaths also respond to the lateral motion (Feigenbaum and Reeve 1977). Other plankton organisms, e.g. copepods, which create a distinct flow field in the water (Bundy and Paffenhöfer 1996, Jiang and Osborn 2004) are most readily detected (Feigenbaum and Maris 1984). Based on this fact and due to the dominance of copepods, chaetognaths feed largely on copepods. The Antarctic *Eukrohnia hamata* preys on the copepodite stages of *Calanus* spp., *Euchaeta* spp., *Metridia gerlachei* and *Rhincalanus gigas* as well as on smaller copepods like *Microcalanus pygmaeus*, *Oithona* spp. and *Oncaea* spp. (Hopkins 1985, 1987; Hopkins and Torres 1989; Øresland 1990, 1995; Froneman et al. 1998). Apart from findings of jellyfish remains and diatoms as transit food items, copepods were the most frequent food items found in the guts of *E. hamata* and *E. bathypelagica* in our study. Unfortunately, they could not be identified to species level. Diatoms were suggested to be ingested accidentally or via herbivorous prey (Feigenbaum 1991). Medusae were also assumed to be artifacts of collecting and preserving methods rather than being true prey items (David 1955; Feigenbaum 1991). These were rarely seen in chaetognaths originating from multinet samples, but frequently found in the guts of chaetognaths from RMT samples. This is supported by the observation that the RMT catches often contained jellyfish. Appendicularians, ostracods and other chaetognaths were documented in the chaetognath's diet (Øresland 1990; Froneman et al. 1998;

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Froneman and Pakhomov 1998). Few chaetognath hooks were observed in *E. hamata* guts, as well as some tintinnids, although the latter prey seems to be more common in young chaetognaths (Pearre 1981). The two acantharians found in the guts of *E. hamata* were in very good condition and therefore probably accidentally ingested by the chaetognaths, instead of being eaten via their copepod prey. To our knowledge no data exist on gut contents of the two deep-living species *E. bathypelagica* and *E. bathyantartica*. Due to several methodological constraints of the gut content analysis, that will be discussed below, these analyses provide only rough estimates of the feeding preferences.

Generally the levels of gut fullness seem to be low in chaetognaths (David 1955; Hopkins 1985, 1987; Hopkins and Torres 1989; Lancraft et al. 1991; Øresland 1995). In our investigation, the number of chaetognaths containing food in their guts ranged between 31 and 48% (FCR total) for *Eukrohnia hamata* and *E. bathypelagica*, irrespective of the state of digestion. In the Australian sector of the Southern Ocean, Johnson and Terazaki (2004) found 15.4 to 48.9% of *E. hamata* specimens with prey in their guts. In many previous studies only the identifiable contents were counted or, in the case of Froneman and Pakhomov (1998), oil droplets were also considered as gut content, which we treated separately. This makes a comparison of the data difficult. If we concentrate on the recognizable food items, generally more than 84% of *E. hamata* or *Sagitta gazellae* had no food in their guts (Øresland 1995, Froneman et al. 1998). This agrees well with our FCR values (up to 4.5% with identifiable content), when we exclude diatoms and jellyfish remains from our data. Froneman et al. (1998) found 0.02 to 0.06 prey items per *E. hamata*, Øresland (1990, 1995) 0.10 to 0.26 and 0.07 to 0.16 prey items per *E. hamata* for summer and winter, which is in the same range as our data (0.01-0.12, jellyfish remains and diatoms excluded). The mean number of prey per chaetognath (NPC) seems to be slightly higher in *Sagitta* compared to *Eukrohnia* species (Øresland 1990: *S. marri*: 0.23, *S. gazellae*: 0.26, *S. maxima*: 0.20).

Sampling methods, e.g. different gears and sampling depths, vary between the reported studies on Antarctic chaetognaths and reveal some drawbacks especially with regard to the gut content analysis. In our investigation, chaetognaths were taken from great depths, i.e. it takes several hours to retrieve the animals from 2000 m depth before preserving them in the laboratory on board ship. Two uncertainties that can also interact may be associated with such long retrieval times, progressed digestion and cod-end feeding. A digestion time of 9.3 h and of 4.9 h is assumed for large and for small copepods respectively (in *Sagitta elegans* at 6°C; Øresland 1987). In the Southern Ocean, Giesecke et al. (2009) estimated a digestion time between 9 and 15.8 h (mean 11.5 h) for *S. gazellae*, also tending to increase with large prey. Although lower temperatures in the Southern Ocean may result in longer digestion times, this process has to be taken into consideration. Cod-end feeding in plankton net hauls is considered to be another problem when applying gut content analysis (Baier and Purcell 1997). Therefore, we excluded from analyses all prey items found in the foreguts. Although cod-end feeding may not have occurred during our sampling process, such a treatment adds to the conservative approach to determine chaetognath feeding. We can also not exclude regurgitation in chaetognaths. Regurgitation and defecation might occur as a stress reaction on capturing or on preservation. Baier and Purcell (1997) presumed based on their investigations that the prey loss in chaetognath guts during sampling was rather



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due to stress-induced gut evacuation than to continued digestion. This could explain the generally low NPC values found in chaetognaths. However, we tried to reduce the stress during the catch by using large cod-ends, thus avoiding crowded samples. Nevertheless, the sampling method seems to have a strong effect on results of chaetognath feeding, and hence it is difficult to draw conclusions on seasonal and species-specific differences in diet composition and feeding activity only on the basis of gut content analyses.

Therefore, we conducted additional fatty acid trophic marker analyses to elucidate diet preferences in the two deep-living species *Eukrohnia bathypelagica* and *E. bathyantartica*. The latter species was of special interest as no identifiable prey items were found in its guts. The fatty acid 18:1(n-9) distinguishes these two chaetognaths very clearly. In *E. bathyantartica* it was a dominant component, whereas *E. bathypelagica* contained only moderate amounts of this fatty acid. As a trophic marker for carnivory (Falk-Petersen et al. 1990), 18:1(n-9) indicates a high level of carnivorous feeding in *E. bathyantartica* which is not surprising. Omnivorous and carnivorous zooplankton is generally known to have wax esters with high amounts of the 18:1(n-9) fatty acid (Lee et al. 2006). However, the ratio  $[18:1(n-9) + 20:1(n-9) + 22:1(n-9)] / [16:1(n-7) + 18:1(n-7)]$  was similar for both species. The higher this value is, i.e. the larger the amount of the three biomarkers for carnivorous feeding are, the more pronounced the degree of carnivory will be. The difference in fatty acid compositions between *E. bathypelagica* and *E. bathyantartica* rather seems to reflect different prey including copepods. The large portions of the short chain fatty alcohols 14:0 and 16:0 again support the high degree of carnivory (Lee et al. 2006) in *E. bathyantartica*. These two fatty alcohols are also major components in the fatty alcohol compositions of copepods like *Rhincalanus gigas* (Kattner et al. 1994) and *Paraeuchaeta antarctica* (Hagen et al. 1995). The fatty acids 20:1(n-9) and 22:1(n-11) and the respective alcohols are considered as biomarkers for calanid copepods such as *Calanoides acutus* (Graeve et al. 1994; Kattner and Hagen 1995). The mean amounts of these long-chain monounsaturated fatty acids were low in both chaetognath species, but the portion of the fatty alcohol 20:1(n-9) was high in *E. bathyantartica*. We can suggest that both chaetognath species feed on calanid copepods. However, *Calanus propinquus*, which produces large amounts of the unusual 22:1(n-9) fatty acid (Hagen et al. 1993), does not seem to be a preferred prey, as indicated by the low level of this fatty acid in both species. The rather high mean portions of 8% and 12% of 16:1(n-7) in *E. bathypelagica* and *E. bathyantartica* could suggest the ingestion of diatoms. However, the chaetognaths probably ingested copepods which fed on diatoms in epipelagic layers or indirectly consumed this marker via carnivorous and/or herbivorous copepods. *Paraeuchaeta antarctica* could be a potential prey species. This carnivorous copepod is known to accumulate considerable amounts of the monounsaturated fatty acid 16:1(n-7) (Hagen et al. 1995). On the other hand, 16:1(n-7) may also be a desaturation product of the fatty acid 16:0.

More detailed information on the dietary composition of the investigated chaetognath species cannot be derived from our analyses, however. Fatty acids (and fatty alcohols) only reflect the dietary composition to a certain extent. With increasing trophic levels the marker signatures may become more blurred.

**Energetics**

C:N ratios higher than 2.9 usually indicate lipid storage (Postel et al. 2000). However, the C:N ratios of the three chaetognath species in combination with the lipid levels generally show that the investigated meso- and bathypelagic chaetognaths do not store substantial amounts of lipids, as compared to e.g. polar copepods. For all three chaetognath species the mean C:N ratio was higher than 4, which is comparable to the ratios and C and N values previously reported (Omori 1969; Schneider 1990). Terazaki (1993) found a C:N ratio of 4.7 for *Sagitta elegans* in the Japan Sea. He supposed that this high ratio might be caused by body lipids, as oil droplets were observed in the intestinal tissue like in meso- and bathypelagic species (or like *Eukrohnia bathyantartica* in our study). *E. hamata* and *E. bathypelagica* also had oil droplets in their guts. These were already reported by several authors for *E. hamata* (Sameoto 1987, Øresland 1990, Froneman et al. 1998, Froneman and Pakhomov 1998). Their function is still unknown, although they are assumed to act as energy store (Kapp 1991), as buoyancy aid or maybe both (Øresland 1990). Hence, the role of these lipid droplets with regard to seasonal and breeding migrations as well as to reproduction is not understood. In both *E. hamata* and *E. bathypelagica* oil droplets were found independent of maturity stage and season.

The dominance of biomembrane fatty acids (16:0, 20:5(n-3) and 22:6(n-3)), as measured in *Eukrohnia bathypelagica*, indicates a limited dependence on lipid reserves (Graeve et al. 1997), but lipids seem to gain in importance with increasing sexual maturity of this species. The higher lipid values in summer only reflect the higher number of mature specimens investigated during this season, as ripe individuals with large ovaries filling the body cavity (maturity stage IV) had maximum lipid contents. The stage V individuals carried only empty brood sacs from which their offspring had been released. A lower lipid level in these specimens is therefore not surprising. Alvarino (1983) reported that the ovaries in this species appear to accumulate fatty tissue. Furthermore, lipid droplets are often observed in zooplankton ovaries, which may partially be transferred to developing oocytes (Lee et al. 2006). In chaetognaths, this is probably an important strategy to support the development of the offspring from oocytes to young chaetognaths that leave their parental brood sacs.

As an explanation for the breeding migration Alvarino (1964) suggested that gonad maturation may increase chaetognath density and therefore cause sinking. A higher lipid content in adult specimens could then partially balance the increased body density. In this case the lipids would act also as buoyancy aids and may cause neutral buoyancy. However, adult individuals are usually found deeper in the water column (e.g. David 1955; Hagen 1985; Kruse 2009). Consequently, there are at least two possibilities: chaetognaths sink either because the lipids cannot balance the mass increase (higher specific gravity) or because they actively swim deeper. If chaetognath density is higher, counteracting mechanisms like voluminous and gelatinous inner parts in the lateral fins as observed in *Sagitta lyra* and *S. hexaptera* (Kapp 1991) are probably not needed in the Antarctic species. As temperature and salinity vary slightly over a large depth range, they do not have to remain at a certain depth. However, stage V specimens of *Eukrohnia bathypelagica* should rise in the water column when they released their eggs, but many of them seem to stay below 1000 m (personal observation). Furthermore, the presence of young chaetognaths throughout the water column further favors the hypothesis that

they actively migrate deeper during maturation. Predator avoidance may be the key factor.

*Eukrohnia bathyantartica* showed no stage-specific differences in its lipid content. However, the lipid level was usually higher (mean 15.4% DM) than in *E. bathypelagica* (mean 11.5% DM). The insignificant differences between maturity stages may partially be explained by their less voluminous ovaries and their smaller number of ova (Kruse 2009). In addition, the brick orange gut of *E. bathyantartica* probably contains a carotenoid pigment with many small oil droplets comparable to the one found in *E. fowleri* (Terazaki 1991). This might be responsible for the relatively higher lipid content in all maturity stages of *E. bathyantartica*. Particularly zooplankton from high latitudes and great depths contain oil droplets distributed throughout the body cavity (Lee et al. 2006 and references therein). It remains obscure though, whether these carotenoids are derived from the prey, e.g. lipid-rich copepods, or whether the chaetognaths synthesise these pigments themselves. Terazaki et al. (1977) suggested for *E. fowleri* and *Sagitta macrocephala* that the carotenoids of the intestinal tissue are produced by the chaetognaths, because these carotenoids have a unique character differing from that of phytoplankton and copepods.

Wax esters were a major component of the lipids in *Eukrohnia bathyantartica* (45.5% TL). They are considered as efficient long-term energy reserves and also serve as buoyancy aid due to their very low density (Hagen 2000). Lee et al. (1971) found a high wax ester content of 34% and 71% TL for unidentified deep-living subtropical chaetognaths with an orange colored gut (probably of the genus *Eukrohnia*). In a second study in the central South Pacific (Lee and Hirota 1973), *Eukrohnia* sp. with an orange colored gut contained a distinctly lower wax ester content with 26% TL. The intestinal oil droplets observed in *E. bathyantartica* may contain wax esters that are missing in species like *E. hamata* or *E. bathypelagica*. For instance a wax ester content of 12% TL was reported for *E. hamata* from the Arctic (TL: 19% DM, Lee 1975), which is comparable to the percentage found in *E. bathypelagica*. Contrary to Lee's data, Hagen (1988) reported wax ester contents up to 40% in *E. hamata* (34.4-39.7%), but slightly lower lipid contents between 11.6 and 14.6% DM. We conclude though that truly bathypelagic species like *E. bathyantartica* probably contain higher amounts of wax esters and rely more on long-term energy reserves, in contrary to species also inhabiting mesopelagic layers like *E. hamata* and *E. bathypelagica*.

*Eukrohnia hamata* and *E. bathypelagica* respired  $0.15 \mu\text{l O}_2 \text{ mg DM}^{-1} \text{ h}^{-1}$  on average. Seasonal differences are not expected due to an assumed year-round activity and feeding at meso- and bathypelagic depths. Our respiration data fit nicely in the range of  $0.10$  to  $0.21 \mu\text{l O}_2 \text{ mg DM}^{-1} \text{ h}^{-1}$  measured for *E. hamata* in Kosterfjorden, western Norway (chaetognaths from 0-200 m depth; Båmstedt 1979). However, this author measured highest respiration rates in spring (May) and lowest rates in winter (February) which we cannot confirm. Båmstedt (1979) additionally reported a respiration rate at  $6^\circ\text{C}$  of  $0.11 \mu\text{l O}_2 \text{ h}^{-1}$  and  $0.86 \mu\text{l O}_2 \text{ h}^{-1}$  per individual *E. bathypelagica* and *E. hamata*, respectively. Our experiments at  $0^\circ\text{C}$  revealed consumption rates of  $0.36$  and  $0.44 \mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ . The difference between the two chaetognath species was more pronounced in Norway, however respiration rates were still in the same range. Data from Thuesen and Childress (1993) for *E. hamata* support our data very well. They measured oxygen consumption rates between  $0.3$  and  $0.5 \mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$  (converted

values) at 5°C in summer. Slight changes between the data may be attributable to the smaller number of experiments and individuals compared to our study and to the different temperatures (Kruse et al. submitted). Previous investigations showed that hydrostatic pressure seems to have only little effect on the metabolic activity of chaetognaths (Thuesen and Childress 1993). These authors observed no significant differences in metabolic rates at 1 and at 101 atm. During our study, oxygen consumption rates were measured at normal surface pressure on chaetognaths mostly originating from 500 to 1000 m depth, with no significant differences between the sampled strata.

Chaetognaths were usually inactive during the experiments. Consequently, our respiration rates may be underestimations considering higher animal activities *in situ*. Thuesen and Childress (1993) reported that chaetognaths have active periods when they search for food or for reproductive partners, and periods of inactivity. Our data may therefore be a good estimate of inactive periods, i.e. basic metabolism.

