



Seasonal ecology and life-history strategy of the high-latitude predatory zooplankter *Parasagitta elegans*

Jordan J. Grigor^{1,2,*}, Janne E. Søreide¹, Øystein Varpe^{1,3}

¹The University Centre in Svalbard, 9171 Longyearbyen, Norway

²Takuvik Joint International Laboratory, Université Laval (Canada)—CNRS (France),
Département de biologie and Québec-Océan, Université Laval, Québec, Québec G1V 0A6, Canada

³Akvaplan-niva, Fram Centre, 9296 Tromsø, Norway

ABSTRACT: Organisms residing in seasonal environments schedule their activities to annual cycles in prey availability and predation risk. These cycles may be particularly pronounced in pelagic ecosystems of the high-Arctic, where the seasonality in irradiance, and thus primary production, is strong. Here we report on the seasonal ecology and life strategy of a predatory planktivore in a high-Arctic fjord (Billefjorden, Svalbard ~78°N). We studied the chaetognath *Parasagitta elegans* (var. *arctica*), an abundant zooplankter of high-latitude seas, focusing on its age structure, seasonal vertical distribution, growth and timing of reproduction. The body-length data (range: 2 to 44 mm) revealed the presence of 3 size cohorts (Cohorts 0, 1 and 2), suggesting a 3 yr life span. Spring and early summer (May/June) was the main spawning season, as revealed by inspection of gonads and the presence of well-developed seminal receptacles prior to high numbers of newborns. Both Cohorts 1 and 2 reproduced, with male gonads maturing first in this hermaphrodite. Growth rates for all cohorts were highest in spring and early summer, and at this time of the year, the youngest year class (Cohort 0) was distributed near the surface where their feeding opportunities may peak. In winter, however, all cohorts were in deeper waters, suggesting seasonal migrations, possibly to follow the distributions of overwintering copepods. Scheduling of growth, maturation and reproduction in Arctic zooplankton populations is important baseline information for predictions of zooplankton responses to environmental change, particularly those associated with timing and phenology, pinpointing the need for more high-resolution studies on zooplankton annual routines.

KEY WORDS: Annual routines · Arctic · Arrow worms · Seasonal environments · Zooplankton

INTRODUCTION

The life histories of Arctic animals have evolved in response to a highly seasonal environment. In the marine pelagic, near-surface biomass shows a strong seasonal signal, caused by both the pulse of primary production (Ji et al. 2013) and the presence of seasonally migrating grazers for corresponding parts of the year (Varpe 2012). High-latitude zooplankton show many adaptations to a seasonal food source, some of which are associated with body lipid content,

diapause and timing and the extent of growth and reproduction (e.g. Falk-Petersen et al. 2009, Varpe 2012). Diel and seasonal vertical migrations (DVM and SVM), observed in various zooplankton species, are also adaptations to the interactions between temporal and spatial distribution of food and predators that occur over varying timescales (Haney 1988). In sum, organisms in seasonal environments have typically evolved schedules of activities over the annual cycle, referred to as annual routines (McNamara & Houston 2008, Varpe 2012).

*Corresponding author: jordangrigo@gmail.com

In the Arctic, the bulk of seasonal studies has focused on the link between primary producers and their grazers (e.g. Søreide et al. 2010, Daase et al. 2013), but planktonic predators (chaetognaths, some copepods, ctenophores, decapods, amphipods etc.) may display similarly marked adaptations to seasonality (e.g. Choe et al. 2003, Dale et al. 2006). In this study we have examined the seasonal ecology and life history of the chaetognath *Parasagitta elegans* var. *arctica* (genus name formerly *Sagitta*).

Chaetognaths form a phylum of gelatinous zooplankton predators, comprising 5 to 15% of global zooplankton biomass (Longhurst 1985) and approximately 200 species worldwide (Ghirardelli 1997). Chaetognaths are hermaphrodites capable of both cross- and self-fertilisation (Alvarino 1992). Three major species can be found in Arctic waters: *Parasagitta elegans*, *Eukrohnia hamata* and *Pseudosagitta maxima*, and they contribute substantially to Arctic zooplankton biomass (Søreide et al. 2003, Hopcroft et al. 2005). However, their roles in energy and elemental flux are not well described, particularly not during the polar night (e.g. Welch et al. 1992). *P. elegans* often dominates chaetognath communities in Arctic shelf seas (Dunbar 1962, Welch et al. 1996), whereas the other 2 species may be more common at meso- to bathypelagic depths offshore (Kosobokova et al. 2011). *P. elegans* is a heterogeneous feeder, but calanoid and cyclopoid copepods are its major prey (see review by Terazaki 2004), and it can consume relatively high portions of the daily secondary production (Samemoto 1987). *P. elegans* is also an important prey item for others, including chaetognaths, amphipods, jellyfish, fish and seabirds (Feigenbaum & Maris 1984 and references therein).

The life cycle of *Parasagitta elegans* varies considerably throughout its distribution range, possibly due to variability in environmental factors such as temperature and food availability (Terazaki 2004). For instance, specimens from the Canadian Arctic may have longer lifespans than those residing at lower latitudes (Dunbar 1962, Terazaki 2004). The number of generations produced in a year also varies considerably, from 0.5 generations at the sub-Arctic setting of Hudson Bay, Canada (65° N; Dunbar 1962), to possibly 5 to 6 in Plymouth, UK (50° N; Russell 1932). Vertical migration behaviour has been less explored in Arctic chaetognaths. In the Arctic, migrations of herbivorous zooplankton have received most attention (Falk-Petersen et al. 2009 and references therein), but several studies have reported both SVM and DVM in lower-latitude populations of *P. elegans* (Terazaki 2004 and references therein).

In order to study the seasonal ecology and life-history strategy of *Parasagitta elegans*, we gathered monthly data in a high-Arctic sill fjord with restricted water mass exchange and seasonal sea ice cover. We investigated the timing of growth, maturation and reproduction as well as age structure and vertical distributions from July 2008 to August 2009. We related our findings to the seasonality of the environment.

