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ORIGINAL PAPER

Polar night ecology of a pelagic predator, the chaetognath *Parasagitta elegans*

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Abstract The annual routines and seasonal ecology of herbivorous zooplankton species are relatively well known due to their tight coupling with their pulsed food source, the primary production. For higher trophic levels of plankton, these seasonal interactions are less well understood. Here, we study the mid-winter feeding of chaetognaths in high-Arctic fjord ecosystems. Chaetognaths are planktivorous predators which comprise high biomass in high-latitude seas. We investigated the common species *Parasagitta elegans* around the Svalbard archipelago (78–81°N) during the winters of 2012 and 2013. Our samples consisted of individuals (body lengths 9–55 mm) from three fjords, which were examined for gut contents ($n = 903$), stable isotopes, fatty acid composition, and maturity status ($n = 352$). About a quarter of the individuals contained gut contents, mainly lipid droplets and chitinous debris, whilst only 4 % contained identifiable prey, chiefly the copepods *Calanus* spp. and *Metridia longa*. The $\delta^{15}N$ content of *P. elegans*, and its average trophic level of 2.9, confirmed its carnivorous position and its fatty acid profile [in particular its high levels of 20:1(n-9) and 22:1(n-11)] confirmed carnivory on *Calanus*. Observations of undeveloped gonads in many of the larger *P. elegans*, and the absence of small individuals <10 mm, suggested that reproduction had not started this early in the year. Its average feeding rate across fjords and years was 0.12 prey ind.$^{-1}$ day^{-1}, which is low compared to estimates of spring and summer feeding in high-latitude environments. Our findings suggest reduced feeding activity during winter and that predation by *P. elegans* had little impact on the mortality of copepods.

Keywords Predator–prey interactions · Polar night · Foraging · Chaetognaths · Arctic · Zooplankton

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Introduction

The Arctic is a highly seasonal environment, with conditions in the marine pelagic varying greatly between summer and winter. The extreme cycles in solar illumination and sea ice cover create strong seasonality in primary production (Ji et al. 2013), which affects food availability for organisms at higher trophic levels (Varpe 2012). Food availability for herbivores such as *Calanus* copepods is severely reduced during the polar night. Many grazers survive winter food shortages by resting at depth and sustaining themselves on storage lipids accumulated when food was last available (e.g. Conover 1988). Although pelagic omnivores and carnivores may experience a less-pulsed food source than for the herbivores, they may also display adaptations to a seasonal food source (e.g. Newbury 1971; Choe et al. 2003; Kraft et al. 2013). However, for many predators we lack knowledge of their feeding opportunities and activities during winter.

The chaetognath *Parasagitta elegans* (Verrill 1873) is highly represented in Arctic mesozooplankton communities, numerically and in biomass terms (e.g. Søreide et al. 2003; Hopcroft et al. 2005). This typically neritic species (Bieri 1959) can exert high predation pressure on Arctic copepods and compete with larval fish (e.g. Samemoto 1978). Some authors have proposed that chaetognaths are not particularly sensitive to seasonality (e.g. Hagen 1999), suggesting that their varied diets (reviewed by Terazaki 2004) and non-visual food search should allow them to find adequate nutrition throughout the year. Lipid-rich copepods, often preferred prey, diapause in large densities and in an unalert state during winter, so they may be easy prey for some carnivores (Darnis et al. 2012). However, some chaetognath species at high latitudes are found to contain considerable amounts of lipids, including wax esters, which may be used for storage (e.g. Lee 1974; Kruse et al. 2010). Furthermore, winter growth rates of *P. elegans* in the Arctic is lower than those in spring and summer (Grigor et al. 2014), and these observations could indicate reduced winter feeding and resting strategies in this chaetognath.

We report here on the winter feeding ecology of *P. elegans* in the European high Arctic. We used three different methods to assess its diet and trophic level: gut content analysis, which records recent feeding, as well as stable isotope and fatty acid trophic marker (FATM) analyses, which provide additional information on its feeding history, over time frames of weeks to months (Graeve et al. 2005). We calculated feeding rates and possible impact on copepod populations. Although we did not expect mid-winter reproduction (e.g. Kramp 1939; Grigor et al. 2014), we also examined their level of maturity, allowing us to infer how close *P. elegans* is to reproducing, which links to how actively individuals are expected to feed.

Materials and methods

Study area

Chaetognaths were collected from waters around Svalbard (78–81°N) during the winters of 2012 and 2013, during the ARCTOS "Polar Night Cruises" (8 to 21 January 2012 and 9 to 18 January 2013).