In consequence of the respiration values, the daily body carbon respired is probably underestimated as well. Our calculated data suggest between 0.45 and 1.1% of body carbon respired per day, which is very low. However, they are similar to data presented for the Antarctic species *Sagitta gazellae* with an average metabolic loss of 0.73% at 0°C (Ikeda and Kirkwood 1989). Metabolic losses of other chaetognaths appear to be higher, e.g. 1.93% for *S. elegans* (converted data from Ikeda and Skjoldal 1989 in Ikeda and Kirkwood 1989). Other Antarctic zooplankton species, e.g. amphipods, copepods and euphausiids, usually have higher daily metabolic losses, varying from 0.44 to 2.75% (at -0.8 to -1.4°C; Ikeda and Mitchell 1982). As our data are in agreement with Ikeda and Kirkwood's data (1989), Antarctic chaetognaths may differ from other zooplankton species in this respect.

### Conclusions

At meso- and bathypelagic depths, *Eukrohnia bathypelagica* and *E. bathyantartica* are suggested to exhibit different modes of feeding and lipid storage. *E. bathypelagica* was characterized by a lower but stage-dependent lipid level, whereas *E. bathyantartica* contained a higher relative amount of total lipids and significant amounts of wax esters. Therefore, lipid storage may be more important in *E. bathyantartica* than in *E. bathypelagica*. Lipid storage was at a medium level during summer and winter in both species, indicating the presence of year-round feeding. In meso- and bathypelagic layers, feeding conditions for chaetognaths are even better in winter, when many copepods overwinter in these layers (Schnack-Schiel and Hagen 1994; Hagen 1999; Auel and Hagen 2005; Laakmann et al. 2009). Based on our analyses of gut contents, fatty acids and respiration, we assume all three *Eukrohnia* species, including *E. hamata*, to be primarily predators of copepods (e.g. calanid copepods and *Paraeuchaeta antarctica*), with generally low oxygen consumption rates and carbon requirements (standard metabolism). Similar fatty acid compositions during summer and winter probably reflect a basically unchanged prey composition. The role of lipids, also in terms of oil droplets, remains unclear. We argue that they could act as buoyancy control as well as energy store in chaetognaths.

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## 5. PUBLICATION III

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## **6. PUBLICATION IV**

### **The role of midwater chaetognaths in Southern Ocean pelagic energy flow**

Svenja Kruse\*, Thomas Brey, Ulrich Bathmann

Alfred Wegener Institute for Polar and Marine Research,  
Am Handelshafen 12,  
D-27570 Bremerhaven, Germany

\*corresponding author:

E-mail: [Svenja.Kruse@awi.de](mailto:Svenja.Kruse@awi.de)

Phone: + 49-471-48311688

Fax: + 49-471-48311149

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### **Abstract**

We estimate the energy flow through meso- and bathypelagic chaetognaths in the Atlantic sector of the Southern Ocean from (1) depth structured chaetognath abundance and body mass data, (2) a general chaetognath respiration model driven by body mass, temperature, water depth and taxon, and (3) published relationships between respiration, production and consumption in chaetognaths. In the 500 to 2000 m depth layer, chaetognath respiration and consumption amount to  $0.28 \text{ g C m}^{-2} \text{ y}^{-1}$  and  $0.56 \text{ g C m}^{-2} \text{ y}^{-1}$ , respectively. Thus, Antarctic midwater chaetognaths consume 0.05% of the copepod standing stock per day or 1% of the daily copepod production in summer. About 2.8% (=  $1.9 \text{ g C m}^{-2} \text{ y}^{-1}$ ) of the annual primary production is required to fuel the midwater chaetognath community via herbivorous copepods. When assuming a 1:1 diet of herbivorous and carnivorous copepods, this share increases to 6.1% (=  $4.1 \text{ g C m}^{-2} \text{ y}^{-1}$ ) of annual primary production. For the whole water column a chaetognath consumption of  $1.7 \text{ g C m}^{-2} \text{ y}^{-1}$  can be estimated. This corresponds to 8.4% (=  $5.6 \text{ g C m}^{-2} \text{ y}^{-1}$ ) and 18.2% (=  $12.2 \text{ g C m}^{-2} \text{ y}^{-1}$ ) of the primary production channeled through herbivorous copepods and through herbivorous and carnivorous copepods, respectively.

**Key words:** Chaetognatha, Antarctica, Midwater, Respiration, Energy budget

### **Introduction**

Chaetognaths are found in all marine habitats, from epipelagic layers to the seafloor. The biomass of these carnivores is estimated to be between 20 and 30% of that of copepods, their principal prey, in the world ocean (Reeve 1970). There is a considerable amount of information on chaetognath feeding ecology, i.e. gut content analyses together with estimates of digestion time and feeding rates (e.g. Sameoto 1987; Falkenhaug 1991; Øresland 1990; Froneman et al. 1998; Giesecke and González 2004), as well as on chaetognath individual metabolism, i.e. respiration measurements (e.g. Reeve et al. 1970; Sameoto 1972; Båmstedt 1979; Welch et al. 1996). However, we know little about the metabolism of Antarctic deep-sea chaetognaths and only few studies have been conducted so far on individual metabolic activity in Antarctic chaetognaths (Ikeda and Kirkwood 1989; Thuesen and Childress 1993; Kruse et al. submitted). The daily metabolic loss of Antarctic chaetognaths is indicated to be lower compared to other chaetognath species at similar temperatures and to other Antarctic zooplankton (Ikeda and Kirkwood 1989; Kruse et al. submitted). Hence, one might ask whether the overall significance of chaetognaths in the Antarctic pelagic food web, particularly their impact on the copepod community, is lower, too. So far, our view on the Antarctic meso- and bathypelagic chaetognath community is rather static, i.e. largely limited to information on taxonomy, abundance and biomass. There are few studies with reasonable resolution in time and space, and most of these are limited to the epi- and mesopelagic realm (e.g. Hagen 1985; Terazaki 1989; Duró et al. 1999; Johnson and Terazaki 2004). The meso- and bathypelagic part of the Antarctic chaetognath community has been studied in detail by Kruse et al. (2009). Their findings indicate that Antarctic midwater chaetognaths may constitute a significant vector in pelagic energy flow.

The present study intends to quantify this ecological impact of Antarctic midwater chaetognaths by combining (1) field data on abundance and body mass with (2) a general chaetognath respiration model derived from published data and own measurements, and (3) published relationships between respiration, production and consumption in chaetognaths.

## Material and methods

### Field sampling

During Antarctic winter 2006 (17 June - 21 August 2006, ANT 23-6) and Antarctic summer 2007/2008 (28 November 2007 - 04 February 2008, ANT 24-2) two expeditions with the RV "Polarstern" were carried out in the Lazarev Sea. The study area was located between 60°-70°S and 3°W-3°E (see Kruse et al. 2009), except for two stations at 52°S 0°E in summer. Twenty-eight stations were sampled with a multinet (MN, 100 µm mesh size; 0.25 m<sup>2</sup> mouth area) in winter, 15 stations in summer. The following standard depth intervals were applied: 2000-1500-1000-750-500-0 m. For further sampling details see Kruse et al. (2009). Additionally, a rectangular midwater trawl (RMT 8: 4.5 mm mesh size, 8 m<sup>2</sup> mouth area; RMT 1: 320 µm mesh size, 1 m<sup>2</sup> mouth area) and a multiple RMT (equipped with three RMT 8 and three RMT 1 nets) were deployed at a few stations during both seasons (Table 1).

**Table 1:** Southern Ocean stations sampled with RMT

Date	Time (UTC)	Latitude	Longitude	Sampling depth
Winter (RMT)				
23.07.06	11:40	61°58.48'S	0°01.56'W	0- ~3000 -0 m
10.08.06	15:18	60°01.31'S	0°00.93'W	0- ~3000 -0 m
13.08.06	01:34	59°54.31'S	2°52.70'E	0- ~3000 -0 m
Summer (multiple RMT)				
03.01.08	07:36	64°28.73'S	2°52.24'E	500-750-1500-1900 m
21.01.08	10:45	62°59.88'S	0°01.18'E	500-1000-2000-2500 m
23.01.08	08:03	59°59.82'S	0°03.24'W	500-1000-2000-2500 m
26.01.08	11:51	52°12.08'S	0°00.23'E	0-1000-1500-2000 m

### Carbon content

Intact chaetognaths of the six species *Eukrohnia bathyantartica*, *E. bathypelagica*, *E. hamata*, *Sagitta gazellae*, *S. marri* and *S. maxima* were selected from the MN and RMT samples. The individuals were sized under a stereomicroscope (Olympus SZX12) to the nearest 0.5 mm (head to tail, excluding tail fin) and immediately frozen at -80°C. Upon return to Alfred Wegener Institute, the chaetognaths were freeze dried for about 24 h and weighted on a Sartorius microbalance (Genius series). Subsequently, the carbon content of the complete animal or of a subsample of pestled animals (weighted on a microbalance Sartorius supermicro 4504 MP8) was determined in a Euro EA Elemental Analyzer. 584 measurements, 328 during winter and 256 during summer, were made in total. Seasonal differences in carbon content

were analyzed by a non-parametric Mann-Whitney-U test for each species ( $\alpha = 0.05$ ).

### Biomass calculation

We tested for differences in carbon content between species by means of analysis of covariance (ANCOVA) (carbon content vs. species and body length as covariate) and a subsequent *post-hoc* Tukey HSD test on differences between means ( $\alpha = 0.05$ , Sokal and Rohlf 1981). Subsequently, we established a multiple linear model of the form

$$\log(C) = a + X_{Taxon1} + b * \log(L) + X_{Taxon2} * [\log(L) - L_{Mean}] \quad (1)$$

to estimate carbon content  $C$  ( $\mu\text{g ind}^{-1}$ ) from body length  $L$  (mm) and taxon specific variables  $X_{Taxon1}$  and  $X_{Taxon2}$  for each taxon. Please note that  $\log(L)$  is adjusted to mean = zero in the interaction term ( $L_{Mean}$ ) in order to make the test for the main effects independent of the test for interaction (“centered polynomials”).

Chaetognath biomass ( $\mu\text{g C m}^{-3}$ ) was then calculated from chaetognath length and abundance (Kruse et al. 2009) for each depth interval and station. A full factorial two-way ANOVA (biomass versus season and depth and season x depth) with subsequent *post-hoc* test on differences between means was applied to check for effects of season and depth on biomass. Prior to this analysis the data were Box-Cox transformed to achieve normality and homogeneity of variances.

### Respiration rate measurements

Respiration rates of *Sagitta gazellae* (caught by RMT in 500 to 1000 m water depth at 64°28.73'S 2°52.24'E) were measured using Winkler titration to determine oxygen concentration as described in Kruse et al. (submitted) for *Eukrohnia hamata* and *E. bathypelagica*. In contrast to Kruse et al. (submitted), two specimens of *S. gazellae* were incubated in each one litre sealed glass bottle filled with filtered (0.7  $\mu\text{m}$  pore size) and oxygen-saturated seawater. For this species, we conducted one experiment with five replicates and two controls without chaetognaths.

### Respiration model

To predict chaetognath respiration from body mass, taxon and environmental parameters, we established a multiple linear model of the form

$$\log(R) = a + b_1 * \log(M) + b_2 / T + b_3 * \log(D) + X_{Taxon} \quad (2)$$

where  $R$  is the respiration rate (Joule/day),  $M$  is the body mass (Joule),  $T$  is the water temperature (Kelvin),  $D$  is the water depth (m), and variable  $X_{Taxon}$  attains a taxon specific value. This model was fitted using our data on *Sagitta gazellae* as well as data from Kruse et al. (submitted), Reeve et al. (1970), Nival et al. (1972), Ivleva (1976), Båmstedt (1979), Ikeda (1989), Ikeda and Kirkwood (1989), Ikeda and Skjoldal (1989), Thuesen and Childress (1993), Welch et al. (1996), Ikeda and Hirakawa (1998), Coston-Clements et al. (2009). The data published by Sameoto (1972) were not used because an *a priori* analysis showed that these values differed consistently and significantly from all other sources, indicating a source specific bias. Respiration and body mass data were converted to Joule/day and Joule respectively by means of general factors summarized in Brey (2001) and Brey et al. (submitted). Multivariate outliers in the sample space [ $\log(M)$ ,  $1/T$ ,  $\log(R)$ ] were identified by Mahalanobis Jackknife

distances (Barnett and Price 1995) and excluded from the model construction. *Heterokrohnia* sp. was included in the family Eukrohniidae, as this was the only data point for the family Heterokrohniidae (following the classification of Casanova 1985).

### Annual respiration and consumption

The respiration rate ( $J \text{ day}^{-1}$ ) of each single individual of all stations during both Antarctic cruises was estimated using the respiration model. From this data base, we inferred the daily chaetognath respiration rate per  $\text{m}^3$  for both seasons and the annual rate per  $\text{m}^2$  for the different depth intervals in the investigated area. By means of a full factorial two-way ANOVA (see above; respiration rate versus season and depth and season x depth) we tested for seasonal and vertical differences in chaetognath respiration.

We used published data on chaetognath assimilation efficiency ( $A/C$ ) of 0.8 (Casper and Reeve 1975, Nagasawa 1985) and gross growth efficiency ( $P/C$ ) of 0.3 (Reeve 1970, Nagasawa 1984, Straile 1997) to estimate total chaetognath energy demand ( $\text{g C m}^{-2} \text{ y}^{-1}$ ;  $1 \text{ g C} = 45.7 \text{ kJ}$ , Salonen et al. 1976). These data indicate that chaetognath consumption is about twice as high as respiration, i.e.:

$$Q_{\text{Chaeto}} = R_{\text{Chaeto}} / (0.8 - 0.3) \quad [\text{g C m}^{-2} \text{ y}^{-1}] \quad (3)$$

To further estimate the amount of primary production  $PP$  that is required to maintain the chaetognath community through its principal food source, pelagic copepods, we used a copepod gross growth efficiency of 0.3 (Landry and Calbet 2004). We assumed that the average chaetognath diet consists either of 100% herbivorous copepods or of 50% herbivorous and 50% carnivorous copepods, as the latter may account for an essential part of the deep living chaetognaths diet:

$$PP_{\text{Chaeto}} = Q_{\text{Chaeto}} / 0.3 \quad \text{and} \quad (4)$$

$$PP_{\text{Chaeto}} = 0.5 * Q_{\text{Chaeto}} / 0.3 + 0.5 * Q_{\text{Chaeto}} / 0.3 / 0.3 \quad [\text{g C m}^{-2} \text{ y}^{-1}] \quad (5)$$

## Results

### Chaetognath biomass

Body length ( $P < 0.0001$ ), taxon ( $P < 0.0001$ ) and the interaction between these two parameters ( $P < 0.0001$ ) affect chaetognath carbon content. Test runs with different taxonomic resolution indicated that the separation into the three groups *Eukrohnia* spp., *Sagitta marri* and other *Sagitta* spp. generated the best tradeoff between model accuracy and model generality:

$$\log(C) = -1.1596 + X_{\text{Taxon1}} + 2.9969 * \log(L) + X_{\text{Taxon2}} * [\log(L) - 1.3898] \quad (6)$$

with  $N = 584$  (six species, Table 2),  $R^2 = 0.874$  and  $P < 0.0001$  for the whole model.  $X_{\text{Taxon1}} = +0.0498$  for *Eukrohnia* spp.,  $+0.1956$  for *S. marri* and  $-0.2454$  for *Sagitta* spp;  $X_{\text{Taxon2}} = +0.4756$  for *Eukrohnia* spp.,  $+0.1283$  for *S. marri* and  $-0.6040$  for *Sagitta* spp. Length specific carbon content was therefore highest in *S. marri*, followed by *Eukrohnia* spp. and *Sagitta* spp. The latter group includes the large *Sagitta* species *S. gazellae* and *S. maxima*. Hence, we used the *S. marri* parameter values to estimate carbon content of small unidentified *Sagitta*.