MATERIALS AND METHODS

Study site

The zooplankton community in Adolfbukta, Billefjorden, on the west coast of Spitsbergen (78° 39.72' N, 16° 44.34' E) was sampled monthly from July 2008 to August 2009. Billefjorden is a threshold fjord with 2 sills at its mouth, which in previous studies have been shown to severely restrict exchange of water masses, particularly the entry of Atlantic water (Nilsen et al. 2008), and hence zooplankton advection into and out of the fjord (Arnkværn et al. 2005). We therefore assume we sampled a single population of *Parasagitta elegans* persisting year-round, an assumption supported by oceanographic data from the 2008 to 2009 mooring (C. Griffiths pers. comm.).

Physical environmental and primary production

Temperature, salinity and *in situ* fluorescence were measured continuously by a mooring placed in close vicinity to our sampling station (<0.5 nautical miles). The depth of the seabed and mooring was 191 m. Four Seabird CTDs measured conductivity, temperature, pressure and density every 12 min at 19, 30, 90 and 180 m. In addition, Vemco temperature miniloggers measured temperature every 20 min at 46, 56, 76, 111, 126 and 151 m. A SeaPoint fluorometer and a light sensor measured fluorescence and photosynthetically active radiation (PAR; 400 to 700 nm) every 12 min at 29 m depth. Only approximate PAR and chlorophyll *a* (chl *a*) data were available from the light sensor and the fluorometer due to the absence of suitable light fluorescence and water samples for calibration during much of the year. The raw PAR and fluorescence data were normalized between 0 and 1 to identify the approximate timing of the phytoplankton bloom. Samples for quantitative chl *a* values were collected at lower resolution, monthly from February to June 2009. The fluorescence data

corresponded well with the quantitative chl *a* data, with values $>1 \mu\text{g chl } a \text{ l}^{-1}$ not obtained before June.

Zooplankton sampling

Depth-resolved mesozooplankton samples were collected once or twice a month from July 2008 to August 2009 (Table S1 in the Supplement at www.int-res.com/articles/suppl/m499p077_supp.pdf). Three different nets were used to collect zooplankton throughout the study period: (1) WP3 (1 m² opening and 1 mm mesh size), (2) WP2 (0.25 m² opening and 0.2 mm mesh size) and (3) MPS (Hydro-Bios multiplankton sampler; 0.25 m² opening and 0.2 mm mesh size). The WP3 was used on the majority of sampling dates, except on dates during the summers of 2008 and 2009, when we used a small boat and thus were unable to sample with this larger net and only with the smaller, more portable WP2. In winter when sampling from sea ice, we were able to sample with both the WP3 and WP2 nets. The heavy MPS was used only from larger research vessels equipped with a crane (Table S1). Sampled depth intervals were standardized to 20–0, 50–20, 100–50 and 180–100 m (MPS and WP2) and 50–0, 100–50 and 180–100 m (WP3). The nets did not sample the ~10 m immediately above the seabed (hyperbenthic zone).

Mesozooplankton samples were fixed in 4% buffered formalin–sea water solution immediately after sampling. Chaetognaths were sorted to the species level. Two species were present: the abundant *Parasagitta elegans* and the rarer *Eukrohnia hamata*. Lengths of all *P. elegans* were measured to the nearest 0.5 mm from the head to the tip of the tail, excluding the caudal fin.

Net sampling efficiency and *Parasagitta elegans* abundance

Since the MPS and WP2 gears had identical opening areas and mesh size, we combined length data collected by these 2 types of gear and compared the sampling efficiency of a ‘combined’ MPS+WP2 type of gear with that of the WP3. The 2 length-frequency distributions differed markedly (Fig. 1). The WP3 was most efficient at capturing individuals above 20 mm, whereas the MPS+WP2 collected the whole *Parasagitta elegans* size range (2 to 44 mm), but the smaller individuals more efficiently than the WP3 (Fig. 1). Since the MPS+WP2 collected the whole size range (Fig. 1) and samples from these

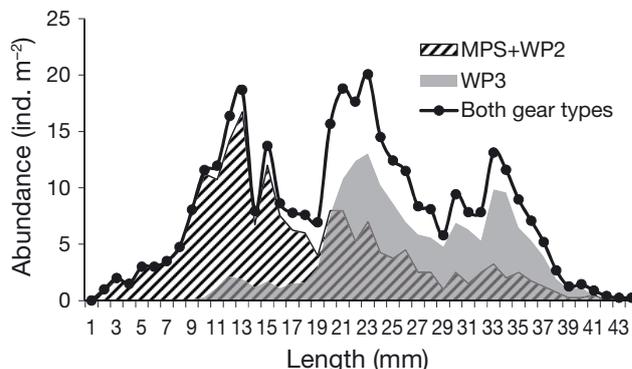


Fig. 1. *Parasagitta elegans*. Length-frequency distributions of *P. elegans* collected by each gear type. Striped area: MPS+WP2 gear (0.25 m² opening area, 0.2 mm mesh size); grey area: WP3 (1 m² opening area, 1 mm mesh size). Sampling efficiency was standardized to ind. m⁻² calculated for the whole water column per sampling date for each gear (i.e. averages of 16 dates for MPS/WP2 sampling and 15 dates for WP3 sampling). The distribution from both gears combined is shown as the black curve. All 4 strata in the water column were sampled on most dates (see Table S1 in the Supplement for the few exceptions). All 1 mm size classes from 2 to 44 mm were represented in our samples

nets were available throughout the year, we used the MPS+WP2 data to investigate monthly trends in population and cohort abundances and vertical distributions. WP3 data were also included when identifying size cohorts in the population, determining growth rates and for maturity analyses, to increase sample size.