The Svalbard archipelago is a meeting place for warm Atlantic water sourced from more southern regions and colder Arctic water from the north. The northward moving West Spitsbergen Current deposits Atlantic water into fjords on the west coast, with one branch finally turning north-east at the top of Spitsbergen and affecting conditions in the Arctic Ocean (Saloranta and Haugen 2001). We sampled three fjords in 2012: Rijpfjorden (station R3), Isfjorden proper, and Adventfjorden, a tributary fjord of Isfjorden (station ISA, see Fig. 1). The latter two locations are hereafter referred to as "Isfjorden". Another fjord, Kongsfjorden, was sampled in 2013, and Rijpfjorden was re-sampled. See Table S1 for full details on the sampling activities. Isfjorden (78°N, 14°E) and Kongsfjorden (79°N, 11.5°E) are influenced by Atlantic water masses and the outer parts are ice free for much of the year (Svendsen et al. 2002; Nilsen et al. 2008), causing important seasonal changes in biodiversity and animal populations in these fjords. Rijpfjorden, in contrast (80°N, 22°E), is influenced by Arctic water, typically remaining ice-covered from December/February to July (Wallace et al. 2010).

Physical and biological environment

At all stations, vertical profiles of salinity, temperature, density, and fluorescence were obtained using a CTD (SBE 9) and processed following standard Sea Bird Electronics (SBE) procedures. In 2012, a steep thermocline was observed in Rijpfjorden between ~70 and 100 m, over which temperature rose to 2 °C and then fell again to 0.5 °C at ~200 m (Fig. S1 in the Supplement). At the mouth of Isfjorden, the thermocline was much weaker, with temperature increasing gradually to 2 °C at ~200 m. At Isfjorden (station ISA), temperature varied little with depth (Fig. S1). At all stations, salinity varied with depth in similar ways to temperature. A strong halocline occurred in Rijpfjorden only, at the same depths as the thermocline (Fig. S1). Fluorescence was very low (<0.6 g l^{-1}) at all stations in January 2012.

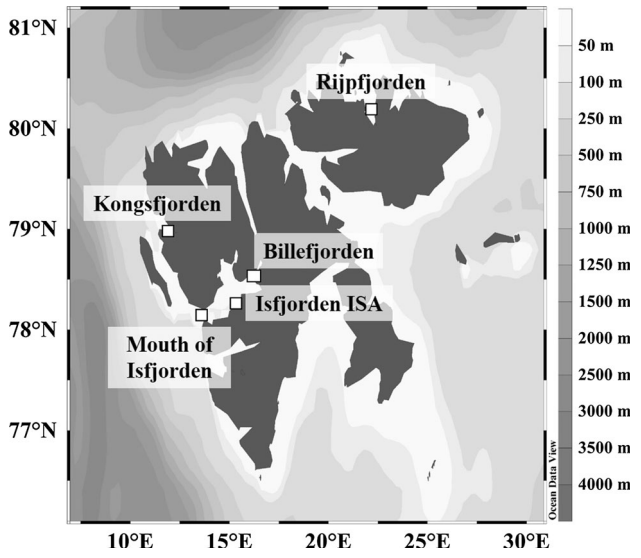


Fig. 1 Map showing the locations of the stations sampled for chaetognaths in January 2012 and 2013

Zooplankton sampling

Horizontal trawls of the large Methot Isaac Kidd gear (MIK, 3.14-m^2 opening, 1.5-mm mesh) were used to obtain large numbers of *P. elegans* for the various dietary analyses (Table S1). MIK sampling depths in Rijpfjorden and Isfjorden (in 2012) captured all water masses in the fjords (melt water, Arctic water/mixed Fram Strait water and Arctic deep water). In contrast, most MIK sampling for chaetognaths in 2013 (Kongsfjorden and Rijpfjorden) was carried out in the upper 20 m (Table S1). This sampling decision was taken to reduce haul time, as chaetognaths can easily become damaged and stressed during net sampling, which poses several problems for gut content analyses (Baier and Purcell 1997).

In Rijpfjorden in 2012, vertical hauls of the smaller Multi-Plankton Sampler gear (MPS, 0.25-m^2 opening, 0.2-mm mesh) were also performed to collect zooplankton community data (see also Daase et al. 2014) and to source smaller *P. elegans* for gut content analyses (sampled strata: 260–200 m, 200–100 m, 100–50 m, 50–20 m, 20–0 m; see Table S1 for details). The MPS captured higher densities of smaller *P. elegans* (10–19 mm) in the upper 20 m than the MIK (0.5 ± 0.4 compared to 0.1 ± 0.1 ind. m^{-3}), but fewer individuals $\geq$20 mm (1.8 ± 1.7 compared to 5.9 ± 8.2 ind. m^{-3}). Individuals <10 mm were not captured by either gear in Rijpfjorden or Isfjorden in 2012. Grigor et al. (2014) similarly showed that the MPS captured the smaller size fraction of *P. elegans* more efficiently than a larger "WP3" net with a 1-m^2 opening. MPS samples collected from Isfjorden ISA on 27 January 2012 were also analysed for abundance data.

