

Role of midwater chaetognaths in Southern Ocean pelagic energy flow

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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 chaetognaths have a mean biomass of 0.109 mg C m⁻³ in summer and 0.146 mg C m⁻³ in winter. Chaetognaths respiration and consumption amount to 282 and 563 mg C m⁻² yr⁻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 g C m⁻² yr⁻¹) of the net 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 g C m⁻² yr⁻¹) of annual primary production. It is estimated that chaetognath consumption for the whole water column is 1.4 g C m⁻² yr⁻¹. This corresponds to 7.1% (= 4.8 g C m⁻² yr⁻¹) and 15.5% (= 10.4 g C m⁻² yr⁻¹) of the primary production channeled through herbivorous copepods and through herbivorous and carnivorous copepods, respectively. Hence, chaetognaths represent an important link between lower and higher trophic levels. To further unravel their role in the ecosystem, additional studies on the meso- and bathypelagic zooplankton community are needed.

KEY WORDS: Chaetognatha · Antarctica · Midwater · Respiration · Energy budget

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INTRODUCTION

Chaetognaths are found in all marine habitats, from epipelagic layers to the seafloor. The biomass of these carnivores is estimated to be about 30% of that of copepods, their principal prey, in the world ocean (Reeve 1970). Antarctic chaetognaths are considered important predators (Pakhomov et al. 1999) and may represent a significant component in the biological carbon pump due to the production of large and fast-sinking fecal pellets (Giesecke et al. 2010). Chaetognath feeding ecology has frequently been studied in terms of gut content analyses, estimates of digestion time and feeding rates (e.g. Øresland 1987, Sameoto 1987, Falkenhaug 1991, Froneman et al. 1998, Giesecke & González 2004). Several respiration measurements provided information on the chaetognath individual metabolism (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 a few studies have been conducted to date on individual metabolic activity in Antarctic chaetognaths (Ikeda & Kirkwood 1989, Kruse et al. 2010).

Evidence suggests that the daily metabolic loss of Antarctic chaetognaths may be lower compared to other chaetognath species at similar temperatures and to other Antarctic zooplankton (Ikeda & Kirkwood 1989, Kruse et al. 2010). Hence, one might ask whether the overall significance of chaetognaths in the Antarctic pelagic food web, particularly their impact on the copepod community, is also lower. Our current knowledge of the Antarctic meso- and bathypelagic chaetognath community is largely limited, and only some information exists on their taxonomy, abundance and biomass. There are few studies with reasonable resolution in time and space, and most of these are limited

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to the epi- and mesopelagic realm (e.g. Hagen 1985, Terazaki 1989, Duró et al. 1999, Johnson & Terazaki 2004). The meso- and bathypelagic part of the Antarctic chaetognath community was studied in detail by Kruse et al. (2009) whose findings indicate that Antarctic midwater chaetognaths may constitute a significant vector in pelagic energy flow due to their relatively numerous occurrence.

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.

MATERIALS AND METHODS

Field sampling. Two expeditions with the RV 'Polarstern' were carried out in the Lazarev Sea during Antarctic winter 2006 (17 June–21 August 2006, expedition ANT 23-6) and Antarctic summer 2007/2008 (28 November 2007–04 February 2008, expedition ANT 24-2). The study area was located between 60–70°S and 3°W–3°E (see Kruse et al. 2009), except for 2 stations located at 52°S 0°E in summer. Samples were taken with a multinet (MN; 100 µm mesh size, 0.25 m² mouth area) at 28 stations in winter and at 15 stations in summer. The following standard depth intervals were applied: 2000–1500, 1500–1000, 1000–750, 750–500, 500–0 m. In this study, the 500 to 2000 m depth range was investigated. For further sampling details see Kruse et al. (2009). A rectangular midwater trawl (RMT 8: 4.5 mm mesh size, 8 m² mouth area; RMT 1: 320 µm mesh size, 1 m² mouth area) and a multiple RMT (equipped with three RMT 8 and three RMT 1 nets) were also deployed at a few stations between about 52° and 64°30' S during winter and summer, respectively (Table 1). The RMT stations were selected at positions separated in time and space and at stations where sufficient additional parameters were available from other groups' measurements.