Size cohort analyses

Analyses of *Parasagitta elegans* size cohorts were performed using the finite mixture distributions (MIXdist) package in the statistical environment RTM (R Development Core Team 2008). This involved the identification of discrete size cohorts (peaks) in monthly pooled length-frequency data. Inspection of length distributions revealed the presence of 3 size cohorts (Fig. S1 in the Supplement), hereafter referred to as Cohorts 0, 1 and 2. MIXdist then uses an automated optimisation process to estimate the average (mean) length and the standard deviation of each cohort. Mean lengths (\pm SD) of the modelled distribution were used to estimate cohort length ranges in each month and these were used to allocate measured individuals into cohorts. The goodness-of-fit was verified by chi-squared statistics. In January, the mean lengths of all 3 cohorts, estimated by MIXdist, contrasted sharply with the December and February values (20.7, 21.7 and 37.4 mm for Cohorts 0, 1 and 2,

respectively). Thus, in January, the values for Cohorts 0 and 2 were set to 13 and 33 mm, to allow realistic growth estimates for all months. For the month of August, length data were available from both 2008 (WP3) and 2009 (MPS; Table S1 in the Supplement). When these August data were analysed for each year separately, the mean lengths of Cohorts 0 and 1 were found to differ by just 0.2 and 0.1 mm, respectively, whereas the mean length of Cohort 2 was 2.2 mm longer in 2009 than in 2008. The August 2008 and 2009 data were pooled for the purposes of our analyses. The length-frequency data suggested reproduction from May to August. Mean cohort lengths in consecutive months were used to estimate monthly growth rates.

Due to our method of defining size cohorts in terms of monthly mean length ranges, some individuals caught could not be allocated to a cohort, and these correspond to the white area directly below the population curve (see Fig. 3). Note that on a few dates, samples were missing from at least 1 depth strata, so total water column abundances on these dates may have been higher than presented here (see Table S1).

Maturity condition

Chaetognaths are hermaphrodites. The male gonads (testes and seminal vesicles) produce and secrete the sperm, whilst the female gonads (ovaries and seminal receptacles) produce the ova and receive sperm from a sexual partner (Alvarino 1992). The seminal receptacles are known to develop in the later stages of the maturation cycle, shortly before reproduction (Russell 1932, Choe et al. 2003). To assess their state of maturity, *Parasagitta elegans* individuals from each month were stained with Borax Carmine solution, and the development of their ovaries and seminal receptacles, and the amount of sperm in their tails, were observed under a stereomicroscope. The same criteria have been used in several other studies to describe *P. elegans* maturity (e.g. Choe et al. 2003). Ovary length was measured to the nearest 0.1 mm. The largest ovaries observed in this study were ~24 mm. Individuals showing advanced ovary development were taken as those with ovaries ≥ 5.4 mm, while shorter ovaries < 5.4 mm were considered to be poorly developed. We assumed the threshold at this size because it was the maximum length of ovaries observed in Cohort 1 during the month of February, when members of this cohort first started to have well-developed seminal receptacles. Although no data on oocyte size or number were

available during this study, other studies suggest that individuals can have many oocytes in their ovaries before they possess well-developed seminal receptacles (e.g. Russell 1932, Choe et al. 2003). Therefore, we assumed that ovaries are ripe at or above 5.4 mm length. This threshold also excluded all Cohort 0 individuals, which we assumed do not reproduce as they had no swollen seminal receptacles. Numbers of individuals with ovaries smaller and larger than 5.4 mm were recorded. Appearance of the seminal receptacles was described according to codes from 0 to 3 (our own approach): Code 0 indicated that no receptacles were visible, Code 3 indicated that receptacles were pronounced and protruding from both ovaries, and Codes 1 and 2 indicated intermediate levels of receptacle development. Numbers of individuals containing high quantities of sperm in the tail (i.e. sperm occupied at least 75% of the tail area) were also recorded.

Vertical distributions

To investigate the vertical distributions of *Parasagitta elegans* throughout the year, abundances in discrete layers of the water column (ind. m^{-3}) were calculated for each sampling date and averaged for each month. Vertical distributions of the population and size cohorts were characterized by their weighted mean depths in the water column (Z_m), with standard deviations (Z_s), using the method of Manly (1977).

RESULTS

Physical and biological environment

Billefjorden was covered with land-fast sea ice from the end of December 2008 until the end of June 2009. During the ice-covered period, near-freezing temperatures (-1.7°C) were observed throughout the whole water column (Fig. 2). In mid-June the sea ice was about to collapse, with many melt holes (~1 m in diameter). Chl *a* data from ice cores confirmed by visual observations of the underside of the sea ice revealed that the ice algal bloom peaked in early May. The phytoplankton bloom commenced approximately 1 mo later (Fig. 2). Temperatures up to 4°C were recorded in the upper 40 m in late summer and early autumn (Fig. 2). From 100 m depth to the bottom, cold waters (less than -1.7°C) persisted throughout the year (Fig. 2).