Sample processing

Upon retrieval of each MIK haul, the cod end was immediately transferred to a marked bucket and diluted up to the 10 l mark. A 0.6 l sub-sample was taken for community analysis and fixed in 4 % buffered formalin–seawater solution. Webster et al. (2013) show presence–absence data for zooplankton in Rijpfjorden from the community samples from 2012. From a second 0.6 l sub-sample, 100 *P. elegans* were randomly picked out for gut content analyses (Table S1) and preserved in 4 % buffered formalin–seawater solution. On the 2012 cruise, 75–150 *P. elegans* were also picked out of this second sub-sample for stable isotope analyses (n individuals = 675, Table S1), and 30 individuals were randomly picked out for fatty acid trophic marker (FATM) analyses (n individuals = 290, Table S1). These samples were frozen at −80 °C until the end of the cruise and then stored at −80 °C for further processing.

Gut content analyses

A total of 202 individuals from 2012 (body lengths 10–55 mm) and 701 from 2013 (body lengths 9–42 mm) were dissected and analysed for gut contents. In 2012, a minimum of 10 individuals were dissected from each MIK haul. In 2013, we examined the guts of all 100 individuals preserved from each MIK haul; 3–10 smaller individuals were sourced from each MPS haul (Table S1).

Parasagitta elegans individuals were measured to the nearest millimetre (excluding the caudal fin) and stained with a solution of lignin-red, used to stain tissues of crustacean prey in their guts (Falkenhaug 1991), and borax carmine, capable of highlighting the gonads of prey (Pierce 1941), diluted 50 times in water. Head widths were measured to the nearest 0.01 millimetre under the binocular microscope. All visible gut contents were described. Detected prey was identified to the lowest possible taxonomic level and photographed using a digital camera connected to a dissecting microscope (Leica DFC 320).

Food-containing ratio and feeding rate

The food-containing ratio (FCR) is the proportion of individuals in a population with food in their gut. Some only include chaetognaths containing identifiable prey in the FCR calculation (FCR_{min}, e.g. Falkenhaug 1991; Kruse et al. 2010). However, this approach may not account for loss of prey items from guts during net towing, due to damage or stress-induced regurgitation (Baier and Purcell 1997, see "Discussion"). Other studies also included individuals with other signs of recent prey digestion (gut lipids and debris, e.g. Samemoto 1978; Froneman and

Pakhomov 1998), which may give an upper estimate of the proportion feeding (FCR_{max}). FCR_{max} measurements may not be appropriate for some chaetognath species, such as those that contain oil vacuoles in the centre of their bodies. This includes another Arctic species, *Eukrohnia hamata* (Möbius 1875), in which oil vacuoles may be for storage or buoyancy (Øresland 1990; Pond 2012, pers. obs.). However, these oil vacuoles do not occur in *P. elegans*. We calculated both FCR_{max} and FCR_{min} for *P. elegans* from each haul. We also calculated feeding rates (FR: no. of prey items consumed ind.$^{-1}$ day^{-1}) according to Eq. (1). Only individuals containing identifiable prey were included in the FR calculation.

$$\mathrm{FR} = \frac{n_{\mathrm{prey}} \times 24}{t_{\mathrm{dig}}} \quad (1)$$

where n_{prey} = mean no. of identifiable prey per chaetognath, and t_{dig} = digestion time in hours. Feigenbaum (1982) suggested a t_{dig} of 10.2 h for *P. elegans* from a laboratory study on starved specimens from Vineyard Sound, maintained at 0 °C. As the water temperature in all our study fjords was close to 0 °C (Fig. S1), we used Feigenbaum's t_{dig} estimate.

Proportions of individuals per haul containing different gut types were analysed using Kruskal–Wallis tests.

Stable isotope analyses

As the ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ in organisms at different trophic levels tend to differ considerably, stable isotope analyses can be used to examine marine food web structure and the transfer of energy between trophic levels (McConnaughey and McRoy 1979). Stable isotope analyses were performed on our 2012 samples at the Institute for Energy Technology in Kjeller, Norway, using similar methods to Søreide et al. (2006). Three replicate samples each containing 25 *P. elegans* were analysed from seven of the MIK hauls, whilst six replicate samples of 25 inds. were analysed from an eighth MIK haul at 225m in Rijpfjorden (Table S1). All *P. elegans* had body lengths within the range of 10–50 mm. The whole body of each chaetognath was used, except lipids and non-dietary carbon (i.e. carbonates), which were removed before analyses by Soxhlet extraction with CH_2Cl_2. Lipids have notably lower levels of ^{13}C than proteins and carbohydrates (van Dongen et al. 2002), and their removal reduces a main source of measurement variability between individuals (Hobson and Welch 1992). C/N ratios were expressed as the deviation from standards in ppt (‰) according to Eq. (2) (Søreide et al. 2006).

$$\delta X = \left[\left(R_{\mathrm{sample}}/R_{\mathrm{standard}}\right) - 1\right] \times 1000 \quad (2)$$

where $X = {}^{13}C$ or ^{15}N and R = the corresponding ratios $^{13}C/^{12}C$ or $^{15}N/^{14}N$. International standards, Pee Dee Belemnite for $\delta^{13}C$ (PDB: USGS 24), and atmospheric air for $\delta^{15}N$ (IAEA-N-1 and 2) were used to determine R. Carbon and nitrogen composition were expressed as percentages of animal dry weight.

