ORIGINAL ARTICLE

Vertical distribution, population structure and developmental characteristics of the less studied but globally distributed mesopelagic copepod *Scaphocalanus magnus* in the western Arctic Ocean

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Scaphocalanus magnus is a large copepod species with a worldwide distribution. Information on the ecology of this species is scarce. In this study, *S. magnus* was collected using vertically stratified net sampling from an ice station in the western Arctic Ocean over a year. The vertical distribution differed between periods of polar night and midnight sun, with core depth distributions of 264–381 m for the polar night and 518–745 m for the midnight sun. The shallower distribution during the polar night may have resulted from the animals moving upwards to find sufficient food during the less productive season. The abundance of early copepodite stages showed clear seasonality. The C2 and C3 stages were abundant June–August and August–September, respectively. After C4, seasonality in abundance was not clear. For C4 and C5, body sizes and masses were greater for males than for females while the opposite was the case for C6. Adult males do not feed and thus have shorter life spans than females, skewing the adult sex ratio towards females. For these mesopelagic particle feeding copepods, a long residence time at C6F suggests that in a varying food environment, it is possible to wait to initiate reproduction until favourable food conditions occur.

KEYWORDS: copepods; mesopelagic; life cycle; vertical distribution

INTRODUCTION

Scaphocalanus magnus is a calanoid copepod of 4.5–5.2 mm total adult length belonging to the Scolecitrichidae and having a worldwide distribution from the Arctic to the Antarctic, including tropical regions (Brodsky, 1950; Tanaka, 1969). To date, there is no evidence of cryptic speciation based on worldwide molecular genetic/phylogeographic analyses for *S. magnus* (Ann Bucklin personal communication). *S. magnus* is a deep-water species, synonymous with *Scaphocalanus acrocephalus* and *Scaphocalanus cristatus* (Vervoort, 1957; Park, 1982). In the Arctic Ocean, although a minor component of total zooplankton biomass, *S. magnus* occurs consistently (Johnson, 1963). During summer, *S. magnus* (=*S. acrocephalus*) is found at 100–300 m and accounts for 0.22–0.28% of the abundance and 1.33–3.58% of the biomass of the total zooplankton community in the Arctic basins (Amundsen, Makarov and Canada Basin) (Kosobokova and Hirche, 2000). For the Pacific-side western Arctic Ocean, *S. magnus* is reported to be an oceanic deep-sea species and characteristic of the basin (Kosobokova and Hopcroft, 2010; Matsuno, 2014; Smoot and Hopcroft, 2017a).

Available ecological information on *S. magnus* mostly focuses on feeding modes, reproduction and others. *S. magnus* have specialized vermiform and brushform sensory filaments on the maxilla and two long vermiform sensory filaments and one short brushform sensory filament on the maxilliped (Park, 1982). Consequently, *S. magnus* are thought to be omnivorous, consuming a wide range of food items ranging from phytoplankton to micro- and mesozooplankton and detritus (Arashkevich, 1969; Blachowiak-Samolyk *et al.*, 2007; Pomerleau *et al.*, 2015). *S. magnus* is a broadcast spawner, producing eggs that are large relative to their body size and with the smallest clutch size (1.6 eggs/clutch) reported for calanoid copepods (Kosobokova *et al.*, 2007; Brun *et al.*, 2017). The carbon and nitrogen mass, protein content and electron transport system activity of *S. magnus* are reported only for the subarctic Pacific (Ikeda *et al.*, 2006). While bioluminescence is common in the mesopelagic copepods, *S. magnus* do not exhibit bioluminescence (Takenaka *et al.*, 2012). *S. magnus* is known to be a host of epibiont suctorian ciliates (Yamaguchi, 2006). While such ecological information is valuable, little information is available for population structure, life cycle and chemical composition, despite the possible worldwide distribution of this species.

In the present study, vertical distributions, seasonal population structure changes, life stage-specific length and mass changes, and moult intervals over an annual cycle were investigated for *S. magnus* using vertically stratified samples collected every 10–14 days over a single year (1997–1998) at an ice station in the western Arctic Ocean. Since ambient environments (e.g. light or food availability) in the Arctic Ocean show greater seasonality, seasonal phenology is expected to be present even for the deep-sea copepods. Adding vertical distribution and population structure observations, measurements of length and mass with each copepodite stage (female and male separation were also made for juveniles based on their morphology) provides deep insights into their development and growth.