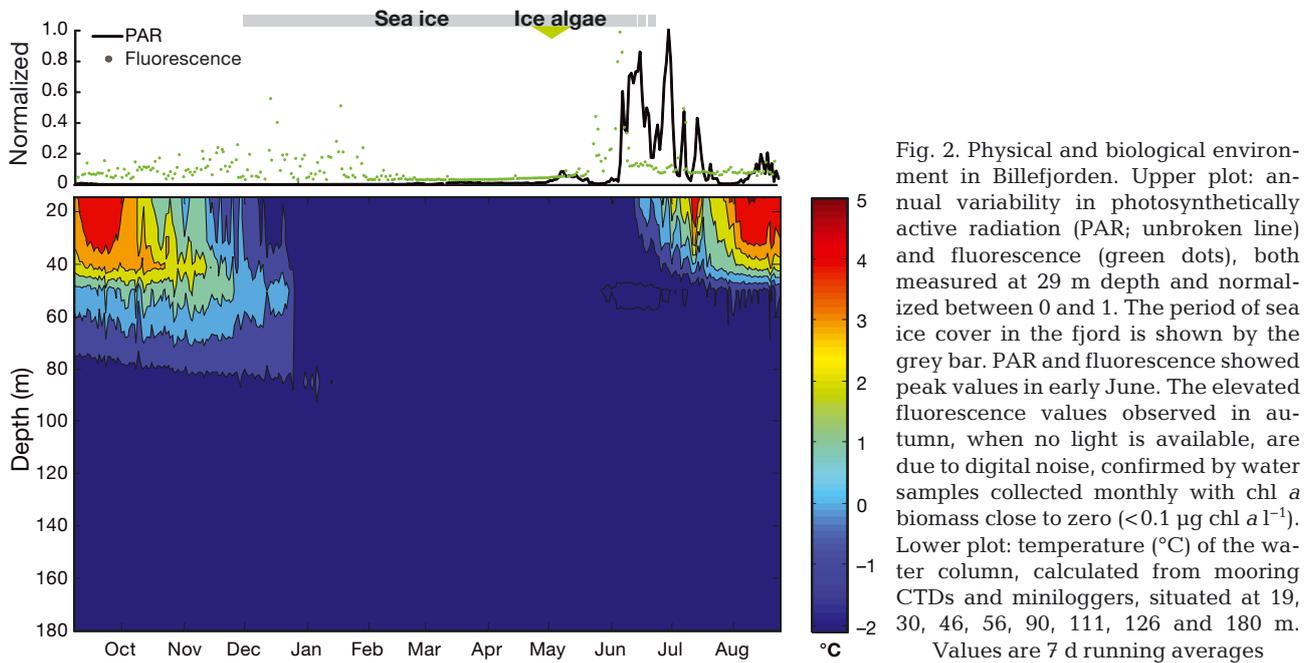


Fig. 2. Physical and biological environment in Billefjorden. Upper plot: annual variability in photosynthetically active radiation (PAR; unbroken line) and fluorescence (green dots), both measured at 29 m depth and normalized between 0 and 1. The period of sea ice cover in the fjord is shown by the grey bar. PAR and fluorescence showed peak values in early June. The elevated fluorescence values observed in autumn, when no light is available, are due to digital noise, confirmed by water samples collected monthly with chl *a* biomass close to zero ($<0.1 \mu\text{g chl } a \text{ l}^{-1}$). Lower plot: temperature ($^{\circ}\text{C}$) of the water column, calculated from mooring CTDs and miniloggers, situated at 19, 30, 46, 56, 90, 111, 126 and 180 m. Values are 7 d running averages

Size cohorts, age structure and reproduction

The *Parasagitta elegans* population size peaked towards the end of July (484 ind. m^{-2}). Relatively high water column abundances ($\geq 344 \text{ ind. m}^{-2}$) also

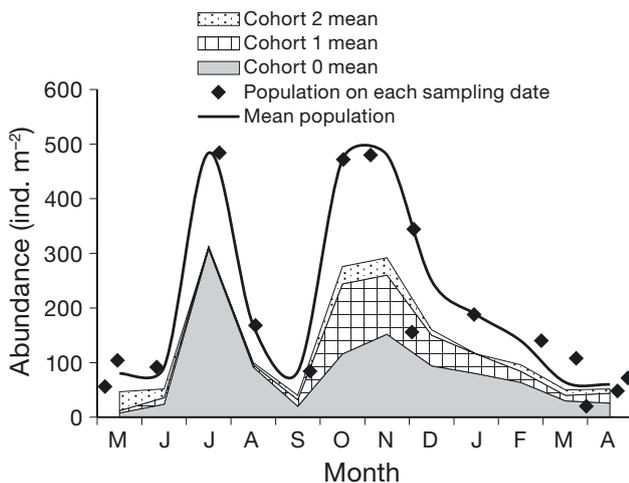


Fig. 3. *Parasagitta elegans*. Integrated abundances of the population on each sampling date (black diamonds) and averaged for each month (black curve), based on MPS+WP2 data only. Although the study did not start in May, this plotting decision was motivated by the finding that May was the start of the main birth season. For exact sampling dates, see Table S1 in the Supplement. Abundances of Cohorts 0, 1 and 2 averaged for each month of the year are shown as the grey area, the hatched area and the stippled area, respectively. In January and July, Cohort 2 was completely absent from the MPS+WP2 samples, but, in January, it was present in WP3 samples

occurred in October, November and December. Population minimums ($\leq 108 \text{ ind. m}^{-2}$) were realized in March, April, May, June and September (Fig. 3).

The main birth month was May, based on the numbers of 2 mm individuals present (16 ind. m^{-2} ; Fig. S1 in the Supplement). Many more individuals $\leq 5 \text{ mm}$ were also captured between May and August (e.g. 52 ind. m^{-2} in July), suggesting that the spawning period extended throughout the summer. There was also some evidence for a winter reproductive episode, since a few smaller individuals ($\leq 5 \text{ mm}$) were also found in December and January (4 to 16 ind. m^{-2}), but they were in insignificant numbers compared to summer. Members of all 3 cohorts were apparently present in the population during all months (although no members of Cohort 2 were identified in July, when the estimated length range of this cohort was particularly narrow). The 3 cohorts were clearly seen in the months of May, August, September, October, November, December and February, but were less distinct in June, July, January, March and April (Fig. S1).

The mean length ranges of Cohorts 0, 1 and 2 during the year were 1.9 to 14.3, 13.0 to 29.7 and 29.0 to 34.2 mm, respectively (Table 1, Fig. 4). Based on the mean lengths of the respective cohorts, the individuals that hatched in May took 1 yr to become Cohort 1 and 2 yr to become Cohort 2 (Fig. 4). Cohort 2 individuals persisted in the population for the whole year, suggesting that some *Parasagitta elegans* in Billefjorden live for 3+ yr.

Table 1. *Parasagitta elegans*. Body length statistics of the 3 size cohorts during 2008 and 2009. Mean values were estimated in the MIXdist library in RTM, along with standard deviations. The goodness-of-fit was verified by chi-squared statistics. See Fig. S1 in the Supplement for monthly length-frequency histograms and Fig. 4 for the continuous growth curve. Values are based on all length data available (WP3-, WP2- and MPS-collected). Monthly growth rates were calculated as the difference in cohort mean length between months. All distributions were normal. na: not applicable