Determination of trophic level

The trophic level (TL) of *P. elegans* in each fjord was calculated as the difference between its average $\delta^{15}N$ content and that of the winter food web baseline, assuming a constant fractionation between trophic levels [Eq. (3), Søreide et al. 2006].

$$\mathrm{TL} = \alpha + \frac{\delta^{15}\mathrm{N}\ P.\ elegans - \delta^{15}\mathrm{N}\ C.\ glacialis}{\Delta N} \quad (3)$$

where α = trophic level of the food web baseline and ΔN = the trophic enrichment factor for $\delta^{15}N$ (average amplification) per trophic level. We took the abundant grazer *Calanus glacialis* ($\alpha = 2$) to represent the winter food web baseline. This decision was made because *P. elegans* are thought to be carnivores that typically do not feed on primary production but feed often on *Calanus*, and primary production is anyway low in winter (pers. comm.: J Søreide).

We used a $\delta^{15}N$ value for *Calanus glacialis* of 9.6 ± 0.2 ‰, estimated for individuals from 300 m in Svalbard fjords during December (Søreide et al. 2008). We used $\Delta N = 3.4$ ‰, also determined for the European Arctic by Søreide et al. (2006).

Fatty acid analyses

Groups of primary producers and some herbivores produce fatty acids that are unique to them, known as fatty acid trophic markers (FATMs, Dalsgaard et al. 2003). Higher consumers possess a lower capacity to synthesise their own fatty acids, or to modify those received from their prey. Therefore, when FATMs persist in a predator for some time with little modification, they can be used to quantify its diet (Dalsgaard et al. 2003).

Determination of the fatty acid signatures of *P. elegans* from Isfjorden and Rijpfjorden (in 2012) were performed on triplicate samples from nine MIK hauls (Table S1) at UNILAB, Tromsø, Norway, using similar methods to Wold et al. (2011). Each sample contained 10 pooled individuals with dry weights between 0.001 and 0.05 g. Total lipid was extracted in 15 ml 2:1 chloroform–methanol with butylated hydroxytoluene (BHT) (Folch et al. 1957). Each sample was supplemented with a known amount of the fatty acid 21:0, as an internal standard, and trans-methylated in methanol containing 1 % sulphuric acid with toluene for

16 h at 50 °C. The relative compositions (%) of FA methyl esters were determined on an Agilent 6890 N gas chromatograph, equipped with a fused silica, wall-coated capillary column with an Agilent 7683 injector and flame ionisation detection. The fatty acid methyl esters were identified and quantified by gas chromatography. Results are given as relative percentages of the various fatty acids identified in specimens from the two fjords. Differences in average fatty acids proportions between sampled depths in Isfjorden and Rijpfjorden were analysed using one-way ANOVA. Differences in the fatty acid profile between fjords was analysed using the Mann–Whitney *U* test (sum rank test).

Mid-winter maturity status

Chaetognaths are hermaphrodites possessing male and female gonads (Alvarino 1992). The male gonads (testes and seminal vesicles) produce and secrete sperm, whilst the female gonads (ovaries and seminal receptacles) produce ova and receive sperm from a sexual partner (Alvarino 1992). Mature *P. elegans* are characterised by advanced ovaries containing large oocytes, high sperm loads filling the tail section of the animal, and pairs of pronounced seminal receptacles and vesicles (Russell 1932; Choe et al. 2003). We described the maturity of 29 of the largest individuals (40–51 mm, 8 × 1 mm size classes), and in 323 smaller individuals (13–39 mm, 26 × 1 mm size classes) in MIK samples from all fjords (both years, Table S1). Measured individuals were stained with borax carmine solution to highlight their gonads (Pierce 1941). Maturity assessments were made under the binocular microscope following the methods of Grigor et al. (2014). Ovaries were measured to the nearest 0.1 mm, and individuals showing advanced ovary development were taken as those with ovaries ≥5.4 mm, whilst shorter ovaries <5.4 mm were considered to be poorly developed. The volume of loose sperm in the tail was estimated to the nearest 25 %. Low sperm loads could suggest that sperm is filling the tail or has already been released. However, when sperm has already been released, remaining sperm appears more sparsely distributed. Therefore, spent individuals can be separated from those which have not yet secreted sperm. The size of the seminal receptacles was also described (see Grigor et al. 2014 for further details).