Carbon content. Intact chaetognaths of the 6 species *Eukrohnia bathyantartica*, *E. bathypelagica*, *E. hamata*, *Sagitta gazellae*, *S. marri* and *S. maxima* were selected from the MN and RMT samples. The size of the individuals was measured 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 the Alfred Wegener Institute, the chaetognaths were

freeze-dried for 24 h and weighed on Sartorius microbalances. Subsequently, either the carbon content of the entire animal or of subsamples of the ground specimen was determined in a Euro Elemental Analyzer. In total, 584 carbon measurements, 328 from winter and 256 from summer, were made. To analyze seasonal differences in carbon content within each species, the data were Box-Cox transformed when necessary to achieve normality and homogeneity of variances (Sokal & Rohlf 1981) and subjected to a *t*-test.

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

$$\log(C) = a + X_{\text{taxon1}} + b \times \log(L) + X_{\text{taxon2}} \times [\log(L) - L_{\text{mean}}] \quad (1)$$

to estimate carbon content C (µg ind⁻¹) from body length L (mm), where variables X_{taxon1} and X_{taxon2} describe the particular effect of each taxon on the relationship between L and C . $\log(L)$ is adjusted to mean = 0 in the interaction term (L_{mean}) in order to make the test for the main effects independent of the test for interaction ('centered polynomials'). Carbon contents were not differentiated by season.

Community chaetognath biomass (µg C m⁻³) was then calculated from chaetognath length and abundance (Kruse et al. 2009) for each depth interval and station (MN only). A full factorial two-way ANOVA (Biomass vs. Season and Depth, and Season × Depth) with a subsequent post-hoc test for 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 750 m water depth at 64° 28.73' S 2° 52.24' E in summer) were mea-

Table 1. Southern Ocean stations sampled with rectangular midwater trawl (RMT)

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

sured using Winkler titration to determine oxygen concentration as described in Kruse et al. (2010) for *Eukrohnia hamata* and *E. bathypelagica*. In contrast to Kruse et al. (2010), 2 unfed specimens of *S. gazellae* were incubated together in a 1 l sealed glass bottle filled with filtered (0.7 µm pore size) and oxygen-saturated seawater (saturation of ~96%) for 11 h. We conducted one experiment consisting of 5 bottles with chaetognaths and 2 controls without chaetognaths for this species.

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

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

where R is the respiration rate (J d^{-1}), M is the body mass (J), T is the water temperature (K), D is the water depth (m), and the variable X_{taxon} represents a taxon-specific value. This model was fitted using our data on *Sagitta gazellae* as well as data from Reeve et al. (1970), Nival et al. (1972), Ivleva (1976), Båmstedt (1979), Ikeda (1989), Ikeda & Kirkwood (1989), Ikeda & Skjoldal (1989), Thuesen & Childress (1993), Welch et al. (1996), Ikeda & Hirakawa (1998), Coston-Clements et al. (2009), and Kruse et al. (2010). The data published by Sameoto (1972) were not used because an *a priori* analysis showed that these values deviated consistently and significantly from all other sources, indicating a source-specific bias. All data were extracted from the respiration data bank of Brey (2010). Using general factors summarized in Brey (2001) and Brey et al. (2010), the body mass and respiration data of *S. gazellae* were converted to J and to J d^{-1} accordingly. Multivariate outliers in the sample space [$\log(M)$, $1/T$, $\log(R)$] ($\alpha = 0.05$) were identified by Mahalanobis Jackknife distances (Barnett & Price 1995) and excluded from the model construction. *Heterokrohnia murina* was included in the family Eukrohniidae, because there was only one data point for the family Heterokrohniidae (following the classification of Casanova 1985).