METHOD

Zooplankton samples were collected during the year-long Surface Heat Budget of the Arctic Ocean (SHEBA) expedition (e.g. Ashjian *et al.*, 2003) from along the ice station drift track through the Canada Basin to the Mendeleev Plain (Electronic supplement 1). Stratified vertical hauls (nominally 0–50, 50–100, 100–200, 200–1500 and 1500–2800 m, depending on bottom depth) were made to just above the seafloor at 10–14 days intervals (total 30 sampling dates) using a 1-m mouth diameter opening–closing net equipped with 53 or 150 μm mesh from 27 October 1997 to 29 September 1998 (Ashjian *et al.*, 2003) (Electronic supplement 2). The samples were preserved with 4% buffered formalin seawater. Vertical profiles of temperature were collected using a conductivity–temperature–depth package. Previous analyses of these samples had enumerated only the dominant zooplankton taxa (Ashjian *et al.*, 2003). In the present analysis, less abundant or rare species were quantified by examining entire samples rather than only quantitative portions (splits).

S. magnus were sorted by copepodite stages. Morphologically, females and males were distinguishable at the C4–C6 stages. At stages C4 and C5, females have a thin, short swimming leg 5 (P5) that extends only to the first 1–2 segments of the urosome while males have thicker, longer P5s that extend to segments 2–3 of the urosome. For details on the morphology of each stage, see Electronic supplement 3 (photographs). A small number of C1 stages of *S. magnus* was present, likely because the diagonal size of the mesh (212 μm) dictated that only stages >C2 [prosome width: 297 ± 19 μm (mean ± standard deviation, $n = 9$)] were collected quantitatively. While we used 53 μm mesh nets for several occasions, because of the usage period (2 months) and depth (0–325 m) were limited (see Electronic supplement 2), the effect of the differences in collection mesh size on the results of this study may be ignored for the deep-dwelling *S. magnus*. Adult female (C6F) specimens with spermatophores attached also were identified (Electronic supplement 3).
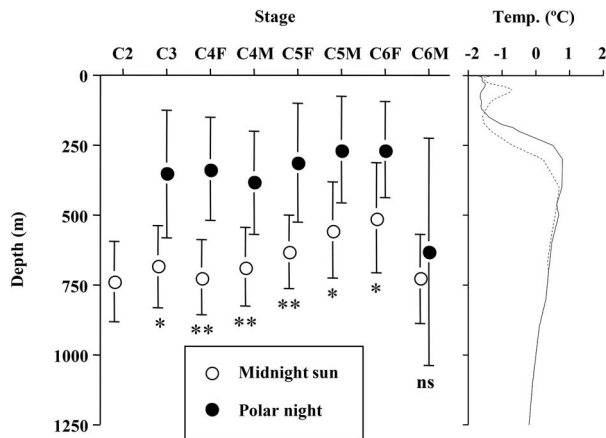
Fig. 1. Ontogenetic changes in the core depth distributions for *S. magnus*. Mean $D_{50\%}$, (symbols) and standard deviations (bars) are shown. Open and solid symbols denote data collected during the periods of the midnight sun (late April to August, $n = 3$) and of the polar night (mid-November to early February, $n = 6$), respectively. The mean temperatures during the midnight sun (solid line) and polar night (dotted line) are shown in the right panel. Differences in $D_{50\%}$ between midnight sun and polar night were tested using a U test. *: $P < 0.05$, **: $P < 0.01$, ns: not significant. Ontogenetic changes within each season were not significant for both midnight sun and polar night ($P > 0.05$, one-way ANOVA).

Seafloor depth varied between 352 and 3850 m over the year-long drift track (Ashjian *et al.*, 2003). Because of this, sampling depths varied from two to eight (number of samples on each date) over 0–100 to 0–3500 m, respectively (Electronic supplement 2). Since *S. magnus* was found primarily below 250 m (see below, Fig. 1), samples with maximum sampling depths shallower than 400 m were omitted from the analysis, reducing the number of available sampling dates to 20 (from an original 30). However, the time interval between the 20 successive dates was at most 1 month, permitting analysis of seasonal abundance and population structure (Electronic supplement 2).

The core depth distribution ($D_{50\%}$) was calculated based on abundances (ind. m^{-2}) in each sampling layer (Pennak, 1943):

$$D_{50\%} = d_1 + (d_2 - d_1) \times \frac{50 - p_1}{p_2}$$

where d_1 is the depth (m) of the upper depth of the 50% individual occurrence layer, d_2 is the maximum depth (m) of the 50% individual occurrence layer, p_1 is the cumulative individual percentage (%) that occurred at depths shallower than the 50% individual occurrence layer, and p_2 is the individual percentage (%) at the 50% individual occurrence layer. The means and standard deviations of the $D_{50\%}$ of each copepodite stage were calculated during the period of the midnight sun (late April–August) and

of the polar night (mid-November–early February), and the differences between them were tested with Mann–Whitney U test. For the evaluation of vertical distributions, data with maximum sampling depths shallower than 900 m and data collected during transitions outside of the periods of the midnight sun or polar night were omitted. According to these criteria, three dates during the midnight sun and six dates during the polar night were retained. For details of sampling depths and dates, see Electronic supplement 2. Ontogenetic changes in vertical distribution were tested by one-way analysis of variance (ANOVA) on the $D_{50\%}$ of each copepodite stage during the midnight sun and polar night.