Results

Chaetognath abundance and prey field

In Rijpfjorden in 2012, the most abundant zooplankton taxa based on the MPS sampling were the larger calanoid copepod *Calanus finmarchicus* and the smaller copepods *Pseudocalanus* spp. (Calanoida) and *Oithona similis* (Cyclopoida) (Table 1). *P. elegans* was the most abundant

Table 1 Total water-column abundances (ind. m^{-3}) of a polar night zooplankton community (Rijpfjorden 2012), ordered according to abundance per taxonomic group

Taxonomic group	Functional (feeding) group	Abundance (ind. m^{-3})
Cyclopoida (Copepoda)	Omnivores	1,467.6
Small Calanoida (Copepoda)	Omnivores	1,257.5
Calanus spp. (Copepoda) CI-AF	Herbivores	881.5
Metridia longa	Omnivore	78.6
Tunicata	Variable between species	36.9
Ctenophora	Carnivores	23.5
Limacina helicina (Pteropoda)	Herbivore	17.3
Parasagitta elegans (Chaetognatha)	Carnivore	5.5
Clione limacina (Pteropoda)	Carnivore	3.9
Other Mollusca	Variable between species	3.9
Isopoda	Variable between species	3.4
Eukrohnia hamata (Chaetognatha)	Carnivore	1.4
Travisiopsis sp. (Polychaeta)	Carnivores	1.2
Harpacticoida (Copepoda)	Variable between species	0.9
Echinodermata	Variable between species	0.6
Hydrozoan medusae	Variable between species	0.6
Euphasiacea	Variable between species	0.3
Apherusa glacialis (Amphipoda)	Herbivore	0.1
Carnivorous Calanoid copepods	Carnivores	0.1
Pseudomma truncatum (Mysidacea)	Omnivore	0.1
Ostracoda	Variable between species	0.1

Net sampling (Multi-Plankton Sampler; 0.25-m^2 opening, 0.2-mm mesh) was used. As larger chaetognaths may have avoided the smaller MPS net (see Grigor et al. 2014), chaetognath abundances presented here are likely to be underestimates. Mean abundances for species and copepod stages were first calculated over two hauls (one at midday and the other at midnight at various depth intervals, see Table S1), and data were summed across all sampling depths. Copepod stages are CI-CV, AM (adult male) and AF (adult female). Functional (feeding) groups were extracted from Søreide et al. (2003). "Small Calanoida" comprised the following taxa: *Acartia longiremis*, Aetideidae CI–CIII, *Bradyidius similis*, *Microcalanus* spp. and *Pseudocalanus* spp. Only taxa with abundances of ≥0.1 ind. m^{-3} are shown

chaetognath, but overall chaetognaths were also less abundant than the non-copepod taxa *Oikopleura* spp. (Tunicata) and *Beroe cucumis* (Ctenophora) (Table 1). Average *P. elegans* abundances in Rijpfjorden MIK trawls ranged from 2.4 ± 1.2 ind. m^{-3} (225 m) to 14.7 ± 7.0 ind. m^{-3} (75 m), comparing relatively well with the MPS results. For further details on the polar night zooplankton community in Rijpfjorden, see Webster et al. (2013), Kraft et al. (2013), and Daase et al. (2014).

Gut contents

Observed gut contents were copepods, chitinous debris, lipid droplets, and other detritus that could not be identified. The proportions of *P. elegans* with gut contents (FCR_{max}) varied between fjords and years (Kruskal–Wallis test, $P < 0.01$), ranging from 9 to 53 % (Fig. 2). Some individuals contained two or more gut content types. Lipid droplets were the most common gut observation overall (Figs. 3, 4), observed in 106 (11.7 %) of the 903 chaetognaths. A total of 33 individuals (3.7 %) contained identifiable copepod prey, including *C. finmarchicus*, *Metridia longa*, and harpacticoid copepods. Proportions containing prey (FCR_{min}) also varied between fjords and years (Kruskal–Wallis test, $P < 0.05$), ranging from 0 to 10 % (Fig. 2). FRs ranged from 0.00 to 0.24 prey ind.$^{-1}$ day^{-1} (mean = 0.12 prey ind.$^{-1}$ day^{-1}). Amongst feeding *P. elegans*, median per haul proportions with prey varied with fjord (Kruskal–Wallis test, $P < 0.005$), but proportions with other gut contents did not ($P > 0.05$, Fig. 3). The relationship between chaetognath head width and body length was linear ($y = 0.031x + 0.37$, $R^2 = 0.79$), and prey was identified in individuals with head widths ≥0.87 mm (Fig. 4). Per haul proportions of *P. elegans* with gut contents increased with head width size class (Kruskal–Wallis test, $P < 0.05$, Fig. 4), but amongst feeders, proportions with each gut content type did not vary with head width ($P > 0.05$, Fig. 4).

Body composition

Values for carbon and nitrogen isotopes varied little between fjords and sampling depths (Table 2). The $\delta^{13}C$ content of *P. elegans* ranged from −22.0 ± 0.3 ‰ (Rijpfjorden) to −21.5 ± 0.2 ‰ (Isfjorden), whilst $\delta^{15}N$ content ranged from 12.5 ± 0.3 ‰ to 12.9 ± 0.1 ‰ (both Isfjorden). Average trophic level (TL) based on the $\delta^{15}N$ content was 2.9, and average *C/N* ratio over fjords and depths was 3.1 (Table 2).