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**Table 2:** Carbon content ( $\mu\text{g C mg DM}^{-1}$ ,  $\pm$  sd, number of measurements in brackets) of six chaetognath species during summer and winter in the Southern Ocean

Species	Carbon content [ $\mu\text{g C mg DM}^{-1}$ ]	
	Summer	Winter
<i>Eukrohnia bathyantartica</i> <sub>a</sub>	324.33 $\pm$ 48.72 (42)	424.30 $\pm$ 70.82 (35) <sub>1</sub>
<i>Eukrohnia bathypelagica</i> <sub>a</sub>	246.23 $\pm$ 72.14 (40)	312.96 $\pm$ 89.38 (43) <sub>1</sub>
<i>Eukrohnia hamata</i> <sub>a</sub>	303.61 $\pm$ 76.53 (72)	393.54 $\pm$ 60.99 (179) <sub>1</sub>
<i>Sagitta gazellae</i>	319.12 $\pm$ 64.69 (40)	274.04 $\pm$ 36.92 (27) <sub>1</sub>
<i>Sagitta marri</i>	313.93 $\pm$ 48.17 (45)	387.34 $\pm$ 79.40 (44) <sub>1</sub>
<i>Sagitta maxima</i>	336.14 $\pm$ 37.42 (17)	-

a: for detailed data on the biochemical composition see Kruse et al. (submitted)

1: significantly different from summer value at  $P < 0.05$

By means of the abundance data of Kruse et al. (2009) we estimated an average midwater (500 to 2000 m) chaetognath biomass of  $0.109 \text{ mg C m}^{-3}$  in summer and  $0.146 \text{ mg C m}^{-3}$  in winter (Table 3). The average biomass was significantly higher in winter than in summer ( $P < 0.01$ ) and significantly higher in the 500 to 750 m depth range compared to deeper strata in general ( $P < 0.01$ ). Integrated over seasons and water depth, average midwater chaetognath biomass amounts to  $199.9 \text{ mg C m}^{-2}$  (sd = 67.2).

**Table 3:** Biomass ( $\mu\text{g C m}^{-3}$ ,  $\pm$  sd) and oxygen consumption ( $\mu\text{g C m}^{-3} \text{ day}^{-1}$ ,  $\pm$  sd, number of multinet stations in brackets) of chaetognaths in different depth intervals during summer and winter in the Southern Ocean (obtained with equations 6 and 7)

	Biomass [ $\mu\text{g C m}^{-3}$ ]		Oxygen consumption [ $\mu\text{g C m}^{-3} \text{ day}^{-1}$ ]	
	Summer	Winter	Summer	Winter
500-750 m	250.2 $\pm$ 119.0 (15)	268.6 $\pm$ 112.5 (28)	1.33 $\pm$ 0.55	1.18 $\pm$ 0.55
750-1000 m	116.4 $\pm$ 56.7 (15)	142.9 $\pm$ 104.1 (28)	0.50 $\pm$ 0.21	0.58 $\pm$ 0.42
1000-1500 m	57.1 $\pm$ 31.2 (15)	118.8 $\pm$ 46.7 (27)	0.22 $\pm$ 0.11	0.42 $\pm$ 0.17
1500-2000 m	85.6 $\pm$ 49.6 (14)	112.2 $\pm$ 65.0 (27)	0.24 $\pm$ 0.08	0.32 $\pm$ 0.15
mean	109.2 $\pm$ 37.5 (14)	145.7 $\pm$ 43.7 (27)	0.46 $\pm$ 0.12	0.54 $\pm$ 0.16

### Respiration model

*Sagitta gazellae*, the single species measured during this study, respired  $0.556 \mu\text{l ind}^{-1} \text{ h}^{-1}$  ( $N = 5$ , sd = 0.176) or  $0.011 \text{ J ind}^{-1} \text{ h}^{-1}$ . Including these data, the data base for the general chaetognath respiration model consisted of 466 measurements referring to 14 species (3 of them identified to genus only). Mahalanobis distances identified 23 outliers, thus reducing the data matrix to 443 data sets (Table 4). Trial runs at different taxonomic resolution (*species*, *family*, *none*) indicated that the parameter *family* provided the best tradeoff between model accuracy and model generality:

$$\log(R) = 10.0264 + 0.6643 * \log(M) - 2957.858/T - 0.3870 * \log(D) + X_{Taxon} \quad (7)$$

with  $N = 443$ ,  $R^2 = 0.832$  and  $P < 0.0001$  for the whole model as well as for each term; with  $X_{Taxon} = +0.1212$  for Eukrohniidae and  $X_{Taxon} = -0.1212$  for Sagittidae. Respiration generally increases with increasing body mass, rising temperature and decreases with increasing depth (Fig. 1). Eukrohniidae have

higher rates than Sagittidae. The respiration rates at low temperatures e.g. 0°C or 273 K increase only slightly with higher body mass compared to chaetognaths at higher temperatures, where a strong increase can be observed. The random distribution of residuals (Fig. 2) indicates that model accuracy is independent of respiration magnitude, i.e. the model has no obvious bias.

### Respiration, grazing upon copepods and indirect impact on primary production

Mean oxygen consumption between 500 and 2000 m depth accounted for 0.46  $\mu\text{g C m}^{-3} \text{ day}^{-1}$  in summer and 0.54  $\mu\text{g C m}^{-3} \text{ day}^{-1}$  in winter (Table 3). Highest rates were found in the 500 to 750 m layer. The respiration rates in the two strata below 1000 m were lowest and did not differ significantly ( $P > 0.05$ ).

Annually, 282  $\text{mg C m}^{-2}$  oxygen are respired by chaetognaths in our investigated area, again with highest rates of 112  $\text{mg C m}^{-2} \text{ y}^{-1}$  between 500 and 750 m depth (Table 5). The corresponding chaetognath consumption is estimated to 563  $\text{mg C m}^{-2} \text{ y}^{-1}$ , and the amount of primary production to maintain this consumption through the copepod food link is about 1877  $\text{mg C m}^{-2} \text{ y}^{-1}$  (100% herbivores) or 4068  $\text{mg C m}^{-2} \text{ y}^{-1}$  (50% herbivores and 50% carnivores). A 1% increase of the share of carnivorous copepods in the diet requires about 2.3% more primary production.

**Table 4:** Taxonomic distribution of chaetognath respiration data used for the construction of the general chaetognath respiration model (reduced by 23 outliers). Sources: 1. Reeve et al. (1970), 2. Ivleva (1976), 3. Båmstedt (1979), 4. Ikeda (1989), 5. Ikeda and Kirkwood (1989), 6. Ikeda and Skjoldal (1989), 7. Thuesen and Childress (1993), 8. Welch et al. (1996), 9. Ikeda and Hirakawa (1998), 10. Coston-Clements et al. (2009), 11. Kruse et al. (submitted) and this study. Species are listed by name as mentioned by the authors

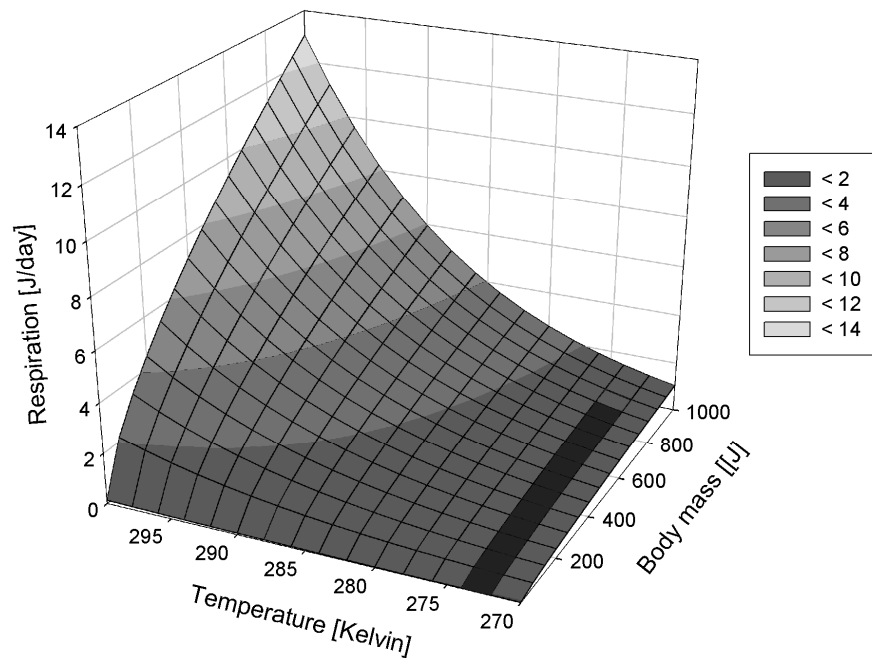
Species	Family	N
<i>Caecosagitta macrocephala</i> <sup>7</sup>	Sagittidae	9
<i>Eukrohnia bathypelagica</i> <sup>11</sup>	Eukrohniidae	13
<i>Eukrohnia hamata</i> <sup>3, 11</sup>	Eukrohniidae	96
<i>Eukrohnia</i> sp. <sup>7</sup>	Eukrohniidae	11
<i>Flaccisagitta</i> sp. <sup>7</sup>	Sagittidae	1
<i>Heterokrohnia</i> sp. <sup>7</sup>	Heterokrohniidae	1
<i>Parasagitta elegans</i> <sup>8</sup>	Sagittidae	77
<i>Pseudosagitta</i> sp. <sup>7</sup>	Sagittidae	15
<i>Sagitta elegans</i> <sup>3, 4, 5, 6, 9</sup>	Sagittidae	16
<i>Sagitta gazellae</i> <sup>4, 5, 11</sup>	Sagittidae	43
<i>Sagitta hispida</i> <sup>1</sup>	Sagittidae	26
<i>Sagitta tenuis</i> <sup>10</sup>	Sagittidae	15
<i>Sagitta</i> sp. <sup>2, 7</sup>	Sagittidae	108
<i>Solidosagitta zetesios</i> <sup>7</sup>	Sagittidae	12
Total		443



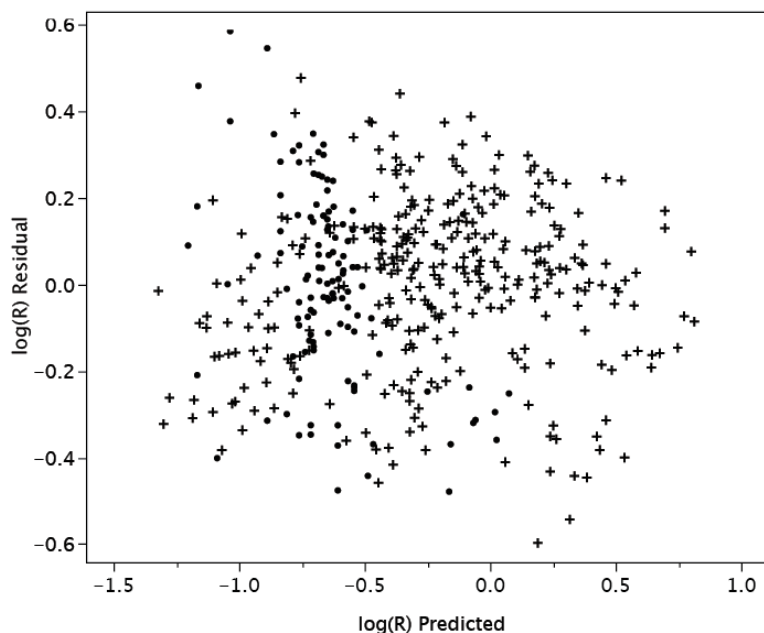
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**Table 5:** Integrated annual respiration  $R$  ( $\text{mg C m}^{-2} \text{y}^{-1}$ ) and corresponding annual carbon consumption  $Q$  ( $\text{mg C m}^{-2} \text{y}^{-1}$ ), as well as annual primary production  $PP$  ( $\text{mg C m}^{-2} \text{y}^{-1}$ ) consumed by chaetognaths in the Southern Ocean.  $n$  = number of mutlinet stations

Depth range	$n$	$R$ [ $\text{mg C m}^{-2} \text{y}^{-1}$ ]	$Q$ [ $\text{mg C m}^{-2} \text{y}^{-1}$ ]	$PP$ [ $\text{mg C m}^{-2} \text{y}^{-1}$ ]	PP- 50% carnivorous copepods [ $\text{mg C m}^{-2} \text{y}^{-1}$ ]
500-750 m	43	112	225	749	1624
750-1000 m	43	51	101	338	732
1000-1500 m	42	64	128	426	924
1500-2000 m	41	54	108	360	779
500-2000 m	41	282	563	1877	4068



**Fig. 1:** 3-D mesh plot of whole body respiration (J/d) versus body mass (J) and temperature (Kelvin) in chaetognaths according to the model  $\log(R) = 10.0264 + 0.6643 \cdot \log(M) - 2957.858/T - 0.3870 \cdot \log(D) + X_{Taxon}$ . Water depth is set to 500 m and taxon effects are neglected, i.e.  $X_{Taxon} = 0$ . The area between 272 and 274 Kelvin coloured in dark grey indicates respiration rates to be expected for Southern Ocean chaetognaths at 500 m water depth



**Fig. 2:** Plot of residual versus estimated  $\log(R)$  of the general chaetognath respiration model  
 $\log(R) = 10.0264 + 0.6643 \cdot \log(M) - 2957.858/T - 0.3870 \cdot \log(D) + X_{Taxon}$ ,  
 $N = 443$ ,  $R^2 = 0.832$ ,  $P < 0.0001$ ;  $X_{Taxon} = +0.1212$  for Eukrohniidae and  
 $X_{Taxon} = -0.1212$  for Sagittidae. (• Sagittidae, + Eukrohniidae)

## Discussion

### Chaetognath biomass distribution

In the upper 300 m of the Atlantic sector of the Southern Ocean, chaetognaths comprise 5 to 30% of zooplankton abundance and biomass (Pakhomov et al. 2000), with *Eukrohnia hamata* and *Sagitta gazellae* being the dominant species. In our investigation area, this corresponds to a summer chaetognath biomass of up to about 5000  $\mu\text{g}$  dry mass (DM)  $\text{m}^{-3}$  (Pakhomov et al. 2000). Lower values are reported from the Weddell Sea, 580  $\mu\text{g}$  DM  $\text{m}^{-3}$  (0-300 m, oceanic community, Boysen-Ennen et al. 1991) and the Croker Passage,  $<3$   $\mu\text{g}$  DM  $\text{m}^{-3}$  (0-1000 m, *E. hamata* and *S. marri*, Lancraft et al. 2004), but this variability may reflect geographical differences, year-to-year variability and sampling gear effects. To obtain an estimate of average annual chaetognath biomass in the 0 to 300 m stratum of the Lazarev Sea, we multiplied Pakhomov's et al. (2000) summer data by the factor 0.5, i.e. presuming high sampling efficiency of the 300  $\mu\text{m}$  bongo net applied (compared to RMT sampling) and generally higher summer biomass. Hence, annual average biomass in the 0-300 m layer is 2500  $\mu\text{g}$  DM  $\text{m}^{-3}$ , corresponding to 825  $\mu\text{g}$  C  $\text{m}^{-3}$  (average C/DM = 0.33, Table 2). In the 500 to 2000 m range, we measured 133  $\mu\text{g}$  C  $\text{m}^{-3}$  (annual mean, Table 3). Integrated across the water column, chaetognath biomass amounts to about 413 mg C  $\text{m}^{-2}$  in the 0 to 500 m range and to 200 mg C  $\text{m}^{-2}$  in the 500 to 2000 m range, i.e. about one third (33%) of total chaetognath biomass is situated in the mesopelagic and bathypelagic realm; and we assume a corresponding depth distribution of chaetognath metabolic activity (see below).

Within the meso-/bathypelagic region, chaetognath biomass decreases with depth and is higher in winter than in summer (Table 3). Nevertheless, winter abundance was lower in the 500 to 750 m layer, thus the higher biomass in

winter owing to the presence of larger and more developed *Eukrohnia hamata* (Kruse et al. 2009).

The share of chaetognaths in total midwater zooplankton of the Southern Ocean can be estimated only. We know that copepod biomass decreases from epipelagic layers to 1000 m in summer (Schnack-Schiel et al. 1998) and probably continues to decrease towards bathypelagic depths. However, reliable quantitative data on copepods and other zooplankton below 1000 m are rare for the Southern Ocean.