Body length (prosome length: PL) and masses (wet mass; WM, dry mass; DM, ash-free dry mass; AFDM) were measured for each stage using formalin-preserved samples. Specimens of each copepodite stage were selected and photographed using a stereomicroscope. The PLs were measured from the images with 10 μm precision using ImageJ (https://imagej.nih.gov/ij/). The WM was determined for batches of pooled specimens (3–19 individuals of each stage) that had been briefly rinsed in distilled water, blotted dry on a filter paper and weighted in a pre-weighed combusted aluminium pan. Those samples then were placed in an oven at 60°C for 5 h and weighed after drying to determine DM. Ash content was determined by weighing the same specimens before and after combustion at 480°C for 5 h; AFDM was then determined by difference. For all determinations, a mass was determined to a precision of 1 μg using a CAHN (C-33) microbalance. Moult increments (MI, %) at C_{n-1}/C_n stage in PL, WM, DM and AFDM were calculated according to the equation of Mauchline (1998):

MI = 100 × (value of C_n—value of C_{n-1})/value of C_{n-1}.

To identify at which stage the growth of PL and masses are achieved, the proportion of growth (PG, %) at C_{n-1}/C_n for PL, WM, DM and AFDM was determined for females and males, treating the values of adults as 100%:

PG = 100 × (value of C_n—value of C_{n-1})/value of adult (C6).

RESULTS

Vertical distribution

The mean vertical distribution core ($D_{50\%}$) of each copepodite stage varied from 264 m (C6F, polar night) to 745 m (C2, midnight sun) (Fig. 1). Depth differences between the midnight sun and the polar night were observed for stages C3–C6F (note that stage C2 did not

occur in polar night samples). The $D_{50\%}$ of C3–C6F ranged from 518 to 745 m (653 ± 86 m, mean $\pm$ standard deviation) during the midnight sun but from 264 to 381 m (322 ± 45 m) during the polar night. Thus, the distribution depths of C3–C6F were shallower during the polar night than during the midnight sun with differences ranging from 25 to 395 m (331 ± 51 m) ($P < 0.05$, U test). In contrast, the $D_{50\%}$ of C6M varied between 628 and 735 m throughout the year and no differences were detected between midnight sun and polar night ($P = 0.593$). Ontogenetic changes in vertical distribution were not detected for C2–C6F/M either during midnight sun or polar night ($P = 0.052$–0.205, one-way ANOVA).

Population structure

During the observation period, there were three transitions in water mass type in the upper water column (Ashjian *et al.*, 2003) that had little effect on the abundances of each copepodite stage of *S. magnus* (Fig. 2). Clear seasonal changes were detected for abundances of C2 and C3, with C2 abundant from June to August, and C3 dominant from August to September. C4 was abundant in August–September and January–February, and C5 and C6 were numerous during May–June. The sex ratio was ~1:1 in C4 and C5 [females were $51.4 \pm 15.6\%$ of C4s and $47.1 \pm 11.4\%$ (mean $\pm$ standard deviation)] of C5s]. However, the sex ratio was skewed towards females at C6 with $84.2 \pm 7.8\%$ of that stage being females. Spermatophores attached to C6F were very scarce, observed seasonally from June to September for only 0–7.7% of the C6F (Fig. 2). On average, the proportion of females were highest in C6 ($44.3 \pm 14.5\%$) while the proportion of males were highest in C5 ($54.6 \pm 14.1\%$) (Fig. 2). Seasonal changes in the relative proportions of C4–C6 were observed for males, with high proportions of C4, C5 and C6 during October–January, February–July and April–July, respectively. However, the relative proportions of those stages remained fairly constant seasonally for females.