Parasagitta elegans fatty acid signature did not differ between Isfjorden and Rijpfjorden (Mann–Whitney *U* test, $P > 0.05$). Similarly, percentage composition of almost all fatty acids did not differ between sampling depths in the two fjords (one-way ANOVA, $P > 0.05$). The high levels of 18:1(n-9) compared with those of 18:1(n-7) strongly indicate carnivory. The *Calanus* fatty acid marker 20:1(n-9) and 22:1(n-11) were both abundant. The dinoflagellate marker docosahexaenoic acid (DHA) 22:6(n-3) was recorded in interestingly high amounts, whilst eicosapentaenoic acid (EPA) 20:5(n-3) was recorded in moderate to high amounts (Table 3).

Mid-winter maturity status

Amongst the largest individuals in the population (body lengths 40–51 mm), 55 % had well-developed seminal receptacles, whereas 93 % had relatively high sperm volumes in their tails (50–100 %) and all had advanced ovaries (≥5.4 mm). In smaller individuals (lengths 13–39 mm), 45 % had well-developed seminal receptacles and 42 % had advanced ovaries; 80 % had synthesised relatively high sperm volumes (filling 50–100 % of the tail area).

Discussion

Studies during the polar night

Studies of plankton ecology in the high Arctic are typically restricted to spring and summer, due to the logistical difficulties of sampling during winter. The polar night cruise, of which our study formed a part, offered unique possibilities for a better understanding of polar night marine ecology (see Berge et al. 2012; Webster et al. 2013; Daase et al. 2014).

We show that the common chaetognath *P. elegans* remains an active carnivore during the polar night. This arrow worm is not in a dormant and non-feeding state although its feeding rates may be considerably lower than in spring and summer, and reproduction is absent (or occurring at very low rates) at this time of year. These observations add to the increasing awareness of activity levels and ecological interactions of pelagic organisms during the polar night.

Feeding activity and rates

Copepods are abundant in Svalbard fjords during winter (Table 1) and as a non-visual predator *P. elegans* should, as opposed to fish and other visual predators, be able to encounter and catch them also during the polar night. The behaviour of some copepods during the polar night (i.e. diapausing in an unalert state) could make them particularly susceptible to predators such as chaetognaths (Darnis et al. 2012). About a quarter of the *P. elegans* individuals showed signs of recent feeding (mainly lipid

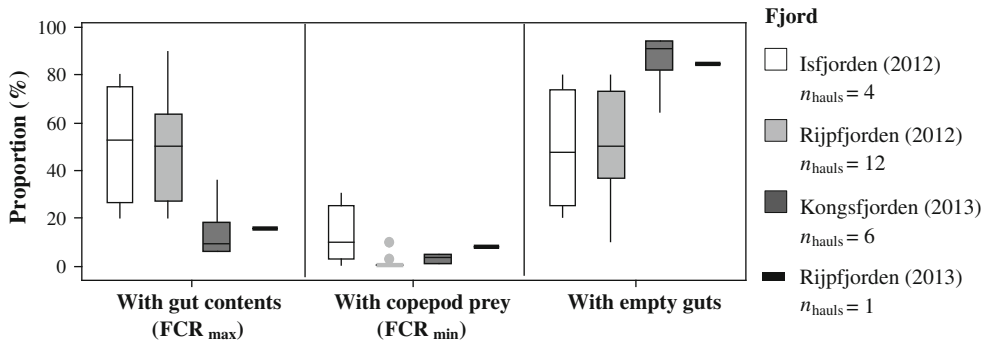


Fig. 2 Proportions (%) of *P. elegans* individuals per haul with gut contents (FCR_{max}), identifiable prey (FCR_{min}), and empty guts in each fjord. The *horizontal line* inside each *boxplot* shows the median of the proportions over multiple haul samples in a fjord. The *lower* and *upper boxes* show the lower and upper quartiles, respectively, and the *vertical lines* outside the boxes the differences between these quartiles and the lowest and highest proportions observed. Each *dot* represents an outlying data point. n_{hauls} = numbers of hauls for each fjord. Hauls with <3 individuals analysed were not included. As only one haul was analysed for Rijpfjorden in 2013, full boxplots could not be shown. See Table 1 for numbers of individuals analysed per haul

Fig. 3 Proportions (%) of feeding *P. elegans* individuals per haul in each fjord with different types of gut content. For details on the features of the boxplots and the data, see Fig. 2