### **Chaetognath respiration**

Our respiration model (Fig. 1) represents an unbiased predictor of chaetognath metabolic rate, with an accuracy that is comparable to other models with similar taxonomic resolution (e.g. Clarke and Johnston 1999; Larson 1987; Seibel 2007; Warwick and Price 1979). Of concern, however, is the distinctly negative effect of water depth on respiration in our model (equation 7). A negative effect of depth on mass specific respiration has been observed in several taxa across a much wider depth range, e.g. Torres et al. (1979), Childress et al. (1990), Thuesen and Childress (1993). Regarding our model, it remains unclear whether this is a residual temperature effect (Thuesen and Childress 1993), a true physiological adaptation (Drazen and Seibel 2007), or just an artifact. For instance, Kruse et al. (submitted) did not find a significant depth effect on respiration rates of *Eukrohnia hamata* and *E. bathypelagica*, albeit rates were measured at normal surface pressure. We think that the apparent depth effect in our model may mask effects of the interplay between species-specific depth distribution and species-specific size range. Thus, the model provides a reasonable estimate of respiration rate for chaetognaths in general, but rather not for a distinct species.

### **Chaetognath energy budget**

It is well established that copepods are the principal food item of chaetognaths. In the Antarctic chaetognaths *Eukrohnia hamata* and *Sagitta gazellae* copepods constitute about 96% and 58% of the diet (Froneman et al. 1998), and in the meso- and bathypelagic *S. zetesios* they account for 72% (North Pacific and Sagami Bay, Japan; Terazaki and Marumo 1982). Other zooplankton, e.g. ostracods, appendicularians and even chaetognaths themselves are usually less important. Thus, considering just copepods as food may be a reasonable simplification in a first attempt to establish a chaetognath community energy budget.

What is the actual impact of midwater chaetognaths on copepod population dynamics? Copepod integrated biomass amounts to 3150 mg C m<sup>-2</sup> for the 500 to 2000 m depth range in summer (derived from the data of Schnack-Schiel et al. 1998), and the corresponding copepod production in this season is about 157.5 mg C m<sup>-2</sup> d<sup>-1</sup>, assuming a daily production rate of 5% (Voronina 1984 in Froneman et al. 1998) and a uniform copepod size composition. Thus, predation by meso- and bathypelagic chaetognaths, 1.5 mg C m<sup>-2</sup> d<sup>-1</sup> (563.2/365, Table 5), corresponds to 0.05% of the copepod standing stock per day in summer, or to 0.98% of copepod daily production. These estimates are rather conservative for two reasons. On the one hand, metabolism and hence energy demand of free living chaetognaths may be distinctly higher than under the restraining conditions of respiration measurement vessels. Previous studies

have shown, for instance, that active metabolism oxygen consumption is about twice as high in crustaceans (Vinberg 1950). On the other hand, by integrating down to 2000 m water depth, we overestimate the copepod biomass at depth, as observations by Schnack-Schiel et al. (1998) indicate that less than 5% of the copepod biomass between 0 and 1000 m depth may be located below 300 m in summer. Therefore, predation impact may be considerably higher on that part of the copepod community accessible for meso- and bathypelagic chaetognaths, and may attain magnitudes comparable to values reported for the epipelagic realm. Published values for Antarctic chaetognath daily consumption in the upper pelagic range between about 0.1 and 5.2% of prey standing stock (*Eukrohnia hamata*: Øresland 1995; *E. hamata* or *Sagitta gazellae*: Froneman and Pakhomov 1998; *E. hamata* and *S. gazellae*: Froneman et al. 1998) and between 7 and 103% of prey production in number (*E. hamata* or *S. gazellae*: Froneman and Pakhomov 1998; *E. hamata* and *S. gazellae*: Froneman et al. 1998).

The winter situation at meso- and bathypelagic depths might be different. In winter, the number of copepods increases at greater depths due to seasonal downward migration (e.g. Schnack-Schiel and Hagen 1994; Atkinson and Sinclair 2000) and production rate is probably much lower at this time of the year (1% daily production rate, Voronina 1984 in Froneman et al. 1998). Chaetognaths also exhibit seasonal vertical migrations (David 1958; Hagen 1999; Kruse et al. 2009). If chaetognaths feed throughout the year, as we assume (Hagen 1999; Kruse et al. submitted), they may have a higher predation impact on the copepod standing stock in winter than in summer.

On an annual basis,  $1.9 \text{ g C m}^{-2} \text{ y}^{-1}$  of primary production are required to maintain the midwater chaetognath community via herbivorous copepods, corresponding to about 2.8% of total primary production ( $67 \text{ g C m}^{-2} \text{ y}^{-1}$  in the pelagic province of the Weddell Sea, Arrigo et al. 2008). If chaetognaths feed on carnivorous copepods, too, as reported for *Euchaeta* spp. (Hopkins 1985; Øresland 1990) this share may increase substantially, up to  $4.1 \text{ g C m}^{-2} \text{ y}^{-1}$  or 6.1% when carnivorous copepods comprise 50% of the diet. Even if the actual contribution of carnivorous copepods to the diet is between 0 and 50%, chaetognaths may play a significant role as consumers in the ecosystem. If we scale up these budget calculations to the whole water column by applying a biomass factor of 2 for the upper 500 m (albeit neglecting the depth effect on respiration), chaetognath consumption amounts to  $1.7 \text{ g C m}^{-2} \text{ y}^{-1}$ , and the primary production required to fuel this consumption through the copepod food chain is between  $5.6 \text{ g C m}^{-2} \text{ y}^{-1}$  (100% herbivorous prey) and  $12.2 \text{ g C m}^{-2} \text{ y}^{-1}$  (50% carnivorous prey), corresponding to 8.4% and 18.2% of the annual primary production, respectively.

Chaetognaths themselves may also represent an important prey for higher trophic levels. Assuming chaetognath production to be 30% of their consumption,  $0.17 \text{ g C m}^{-2} \text{ y}^{-1}$  is available for their predators, e.g. amphipods and myctophid fish (Hopkins 1985; Hopkins and Torres 1989; Perissinotto and McQuaid 1992; Pakhomov et al. 1996) between 500 and 2000 m. Our findings therefore support the view that in Antarctic waters the mesopelagic zooplankton plays a significant role in energy transfer from primary production to higher trophic levels.

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## 7. SYNOPTIC DISCUSSION

The following synopsis will provide combined information and additional discussion based on substantial published literature (including the four publications for this thesis) and also on additional unpublished results of the author. The first chapter will focus on species identification and special features that I observed in some chaetognaths but are not included in the publications. The second chapter concentrates on the life history of the chaetognaths (**publications I and II**), which includes the maturity and life cycle and the breeding periods. A third chapter (**publications I to III**) will discuss the distribution patterns first in the context of hydrography, feeding and reproduction. Then further attention will be paid to the species-specific differences in distribution and their adaptations to the environment. The last chapter elucidates the estimated role of chaetognaths in the ecosystem (**publications I, III and IV**). Specific topics are discussed in detail in the respective publications.

### 7.1 Species identification and special features in chaetognaths

During this study ten different species were found in the Southern Ocean. They were identified with the relevant literature (Alvariño 1969; O'Sullivan 1982; Casanova 1986; 1999; Kapp 1991b). Even though extensive studies on the taxonomy were made and published in thorough and detailed descriptions, specimens of certain species are still difficult to distinguish.

This is especially true for the two species *Eukrohnia hamata* (max. length: 43 mm) and *Eukrohnia bathypelagica* (max. length: 23 mm). Alvariño described the differences of these two species and the taxonomic problems in detail (Alvariño 1962), however, the defining characters are often not distinct. She suggested that some authors mistakenly identified *E. bathypelagica* as *E. hamata*. Dawson (1968) found *E. hamata* individuals carrying brood sacs that Alvariño (1990) assigned to *E. bathypelagica*. Moreover, Alvariño (1962) assumed that the drawing given for maturity stage V in *E. hamata* by Kramp (1939) belongs again rather to *E. bathypelagica* than to the spent stage of *E. hamata*. However, the maturity stage descriptions of Kramp (1939) were used in this study. No spent stages of *E. hamata* were found which could prove or disprove Alvariño's suggestion. I agree that the picture of stage V mentioned earlier is very similar to *E. bathypelagica*, which is characterized by its curled ovaries. Nevertheless, the spent stages of *E. hamata* could look similar (except for the fins) with shrinking ovaries probably slightly shorter and total body length longer than in *E. bathypelagica*. However, in the Southern Ocean *E. bathypelagica* seems to be larger (up to 26 mm in this study) than the 23 mm usually expected and might overlap in length with *E. hamata*.

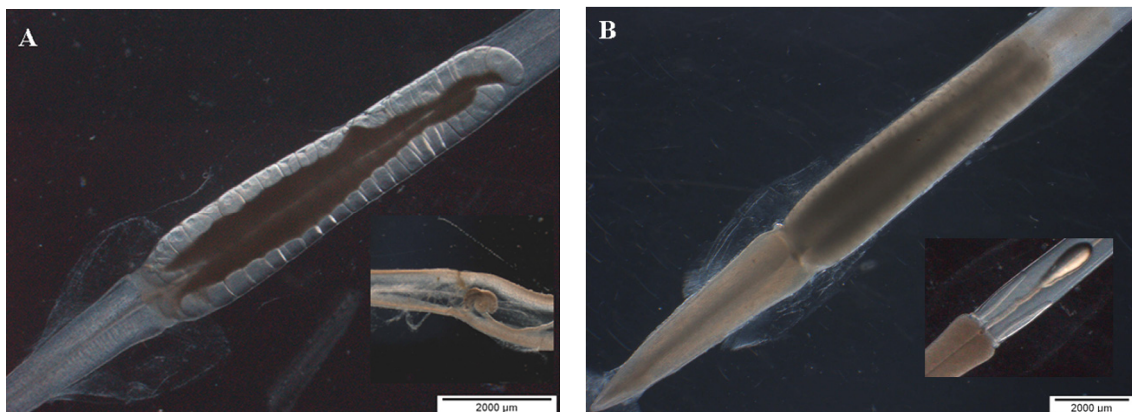
The younger stages of the two species in question with small developing ovaries and the mature stages with large ripe ova are usually easy to identify, especially when the fins are complete. This is shown in Figures 5A and B. In young stages the ovaries of *E. bathypelagica* are curled (5A), whereas they are straight in *E. hamata* (5B). Ripe ovaries are proportionally longer and the ova are larger in *E. bathypelagica* than in *E. hamata*. Usually the ova are arranged in two, occasionally in three rows in *E. bathypelagica*, and in four rows in *E. hamata* (Alvariño 1983). Juvenile specimens and specimens in which the ovaries continue to develop, i.e. intermediate to those shown in Figures 5, are

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often difficult to identify. Due to missing characters, the juveniles (<6 mm length) and some other smaller specimens (generally <10 mm) could not be identified to species level for this thesis.

According to Terazaki (1991) the juveniles of these two species may be distinguished. He compared the juvenile *E. hamata* of 2.4 mm length, which were observed by Dawson (1968), with *E. bathypelagica* of 2.5 mm length covered with alveolar tissue and three to six pairs of hooks on the head at hatching. If Alvariño's (1990) assumption that Dawson (1968) found *E. bathypelagica* is true, however, he was comparing the same species. This debate however cannot be resolved here.

Furthermore, an alveolar tissue on the entire body surface is a common feature in juvenile *Eukrohnia* specimens in the marsupial sacs and shortly after hatching (Kapp 1991a). It seems though, that this tissue may be thicker or thinner depending on the species. *E. bathyantartica* appears to have a slightly thicker alveolar tissue than *E. bathypelagica* and may have a slight orange pigmentation. When the chaetognaths are maturing, the appearance of the ovaries should distinguish between *E. hamata* and *E. bathypelagica* as explained above. The tip of the ovaries in *E. bathypelagica* is usually still curled when growing, whereas they should remain straight in *E. hamata*. Sometimes it appears that the tip in *E. hamata* is also slightly curved and can cause confusion. If coiling of the ovaries occurs due to changes in pressure or due to shrinkage during preservation (Alvariño 1967), it might also be seen in *E. hamata*. Although the tail – body length relationship is considered a valuable character to separate these two species in general (Alvariño 1962; Dinofrio 1973; Sands 1980), the transition in this respect is somewhat variable. Consequently I conclude that several characters are definitely necessary and have to be taken into consideration to distinguish between these species. These characters include fins, ovaries (length, form, ova size, number of ova rows), tail and body length.

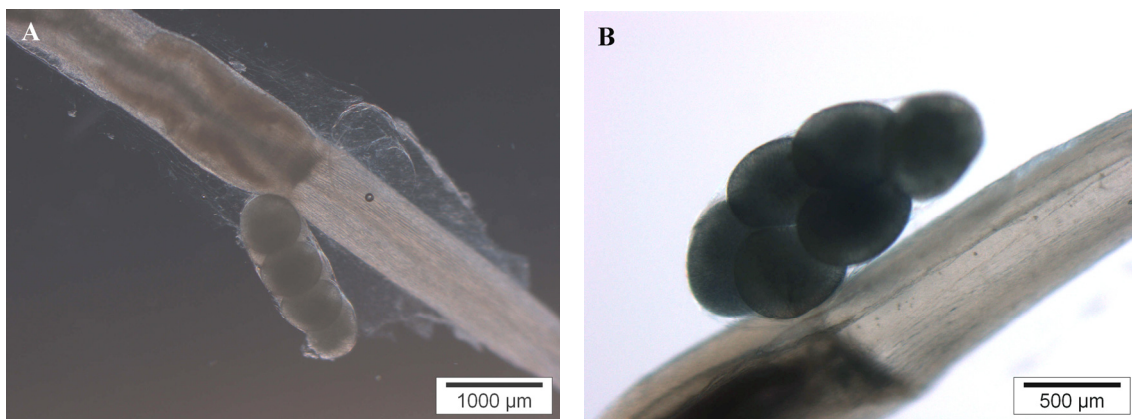


**Fig. 5:** Posterior parts of chaetognaths. *Eukrohnia bathypelagica* (A) with large ova in the ovaries and receptaculum seminis filled with sperm (maturity stage IV, after Alvariño 1967), B, *Eukrohnia hamata* with ova in the ovaries (maturity stage III-IV after Kramp 1939). Picture inserts showing the posterior parts of the trunk in young chaetognaths: A, lateral view of curled ovaries of *E. bathypelagica* (maturity stage I); B, straight ovaries of *E. hamata* (maturity stage II). The scales refer only to the large pictures

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Apart from these observations on species differentiation, some interesting features among the chaetognaths were observed and shall be briefly mentioned here.

One specimen was found carrying brood sacs with very few eggs (Figs. 6A and B). One brood sac lost its eggs during preservation, but it also contained a low number of eggs. So a partial loss of eggs from the sac can be excluded. Unfortunately the anterior part, including head and ventral ganglion, of this chaetognath was missing and so species identification was not possible. It seems clear though, that this specimen did not belong to *E. hamata*, *E. bathypelagica* or *E. bathyantartica*. Based on the characteristics of one pair of lateral fins and the presence of brood sacs, it is clearly an *Eukrohnia* species. The low number of six eggs in one sac indicates that it might be *E. macroneura* or a very similar species.

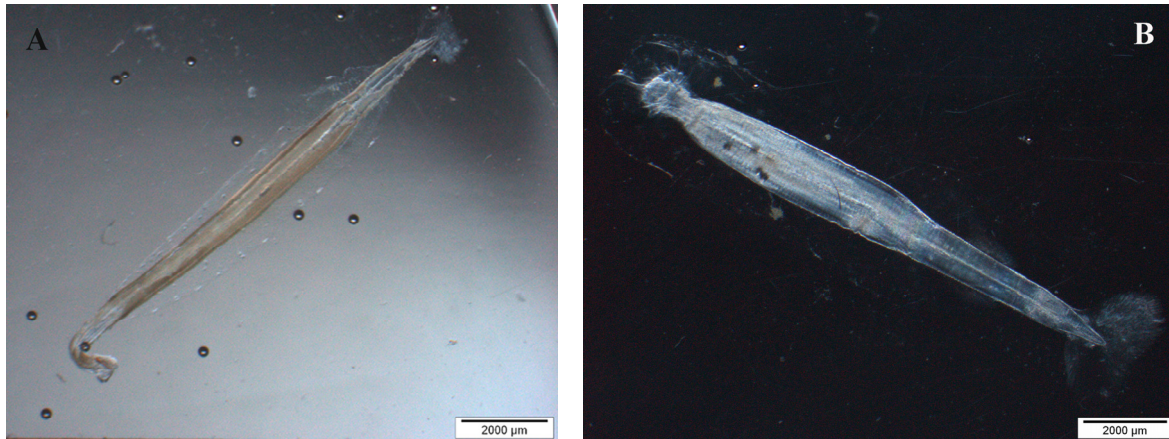


**Fig. 6:** Posterior part of an unidentified *Eukrohnia* specimen carrying one empty and one full brood sac (A) and a close-up of the intact sac with six eggs (B)

Furthermore, a specimen of the genus *Eukrohnia* was found with a greenish cover especially on the lateral margin of its complete body (Fig. 7A). This specimen originated from 750 to 1000 m depth. The origin of the greenish color remained unclear. Microbial colonization of chaetognath body surfaces has already been observed occasionally (Nagasawa 1991). This biofouling might involve marine bacteria, fungi and/or cyanobacteria. No evidence of identification of the micro-organisms is known to the author and whether they are indeed external parasites is still unknown (Nagasawa 1991).