Month	n	Cohort 0		Cohort 1		Cohort 2		Goodness-of-fit		
		Mean length ± SD (mm)	Mean monthly growth rate (mm mo ⁻¹)	Mean length ± SD (mm)	Mean monthly growth rate (mm mo ⁻¹)	Mean length ± SD (mm)	Mean monthly growth rate (mm mo ⁻¹)	df	χ ²	p
May	126	1.9 ± 0.8	6.4	13.0 ± 1.5	9.4	30.0 ± 3.7	2.5	38	38.37	0.45
Jun	23	8.3 ± 4.7	0.3	22.4 ± 1.9	0.5	31.8 ± 3.5	0.7	38	44.77	0.21
Jul	121	8.6 ± 2.8	2.3	22.8 ± 0.9	-0.9	32.4 ± 0.1	-0.4	18	15.84	0.60
Aug	255	11.0 ± 3.4	0.0	22.0 ± 1.8	-1.0	32.0 ± 2.9	0.0	35	22.54	0.95
Sep	481	11.0 ± 1.3	1.8	20.9 ± 2.4	1.2	32.0 ± 3.1	1.1	30	40.11	0.10
Oct	401	12.8 ± 2.2	-0.5	22.1 ± 2.6	0.4	33.2 ± 2.8	0.1	33	36.48	0.31
Nov	504	12.3 ± 2.0	0.6	22.5 ± 2.7	0.3	33.3 ± 3.1	-0.5	33	46.02	0.07
Dec	678	12.9 ± 2.9	0.1	22.8 ± 2.7	-1.2	32.8 ± 3.7	0.2	38	67.96	0.002
Jan	110	13.0 ^a ± 3.8	0.3	21.6 ± 4.0	1.4	33.0 ^a ± 5.2	0.5	43	45.83	0.36
Feb	146	13.3 ± 3.3	-0.2	23.0 ± 3.1	3.8	33.5 ± 3.5	-0.3	39	43.36	0.29
Mar	82	13.1 ± 2.2	1.2	26.8 ± 5.4	-1.7	33.2 ± 2.7	1.0	32	22.50	0.89
Apr	237	14.3 ± 4.2	-1.3	25.1 ± 4.1	4.1	34.2 ± 2.6	na	37	25.72	0.92

^aValue fixed by user

Cohort abundances

Cohort 0 was the most abundant cohort (Fig. 3). It comprised most of the individuals during the population peak in July (308 ind. m⁻², when it had a mean length of 8.6 mm), and the secondary peak in November (152 ind. m⁻², mean length = 12.3 mm). From January to June, Cohort 0 formed relatively low abundances (8 to 80 ind. m⁻²). Abundances of Cohort 1 peaked from October to November (108 to 128 ind. m⁻²; Fig. 3). In comparison, Cohort 2 was generally rare, but dominated the population in May (34 ind. m⁻²) after developing from Cohort 1 (Fig. 3).

Growth

The estimated annual growth rates of Cohorts 0, 1 and 2 were 11.1, 16.2 and 5.0 mm yr⁻¹, respectively,

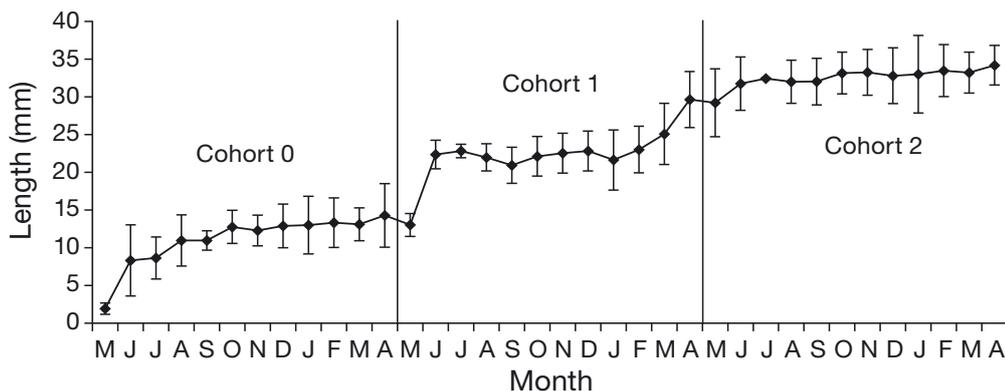


Fig. 4. *Parasagitta elegans*. Continuous growth curve (mean ± SD) for the Billefjorden population, produced from the mean lengths of the 3 size cohorts in adjacent months. Peak growth in all cohorts occurred between May and June

with half or more (depending on cohort) of this growth taking place between May and June (Table 1, Fig. 4). From August until May, growth of both Cohorts 0 and 2 remained low (~2 mm). Considerable growth at other times of the year was suggested only for Cohort 1, which gained 6.6 mm from February to April (Table 1, Fig. 4).

Maturity

The mean (± SD) ovary length of all individuals investigated in this study was 2.9 ± 2.6 mm, and the mean ovary lengths of Cohorts 0, 1 and 2 were 0.5 ± 0.4, 1.9 ± 1.1 and 5.1 ± 2.4 mm, respectively. No Cohort 0 individuals showed advanced ovary development (i.e. had ovaries ≥5.4 mm) (Table 2). Cohort 1 observations revealed that time of maturation differed for male versus female function, with male

Table 2. *Parasagitta elegans*. Percentages of individuals in each size cohort during 2008 and 2009 with advanced female (ovaries measuring ≥ 5.4 mm) and male gonads ($\geq 75\%$ of the tail section containing sperm), and with pairs of pronounced seminal receptacles. See 'Materials and methods' for further details. Data in **bold** indicate cohorts in which 10 or more individuals were examined per month. n: number of individuals examined; nd: no data

Month	Ovaries ≥ 5.4 mm		Sperm load		Seminal receptacles	
	n	% present	n	% high	n	% present
Cohort 0						
May	4	0	4	0	4	0
Jun	4	0	6	0	4	0
Jul	2	0	77	0	2	0
Aug	4	0	27	0	4	0
Sep	1	0	11	0	28	0
Oct	39	0	40	0	40	0
Nov	68	0	70	0	70	0
Dec	91	0	93	0	80	0
Jan	19	0	19	0	16	0
Feb	31	0	27	0	20	0
Mar	15	0	16	0	7	0
Apr	15	0	17	0	12	0
Cohort 1						
May	6	0	6	0	5	0
Jun	3	0	3	0	3	0
Jul	1	0	1	0	1	0
Aug	72	0	74	0	73	0
Sep	180	0	190	0	40	0
Oct	107	0	111	3.6	111	0
Nov	166	0	174	23.6	144	0
Dec	291	0	294	43.5	281	0
Jan	52	0	52	57.7	47	0
Feb	31	6.5	36	38.9	32	3.1
Mar	31	22.6	33	48.5	29	13.8
Apr	122	21.3	159	67.3	124	58.9
Cohort 2						
May	71	1.4	74	44.6	61	73.8
Jun	4	0	4	50.0	4	0
Jul	0	ND	0	ND	0	ND
Aug	58	1.7	59	57.6	58	0
Sep	137	2.9	140	62.9	58	50.0
Oct	121	31.4	123	95.9	123	0
Nov	98	64.3	104	94.2	83	7.2
Dec	82	75.6	83	77.1	80	1.3
Jan	13	61.5	13	92.3	13	38.5
Feb	40	90.0	39	89.7	42	7.1
Mar	14	100.0	15	73.3	10	90.0
Apr	86	44.2	52	71.2	86	93.0