Length and mass

PL ranged from 1.03 mm (C2) to 3.80 mm (C6F) and increased with development (Table I). Masses (Y: WM, DM and AFDM, µg) and PLs (X: mm) had highly significant relationships, expressed as power functions ($Y = a X^b$) ($r^2 = 0.991$–0.993, $P < 0.0001$), with b between 3.024 and 3.349. Males tended to be larger and heavier than females at stages C4 and C5 (Table II). In particular, the masses of C5M were 1.39–1.67 times heavier than those of C5F ($P < 0.0001$; U test, Tables I and II). Female C6s tended to be longer (PL) and heavier in WM ($P < 0.0001$)
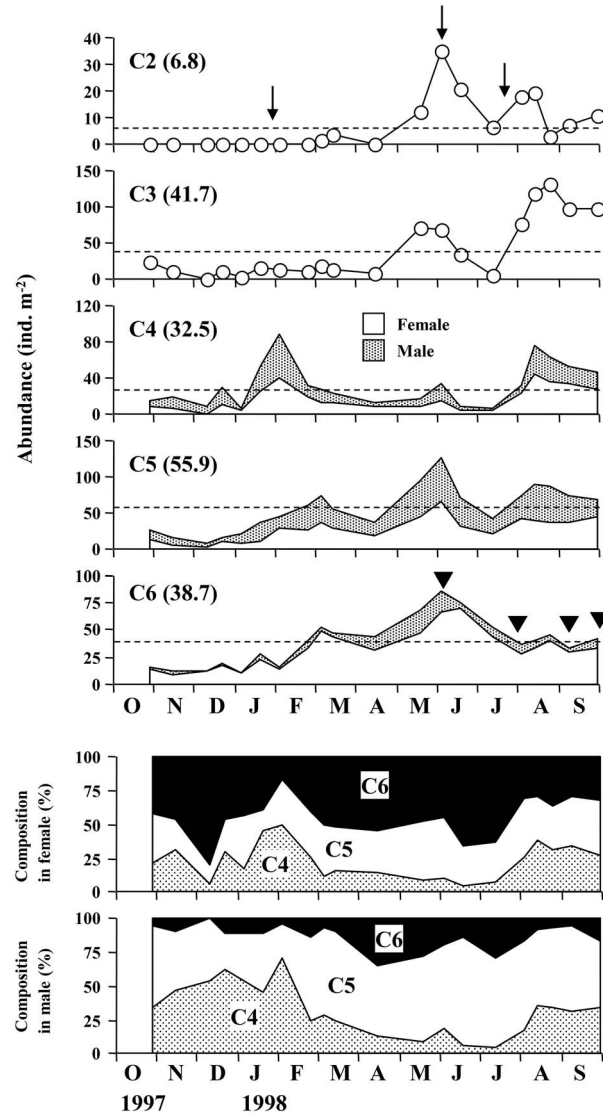
Fig. 2. Seasonal abundance of each copepodite stage of *S. magnus*. Females and males were morphologically distinguishable for stages C4–C6. Stage compositions within the female and male populations are shown in the bottom panels. Arrows in the upper panel indicate timings of water mass changes (cf. Ashjian *et al.*, 2003). Solid triangles in the C6 panel represent occurrences of spermatophore-attached C6F. Horizontal dashed lines and values in the parentheses show annual mean abundances for each stage (ind. m^{-2}).

than male C6, but no differences were observed for DM and AFDM (Table II).

Chemical composition

The water content ranged between $75.6 \pm 1.6\%$ WM (mean $\pm$ standard deviation) of C5M and $85.9 \pm 2.6\%$ WM of C4F, and was significantly different between stages ($P < 0.0001$, one-way ANOVA, Table I). The

Table I: Summary data as the mean ± standard deviation of prosome length (PL), wet mass (WM), dry mass (DM), ash-free dry mass (AFDM), water content (WATER, % of WM) and organic content (AFDM, % of DM) for S. magnus

Stage	PL (mm)	WM (μg)	DM (μg)	AFDM (μg)	WATER (% of WM)	AFDW (% of DM)
C2	1.03±0.03 (9)	77.71±6.02 (4)	12.13±1.28 (4)	11.11±1.00 (4)	84.4±0.6 (4)	91.7±1.4 (4)
C3	1.54±0.06 (9)	257.2±20.4 (6)	43.27±3.81 (6)	40.00±3.49 (6)	83.1±1.3 (6)	92.5±0.9 (6)
C4F	2.02±0.13 (14)	800.2±138.6 (6)	110.7±15.5 (6)	100.6±14.4 (6)	85.9±2.6 (6)	90.8±0.5 (6)
C4M	2.29±0.09 (12)	881.9±72.6 (6)	154.4±11.9 (6)	141.1±11.1 (6)	82.4±1.2 (6)	91.4±0.5 (6)
C5F	2.97±0.06 (9)	2024±87 (5)	421.2±19.1 (5)	387.8±18.3 (5)	79.2±0.8 (5)	92.1±0.7 (5)
C5M	3.20±0.07 (10)	2810±156 (5)	687.9±74.7 (5)	647.6±75.0 (5)	75.6±1.6 (5)	94.1±0.8 (5)
C6F	3.80±0.08 (10)	3747±119 (5)	771.5±78.2 (5)	706.6±79.9 (5)	79.4±2.2 (5)	91.5±1.2 (5)
C6M	3.50±0.08 (10)	3214±106 (5)	690.5±30.2 (5)	640.2±28.1 (5)	78.5±0.6 (5)	92.7±0.3 (5)