One beheaded chaetognath was caught during the summer expedition (Fig. 7B). The body was closing where the anterior part of this specimen is missing. This phenomenon of wound healing in chaetognaths has already been observed by several authors in the past (reviewed by Pearre 1991). Duvert et al. (2000) showed in experiments with *Sagitta* and *Spadella* that the muscles contract and the gut closes the wound after beheading. Astonishingly they may survive some time and are still able to lay eggs or to mate with other mature specimen even after decapitation. Regeneration of the head is probably not possible and nutrient uptake may then occur through the integument (Duvert et al. 2000).

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**Fig. 7:** *Eukrohnia* sp. with cover (greenish when alive, A) and a beheaded chaetognath found (B) in the Southern Ocean

### 7.2 Chaetognath life history

#### *Maturity cycle*

The maturity stage composition of the four species *Eukrohnia hamata*, *E. bathypelagica*, *E. bathyantartica* and *Sagitta marri* were studied in detail and assigned to stages according to Kramp (1939), Alvariño (1967, 1969; drawings therein and Tables 1 and 2) and David (1955). Stage I specimens followed the descriptions given in the classifications or the given characteristics were not yet developed in these young chaetognaths. The identification included five maturity stages from stage I, immature, to stage V, spent specimens. Only the young *Eukrohnia* specimens smaller 6 mm in length were not treated as stage I, but as *Eukrohnia* juveniles.

More mature stages (usually III and IV) were only found in low numbers in *E. hamata* and *S. marri*, a matter which will be discussed later. In *E. bathypelagica* and *E. bathyantartica* comparatively numerous specimens were attributed to stages III and IV, and even specimens with marsupial or brood sacs were found (Stage V). The assignment to a distinct maturity stage was not always clear though. Especially in *E. bathyantartica* spermatozoa were often still observed in specimens with ripe ova or even with brood sacs. As the ontogenetic development is continuous, the transition from one stage to the next is fluent. Therefore more attention had to be paid to the development of the ovaries than to the male reproductive organs, but the latter was still taken into account.

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**Table 1:** Maturity stage classification of *Eukrohnia bathypelagica* according to Alvariño (1967)

<i>Eukrohnia bathypelagica</i>		
Stage	Male gonads	Female gonads
I	Testes as fine tubes; seminal vesicles beginning to appear; vas deferens well developed	Ovaries small curled tubes
II	Tail filled with spermatids and sperm; seminal vesicles getting filled	Ovaries curled at top, reaching up to level of top of rayed zone in the paired fins
III	Tail full or partially empty; seminal vesicles full or broken	Ovaries curled at the top, reaching up to 2/3 from ventral ganglion, in the distance to caudal septum
IV	Tail empty; seminal vesicles broken	Ovaries filling body cavity, reaching up to 1/3 from ventral ganglion, in distance from there to caudal septum

**Table 2:** General maturity stage classification for chaetognaths according to Alvariño (1969), translated in Alvariño et al. (1983b) and here applied for *Eukrohnia bathyantartica*

<i>Eukrohnia bathyantartica</i>		
Stage	Male gonads	Female gonads
I	Testes begin to develop	Ovaries begin to appear as fine, short tubes
II	Testes occupy caudal cavity and appear full of spermatogonia.* Seminal vesicles begin to develop	Ovaries occupy greater length of general trunk cavity. Ova are small
III	Tail is full of sperm, which begins to pass into seminal vesicles	Ovaries continue to grow in length and diameter. Ova increase in size
IV	Tail appears empty of sexual products. Seminal vesicles are full or broken after discharging gametes during copulation	Ovaries attain maximum length, extending to different levels along the trunk, depending on species; also attain maximum diameter. Ova are mature. Seminal receptacle appears full of sperm

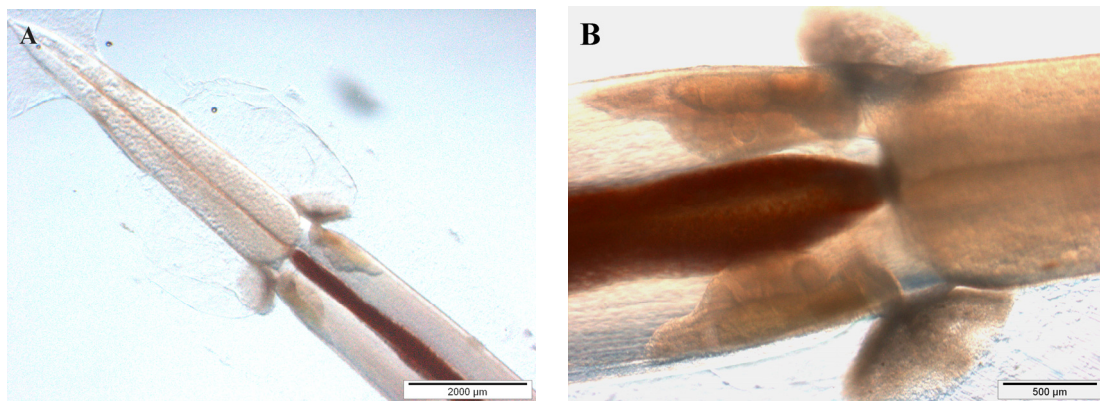
\* Some authors consider the tail as male reproductive organ, but the testes are only slender organs within the tail segment. Therefore testes do not fill the caudal cavity, but the spermatogonia may start to fill the tail segment at this stage.

The differentiation between stage V and younger stages (I and II) was problematic in *E. bathypelagica* and *E. bathyantartica*. Stage V specimens may look equal and may therefore be mixed up with stage I or II specimens when undergoing a second maturity or spawning cycle. The ovaries in *E. bathypelagica* seem to shrink during ova release and possibly regenerate somehow afterwards. Reeve and Cospér (1975) reported difficulty in distinguishing animals that possess eggs for the first time from animals that have already laid eggs only on the basis of ovarian characteristics. In some specimens in this study the ovaries were small and curled as in young specimens, but the fins were strongly bent dorsally. The formation of the fins indicated that they had already carried young in brood sacs and that they possibly pass through a second maturity cycle. Remains of empty brood sacs

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were seen, but not as easily visible in *E. bathypelagica* as in *E. bathyantartica* however, probably because the sac membrane is thinner and more easily damaged. Moreover, the seminal vesicles were hardly visible in any of these *E. bathypelagica* specimens. In contrast the transition to the next maturity cycle in *E. bathyantartica* seems to be progressive. The ovaries do not shrink and oocytes seem to begin to grow right after egg release or juvenile hatching (here considered as stage V but = stage II, Fig. 8). Maturation and spawning may rather be cyclic processes than single events in one lifetime as indicated by Ghirardelli (1968) and Reeve (1970a) for example.

The succession of at least two maturity cycles may also partially explain the strong overlap of body lengths observed between subsequent maturity stages (publication II) which was also reported by Alvariño et al. (1983b) in both species. Sands (1980) even reported no significant differences in lengths of the different stages for *E. bathypelagica*. The chaetognaths may continue to grow while they undergo the maturity cycles, even if on a lower level with increasing maturity. They probably invest more in the development of male and female gonads than in growth at these stages in the first maturity cycle and generally in any further cycle. We do not know how fast these species grow and how long generation time is in the Southern Ocean. Different generations might be similar in length. The succession of several maturity cycles and the shrinkage of specimens after egg release, which is assumed to occur in chaetognaths (discussed by Pearre 1991), might strengthen the overlap of lengths. Other factors such as the quality and quantity of food supply and temperature may also cause differences in size at various stages of maturity (Alvariño 1992).



**Fig. 8:** Posterior part of *Eukrohnia bathyantartica* carrying empty brood sacs (A). The tail is partially filled with sperm and the ovaries appear to contain few small ova. Picture B is a close-up of the ovaries in picture A

Because of their exceptional abundance in summer, *Eukrohnia* specimens smaller than 6 mm in length were defined as juveniles during this study. They were difficult to identify at the species level and thus treated as one group (including *E. hamata*, *E. bathypelagica* and *E. bathyantartica*). During winter *Eukrohnia* juveniles were largely missing, which may also partially be explained by several maturity cycles. If the juveniles found during our studies would belong to *E. bathypelagica*, which is by no means clear, we might have sampled during a reproduction break in between two maturity cycles. The absence of juveniles may also result from a reproduction break in *E. hamata* for the time of

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sampling. However, both suggestions would not entirely explain the missing juveniles, because *E. bathypelagica* with empty brood sacs were also present in winter. On the other hand, as long as we do not know the time between two maturity cycles, the few numbers of juveniles (<6 mm) cannot be explained. Another explanation could be a migration of the *Eukrohnia* juveniles to a depth above 500 m. The juveniles of *E. bathyantartica* were easier to distinguish from the other two *Eukrohnia* species and thus exceptional. Young *E. bathyantartica* are generally few, probably due to the lower number of offspring in the brood sacs, but present during both seasons. Young, but larger *Eukrohnia* specimens of 6 to 8 mm length were present and *S. marri* juveniles of 3 to 5 mm length were also caught. A reproduction break as a reason for the absence of *Eukrohnia* juveniles in winter can therefore not be excluded.

### *Breeding periods and life cycles*

Reproduction in the deep-living species *Eukrohnia bathypelagica* and *E. bathyantartica* is probably intensive and may be continuous. During both seasons all maturity stages were caught with a considerable portion of stage III to V specimens, especially in *E. bathypelagica*. In *E. hamata* and *Sagitta marri* a comparatively small number and small relative portion of adult stage IV specimens was present. The proportion of maturity stage III specimens was also small. These two species have a wide vertical distribution in the Southern Ocean, usually also occurring shallower than *E. bathypelagica* and *E. bathyantartica*. Reproduction might therefore be triggered by different parameters between the four chaetognath species. The reason for the low portion of mature specimens in *E. hamata* and *S. marri* is not clear. Either species occurrence in deeper layers, low reproduction and/or missed reproduction maxima may explain our findings and possible causes will be discussed below.

Adult individuals of *E. hamata* and *S. marri* may occur below 2000 m depth and would have been missed with our multinet. Data obtained from sampling with the rectangular midwater trawl (RMT), which are not presented in the manuscripts, also indicate maturation at greater depths. Stratified sampling (at four stations) with the RMT was conducted in summer, with two nets descending to 2500 m depth, one down to 1900 and a fourth net down to 2000 m. Three RMT stations were sampled in winter, from the surface to about 3000 m depth (5000 m wire length) and back to the surface. Unfortunately these oblique samples lack depth resolution. Maturing and adult *E. hamata* and *S. marri* (stage III and IV) were observed in these samples, but young maturity stages (I and II) dominated. No *E. hamata* specimens with brood sacs occurred in these samples as observed in the multinets, although *E. bathyantartica* specimens carrying empty sacs were also present in the RMT samples. Consequently it is difficult to determine whether or not we missed deep-living adult specimens.

Based on the differences in length-frequency distribution, I propose that reproduction in *E. hamata* and in *S. marri* is less pronounced than in the two deep-living species *E. bathypelagica* and *E. bathyantartica*. A continuous low level of reproduction has also been presumed for *E. hamata* in Gerlache Strait, Antarctic Peninsula by Øresland (1995). Low relative portions of stage III specimens and no stage IV specimens were reported for *S. marri* (Hagen 1985) and for *E. hamata* (Hagen 1985; Johnson and Terazaki 2004) down to 1000 m

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depth. Sands (1980) also found only low proportions of stage III specimens and very low proportions of stage IV specimens of *E. hamata* in West Norway (0.5% and 0.1% of the population throughout the year). She stated that confusion with *E. bathypelagica* can be excluded due to the anatomical structures, as discussed in the previous part of this synthesis, and due to the different body proportions; I agree with her conclusions. Therefore it can be concluded that a year-round low reproduction level is probable for this species.

From other regions and reports we know that adult *E. hamata* may reach a length of up to 40 mm (Sands 1980). Kramp (1917, 1939) reported *E. hamata* specimens of 26 mm, being far from maturity, and still immature specimens as long as 37 mm (probably comparable with stage II and younger in this study) in Greenland waters. From the observations in the multinets and RMTs of this study, it can be suggested that *E. hamata* may reach maturity already at a length below 30 mm, but the length range at full maturity may be wide. Very large animals far beyond 30 mm were not captured, however. If maturity is reached at a length of more than 30 mm for the largest part of one generation in the Southern Ocean, then we could have missed the reproduction maxima. This would imply that maturing chaetognaths still continue to grow significantly in length, which is doubtful. *E. hamata* grows in length between stages I and II (Sameoto 1987) and this during its first growth season (Sands 1980). In the second growth season, and accordingly in the second year, *E. hamata* sexually matures (Sands 1980). Thus, growth in length is low at greater maturity. Moreover, the breeding season of *E. hamata* off the west coast of Greenland may start in spring, reach a maximum in late summer and decrease again in fall (Kramp 1939). Kramp (1939) suggested that breeding may continue during the winter in deep water. Sands (1980) further observed breeding maxima in spring and fall, with a continuous low level throughout the summer in Korsfjorden, West Norway. Consequently we may have sampled before the reproduction maximum at the end of summer or fall, and in winter when reproduction is probably on a constant low level. Our data for *S. marri* support this hypothesis very closely. A high number of young specimens during summer and winter (<12 mm) suggest intensive reproduction periods in spring and fall. The few adult specimens may indicate continuous, but low, reproduction during both winter and summer. Hence, reproduction could be continuous in all four abundant species, even if the level of reproduction may vary strongly among the species.

The life cycles of the four chaetognath species are difficult to decipher. Not much is known on the life cycle of *E. bathypelagica*, *E. bathyantartica* and *S. marri*. Only *E. hamata* has been investigated in more detail. Most literature data are based on sampling during one season, primarily summer, and therefore more extensive seasonal observations and life cycle studies on these species are rare. Most studies on the reproduction and life cycle of *E. hamata* were reported from the northern hemisphere. Bogorov (1940) reported a biennial life cycle and breeding in fall in the Barents Sea. Also Sands (1980) and Sameoto (1987) suppose a life span of two years in *E. hamata* for Korsfjorden, West Norway, and Baffin Bay, west of Greenland. A biennial life cycle can also be assumed for the Antarctic because growth may be slow, but final proof is still missing. *E. bathypelagica* and *E. fowleri* are assumed to breed the whole year in the deep North Pacific (Terazaki and Miller 1986). All stages of maturity (I to



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IV) in *E. bathypelagica* seem to be present throughout the year in Korsfjorden (Sands 1980). Alvariño et al. (1983b) reported stages I to IV for both *E. bathypelagica* and *E. bathyantartica* for all four seasons in the Southern Ocean. My observations for *E. bathypelagica* and *E. bathyantartica* in the Southern Ocean support the previous results, although I have to admit that the bimodal length–frequency distribution in both species rather indicates several reproduction phases. The possible continuity of breeding and a probable presence of multiple cohorts produced by a single adult generation make it difficult to evaluate growth rates and generation lengths, however. Furthermore, the state of population structures in two seasons is not sufficient to provide evidence to the number of present generations and the duration of each maturity stage of the investigated species. Alvariño (1994) pointed out that deep-living species mature only once a year as polar species, but that their life span may include several maturity cycles. This in consequence leads to the assumption that there are not only several cohorts, but also several generations present which may ensure year-round reproduction.

### 7.3 Distribution patterns and adaptations to the environment

The distribution of chaetognaths may be influenced by different abiotic and biotic parameters. Notably hydrography, feeding and reproduction may affect species distribution patterns. Species-specific adaptations bring success in a given environment such as the Southern Ocean and especially the deep-sea. The following discussion of distributions and life strategies of the investigated species will elaborate on these aspects.