Annual respiration and consumption. The respiration rate (J d^{-1}) of each single individual from all MN stations during both Antarctic cruises was estimated using the calculated individual chaetognath biomass and the respiration model. From this data base, we inferred the daily chaetognath respiration rate per m^3 for both seasons and the annual rate per m^2 for the different MN depth intervals in the investigated area. By means of a full factorial two-way ANOVA (see 'Biomass calculation'; Respiration rate vs. Season and Depth, and Season \times Depth), we tested for seasonal and vertical differences in chaetognath respiration. To achieve normality and homogeneity of variances, the data were Box-Cox transformed prior to this analysis.

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

$$Q_{\text{chaeto}} = R_{\text{chaeto}} / (0.8 - 0.3) \quad (3)$$

To estimate the amount of primary production (PP_{chaeto}) ($\text{g C m}^{-2} \text{ yr}^{-1}$) 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 (Straile 1997, Landry & 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:

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

$$PP_{\text{chaeto}} = 0.5 \times Q_{\text{chaeto}} / 0.3 + 0.5 \times Q_{\text{chaeto}} / 0.3 / 0.3 \quad (5)$$

A gross growth efficiency of 0.3 can also be estimated for other zooplankton species. Therefore we assume that the same amount of primary production is needed, even if other zooplankton are constituents of the chaetognath diet.

RESULTS

Chaetognath biomass

Body length (ANCOVA, $p < 0.001$), taxon ($p < 0.001$) and the interaction between these 2 parameters ($p < 0.001$) affect chaetognath carbon content. Test runs with different taxonomic resolution indicated that the separation into the 3 groups *Eukrohnia* spp., *Sagitta marri* and other *Sagitta* spp. generated the best trade-off between model accuracy and model generality:

$$\log(C) = -1.1596 + X_{\text{taxon1}} + 2.9969 \times \log(L) + X_{\text{taxon2}} \times [\log(L) - 1.3898] \quad (6)$$

with $N = 584$ (6 species, Table 2), $R^2 = 0.874$ and $p < 0.001$ 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 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*.

Based on the abundance data of Kruse et al. (2009), we estimated an average midwater (500 to 2000 m) chaetognath biomass of 0.109 mg C m⁻³ in summer and 0.146 mg C m⁻³ in winter (Table 3). The biomass was significantly higher in winter (ANOVA with Tukey's post-hoc test, $p < 0.01$) and in the 500 to 750 m depth range (ANOVA with Tukey's post-hoc test, $p < 0.001$). The midwater chaetognath biomass integrated over water depth and averaged over season was 199.9 mg C m⁻² (SD = 67.2).

Respiration model

Sagitta gazellae respired 0.556 $\mu\text{l ind.}^{-1} \text{h}^{-1}$ (SD = 0.176, N = 5) or 0.011 J ind.⁻¹ h⁻¹. Including these data and the data on *Eukrohnia* (Kruse et al. 2010), the database for the general chaetognath respiration model consisted of 466 measurements spanning 13 species (3 of them identified to genus only). Mahalanobis distances identified 23 outliers, thereby 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:

$$\log(R) = 10.0264 + 0.6643 \times \log(M) - 2957.8576/T - 0.3870 \times \log(D) + X_{\text{taxon}} \quad (7)$$

Table 2. Carbon content \pm SD (no. of measurements in parentheses) of 6 chaetognath species during summer and winter in the Southern Ocean. DM: dry mass; (-) no data. * $p < 0.05$: significantly different from summer value

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

^aFor detailed data on the biochemical composition see Kruse et al. (2010)

Table 3. Biomass (no. of multinet stations in parentheses) and oxygen consumption \pm SD of chaetognaths at different depth intervals during summer and winter in the Southern Ocean (obtained by Eqs. 6 & 7)