Regression statistics for body allometry

	WM-PL	DM-PL	AFDM-PL
Constant (a)	75.34	10.69	9.795
Power (b)	3.024	3.341	3.349
r^2	0.993	0.992	0.991
P	<0.0001	<0.0001	<0.0001

one-way ANOVA

	WATER	AFDM
df	7	7
F	24.3	5.43
P	<0.0001	<0.0001
Tukey-Kramer	C5M C6M C5F C6F C4M C3 C2 C4F	C4F C4M C6F C2 C5FC3 C6M C5M

(P < 0.05)

The number of replicates is shown in the parentheses. For analysing body allometry, the power regression model $Y = a.X^b$ was used, where Y is WM, DM or AFDM (μg) and X is PL (mm). Differences between stages in WATER and AFDM were tested by one-way ANOVA and post hoc test (Tukey-Kramer). Any two stages not underscored by the same line are significantly different.

Table II: Comparisons between S. magnus female and male prosome length (PL), wet mass (WM), dry mass (DM) and ash-free dry mass (AFDM) for stages C4–C6

Stage	PL	WM	DM	AFDM
C4	F = M^{ns}	F < M****	F < M***	F < M***
C5	F < M****	F < M****	F < M****	F < M****
C6	F > M****	F > M****	F = M^{ns}	F = M^{ns}

For raw data of each parameter, see Table I. Differences between female (F) and male (M) were tested using the Mann–Whitney *U* test. ***: $P < 0.001$, ****: $P < 0.0001$, ns: not significant.
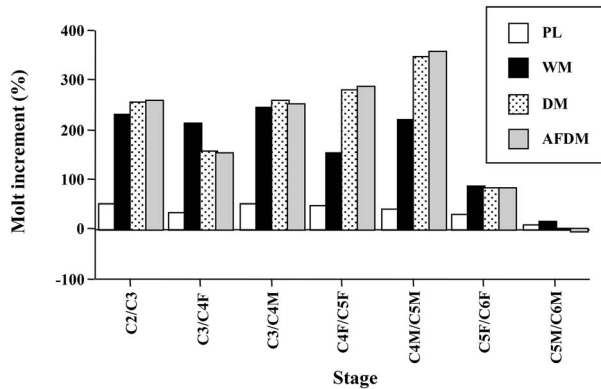

Fig. 3. Moult increment (MI) in prosome length (PL) and masses for *S. magnus* (WM: wet mass, DM: dry mass, AFDM: ash-free dry mass). Raw data are shown in Table I.

Fig. 4. The proportional increase in length and mass as a percentage of the C6 values by the stage for *S. magnus*. Raw data are shown in Table I. (PL: prosome length, WM: wet mass, DM: dry mass, AFDM: ash-free dry mass).

organic content was between $90.8 \pm 0.5\%$ DM at C4F and $94.1 \pm 0.8\%$ DM at C5M and also was significantly different between stages ($P < 0.0001$, one-way ANOVA, Table I). It is notable that males always had lower water content and higher organic content than females within the same copepodite stage (Table I).

Moult increment

The MI of PL of adjacent stages were 9.4–49.3%, while those of masses (WM, DM and AFDM) ranged from −1.1 to 358.8% and showed greater differences (Fig. 3). The MI also differed substantially between females and males. For both C3/C4 and C4/C5, MIs of males were larger and greater than females, especially for the mass measurements. For the moult from C5 to C6, all female growth was positive while male growth was extremely small, including negative growth in AFDM.