#### *Hydrography*

The significance of hydrography (Fig. 2) for determining distribution of meso- and bathypelagic chaetognaths in the Southern Ocean is not obvious due to the observed patchiness in chaetognath abundance. The only distinct effect was seen in *Eukrohnia bathypelagica* which seemed to have higher abundances in the Polar Frontal Zone (PFZ) than in the Weddell Gyre (WG) and the Coastal Current (CC). This may be due to a salty and warm intermediate layer located between 200 and 1500 m depth in this region (Schröder and Fahrbach 1999). The upper part of this warm Circumpolar Deep Water (CDW) originates in the Atlantic, whereas the lower CDW, characterized especially by its high salinity, is an inflow from the Pacific and partially Indic (E. Fahrbach personal communication). However, the generally high zooplankton abundances found in the Antarctic Polar Front (APF) were not observed in the meso- and bathypelagic chaetognaths. After Voronina (1968), highest zooplankton concentrations should be located in the upper 100 m, where cold Antarctic Surface Water (ASW) converges with warmer Subantarctic Surface Water. The ASW sinks with high downward velocities. However, the sinking speed is not sufficient to transport the animals (Voronina 1968). As zooplankton may resist the downward movement, they do not necessarily sink and thus, remain in the convergence zone. Consequently the plankton biomass may increase about 10 % on average in the upper 100 m (Voronina 1968).

No horizontal transport in the upper layer takes place across the convergence. Horizontal transport is confined to the Subantarctic Intermediate Water from south to north, and below in the CDW from north to south.

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Consequently, highest numbers and biomass of chaetognaths and particularly of *E. hamata* should be found in near surface layers and probably not at meso- and bathypelagic depths. Moreover, our two stations at about 52°S were likely located at the southernmost edge of the Antarctic convergence and did not catch the full impact of the prevailing hydrographical conditions.

The APF may present something of a barrier for the distribution of species. It is considered a boundary for *Sagitta marri*, but not for the distribution of *S. gazellae* (Pierrot-Bults and Van der Spoel 1979). However, it can be assumed that there is no strict restriction especially in the meso- and bathypelagic species. *S. marri* may occur even north of the APF (Alvariño et al. 1983a,b). *S. macrocephala*, a mesopelagic cosmopolitan species (Alvariño et al. 1965), was only caught in samples in the vicinity of the APF during this study. This species might occur to the south when it is carried with Circumpolar Deep Water coming from the north. Generally it seems to be more frequent in the Subantarctic than in the Antarctic (David 1958). The same may be true for *E. fowleri* and *S. planctonis*, which were reported in the Southern Ocean too (Alvariño et al. 1983a,b), but were not captured during the present investigation. On the basis of several reports (Alvariño et al. 1983a,b; Duró et al. 1999) it can be assumed that the distribution of these two species is more to the north of the APF too. Whereas *S. macrocephala*, *S. planctonis* and *E. fowleri* are found in deep waters, the Subantarctic *S. maxima* occurs preferably between 150 and 500 m and is rarely observed down to 1500 m depth (David 1958). Its occasional findings to the south were considered as losses of population such as seen in *S. marri* to the north. David (1958) further assumed that Antarctic Intermediate Water mixes with the warm CDW in the vicinity of the Antarctic convergence and this may cause an extension of *S. maxima*'s distribution in deeper layers to the south. Highest numbers of this species in both multinets and RMTs (see Appendix I) in the PFZ and low numbers generally in the Lazarev Sea support David's suggestions. The APF can therefore be regarded as a partial boundary for species distribution, which also may have influence on the vertical distribution of species.

### *Food and reproduction*

Feeding can also be regarded as a determinant for the vertical distribution of chaetognaths. The seasonal migration which has been observed especially in *Sagitta marri*, *Eukrohnia hamata* and *E. bathypelagica* may be attributed to the necessity to follow the migrating copepods in winter. It is difficult to prove this because gut content analyses do not reveal a substantial insight into the diet of chaetognaths. Only transit food items (i.e. jellyfish remains and diatoms), some protozoans as well as parts of chaetognaths and copepods could be identified as their prey. Among the copepod remains few mandibles of the type shown on Figure 9A and only one complete copepod (Fig. 9B) were found in *E. hamata* and *E. bathypelagica* respectively in winter. To date no species name has been assigned to these two copepod remains. It is probable that they more likely belong to deep-water copepod species than to the very abundant copepods occurring at shallower depths.

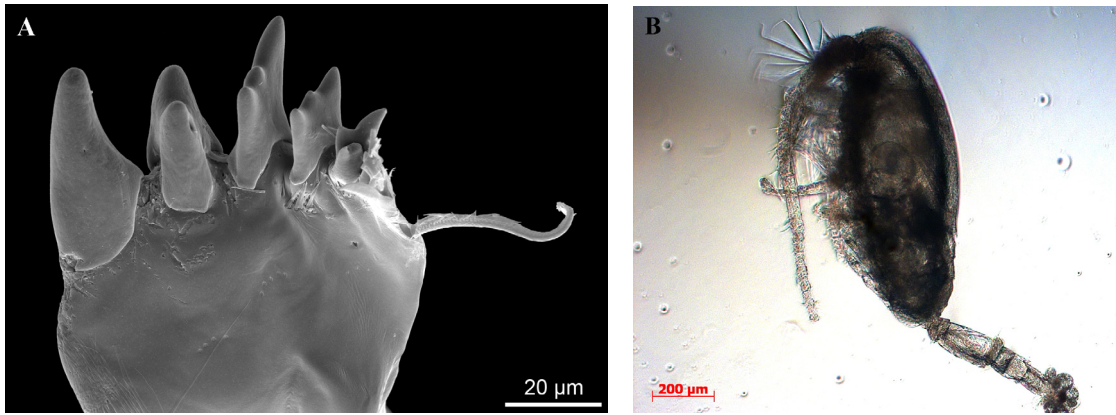
From the fatty acid analyses of *E. bathypelagica* and *E. bathyantartica* we assume that they primarily prey on copepods like calanid copepods and *Paraeuchaeta antarctica* for example. However, these two chaetognaths show distinct differences in their fatty acid composition. *E. bathypelagica* contains

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high amounts of the biomembrane fatty acid 22:6(n-3), whereas *E. bathyantartica* had a high portion of 18:1(n-9), a trophic marker for carnivory (Falk-Petersen et al. 1990). *E. bathyantartica* was further characterized by a higher fatty alcohol content, indicating wax esters as long-term energy reserves and also buoyancy aids (Hagen 2000) in this species. High portions of the fatty alcohols 14:0 and 16:0 were measured which are major components in the copepods *Rhincalanus gigas* (Kattner et al. 1994) and *Paraeuchaeta antarctica* (Hagen et al. 1995). With 15.4% dry mass (DM) in *E. bathyantartica* and 11.5% DM in *E. bathypelagica* (detailed data provided in Appendix II) the general lipid content was on a lower level compared to Antarctic copepods (e.g. up to 56% DM for *Calanus propinquus* in summer; Hagen et al. 1993). The lipid content within *E. bathypelagica* differed between maturity stages, with elevated values in ripe specimens (maturity stage IV). Hence, chaetognaths probably feed throughout the year and do not store large energy reserves. To cover their metabolic demands, it may be necessary for the chaetognaths to follow their prey in winter. Especially as *E. bathypelagica* and *E. bathyantartica* reproduce during summer and winter food uptake is important. However, not all copepods migrate to great depths in winter. For example, only one part of the *Calanus propinquus* population migrates below 200 m, whereas the remainder stays near the surface (Bathmann et al. 1993; Schiel 1998). Moreover, a vertical migration in *E. bathyantartica* was not really detectable. Although this species appeared to rise to shallower depths in the CC in winter, no definite conclusions can be drawn, as we probably missed a part of its population below 2000 m depth. *E. fowleri*, a closely related species of *E. bathyantartica*, shows in comparison a biomass peak in the 2000 to 2500 m layer in the region of the Kurile-Kamchatka Trench (Vinogradov 1970). In *S. gazellae* seasonal and breeding migration seem to be linked (David 1965). A deeper distribution was observed for *E. hamata* (David 1958) and *S. marri* (Mackintosh 1937) in winter which matches with the results of this study. Unfortunately, no fatty acid analyses were conducted on these two species, therefore their connection to the copepod prey distribution cannot be clarified. A link to the breeding behavior is not obvious either. As discussed in the previous section, reproduction in *E. hamata* and *S. marri* might take place during all seasons at different degrees. Even if reproduction occurs throughout the winter and is coupled with a migration of specimens to deeper layers, reproduction in summer, in combination with an average shallower distribution, cannot be explained. If prey is the determining factor, mature chaetognaths would be expected to stay in the upper layers. Possible changes in the vertical distribution of *E. bathypelagica* are even more difficult to clarify, as the population structure remained more or less the same during winter and summer. Therefore other parameters than reproduction seem to influence vertical distribution and migration from summer to winter. Feeding seems to be one probable parameter.

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**Fig. 9:** Mandibular gnathopod found in two guts of *Eukrohnia hamata* specimens below 1000 m depth (A, photo taken by Jan Michels) and a unidentified copepod originating from *Eukrohnia bathypelagica*'s gut (B)

Even if food may be the main determinant for the seasonal vertical distribution, reproduction plays a key role for the ontogenetic vertical distribution in chaetognaths. In *E. hamata*, *S. marri* and *E. bathypelagica* higher maturity stages were caught with increasing depth. In *E. bathyantartica* a vertical segregation of maturity stages was indicated. *E. bathyantartica* has a deep-mesopelagic and bathypelagic distribution and therefore this segregation pattern is likely not as developed as in *E. hamata* for example. Furthermore, one part of its population may be found even below our sampling depth as mentioned before. A higher excess density of specimen due to the development of the ovaries and ova, may cause a sinking of the maturing specimens (Alvariño 1964, 1965; Kapp 1991c). The development of counteracting mechanisms such as voluminous and gelatinous inner parts is probably not necessary, as these chaetognaths do not need to stay at a certain depth. Oil droplets found in *E. hamata* and *E. bathypelagica* may partially act as such counteracting mechanisms or buoyancy aids, this might be combined with the function as energy reserves (Øresland 1990; Kapp 1991c). However, if an increased excess density would be the only reason, stage V specimens would rise in the water column after releasing their young. Although many of the spent adults were still found below 1000 m. Furthermore, young specimens are usually found throughout the entire water column rather than only concentrated in the upper layers. David (1958) hypothesized that the descent to deeper layers is “a behavioural relic of some deep-living ancestral form”. Alvariño (1965) also assumed that the “ontogeny is a replica of the phylogeny”. However, it has since been hypothesized that cold water taxa are usually ancestral to deep water taxa (Van der Spoel and Heyman 1983) and that the bathypelagic zone was the latest to be populated (Pierrot-Bults and Van der Spoel 1979). Thus, phylogeny seems to be no explanation for the vertical migration of maturing chaetognaths. Another possible reason for deep migration may be the escape from predators (Alvariño 1965). In the absence of the necessity to stay at a certain depth, i.e. in a defined temperature and salinity regime, predator avoidance appears to be a probable reason for the descent of maturing chaetognaths. Nevertheless, the factors triggering the vertical segregation or migration of maturity stages especially in *E. hamata*, *S. marri* and *E. bathypelagica* are not completely understood.

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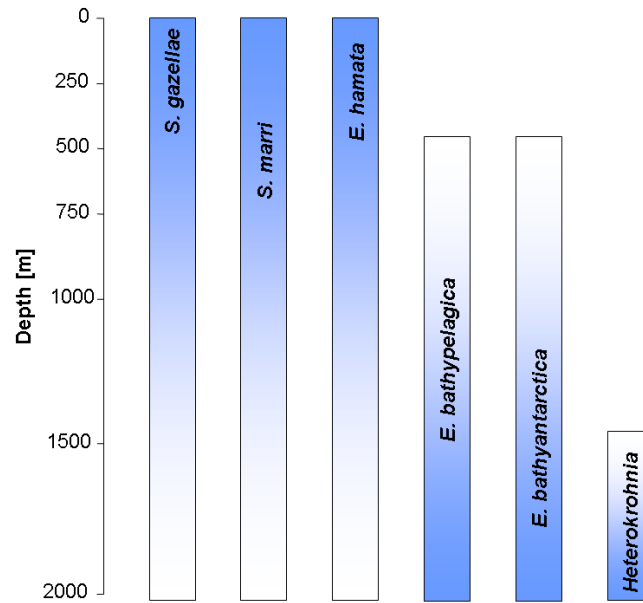
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Food and reproduction are closely linked and food may be an important parameter for reproduction (Terazaki and Miller 1986; Alvariño 1994), even though the effect of food for growth and development is not as well documented as for temperature (Pearre 1991). Both concentration and composition of food may affect the growth rate and generation length in chaetognaths (reviewed by Pearre 1991). The duration of the maturity stage may be influenced and the population structure may consequently be shaped by the food supply. Therefore a link of the ontogenetic to the seasonal migration cannot be excluded.

### *Species-specific differences and adaptations*

The chaetognath community of the Southern Ocean comprises of a low number of species which show differences in their vertical distribution patterns (Fig. 10). *Eukrohnia hamata* is the most abundant species in the Southern Ocean with highest numbers in the upper 500 m (David 1965) or the layer between 200 to 750 m (Hagen 1985). Nevertheless, it may occur down to more than 4000 m depth (Alvariño et al. 1983b). *Sagitta gazellae* is very common in the upper 400 m (Hagen 1985), with highest densities in the 50 to 100 m layer (David 1965). However, this species may occur in low numbers down to 3000 m, with especially the advanced maturity stages inhabiting greater depths (David 1955). Only few *S. gazellae* were found also in our meso- and bathypelagic samples. *E. hamata* and *S. gazellae* show a distinct overlap in distribution in the near surface layers, but *E. hamata* generally has a wider vertical distribution. *S. marri* is most common at mesopelagic depths within the 200 to 1000 m depth range (Alvariño et al. 1983a; Hagen 1985). This species shows some slight overlap with the previous two species, but has a deeper distribution maximum. It rather overlaps with *E. macroneura* which was especially found between 750 and 1500 m, but still in distinctly smaller numbers than *E. hamata* and *S. marri*. The two deep-living species *E. bathypelagica* and *E. bathyantartica* increase in number with increasing depth. Both showed highest numbers between 1000 and 2000 m depth in the Lazarev Sea. However, it appears that *E. bathypelagica* already inhabits the lower mesopelagial (especially in summer), whereas *E. bathyantartica* is a more typical bathypelagic species and probably the most numerous chaetognath species found below 1500 m depth (David 1964). Both seem to partially displace *E. hamata*, as its distribution decreases with increasing depth. Below 2000 m *Heterokrohnia mirabilis* appears as bathypelagic species. Other *Heterokrohnia* like *H. fragilis* may also be found at bathypelagic depths, but always few in number. There seem to be niches for the different species. Overlaps in distribution rather occur between species of different genera than between species of the same genus, as already noted by David (1958), although *E. bathypelagica* and *E. bathyantartica* show a strong overlap.

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**Fig. 10:** Vertical distributions and depth ranges of the Antarctic chaetognaths *Sagitta gazellae*, *S. marri*, *Eukrohnia hamata*, *E. bathypelagica*, *E. bathyantartica* and the genus *Heterokrohnia*. Blue shading and position of species names indicate centers of occurrence as found during this study and reported in literature

The vertical distributions of the juveniles differ from those of the maturing chaetognaths and adults, however. The juvenile *Eukrohnia* specimens (<6 mm) were distributed between 500 and 2000 m with a maximum in the 500 to 1000 m layer during this study in summer. These juveniles might include specimens of *E. hamata*, *E. bathypelagica* and only some *E. bathyantartica*. *E. bathyantartica* juveniles occurred preferentially below 1000 m depth. The young and small *S. marri* (<6 mm) were also found especially between 500 and 1000 m depth in summer. Duró and Gili (2001) also reported *E. hamata* juveniles concentrated in the 500 to 1000 m depth range in the Weddell Sea in late spring. Young *S. marri* were observed at mesopelagic depths, whereas juvenile *S. gazellae* were caught above or within the thermocline (between 200 and 100 m; Duró and Gili 2001). This vertical segregation of juveniles was already reported by David (1955). Juveniles of *E. hamata*, *S. planctonis* and *S. maxima* (2-5 mm length) occur deeper than *S. gazellae* juveniles (David 1955), the latter probably hatching at 250 m depth (David 1965). Juveniles of *E. hamata* and *S. gazellae* are vertically separated, whereas their main distributions of the other stages generally overlap. Probably there is not only a spatial separation between these two species. It has been assumed that these two species have a different timing of their life cycles (Timonin 1968). *E. hamata* is suggested to have a two year life cycle, as described earlier, whereas *S. gazellae* has probably only a one year life cycle (David 1955). This mechanism may adjust competitive relations between the species (Timonin 1968).