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

with N = 443, R² = 0.832 and $p < 0.001$ for the whole model as well as for each term; with $X_{\text{taxon}} = +0.1212$ for Eukrohniidae and $X_{\text{taxon}} = -0.1212$ for Sagittidae. Respiration per individual generally increases with increasing body mass and rising temperature, and it decreases with increasing depth (Fig. 1). Eukrohniidae have higher rates than Sagittidae. The respiration rates

Table 4. Taxonomic distribution of chaetognath respiration data used for the construction of the general chaetognath respiration model (reduced by 23 outliers). N: number of data

Species	Family	N	Source
<i>Caecosagitta macrocephala</i>	Sagittidae	9	Thuesen & Childress (1993)
<i>Eukrohnia bathypelagica</i>	Eukrohniidae	13	Kruse et al. (2010)
<i>Eukrohnia hamata</i>	Eukrohniidae	96	Båmstedt (1979), Kruse et al. (2010)
<i>Eukrohnia</i> spp. (<i>E. hamata</i> , <i>E. fowleri</i>)	Eukrohniidae	11	Thuesen & Childress (1993)
<i>Flaccisagitta hexaptera</i>	Sagittidae	1	Thuesen & Childress (1993)
<i>Heterokrohnia murina</i>	Heterokrohniidae	1	Thuesen & Childress (1993)
<i>Parasagitta elegans</i> ^a	Sagittidae	77	Welch et al. (1996)
<i>Pseudosagitta</i> spp. (<i>P. lyra</i> , <i>P. maxima</i>)	Sagittidae	15	Thuesen & Childress (1993)
<i>Sagitta elegans</i> ^a	Sagittidae	16	Båmstedt (1979), Ikeda (1989), Ikeda & Kirkwood (1989), Ikeda & Skjoldal (1989), Ikeda & Hirakawa (1998)
<i>Sagitta gazellae</i>	Sagittidae	43	Ikeda (1989), Ikeda & Kirkwood (1989), present study
<i>Sagitta hispida</i>	Sagittidae	26	Reeve et al. (1970)
<i>Sagitta tenuis</i>	Sagittidae	15	Coston-Clements et al. (2009)
<i>Sagitta</i> spp.	Sagittidae	108	Ivleva (1976), Thuesen & Childress (1993)
<i>Solidosagitta zetesios</i>	Sagittidae	12	Thuesen & Childress (1993)
Total		443	

^aTreated as 1 species (*Sagitta elegans* = *Parasagitta elegans*)

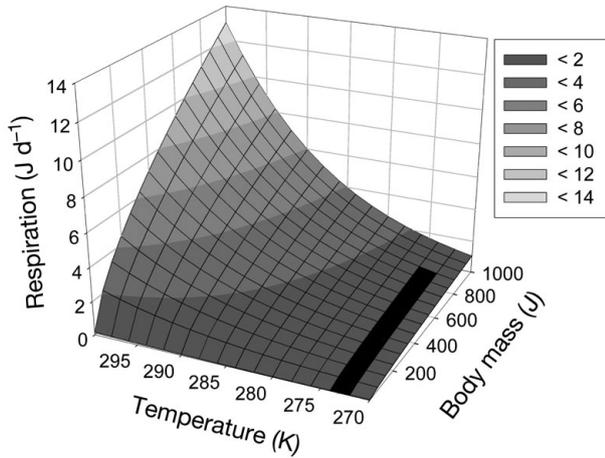


Fig. 1. Individual respiration (R ; J d^{-1}) vs. body mass (M ; J) and temperature (T ; K) in chaetognaths according to the chaetognath respiration model: $\log(R) = 10.0264 + 0.6643 \times \log(M) - 2957.8576/T - 0.3870 \times \log(D) + X_{\text{taxon}}$ (Eq. 7). Water depth (D) is set to 500 m and taxon effects are neglected, i.e. $X_{\text{taxon}} = 0$. Black area between 272 and 274 K: respiration rates to be expected for Southern Ocean chaetognaths at 500 m water depth

at low temperatures (e.g. 0°C or 273 K) increase only slightly with higher body mass. In contrast, chaetognath respiration rates increase strongly at higher temperatures. 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