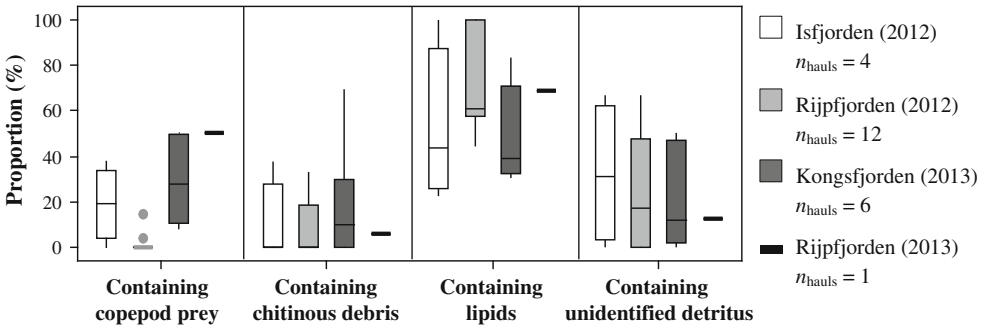
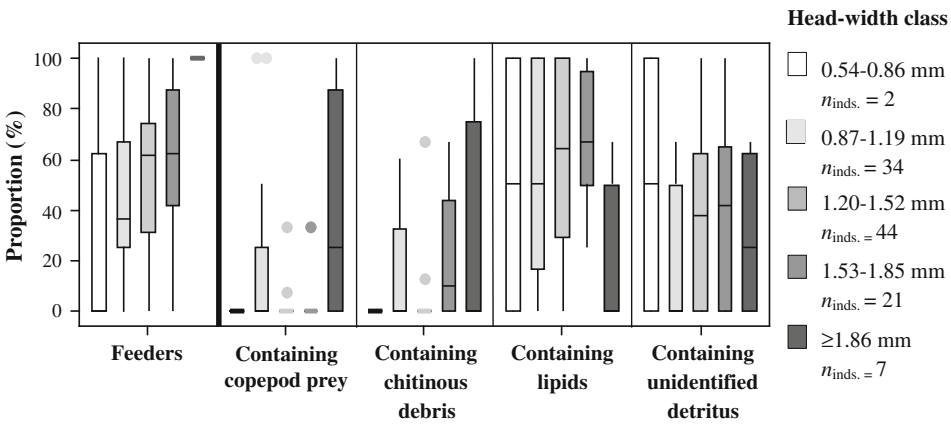


Fig. 4 Gut contents in ascending head width size classes: proportions of *P. elegans* (%) per haul with gut contents and of feeders with each gut content type. Includes all dissected specimens from Isfjorden (50 individuals, 4 hauls) and Rijpfjorden (152 individuals, 13 hauls) in 2012. For details on the features of the boxplots and the data, see Fig. 2. $n_{inds.}$ = total numbers of individuals for each size class



droplets). The body of *P. elegans* does not contain a centralised oil vacuole, suggesting that all lipid droplets in *P. elegans* guts remained from recently digested prey, yet only 4 % contained identifiable prey. Based on Feigenbaum's (1982) digestion time estimate of 10.2 h at 0 °C (likely longer in colder waters), our findings would

Table 2 Stable carbon and nitrogen isotope values for *P. elegans* by the MIK (3.14-m^2 opening, 1.5-mm mesh) at various trawl depths (20, 30, 35, 60, 75, and 225 m) in Isfjorden and Rijpfjorden (2012)

Location	Trawl depth (m)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	DW %C	DW %N	*C/N*	TL
Mouth of Isfjorden	250	−21.7 ± 0.0	12.5 ± 0.3	48.4 ± 0.5	15.6 ± 0.4	3.1 ± 0.0	2.9
Isfjorden (ISA)	30	−21.5 ± 0.2	12.9 ± 0.1	48.4 ± 0.4	15.5 ± 0.1	3.1 ± 0.0	3.0
-"-	35	−21.5 ± 0.1	12.8 ± 0.2	47.9 ± 1.1	15.4 ± 0.4	3.1 ± 0.0	2.9
-"-	60	−21.6 ± 0.1	12.9 ± 0.1	48.3 ± 0.8	15.5 ± 0.4	3.1 ± 0.0	3.0
Rijpfjorden	20	−22.0 ± 0.0	12.5 ± 0.2	48.7 ± 0.3	15.8 ± 0.1	3.1 ± 0.0	2.9
-"-	75	−21.8 ± 0.2	12.5 ± 0.2	48.0 ± 0.2	15.4 ± 0.0	3.1 ± 0.0	2.9
-"-	75	−22.0 ± 0.3	12.6 ± 0.3	48.9 ± 0.4	15.7 ± 0.2	3.1 ± 0.0	2.9
-"-	225	−21.8 ± 0.1	12.5 ± 0.1	48.6 ± 0.4	15.8 ± 0.2	3.1 ± 0.0	2.9

The average $\delta^{13}C$ and $\delta^{15}N$ composition (‰) in replicate samples (usually three but six from 225 m in Rijpfjorden) containing 25 pooled individuals (10–50 mm), average proportions of animal dry weight (DW) comprising carbon and nitrogen (%), and *C/N* weight ratios. All values are accompanied by standard deviations. Trophic levels (TL) were calculated for *P. elegans* from each fjord from mean $\delta^{15}N$ (‰) values (see "Methods")