Differences between species and especially between the genera *Eukrohnia* and *Sagitta* are also seen in their breeding behavior. Whereas *Sagitta* species usually release their eggs into the water column, *Eukrohnia* species keep them in their marsupial sacs until they hatch. The development of the eggs to juveniles in brood sacs is shown in Figures 11A-F. Many authors wrongly call

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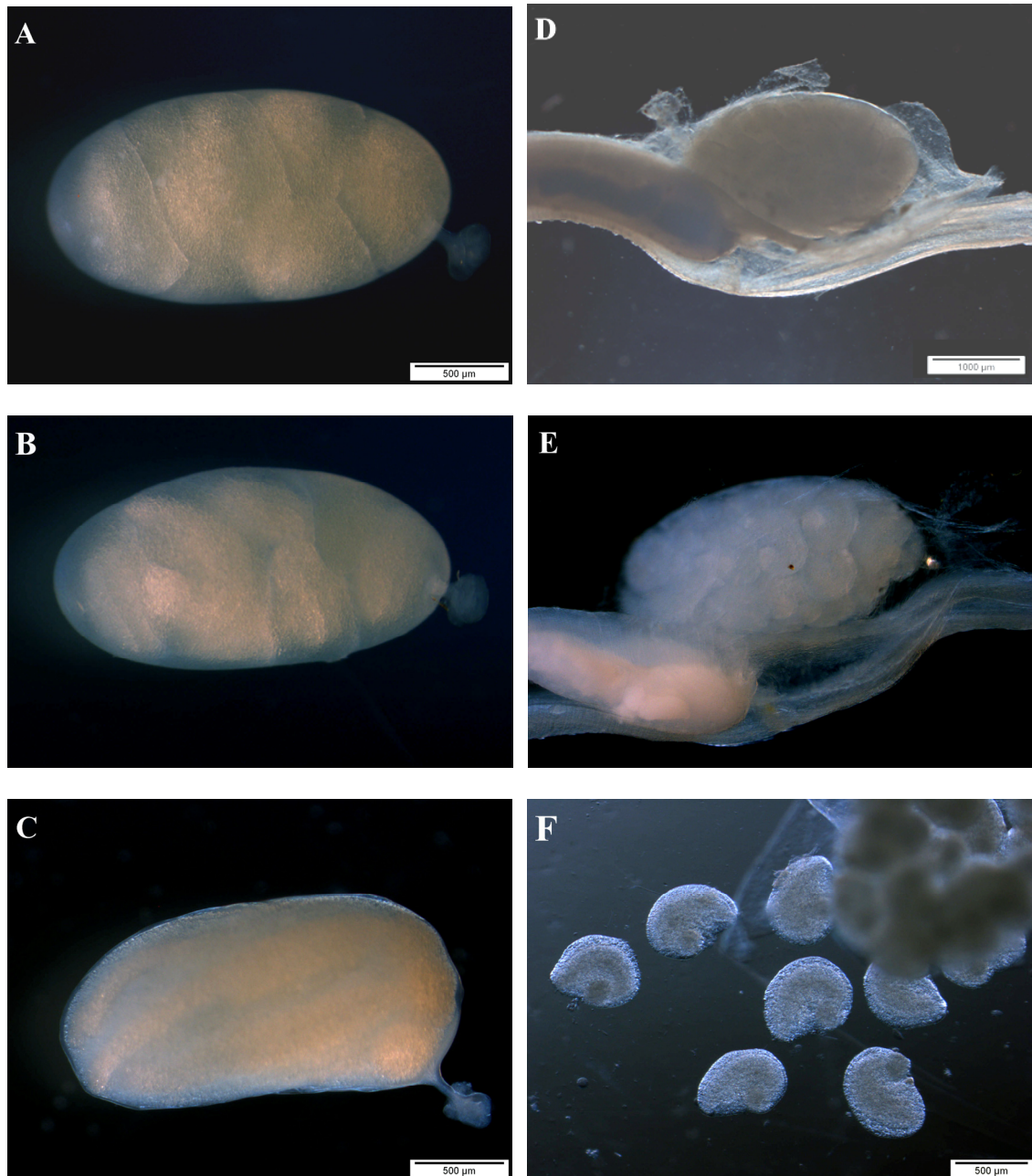
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the young developing chaetognaths larvae, although they continue to develop adult organs from embryonic structures after hatching and do not undergo a metamorphosis (Kapp 1991a). It is more correct to call them juveniles as soon as they are hatched. Alvariño (1968) defined brood phases for *E. bathyantartica* which were slightly modified and applied to both deep-living species *E. bathypelagica* and *E. bathyantartica*. The Figures 11A-F show the brood phases II to IV, with phase II: brood sac filled with mature eggs (Figs. 11A,D), phase III: brood sac with eggs containing embryos in a single coil (Figs. 11B,E) and phase IV: brood sacs with eggs containing double coiled embryos or hatched juveniles (Fig. 11C). In both species all three phases were observed. Compared to *E. bathyantartica*, the marsupial sac of *E. bathypelagica* is thinner (Fig. 11F), but it is protected by the broad lateral fins which are bent dorsally. This is characteristic for *E. bathypelagica*, and is not as conspicuous in *E. hamata* (Alvariño 1962). *E. bathyantartica*'s fins are also only slightly bent dorsally. It is suggested that hatching and release of the *Eukrohnia* young is stimulated and synchronized by extracts of the adults when environmental conditions are favorable (Alvariño 1990). Unfortunately no marsupial sacs were found in *E. hamata* which is also known to carry their young (e.g. MacGintie 1955; Dawson 1968; Timofeev 1998). It can be assumed that the development of brood sacs is an adaptation to the environment (e.g. predation impact or food availability), considering polar regions as well as meso- and bathypelagic depths. *S. marri* and *S. gazellae* for instance migrate to greater depth for breeding (David 1965), but release their eggs freely into the water column and generally have larger numbers of eggs.

*E. bathypelagica* carried a higher number of eggs (86 to 128) than *E. bathyantartica* (8 to 13 eggs). Alvariño (1983) found 20 ova per ovary in *E. bathyantartica* and 42 ova per ovary in *E. bathypelagica*. Terazaki and Miller (1982) found *E. bathypelagica* with 19 to 30 eggs in the North Pacific. This shows that differences in egg number exist not only between species, but also within a species.

Egg numbers may even vary within a year and between years (Alvariño 1994). Such differences are often closely linked to the food supply. However, even if seasonality is stronger in polar regions, it does not necessarily follow that the available food for chaetognaths differs significantly throughout the year. When copepods like *Calanus propinquus* or *Microcalanus pygmaeus* migrate deeper in the Southern Ocean in winter (Schiel 1998), they may represent possible prey for the chaetognaths. These two species are not diapausing during winter and might therefore be detected by chaetognaths. *Calanoides acutus* on the contrary undergoes a diapause (Schiel 1998) and stays probably more or less motionless at depths below 500 m. As chaetognaths need to sense locomotion, only winter active copepods may be potential prey. The conditions in the Antarctic may therefore be not much more unfavorable than the conditions in more temperate regions, especially when food quality is also high due to lipid rich overwintering copepods. Moreover, chaetognaths may resort to cannibalism, if copepod prey density is low. Good food conditions could also illuminate the lack of large lipid storage in chaetognaths.

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**Fig. 11:** Marsupial sacs of *Eukrohnia bathyantartica* (A-C) and *Eukrohnia bathypelagica* (D-F) at different stages of development: stage II (A, D), stage III (B, E, F), stage IV (C). Scale bars are given in the pictures. Picture B was taken at the same magnification as A and C, picture E with an about 20% higher magnification than picture D

High numbers of eggs are usually observed in “poor” areas and in species living under stress (e.g. bathypelagic and cold water species; Alvariño 1994). Alvariño (1983) stated in addition that ova number is lower and ova size is larger in tropical species (with a short life span and a continuous reproduction cycle), and in species with brood sacs than in species of cold and temperate waters. The latter species often lay their eggs freely into the water column and reach high numbers of about 1600 ova per specimen, for instance in *Sagitta gazellae* (Alvariño 1983). Although the egg number in brood sacs may generally be lower compared to the cold water species releasing their eggs freely, the difference



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between *E. bathypelagica* from different regions may represent climatic and temperature differences respectively. A decrease of egg numbers from the poles to the tropics may therefore be possible even in species carrying brood sacs.

Moreover, population size may also affect the number of offspring. In large epipelagic populations for instance lower numbers of eggs may be produced compared to small populations with high reproductive effort (Alvariño 1994). Hence, the discrepancy seen within *E. bathypelagica* may be due to differences in food supply, the harsher environmental conditions in polar regions or possibly due to different population sizes.

While this intra-specific variability cannot be elucidated, the differences between *E. bathypelagica* and *E. bathyantartica* may be explained by different strategies to achieve reproduction success. *E. bathypelagica* eggs were small (about 460 x 560 µm), but numerous, compared with *E. bathyantartica*'s eggs about 700 x 1090 µm, but fewer in number. It can be assumed that the better the brood care, the lower the number of eggs. Alvariño (1994) stated that both strategies could maintain the same annual cycle. Even if fecundity may be defined as "the number of eggs produced per individual per species and geographic location" (Alvariño 1994), large eggs may result in a comparable reproductive success by producing larger juveniles at time of hatching which are better suited to survive. Being at least 1.5 mm in length at hatching both deep-living *Eukrohnia* species are larger than many *Sagitta* juveniles, but a larger size may again outweigh a large egg number. Relatively large numbers of eggs as seen in *E. bathypelagica* can be assumed for *E. hamata*. Timofeev (1998) found 120 to 151 eggs per specimen in Arctic *E. hamata*. Following Alvariños' (1983) observations of 130 ova per ovary, *E. hamata* specimens may even possess 260 eggs each. As *E. hamata* is the most abundant *Eukrohnia* species and possibly reproducing on a low level, such a number may be necessary to sustain the population.

Meso- and bathypelagic chaetognaths occur in lower numbers compared to their epipelagic counterparts. Although self-fertilization could ensure successful reproduction at great depth, there is no proof to which extent self- or cross-fertilization do occur. In *E. bathypelagica* protandry seems to be stronger than in *E. bathyantartica*, as tail and seminal vesicles were usually empty when they carried large ova in the ovaries (stages IV). In few specimens of *E. bathyantartica* protandry seemed only to be slight, as large and ripe ova occurred at the same time as filled seminal vesicles (receptaculum seminis empty). As early as 1917 Kramp had reported that *E. fowleri* is only slightly protandric, too. Furthermore, it can be hypothesized that self-fertilization may even occur when protandry is strong. The sperm might be stored in the receptaculum seminis until the ova are ripe. However, it is still unknown what really happens in nature. Self-fertilization may therefore be possible and cannot be excluded as an adaptation to living at great depth.

### 7.4 Estimated role of chaetognaths in the ecosystem

Chaetognaths play an important role in the food web as the primary predators of copepods (e.g. Sullivan 1980; Terazaki and Marumo 1982; Bone et al. 1991). They are estimated to have a biomass of 20 to 30% of that of copepods in the world oceans (Reeve 1970a) and can therefore be considered a taxon rich in

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numbers and biomass, with highest concentrations occurring in the upper hundreds of meters of the water column. Although their abundance decreases with depth, chaetognaths may still show high numbers in the mesopelagic zone, especially when reproduction takes place and many juvenile chaetognaths appear. In winter their abundance below the epipelagic layer may further be enhanced when chaetognaths, particularly the dominating species *Eukrohnia hamata* and *Sagitta marri*, undergo seasonal vertical migrations. Average chaetognath biomass can consequently reach approx.  $270 \mu\text{g C m}^{-3}$  between 500 and 750 m in winter, compared to  $250 \mu\text{g C m}^{-3}$  in summer. The biomass in the upper 300 m is with up to about  $5000 \mu\text{g dry mass (DM) m}^{-3}$  (Pakhomov et al. 2000) or  $1650 \mu\text{g C m}^{-3}$  (assuming a carbon content of  $330 \mu\text{g C mg DM}^{-1}$ ) significantly higher. However, as chaetognaths may feed throughout the year due to more or less continuous food availability (Hagen 1999), they may exert a distinct predation pressure especially on the copepod community.

The study of the feeding behavior of the meso- and bathypelagic chaetognaths *E. bathypelagica* and *E. bathyantartica* has shown that both species feed on copepods independent of their maturity stage and of the season, although standard metabolism of *Eukrohnia* seems to be low. *E. hamata* and *E. bathypelagica* respired only  $0.15 \mu\text{l O}_2 \text{ mg DM}^{-1} \text{ h}^{-1}$ . This is probably an oxygen consumption we can expect when the chaetognaths of this genus lie in wait for their prey. Their active metabolism respiration might be higher. For crustaceans this respiration during active periods was suggested to be about twice as high as standard metabolism respiration (Vinberg 1950). Nevertheless, our developed respiration model on the basis of own and of numerous chaetognath respiration data from the literature allowed a good estimate of total respiration of meso- and bathypelagic chaetognaths in the Southern Ocean. Oxygen consumption reached an average rate of  $0.46 \mu\text{g C m}^{-3} \text{ day}^{-1}$  in summer and  $0.54 \mu\text{g C m}^{-3} \text{ day}^{-1}$  in winter between 500 and 2000 m water depth in this study. The estimated carbon consumption was then  $0.56 \text{ g C m}^{-2} \text{ y}^{-1}$  and may be equal to 0.05% of the copepod standing stock per day in summer. This predation impact is lower than the data reported for the epipelagic layer. Øresland (1995) assumed an impact of up to 0.2% of the copepod standing stock per day by number solely for the abundant *E. hamata*, whereas Froneman et al. (1998) estimated 0.3 to 1.2% for *E. hamata* and *S. gazellae* that is somewhat higher than the above mentioned biomass consumption, if the size spectrum of copepods is rather uniform. Only data from observations near Prince Edward Island were distinctly higher (Froneman and Pakhomov 1998). Considering higher metabolic rates for meso- and bathypelagic chaetognaths as indicated before and probably overestimated copepod biomass, the predation impact would be higher.

The primary production needed to maintain the consumption by chaetognaths via herbivorous copepods may amount to 2.8% below 500 m depth. If their diet also consists of carnivorous prey, however, the amount may be 6.1% (1:1 diet of herbivorous and carnivorous copepods). Considering the water column from 0 to 2000 m, values of 8.4% and 18.2% respectively could be estimated. Chaetognaths may therefore exhibit a significant impact on the copepod community and play an important role in transfer of energy. This is especially true as they themselves may represent prey for higher trophic levels like myctophid fishes (Perissinotto and McQuaid 1992; Pakhomov et al. 1996).

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In the last two decades some studies on the role of chaetognaths in the vertical carbon flux were conducted (Dilling and Alldredge 1993; Giesecke et al. 2009). These studies reveal a significant contribution of this abundant zooplankton group to the vertical carbon flux via the production of large, fast-sinking fecal pellets. Giesecke et al. (2009) estimated that *Sagitta gazellae* may contribute 5 and 12% of the total vertical carbon flux in summer and winter, respectively, at 360 m depth in the Lazarev Sea. Chaetognath abundance and/or defecation must be high for such a substantial contribution (Giesecke et al. 2009). The number of *S. gazellae* at meso- and bathypelagic depths during this study is low compared to the epipelagial. Therefore their impact at this depth zone is assumed to be low. The contribution of *Eukrohnia* specimens to carbon flux is still unclear. As experiments with this genus are challenging, rarely any data on their fecal pellet production and sinking rates exist.