Respiration rates were similar during both seasons, accounting for $0.46 \mu\text{g C m}^{-3} \text{ d}^{-1}$ in summer and $0.54 \mu\text{g C m}^{-3} \text{ d}^{-1}$ in winter between 500 and 2000 m depth (Table 3). Depth had a significant effect on chaetognath respiration (ANOVA, $p < 0.001$). The highest rates were found in the 500 to 750 m layer. In the 2 strata below 1000 m, the rates were the lowest, and the values did not differ significantly (ANOVA with Tukey's post hoc test, $p > 0.05$).

Table 5. Integrated annual respiration (R) and corresponding annual carbon consumption (Q), and annual net primary production (PP) used by chaetognaths in the Southern Ocean. N = number of multinet stations

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

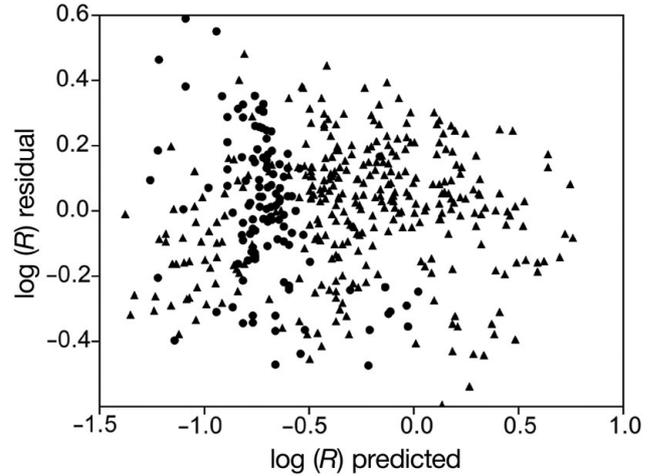


Fig. 2. Residual vs. estimated $\log(R)$ of the general chaetognath respiration model: $\log(R) = 10.0264 + 0.6643 \times \log(M) - 2957.8576/T - 0.3870 \times \log(D) + X_{\text{taxon}}$ (Eq. 7; see Fig. 1 for definitions). $N = 443$, $R^2 = 0.832$, $p < 0.001$; $X_{\text{taxon}} = +0.1212$ for Eukrohniidae and -0.1212 for Sagittidae. (●): Sagittidae; (▲): Eukrohniidae

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

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, with *Eukrohnia hamata* and *Sagitta gazellae* being the dominant species (Pakhomov et al. 2000). In our study area, this corresponds to a summer chaetognath biomass of up to $\sim 5000 \mu\text{g dry mass (DM) m}^{-3}$ (Marginal Ice Zone; Pakhomov et al. 2000). Lower values (averages) are reported from the Weddell Sea ($\sim 580 \mu\text{g DM m}^{-3}$, 0–300 m, oceanic community; Boysen-Ennen et al. 1991) and the Croker Passage ($< 36 \mu\text{g DM m}^{-3}$, 0–1000 m, *E. hamata*, *S. gazellae* 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 500 m stratum of the Lazarev Sea, we used the data published by Ward et al. (1995) for South Georgia that are based on 200 μm mesh sampling. These authors provided a vertical profile for chaetognaths in summer with a mean biomass of $\sim 2500 \mu\text{g DM m}^{-3}$ for the upper 500 m. The winter biomass in the upper water column is usually lower than in summer. Zooplankton volume data reported by Foxton (1956) for the upper 100 m indicate higher values by a factor of ~ 3 in summer than in winter in the Antarctic. The mean zooplankton volume in the 0 to 1000 m layer at these latitudes was nearly the same during both seasons (Foxton 1956). Based on Foxton's information, we assume the summer chaetognath biomass to be higher by a factor of 2 compared to winter in the 0 to 500 m layer, which results in chaetognath biomass estimates of $2500 \mu\text{g DM m}^{-3}$ for summer and $1250 \mu\text{g DM m}^{-3}$ for winter. Hence, annual average biomass in the 0 to 500 m layer is $1875 \mu\text{g DM m}^{-3}$, corresponding to $619 \mu\text{g C m}^{-3}$ (average $\text{C/DM} = 0.33$, Table 2). In the 500 to 2000 m range, we measured $133 \mu\text{g C m}^{-3}$ (annual mean, Table 3). Integrated across the water column, chaetognath biomass amounts to $\sim 309 \text{ mg C m}^{-2}$ in the 0–500 m range and to 200 mg C m^{-2} in the 500–2000 m range. Therefore, 39% of total chaetognath biomass is situated in the meso- and bathypelagic realm. We assume a corresponding depth distribution of chaetognath metabolic activity (see 'Chaetognath energy budget').