gonads (observed in autumn; Table 2) preceding advanced ovaries (first observed in spring; Table 2). In both Cohorts 1 and 2, advanced ovaries peaked in spring, and, in Cohort 2, they were also observed in late autumn–winter (Table 2). Individuals started to show high volumes of sperm in their tails ($\geq 75\%$ of the tail area), at approximately 1.5 yr of age. In April, $\sim 70\%$ of Cohort 1 individuals had reached these high amounts of sperm in their tails (Table 2). Similarly to advanced ovaries, high sperm loads were relatively common in Cohort 2 throughout the year. Pairs of

well-developed seminal receptacles (i.e. Code 3) were present in members of both Cohorts 1 and 2, with high proportions (up to 93%) of individuals in both cohorts possessing these in March, April and May. As with advanced ovaries, seminal receptacles were also frequently observed in members of Cohort 2 in late autumn–winter (Table 2).

Vertical distribution and seasonal migration

Parasagitta elegans occupied much of the water column (Figs. 5a & 6). The peak primary production months, May, June and July (also the month of peak *P. elegans* abundance) were characterized by a shallower distribution of Cohort 0 than in other months of the year (Figs. 5b & 6). A 2-sample *t*-test revealed that the average mean depth of Cohort 0 was shallower at this time (May to July) than in autumn (August to October; $df = 3$, $t = -3.44$, $p = 0.041$). However, the vertical distribution of Cohort 0 did not vary between the remaining adjacent 3 mo periods of the year. No differences in the vertical distributions of Cohorts 1 and 2 were observed between any 3 mo consecutive periods (2-sample *t*-tests, $p > 0.05$). Cohort 1 (Fig. 5c) and Cohort 2 (Fig. 5d) seemed to show affinities for relatively deeper waters, and Cohort 2 was absent from the upper 50 m during 10 mo of the year. The generally low abundances of Cohort 2 throughout the year may make some of the mean depth estimates for this cohort unreliable.

DISCUSSION

Based on our findings, the life history of *Parasagitta elegans* in Billefjorden can be summarized by the following key points: (1) the population comprises 3 size cohorts corresponding to age classes; hence, the potential lifespan is at least 3 yr; (2) Cohort 1 individuals develop male gonads prior to female gonads, while members of Cohort 2 possess

advanced male and female gonads year-round; (3) the presence of mature female gonads in Cohorts 1 and 2 prior to the appearance of high numbers of small (≤ 5 mm) newborns from May to July suggests spring and early summer to be the main spawning season; (4) length-growth in all 3 cohorts mainly occurs in summer and; (5) the vertical distribution of Cohort 0 was significantly shallower during the summer productive period than in autumn, whereas Cohorts 1 and 2 were typically distributed in deeper waters year-round.

Lifespan and cohort dynamics

Three cohorts and a potential lifespan of at least 3 yr agree well with reports from other locations around Spitsbergen and the Barents Sea (Falken- haug 1993, Timofeev 1995), as well as the Kara Sea (Timofeev 1989). *Parasagitta elegans* populations residing at lower latitudes with warmer temperatures have considerably shorter lifespans, e.g. 3 mo at St. Margaret's Bay in the West Atlantic (33 to 44° N; Samemoto 1971). Russell (1932) reported generation times and breeding cycles of a little over 1 mo in Ply-

mouth, UK, although Russell may have sampled different populations during his 1 yr study (Jakobsen 1971).

The 3 discrete size cohorts observed in our study also agree well with several other studies from Arctic and sub-Arctic areas (e.g. Dunbar 1962, Welch et al. 1996). Cohorts were relatively obvious in many months. During the less clear months, this seemed to be due to the absence of a clear Cohort 2 peak. Overall, Cohort 2 was the rarest of the size cohorts. However, the maximum size remained around 40 mm in all months, showing that the larger individuals were never completely absent (see the discussion below on their potential hyperbenthic distribution) and also pointing towards a lifespan >3 yr for some individuals. In June and July, the absence of this peak can be attributed to the lack of WP3 sampling. The WP3 net proved to be more efficient at capturing the larger individuals (Fig. 1). Cohort 1 grew much faster than Cohort 2 throughout the year, the latter most likely investing more energy in reproduction than in growth. In January, some Cohort 1 individuals had already attained the lengths of the smaller Cohort 2 individuals, causing an overlap in the distributions of Cohorts 1 and 2.