The proportion of PL growth (as a percentage of the mean adult female and male values) did not vary with a stage between males and females, with the largest proportions for both seen for the <C2 (27.1–29.4%) (Fig 4). By contrast, proportions for changes in mass (WM, DM and AFDM) in the older stages differed between males and
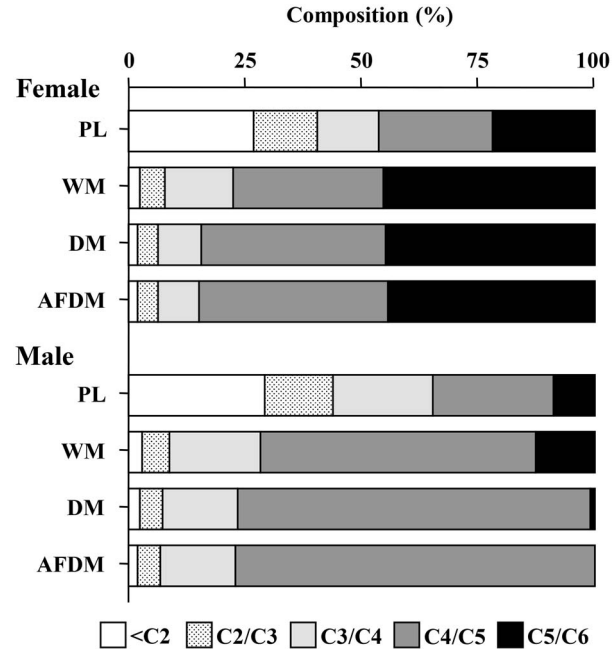
females. Females had the greatest increase in mass (45.1–46.0%) as C6 with substantial increases also during C5 while males had the largest increase (60.0–79.1%) as C5.

DISCUSSION

Vertical distribution

In the present study, C3–C6F of *S. magnus* were distributed at 518–745 m during the period of the midnight sun and at shallower depths, 264–381 m, during the polar night (Fig. 1). By contrast, C6M was found between 628 and 735 m with no day–night difference. Since water temperature did not vary between polar night and midnight sun, the seasonal changes in vertical distributions do not appear to be related to water temperature.

The vertical distribution of *S. magnus* has been reported previously. In the Arctic Ocean central basin, *S. magnus* had a distribution centre at 50–500 m during the summer (midnight sun) (Mumm *et al.*, 1998; Kosobokova and Hirche, 2000; Auel and Hagen, 2002). Elsewhere, *S. magnus* occurred below 150 m in the Bering Sea (Minoda, 1971), 495–775 m in the Oyashio region (Furuhashi, 1966), 500–1000 m in the Sargasso Sea (Deevey and Brooks, 1977), 570–950 m in the Canary Islands (Roe, 1972) and 1000–3000 m in the equatorial Indian Ocean (Grice and Hulsemann, 1967). Thus, the distribution depth of *S. magnus* becomes deeper at lower latitudes, presumably as this cold-water species avoids warm surface waters.

Diel vertical migration (DVM) is a common pattern in calanoid copepod vertical distribution (e.g. Mauchline, 1998). However, the temporal sampling of the net tows in this study did not permit identification of true DVM. The seasonal day–night differences are somewhat analogous, although on a completely different temporal scale (months vs. a day). DVM of *S. magnus*, has been reported in the North Atlantic Rockall Trough with the day distribution peak at 500 m and the night distribution peak at 100 m (Mauchline, 1998). In the Canary Islands, peak abundance was reported at 800 m during the day and at 660 m during the night, shoaling slightly (Roe, 1972). On the other hand, no DVM was reported in the Bering Sea (Minoda, 1971) or in the Arctic Ocean, likely because the sampling was conducted in summer during the midnight sun (Mumm *et al.*, 1998; Kosobokova and Hirche, 2000; Auel and Hagen, 2002).

Why are *S. magnus* found at shallower depths during the polar night in this study? It has been reported that deep-sea copepods in polar regions have different vertical distributions and preferred food items than other species of the same family and genus from outside polar regions (Laakmann *et al.*, 2009). For the Scolecitrichidae, to which *S. magnus* belongs, altering the vertical distribution and body size in the mesopelagic layer is known to maintain sympatric species diversity (Kuriyama and Nishida, 2006). In the Beaufort Sea Scolecitrichidae' depth distributions are known to differ within the family and genus, with *Scolecithricella minor* at the shallowest depths (0–500 m), *S. magnus* at intermediate depths (200–500 m) and *Scaphocalanus brevicornis* at greatest depths (300–1000 m) (Smoot and Hopcroft, 2017b). Additionally, vertical partitioning within the *Scaphocalanus* genus has been reported in the central Arctic Basin, with the shallowest for *S. magnus*, intermediate for *S. brevicornis* and the deepest for *S. polaris* (Kosobokova *et al.*, 2011). These observations suggest that competition for food is strong in the Arctic Ocean.