Within the meso-/bathypelagic region, chaetognath biomass decreases with depth. The biomass is higher in winter than in summer (Table 3). In the 500 to 750 m layer, where the abundance was lower in winter, the higher biomass results from the presence of larger and more developed *Eukrohnia hamata* (Kruse et al. 2009).

The fraction of total midwater zooplankton in the Southern Ocean that represent chaetognaths can only be estimated. 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. Warwick & Price 1979, Larson 1987, Clarke & Johnston 1999, Seibel

2007). Of concern, however, is the distinctly negative effect of water depth on respiration in our model (Eq. 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 & Childress (1993). Regarding our model, it remains unclear whether this is a residual temperature effect (Thuesen & Childress 1993), a true physiological adaptation (Drazen & Seibel 2007), or just an artifact. For instance, Kruse et al. (2010) did not find a significant depth effect on respiration rates of *Eukrohnia hamata* and *E. bathypelagica*, although rates were measured at normal surface pressure. The relationship between respiration and depth remains a topic of debate. One party reported a decline in copepod respiration with depth (Ikeda et al. 2006, Ikeda 2008), whereas other findings support the absence of large depth-related declines in species without image-forming eyes (Childress & Thuesen 1992, Childress et al. 2008). It is possible that the apparent depth effect in our chaetognath 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 not for a distinct species.

Physical, chemical and biological parameters like pressure, oxygen concentration, pH and food may influence respiration rates as well (Hernández-León & Ikeda 2005). However, zooplankton species react differently to these factors, some of which have been shown to be negligible for chaetognaths. Experiments at 0.101 and 10.1 MPa (equivalent to 0 and 1000 m depth) have shown, for example, that hydrostatic pressure has no significant effect on oxygen consumption rates of chaetognaths (Childress & Thuesen 1993). Therefore, pressure was not included in the respiration experiments or in the model. Respiration rates are also influenced by the percentage of oxygen saturation. Generally, a saturation of 70 to 80% is suggested as a limit above which the zooplankton respiration is little affected by the oxygen concentration (with few exceptions, Ikeda 1977a). Low oxygen concentrations, associated with the oxygen minimum layer for example, might influence chaetognath respiration rates, however. In addition, the pH may decrease in this layer. Chaetognaths are sensitive to a lowered pH (Yamada & Ikeda 1999). To our knowledge, no studies have evaluated the effect of pH changes on respiration of chaetognaths; thus it was not possible to include this parameter in our model. Furthermore, respiration rates are significantly influenced by feeding conditions (Ikeda et al. 2000). The rates are usually lower in starved animals than in non-starved animals (e.g. Ikeda 1977b, Brey 2010); accordingly, oxygen con-

sumption rates and ingestion rates are often positively correlated. However, the influence of feeding on zooplankton metabolism is rather complex and may be affected, amongst other things, by different kinds of prey and species-specific differences in nutritional and metabolic status of predators (Ikeda et al. 2000). In addition, bacterial activity during chaetognath experiments might also overstate measured animal oxygen consumption. We consider this effect to be negligible in our experiments due to prefiltration of water, unfed chaetognaths and hence low excretion. Considering the complexity of the various interacting factors, the presented model, even if simplified, yields the best approximation at present.