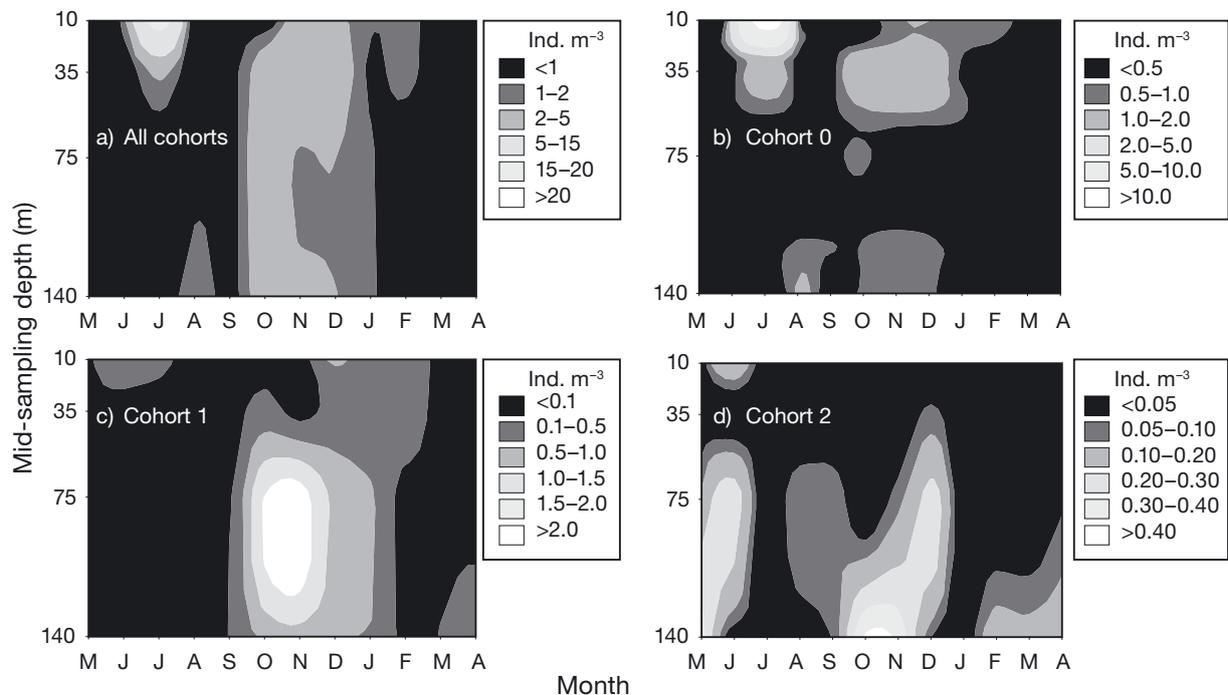


Fig. 5. *Parasagitta elegans*. Contour plots showing the seasonal vertical distributions of (a) the whole population and (b–d) the 3 size cohorts, based on MPS+WP2 data. Each sampled strata is represented on the y-axis by its mid-depth. For those months when data were collected on 2 sampling dates, the abundances shown are averages. Plots were produced in Minitab 16™ using the Distance interpolation method. Note the different scales for abundance in each plot and that Cohort 2 individuals were absent in the MPS+WP2 samples in January and July

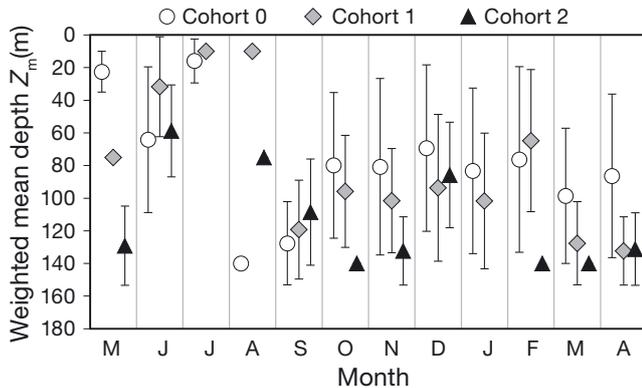


Fig. 6. *Parasagitta elegans*. Weighted mean depth of occurrence in the water column (Z_m) of Cohorts 0, 1 and 2 throughout the year, plus standard deviation (Z_s) bars, based on MPS+WP2 data. As Cohort 2 was not present in the MPS+WP2 samples in January and July, no data are presented for Cohort 2 in these months. In some other cases, abundances were too low to allow standard deviations

Spring–summer strategy: breeding, intense feeding and elevated growth rates

The main period of reproduction for *Parasagitta elegans* in Billefjorden was spring and early summer. The mean length of Cohort 0 in May was very close to the reported length of newly hatched larvae (~1.2 mm; Kotori 1976), indicating that this is the start of the main spawning period. Individuals <6 mm were captured in May, June, July and August, peaking in July, suggesting that the reproductive season is relatively long, at least compared to some estimates for this species in the North Pacific (e.g. Kotori 1999 and references therein) and North Atlantic Oceans (e.g. Conway & Williams 1986, Tiselius & Peterson 1986). Peak spring/summer breeding is common in *P. elegans* at high latitudes (e.g. Kramp 1939, Samemoto 1971), but a breeding season lasting from July into the winter was reported in sub-Arctic Hudson Bay (Dunbar 1962). In temperate regions, breeding seasons can typically be even longer (Terazaki 2004 and references therein). Higher temperatures and less pulsed food availability in the south, and thus the potential for continuous growth and development, are potential explanations for this latitudinal pattern. The vertical distribution of Cohort 0 was particularly shallow during the main reproductive and primary production period in the fjord (May, June and July). Although *P. elegans* var. *arctica* may reproduce at depth (e.g. Kramp 1939, Samemoto 1987), its buoyant eggs rise and typically hatch near the surface (Hagen 1999 and references therein). By emerging in relatively shallow waters in early summer, Cohort 0 individuals have access to a wide

range of copepod prey, which graze and reproduce during the ice algal and phytoplankton blooms (Søreide et al. 2010). For these small chaetognaths, prey size is an important factor. Saito & Kiørboe (2001) showed that *P. elegans* <5 mm in the North Sea fed almost exclusively on prey <350 μ m in length. In Billefjorden, the prey in this size range is represented by small cyclopoids such as *Oithona similis*, as well as *Calanus* nauplii and the young *Calanus* stages. The early stages of *Calanus glacialis*, CI and CII are also available prey sources, and these young developmental stages also peaked in the upper 50 m in June and July in Billefjorden (Bailey 2010).