In the Arctic Ocean, because of the constant solar radiation during summer, primary production and export-sinking flux have seasonal peaks in summer (Lalande *et al.*, 2019). Conversely, during the polar night, without radiation, primary production is much reduced or absent and particle flux to the deep sea is lower (Lalande *et al.*, 2019). Sinking particle flux from the surface layer in the ocean is known to decrease exponentially with increasing depth (Suess, 1980; Pace *et al.*, 1987). Therefore, during winter, *S. magnus* may ascend to the shallower depths to exploit the presumably greater food availability. During C6, feeding appendages of males degenerate, digestive tracts become thread-like, and animals cease feeding (Harding, 1974), so there is no need for them to ascend to find food during the polar night (Fig. 1) and they can remain in the deep layer during both midnight sun and polar night to avoid predation. This behaviour can be thought of as an analogue to DVM, although on a longer temporal scale, since upwards migration is similarly motivated by food availability and downwards migration by avoidance of predation.

Abundance and biomass

Abundances of *S. magnus* in the Arctic Ocean from previous studies are comparable to those seen in this study (ca. 100–>200 ind. m^{-2}, Table III). However, the biomass of *S. magnus* from around Svalbard (4 ± 15 mg DM m^{-2}) is much lower than in this study (65.2 ± 31.8 mg DM m^{-2}). Most of the sampling locations from that study were in water depths of shallower than ~500 m. It may be that *S. magnus* is less abundant there because they prefer greater water depths (518–745 m) during the midnight sun (Fig. 1). The abundance and biomass of *S. magnus* in this study corresponded with the reported values in the Canada Basin (Kosobokova and Hopcroft, 2010) (Table III).

Difference in development time between females and males

Although cohort development to C2–C3 could be traced for *S. magnus*, it was unclear after C4 stages (Fig. 2). This uncertainty likely resulted because development times differ between females and males. Comparisons of the ratio of C4–C6 for each sex showed distinct differences in cohort growth, especially for males (Fig. 2). The difference in development time between females and males is most prominent in C6. Since C6M are not feeding, their longevity should be short. This short duration has a marked effect on the sex ratio of *S. magnus* in the C6 stage. The sex ratio of C4 and C5 was ~1:1, whereas in C6 it

Table III: Comparison of abundance and biomass of S. magnus in the Arctic Ocean

Location	Season	Depth	Mesh size	Abundance	Biomass	References
		(m)	(µm)	(ind. m^{-2})	(mg DM m^{-2})	
Nansen, Amundsen and Makarov Basin	Jun.–Oct.	0–500	150–300	100– > 200	-	Mumm *et al.* (1998)
Central Arctic Ocean	Aug.–Sep.	0–1500	200	174.7	-	Auel and Hagen (2002)
Northern Svalbard waters	May–Aug.	0–600	180	-	4 ± 15	Blachowiak-Samolyk *et al.* (2008)
Canada Basin	June–July	0–3000	150	200 ± 22*	48.5 ± 3.5*	Kosobokova and Hopcroft (2010)
Western Arctic Ocean	Year round	0–2800	53, 150	176.0 ± 101.1	65.2 ± 31.8	This study

Where available, means ± standard deviations are shown. *: standard errors.

was largely skewed towards females (Fig. 2). In a study of C6 *S. magnus* sex ratios in the Canary Islands, males were only 2.7–12.1% of the total C6 population and females predominated (Roe, 1972), similar to the annual average percentage of adult males (15.8 ± 7.8%) from the present study.

The proportions of C4–C6 in the female and male populations reflect the residence time in each stage of development (cf. Mauchline, 1998). High proportions were seen in the female C6 and male C5 stages, with females quickly developing to C6F and males spending longer as C5M. It is well known that the reproduction of most copepods is dependent on food availability (Mauchline, 1998). Thus, spending a long time as C6F permits females to reproduce in response to periods of greater food availability within that stage duration (Yamaguchi and Ikeda, 2000b). Males are potential competitors for available food. The cessation of male feeding thus reduces competition for food with other life stages. This may explain why the feeding appendages of the C6M degenerate in several mesopelagic families (Euchaetidae, Aetideidae, Scolecitrichidae; Yamaguchi and Ikeda, 2000b).

Developmental characteristics

In this study, weights were determined for formalin-preserved individuals, potentially resulting in underestimates because of the dissolution of organic matter during storage (Fudge, 1968; Hopkins, 1968). Nonetheless, the magnitude of the error caused by formalin preservation is relatively small and unimportant for broad comparisons between stages of dissimilar species (Gruzov and Alekseyeva, 1970). The DM of *S. magnus* has been reported in the Greenland Sea to be 722 ± 23 µg for C6F and 635 ± 62 µg for C6M (Richter, 1994) corresponding closely to the DMs measured in this study (772 ± 78 µg (C6F) and 691 ± 30 µg (C6M), respectively, Table I). Here, allometric formulas were obtained between PL and body masses (WM, DM and AFDM), with power (*b*)

between 3.024–3.349. According to Mauchline (1998), the power (*b*) of allometric equations between PL and body mass of calanoid copepods usually lies between 2.5 and 3.3, corresponding to the values observed in the present study. The difference in power is considered to be due to the body shape of each species (Gruzov and Alekseyeva, 1970).