## 8. CONCLUSIONS AND PERSPECTIVES

The Antarctic meso- and bathypelagic chaetognath community consists of at least ten species. Multiple morphological characters are necessary for clear determination of different species and maturity stages, and have to be consulted especially when distinguishing *Eukrohnia hamata* and *E. bathypelagica*. *E. hamata* and *Sagitta marri* are the dominating species, whereas *E. bathypelagica* and *E. bathyantartica* are the typical meso- and bathypelagic chaetognaths. Each species seems to inhabit its own vertical and horizontal region, more or less overlapping in distribution with other chaetognath species. Due to a high variability in chaetognath abundance between the stations, the effect of water masses on species distribution is difficult to identify. The Antarctic Polar Front and the associated water mass seem to have a minor impact on the chaetognath distribution below 500 m, and do not act as a strict boundary for the distribution of meso- and bathypelagic chaetognaths. The principle determinants of abundance and species composition are water depth and season. Hence, total abundance and biomass decrease with increasing depth, showing highest numbers between 500 and 1000 m within the 500 to 2000 m sampling range. Seasonality can be observed in *E. hamata* and *S. marri*, both showing a deeper distribution in winter than in summer. The vertical segregation of maturity stages is assumed to be a common pattern in all four abundant species to different degrees.

The population structures in *E. hamata*, *E. bathypelagica*, *E. bathyantartica* and *S. marri* appear to be complex. The low numbers of stage III and IV specimens in *E. hamata* and *S. marri* indicate either an occurrence of adults below 2000 m, general low reproduction and/or missed reproduction maxima. Reproduction in *E. bathypelagica* and *E. bathyantartica* is probably continuous throughout the year. Chaetognaths were believed to die after reproduction, however this study demonstrates that a succession of at least two maturity cycles can be assumed in these two deep-living species. Both species protect their young in brood sacs in the harsh environment of the deep sea, but show different strategies for successful reproduction. *E. bathyantartica* has a small number of large eggs, whereas *E. bathypelagica* carries numerous and smaller eggs. The life cycles of the four species are not possible to elucidate only on the basis of two sampling seasons, however.

*E. hamata*, *E. bathypelagica* and *E. bathyantartica* feed in summer and winter, with copepods as favorite prey. They possibly follow the migrating copepods in winter. To study chaetognath feeding, fatty acid analyses together with gut content analyses have been carried out because chaetognaths with identifiable content are rarely caught. Higher lipid contents are found in *E. bathyantartica* than in *E. bathypelagica*, although lipid storage does not seem to be of high importance in chaetognaths. The metabolism of Antarctic chaetognaths is on a lower level compared to other Antarctic zooplankton, indicated by very low metabolic losses of body carbon. Their impact as predators on the copepod community even in the meso- and bathypelagic zone of the Southern Ocean may be high.

To receive a complete picture of the deep-water chaetognath community, further seasonal deep sampling is necessary. New species and also new distribution patterns of existing species can still be expected at these depths in

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the Southern Ocean, as indicated by the observations during this study. Furthermore, genetic analyses may complement and support morphological studies and species identification. Genetical analyses may also elucidate whether the cosmopolitan *Eukrohnia hamata* is one species or whether there are cryptic species. As differences in maximum lengths seem to exist between the Antarctic and the Greenland Sea for example, the chance of cryptic species under this complex is high. On the other hand a gene-flow associated with the thermo-haline circulation as mentioned above may exist. This would counteract the development of species differentiation.

There is still much to be learned on the biology of the meso- and bathypelagic chaetognaths. The present study was a first attempt to focus on this topic. Extensive seasonal sampling from the epipelagial to the bathypelagial could further reveal new insights into the life cycles of the abundant deep-living species. Fatty acid and trophic marker analyses may provide additional information on their feeding behavior, as experimental approaches with these delicate animals are difficult to conduct. In this context, it would be essential not only to investigate the chaetognath community, but also the copepod community as their potential prey. Data on copepods below 1000 m are basically missing for the Southern Ocean. Such datasets would allow a more realistic estimate of the chaetognath predation impact. Moreover, the comparison of copepod and chaetognath distribution patterns would allow us to prove or disprove the link between their seasonal migration patterns. Recently, Kosobokova and Hopcroft (2009) studied the mesozooplankton community in the Arctic Canada Basin down to 3000 m depth. They showed that copepods increased in importance between 1000 and 2000 m depth, whereas chaetognaths declined abruptly below 1000 m. Additionally, they observed a number of new zooplankton species. A comparable study for the Southern Ocean is a matter of particular interest.

In a second step the biology of midwater zooplankton could reveal information on their influence on the particle flux at these depths. The process of a better understanding of the deep-water chaetognaths and their biology must go on in order to deliver a valuable contribution to the further research of the Antarctic deep-water zooplankton community.

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## APPENDIX

### I.

Chaetognath abundance and species composition from deep RMTs (Rectangular Midwater Trawl) are presented for the winter 2006 and the summer 2007/2008 in the Southern Ocean. A station list for both expeditions is given in Table A. Estimated chaetognath abundance (ind. 1000 m<sup>-3</sup>) and species composition (%) is shown in Table B (winter) and in Tables C-F (summer). The nets were not equipped with a flowmeter. In order to calculate zooplankton abundance, the sampled volume was estimated via rope length, time and ship speed.

**Table A:** Station list of deep RMTs

Station	Date	Time (UTC)	Latitude	Longitude
Winter (RMT)				
506	23.07.06	11:40	61°58.48'S	0°01.56'W
529	10.08.06	15:18	60°01.31'S	0°00.93'W
532	13.08.06	01:34	59°54.31'S	2°52.70'E
Summer (multiple RMT)				
39	03.01.08	07:36	64°28.73'S	2°52.24'E
62	21.01.08	10:45	62°59.88'S	0°01.18'E
68	23.01.08	08:03	59°59.82'S	0°03.24'W
84	26.01.08	11:51	52°12.08'S	0°00.23'E

**Table B:** Estimated total chaetognath abundance (ind. 1000 m<sup>-3</sup>) and chaetognath composition (%) at three different RMT stations in winter. The RMT sampled from the surface to about 3000 m and back to the surface (5000 m rope length)

Station	506	529	532
<i>Eukrohnia hamata</i>	44.79	33.70	35.64
<i>E. bathypelagica</i>	5.65	6.91	6.93
<i>E. bathyantartica</i>	5.59	7.03	8.66
<i>Eukrohnia</i> spp.	4.89	2.06	3.28
<i>Sagitta marri</i>	10.95	12.97	11.76
<i>S. maxima</i>	1.16	1.33	0.55
<i>S. gazellae</i>	26.03	35.39	32.91
<i>Sagitta</i> spp.	0.93	0.61	0.27
Estimated abundance (ind. 1000 m <sup>-3</sup> )	7.15	3.44	4.22

APPENDIX

**Table C:** Estimated total chaetognath abundance (ind. 1000 m<sup>-3</sup>) and chaetognath composition (%) at three different depths of RMT station 39 in summer

Depth range (m)	500-750	750-1500	1500-1900
<i>Eukrohnia hamata</i>	64.10	55.87	20.26
<i>E. bathypelagica</i>	5.13	10.53	35.95
<i>E. bathyantartica</i>	0.43	10.12	37.25
<i>Eukrohnia</i> spp.	0.00	1.21	0.00
<i>Sagitta marri</i>	8.55	12.96	3.92
<i>S. maxima</i>	2.14	4.05	0.65
<i>S. gazellae</i>	19.66	5.26	1.96
<i>Sagitta</i> spp.	0.00	0.00	0.00
Estimated abundance (ind. 1000 m <sup>-3</sup> )	33.43	10.74	5.28

**Table D:** Estimated total chaetognath abundance (ind. 1000 m<sup>-3</sup>) and chaetognath composition (%) at three different depths of RMT station 62 in summer

Depth range (m)	500-1000	1000-2000	2000-2500
<i>Eukrohnia hamata</i>	45.28	34.09	42.86
<i>E. bathypelagica</i>	3.14	2.27	7.14
<i>E. bathyantartica</i>	3.77	29.55	28.57
<i>Eukrohnia</i> spp.	0.00	0.00	0.00
<i>Sagitta marri</i>	11.95	11.36	0.00
<i>S. maxima</i>	1.26	4.55	0.00
<i>S. gazellae</i>	34.59	18.18	21.43
<i>Sagitta</i> spp.	0.00	0.00	0.00
Estimated abundance (ind. 1000 m <sup>-3</sup> )	10.60	1.42	0.60

**Table E:** Estimated total chaetognath abundance (ind. 1000 m<sup>-3</sup>) and chaetognath composition (%) at three different depths of RMT station 68 in summer

Depth range (m)	500-1000	1000-2000	2000-2500
<i>Eukrohnia hamata</i>	41.19	23.70	11.32
<i>E. bathypelagica</i>	3.89	7.51	16.98
<i>E. bathyantartica</i>	2.07	30.64	49.06
<i>Eukrohnia</i> spp.	0.26	2.89	1.89
<i>Sagitta marri</i>	19.95	9.25	5.66
<i>S. maxima</i>	2.33	4.05	0.00
<i>S. gazellae</i>	30.31	21.97	15.09
<i>Sagitta</i> spp.	0.00	0.00	0.00
Estimated abundance (ind. 1000 m <sup>-3</sup> )	10.03	2.51	2.30



APPENDIX

**Table F:** Estimated total chaetognath abundance (ind. 1000 m<sup>-3</sup>) and chaetognath composition (%) at three different depths of RMT station 84 in summer

Depth range (m)	0-1000	1000-1500	1500-2000
<i>Eukrohnia hamata</i>	28.28	45.73	51.11
<i>E. bathypelagica</i>	1.29	2.51	7.04
<i>E. bathyantartica</i>	3.08	1.01	18.52
<i>Eukrohnia</i> spp.	2.83	1.51	0.37
<i>Sagitta marri</i>	6.68	11.06	4.81
<i>S. maxima</i>	36.50	33.67	10.74
<i>S. gazellae</i>	20.31	4.52	7.41
<i>S. macrocephala</i>	0.26	0.00	0.00
<i>Sagitta</i> spp.	0.00	0.00	0.00
Unid. chaetognath	0.77	0.00	0.00
Estimated abundance (ind. 1000 m <sup>-3</sup> )	12.75	9.26	7.50

The last net should have sampled the 500 to 1000 m depth range, but the net did not close completely and stayed open up to the surface.

APPENDIX

II.

The following tables show the summarized results of length, body composition and daily metabolic loss (% body carbon) of *Eukrohnia hamata* (A), *E. bathypelagica* (B) and *E. bathyantartica* (C) at different depths in summer (1) and winter (2). A lower number of nitrogen and thus C:N data were obtained for *E. hamata* and *E. bathyantartica* in summer (number of specimens given in brackets). Body carbon respired was calculated for each specimen using an average respiration rate of 0.15  $\mu\text{l O}_2 \text{ mg dry mass}^{-1} \text{ h}^{-1}$  (see publication III for calculation details).

DM: dry mass, n: number of specimens

**Table A1: *Eukrohnia hamata* (summer)**

Depth range (m)		500-750	750-1000	500-1000	1000-1500	1500-2000	1000-2000
n		43 (42)	8	4	3 (2)	6	8
Length (mm)	Mean	19.4	21.5	26.0	16.3	27.3	26.1
	sd	4.3	4.8	1.2	4.7	1.5	1.1
Dry mass (mg)	Mean	2.0	2.7	4.1	0.9	6.6	4.3
	sd	1.4	1.6	0.8	0.6	1.5	0.9
Carbon (% DM)	Mean	28.5	32.5	31.1	27.6	38.3	32.8
	sd	7.6	6.3	1.4	4.0	2.7	10.2
Nitrogen (% DM)	Mean	6.5	6.8	7.7	7.0	7.7	7.2
	sd	1.7	1.4	0.2	0.6	0.6	3.0
C:N ratio	Mean	4.4	4.8	4.0	4.3	5.0	4.9
	sd	0.6	0.9	0.1	0.0	0.6	1.1
Body carbon respired (%)	Mean	0.74	0.61	0.62	0.71	0.50	0.64
	sd	0.26	0.12	0.03	0.10	0.04	0.22

APPENDIX

**Table A2:** *Eukrohnia hamata* (winter)

Depth range (m)		500-750	750-1000	1000-1500	1500-2000	2000-3000
n		62	36	50	30	1
Length (mm)	Mean	20.9	21.3	23.3	24.2	26.0
	sd	2.9	3.5	2.7	2.8	-
Dry mass (mg)	Mean	2.0	2.2	2.7	2.8	4.6
	sd	1.0	1.2	1.2	1.3	-
Carbon (% DM)	Mean	38.4	40.2	38.5	41.7	39.8
	sd	5.9	7.2	5.8	5.1	-
Nitrogen (% DM)	Mean	8.0	7.9	7.6	7.7	7.4
	sd	1.1	1.5	1.1	1.0	-
C:N ratio	Mean	4.8	5.2	5.1	5.6	5.4
	sd	0.8	1.1	0.9	1.2	-
Body carbon respired (%)	Mean	0.51	0.50	0.51	0.47	0.48
	sd	0.07	0.13	0.10	0.06	-

**Table B1:** *Eukrohnia bathypelagica* (summer)

Depth range (m)		500-750	750-1000	1000-1500	1500-2000
n		12	4	9	15
Length (mm)	Mean	21.5	18.8	18.9	22.6
	sd	1.5	1.7	2.6	1.6
Dry mass (mg)	Mean	1.9	1.6	1.8	4.0
	sd	0.5	0.8	1.1	1.6
Carbon (% DM)	Mean	17.3	21.3	27.9	29.4
	sd	2.2	4.6	6.7	5.5
Nitrogen (% DM)	Mean	4.7	5.0	6.0	6.5
	sd	0.8	0.7	1.1	0.8
C:N ratio	Mean	3.7	4.3	4.6	4.5
	sd	0.2	0.4	0.7	0.6
Body carbon respired (%)	Mean	1.13	0.94	0.72	0.68
	sd	0.14	0.25	0.16	0.14

APPENDIX

**Table B2: *Eukrohnia bathypelagica* (winter)**

Depth range (m)		500-750	750-1000	1000-1500	1500-2000	2000-3000
n		5	5	19	13	1
Length (mm)	Mean	22.6	20.8	21.1	23.1	23.0
	sd	1.1	2.4	2.2	2.0	-
Dry mass (mg)	Mean	1.6	1.7	2.0	3.0	1.6
	sd	0.4	0.8	1.1	1.6	-
Carbon (% DM)	Mean	24.1	30.0	33.6	31.9	21.4
	sd	2.0	8.7	10.2	7.7	-
Nitrogen (% DM)	Mean	6.4	7.4	7.0	7.0	5.4
	sd	0.6	1.7	1.3	1.0	-
C:N ratio	Mean	3.8	4.0	4.7	4.5	4.0
	sd	0.1	0.3	1.1	0.7	-
Body carbon respired (%)	Mean	0.80	0.68	0.63	0.64	0.90
	sd	0.07	0.19	0.21	0.16	-

**Table C1: *Eukrohnia bathyantartica* (summer)**

Depth range (m)		1000-2000	2000-2500
n		34 (33)	8
Length (mm)	Mean	21.6	23.6
	sd	5.7	2.4
Dry mass (mg)	Mean	3.5	3.2
	sd	2.7	1.3
Carbon (% DM)	Mean	32.1	34.0
	sd	5.2	3.3
Nitrogen (% DM)	Mean	6.8	7.2
	sd	1.1	0.5
C:N ratio	Mean	4.8	4.7
	sd	0.9	0.3
Body carbon respired (%)	Mean	0.62	0.57
	sd	0.10	0.06

APPENDIX

**Table C2:** *Eukrohnia bathyantarctica* (winter)

Depth range (m)		500-750	1000-2000	2000-3000	0-3000
n		1	16	2	16
Length (mm)	Mean	25.0	19.0	21.5	24.1
	sd	-	4.9	3.5	1.7
Dry mass (mg)	Mean	2.4	1.6	2.0	2.9
	sd	-	1.0	1.1	0.7
Carbon (% DM)	Mean	45.5	36.5	44.3	47.9
	sd	-	4.1	5.2	4.9
Nitrogen (% DM)	Mean	8.1	7.6	7.4	9.3
	sd	-	1.1	1.0	1.1
C:N ratio	Mean	5.6	4.9	6.1	5.2
	sd	-	0.8	1.5	0.9
Body carbon respired (%)	Mean	0.42	0.53	0.44	0.41
	sd	-	0.06	0.05	0.04

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