Having already developed advanced ovaries and synthesized considerable amounts of sperm, members of Cohort 1 possessed well-developed seminal receptacles in March/April, suggesting that they will be able to reproduce in the next days to weeks. Once eggs are laid, they may hatch within ~2 d (Brusca & Brusca 1990). In Cohort 1, male gonads developed earlier than female gonads (sex-specific maturation), with ovaries reaching advanced stages several months after male gonads. This difference may lead to some individuals functioning first as males and then as both males and females (Alvarino 1992). This could be an adaptation to ensure cross-fertilisation, and may increase overall fecundity as female fecundity is likely to be more dependent on body size than the male component. Some authors have suggested that chaetognaths die after laying their first batch of eggs (e.g. Russell 1932, Alvarino 1992), but, in our study, the persistence of Cohort 2 throughout the year rather suggests that they may be iteroparous, reproducing several times before dying (also suggested by others: Conway & Williams 1986 and references therein). Maturity data support this, showing that they may reproduce during both their second and third year. However, in Cohort 2, observations of advanced ovaries fell drastically in April, and from May to August few Cohort 2 individuals possessed advanced ovaries. This could possibly be due to ovary shrinkage after egg laying (Dallot 1968), although very few large specimens were collected in June and July, since we did not sample with the WP3 in these months. Observations of advanced ovaries in Cohort 2 increased again in autumn and peaked in this cohort in March. However, these observations were only indicative of iteroparity, and a semelparous strategy could also give rise to the same observations, given age-specific reproduction (as well as variability among individuals with respect to timing within the season).

Autumn–winter strategy: maturation, possible migrations and reduced growth rates

There is evidence in our study that Cohort 0 individuals hatching in spring–summer migrate to deeper waters as they age, possibly to reduce their exposure to visually searching predators or to follow the depth distributions of their prey. Chaetognaths are tactile predators, using hair fans to sense prey vibrations in the water column (Saito & Kiørboe 2001 and references therein). In autumn and winter, feeding opportunities for older chaetognaths may peak at depth. For instance, the calanoid copepods of the genus *Calanus* diapause at depth (Falk-Petersen et al. 2009). These copepods are very abundant in Billefjorden (Arnkvaern et al. 2005, Bailey 2010) and may be important prey for older chaetognaths.

Parasagitta elegans growth rates in autumn and winter generally fell below those in spring and summer, which could suggest reduced feeding rates and, furthermore, little direct impact of these arrow worms on the overwintering populations of copepods (in agreement with unpublished data from Grigor et al.). Cohort 2 had low growth rates throughout the year (total growth of 5 mm), suggesting little growth after maturation, in agreement with results from Baffin Bay (Samemoto 1987) and Resolute (Welch et al. 1996). Cohort 1, however, grew considerably from around 23 mm in February to 30 mm in April. Whilst this strong growth could be an artefact of our method of detecting size cohorts from length-frequency data, Welch et al. (1996) similarly observed high winter growth rates for adolescents in the cold environment of Resolute (Canadian Arctic). Saito & Kiørboe (2001) showed that individuals >12.5 mm can feed on many prey size classes >250 μm , suggesting that adolescents and adults are unlikely to face food shortages in winter. *Calanus* abundances dropped drastically from February to April (Bailey 2010), and predation from Cohort 1 could have played a role.

MPS data suggested that the *Parasagitta elegans* population had an apparent minimum in September (84 ind. m^{-2}) before reaching a second peak in November. However, the WP3 data did not reveal the same trough in September, showing mean abundances of 153 ind. m^{-2} , which were more comparable with the August and October values. The large difference in abundances between the MPS and WP3 nets may be due to patchiness, which always poses a problem when sampling macrozooplankton, combined with the fact that the MPS data were obtained during the day, whereas the WP3 data were sampled at night. The MPS data suggest that Cohort 0 abun-

dances increased ~6-fold from September to October, which may suggest some autumn production. However, the abundance of the other cohorts increased similarly to Cohort 0, and no individuals <6 mm were found in September or October, which points to no autumn reproduction. A few individuals <6 mm occurred in December, January and February, suggesting some winter reproduction in Billefjorden. These could be the offspring of Cohort 2, which possessed advanced ovaries at this time, and a few members of Cohort 2 also possessed swollen seminal receptacles in autumn and winter. However, <6 mm individuals comprised <5% of the *P. elegans* population in these months, compared with up to 13% of those caught in summer months, and the proportion of *P. elegans* with mature gonads in winter was much lower than in spring (for ovaries) and early summer (for receptacles). The lack of mature individuals during the polar night agrees well with results from other Svalbard fjords in 2012 and 2013 (J. J. Grigor et al. unpubl. data).

Potential migration behaviours of larger chaetognaths in the lower part of the water column may also explain the second population peak in November. We did not sample the lower 10 m above the seabed during our study, the hyperbenthic zone where high abundances of large chaetognaths can occur (Choe & Deibel 2000). In fact, image analysis of the hyperbenthic community in Kongsfjorden (Svalbard) in autumn 2012 showed high abundances of chaetognaths just above the sea floor (J. Laudien pers. comm.). ROV recordings made in Baffin Bay (Canadian Arctic) in August 2013 also showed high densities of large chaetognaths in the hyperbenthic zone (bottom depth was ~370 m). They hovered in position above the seabed until approached by the ROV and then quickly darted away (L. Fortier unpubl. data). Similarly Choe & Deibel (2000) showed that 25% of the total *Parasagitta elegans* biomass in the water column occurred in the lowest 1 m, and Mature Stage III comprised $46 \pm 26\%$ of the chaetognaths here throughout the year. In our study, measured abundances of Cohorts 1 and 2 in October and November were much higher than in autumn, possibly because they migrated upward in the water column, and thus were more representatively sampled by our nets.

Concluding remarks and outlook

Our study shows the importance and potential of field campaigns with high temporal resolution within the annual cycle. As a result of this design, we ob-

tained robust knowledge of the scheduling of the major events in the life cycle of *Parasagitta elegans* in the highly seasonal environments of the high Arctic. High-resolution seasonal sampling is important for proper parameterisation and development of life-history and annual routine models for this and similar species (Varpe et al. 2007). Such models are needed for an improved understanding and quantification of life-history trade-offs and for predictive powers in studies of environmental change (McNamara & Houston 2008, Varpe 2012). Further studies of chaetognath reproductive strategies, including sex allocation and energy storage (Pond 2012) are particularly interesting avenues. We recommend a continued focus on abundant predatory zooplankton, especially on gelatinous plankton, which, due to their non-visual food search, may be less restricted by seasonality at high latitudes than grazers and visual predators.

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