The water content (75.6–85.9% WM) of *S. magnus* measured in this study was in the range of most copepods (67–92% WM, Båmstedt, 1986). The organic matter (=AFDM) content (90.8–94.1% DM) of *S. magnus* also corresponded well to the range (70–98% DM) and mode (92–94% DM) seen for copepods (Båmstedt, 1986). Noteworthy here is that males had a lower water content and a higher AFDM content than females when compared within the same developmental stages of C4–C6 ($P < 0.0001$, one-way ANOVA, Table I).

MI of the copepodite stages of calanoid copepods are known primarily for epipelagic species, with observed MI in PL between 14.5 and 29.3% and in DM of 61.7–94.0% (Mauchline, 1998). Here, the MI of *S. magnus* was between 9.4 and 49.3% in PL and 0.4–345.5% in DM (Fig. 3). The maximum reported values of MI for DM of mesopelagic copepods are 498% (*Heterorhabdus tanneri*, Yamaguchi and Ikeda, 2000a) and 550% (*Paraeuchaeta elongata*, Ikeda and Hirakawa, 1996). Thus, the MIs, expressed as DM, of mesopelagic copepods are much greater than those of epipelagic copepods. For *S. magnus*, it is notable that the MIs of both C3/C4 and C4/C5 were larger in males than in females, and this pattern was pronounced in DM and AFDM (Fig. 3). On the other hand, in C5/C6, all female growth was positive, but male growth was extremely small, and negative growth was seen in AFDM.

S. magnus in the Arctic Ocean and the aetideid copepod *Gaetanus* (= *Gaidius*) *variabilis*, a medium-sized (PL of 3.02 mm in C6F) mesopelagic copepod found at 600–1000 m in the Oyashio region, are similar in several aspects of their ecology. Both are suspension feeders and omnivores and both have feeding appendages that degenerate at C6M (Yamaguchi *et al.*, 2005, 2007). At

C4 and C5, *S. magnus* males were often larger (PL) and heavier than females, while the opposite was seen at C6, where females were often larger and heavier than males (Tables I and II). Remarkable differences in the proportional increases in DM and AFDM by stage also were observed between males and females. Thus, the greatest increases were seen in the C6 for females, while for males the greatest proportional increase occurred during the C5 stage (Fig. 4). These weight differences are believed to result in part from the cessation of feeding by C6M (Harding, 1974) and a short duration of the C6M stage (Fig. 4) relative to the long stage residence time for females. Also, female C4 and C5 stage duration are short, resulting in lower growth and mass than males at the same developmental stage (Tables I and II).

The same pattern (the males larger and heavier than females in C4 and C5, and the females larger and heavier than males in C6) is seen for *G. variabilis* (Yamaguchi and Ikeda, 2000b). The mass difference between females and males of *G. variabilis* stages C4 and C5 are largest in DM and AFDM, with M:F in DM and AFDM being 1.33–1.37 in C4 and 1.74–1.86 at C5 (Yamaguchi and Ikeda, 2000b). The mass difference between females and males in C4 and C5 of *S. magnus* was also the largest in DM and AFDM, with M:F of 1.39–1.40 at C4 and 1.63–1.67 at C5 (Table I). Patterns in water content and moult increments with stage and sex also were comparable between the two species (Yamaguchi and Ikeda, 2000b). It is possible that *S. magnus* and *G. variabilis* occupy similar ecological niches in their respective ocean habitats.

CONCLUSION

Through this study, ecology (vertical distribution, population structure and developmental characteristics) of mesopelagic copepod *S. magnus* was evaluated. Since seasonality in environmental parameters (light and food availability) is large, their vertical distribution and population structure, especially early copepodite stages, showed seasonality which related to their adaptation for these conditions. In addition to these ordinary observations (counting with each stage), measurements of length and masses (WM, DM and AFDM) with each stage throughout the life stages provide deep insights on the growth and development of the mesopelagic copepods. This study emphasizes the importance and usefulness of the measurements of weights with each copepodite stage especially for studies on the life cycle of the longer lived mesopelagic copepods.

SUPPLEMENTARY DATA

Supplementary data can be found at *Journal of Plankton Research* online.

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