Chaetognath energy budget

It is well established that copepods are the principal food source of chaetognaths. In the Antarctic chaetognaths *Eukrohnia hamata* and *Sagitta gazellae*, copepods constitute ~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 & Marumo 1982). Other zooplankton, including ostracods, appendicularians and even chaetognaths themselves, usually represent a smaller percentage of the chaetognath diet. Hence, assuming that copepods are the only source of food is a reasonable simplification for 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⁻² for the 500–2000 m depth range in summer (derived from the data of Schnack-Schiel et al. 1998 for 0–1000 m), and the corresponding copepod production in this season is ~157.5 mg C m⁻² d⁻¹, assuming a daily production rate of 5% (Voronina 1984 in Froneman et al. 1998) and a uniform copepod size composition. Thus, the predation by meso- and bathypelagic chaetognaths of 1.5 mg C m⁻² d⁻¹, estimated in our study (563/365, 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 conservative for 2 reasons. On the one hand, metabolism and hence energy demand of free-living chaetognaths may be higher than in the restraining conditions of respiration measurement vessels. Previous studies have shown, for instance, that active metabolism oxygen consumption is nearly 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. Less than 5% of the copepod biomass between 0 and 1000 m depth is located below 300 m in summer (Schnack-

Schiel et al. 1998). Therefore, predation impact may be considerably higher on the part of the copepod community that is accessible to 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 zone range between 0 and 5.2% of the copepod standing stock for *Eukrohnia hamata* and between 0 and 3.2% for *Sagitta gazellae* (Øresland 1990, 1995, Froneman & Pakhomov 1998, Froneman et al. 1998). This corresponds to up to 103% of the daily copepod production in number for *E. hamata* and up to 63% for *S. gazellae* (Froneman & Pakhomov 1998, Froneman et al. 1998).

The winter conditions 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 & Hagen 1994, Atkinson & Sinclair 2000), and their 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, Kruse et al. 2009). If chaetognaths feed throughout the year, as we assume (Hagen 1999, Kruse et al. 2010), they may have a higher predation impact on the copepod standing stock in winter than in summer.

On an annual basis, 1.9 g C m⁻² yr⁻¹ of primary production is required to maintain the midwater chaetognath community via herbivorous copepods, corresponding to ~2.8% of net primary production (67 g C m⁻² yr⁻¹ integrated over the upper 100 m in the pelagic province of the Weddell Sea, Arrigo et al. 2008). If chaetognaths also feed on carnivorous copepods, such as *Euchaeta* spp. (Hopkins 1985, Øresland 1990), the required primary production may significantly increase. Assuming carnivorous copepods to comprise 50% of the diet, the required primary production increases to 4.1 g C m⁻² yr⁻¹ or 6.1%. 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. For the whole water column, chaetognath consumption amounts to 1.4 g C m⁻² yr⁻¹, if we scale up these budget calculations by applying a biomass factor of 1.5 for the upper 500 m (albeit neglecting the depth effect on respiration). The primary production required to fuel this consumption through the copepod food chain is between 4.8 g C m⁻² yr⁻¹ (100% herbivorous prey) and 10.4 g C m⁻² yr⁻¹ (50% carnivorous prey), corresponding to 7.1 and 15.5% of the annual net primary production, respectively.

Chaetognaths themselves may also represent an important prey for higher trophic levels. Assuming chaetognath production to be 30% of their consump-

tion, $0.17 \text{ g C m}^{-2} \text{ yr}^{-1}$ is available for their predators, e.g. amphipods and myctophid fish (Hopkins 1985, Hopkins & Torres 1989, Perissinotto & McQuaid 1992, Pakhomov et al. 1996), between 500 and 2000 m. Our findings, therefore, support the view that the mesopelagic zooplankton in Antarctic waters play a significant role in energy transfer from primary production to higher trophic levels.

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