Table 3 Average fatty acid profile for *P. elegans* in 2012

Fatty acid	Mean % Isfjorden (*n* samples = 12)	Mean % Rijpfjorden (*n* samples = 17)
14:0 FA	5.02 ± 2.09	4.13 ± 0.62
14:1(n-5) FA	0.54 ± 0.06	0.52 ± 0.08
15:0 FA	0.72 ± 0.07†	0.73 ± 0.06
16:0 FA	11.91 ± 1.16	12.65 ± 1.47
16:1(n-5) FA	2.97 ± 0.41	3.30 ± 0.39
16:1(n-7) FA	7.13 ± 0.27	6.05 ± 0.33
18:0 FA	1.09 ± 0.13	1.18 ± 0.20
18:1(n-7) FA	1.95 ± 0.28	1.74 ± 0.18
18:1(n-9) FA	5.35 ± 0.65	5.82 ± 0.54
18:2(n-6) FA	1.28 ± 0.11†	1.35 ± 0.09
18:3(n-3) FA	1.11 ± 0.11	1.37 ± 0.07
18:4(n-3) FA	1.76 ± 0.63	2.35 ± 0.35
20:1(n-9) FA	14.80 ± 1.02	11.46 ± 1.71
20:4(n-3) FA	0.82 ± 0.10	0.99 ± 0.07
20:5(n-3) FA (EPA)	11.41 ± 0.68	12.73 ± 0.75
22:1(n-11) FA	6.77 ± 1.38	5.69 ± 0.71
22:1(n-7) FA	0.47 ± 0.02	0.78 ± 0.30
22:5(n-3) FA	0.60 ± 0.14	0.69 ± 0.15
22:6(n-3) FA (DHA)	18.01 ± 2.33	18.81 ± 1.99
24:1(n-9) FA	2.88 ± 0.21	3.81 ± 0.62

Results are given as average percentages of the various fatty acids identified across all samples from Isfjorden and Rijpfjorden (see "Methods"), alongside the standard deviations. Only fatty acids with mean percentages of ≥0.5 ± 0.1 across both fjords are shown. In Isfjorden, the mean percentages of 15:0 FA and 18.2(n-6) FA differed between sampling depths (indicated by a † symbol, one-way ANOVA, $P < 0.05$). In Rijpfjorden, the proportion of every fatty acid was similar between sampling depths (one-way ANOVA, $P > 0.05$)

suggest that most individuals had not fed for several hours before their capture. In contrast, Falkenhaug (1991) identified prey in 36 % of the *P. elegans* population collected from the Barents Sea in summer. Our average estimate of per capita feeding in *P. elegans* was 0.12 prey ind.$^{-1}$ day^{-1}, corresponding to 0.66 prey ind.$^{-1}$ m^{-3} consumed per day by the *P. elegans* population (based on the abundance data in Table 1). Their predation impact on *Calanus* is therefore low given the high *Calanus* abundances (Table 1, see also Daase et al. 2014). *Calanus* are assumed to be in a dormant, non-feeding state during winter (Falk-Petersen et al. 2009). Daase et al. (2014) reported on *Calanus* from the same cruise in 2012 and found that the *C. finmarchicus* population in Rijpfjorden comprised mainly copepodite stage CV and some CIVs, which could indicate overwintering. However, these authors also noted that "the bulk of the *C. finmarchicus* and *C. glacialis* population was found close to the surface and not at greater depth where they presumably should overwinter", suggesting they were not in an unalert dormancy phase, at least not in January. If not, these copepods may be more alert to the presence of predators than assumed, allowing them to avoid or escape chaetognaths.

Our FR estimate is similar to that obtained for immature specimens in northern Sweden in autumn–winter (0.2 prey ind.$^{-1}$ day^{-1}) and much lower than reported for spring–summer (0.7–0.9 prey ind.$^{-1}$ day^{-1}, Øresland 1987). These findings suggest that feeding rates for *P. elegans* at high-latitude drop during winter, corresponding well with the reduced growth rates observed during winter (Grigor et al. 2014), and the lack of reproduction at this time of year (this study). In less seasonal environments, energetic requirements may vary less between the seasons, accounting for relatively higher feeding rates at lower latitudes, also during winter and early spring (e.g. up to 1.33 prey ind.$^{-1}$ day^{-1} in Vineyard Sound, Feigenbaum 1982).

However, care should be taken when comparing estimates of feeding rates between studies, because each study detects prey with various levels of precision. For example, we did not search for mandible remains in guts to detect further signs of recent copepod digestion, as in other studies (e.g. Falkenhaug 1991; Giesecke and Gonzalez 2004). Feeding estimates in chaetognaths are also highly sensitive to sampling methodology. As well as the risk of damage to their fragile bodies, stressed chaetognaths may also regurgitate gut contents, leading to underestimates of true feeding rates. Baier and Purcell (1997) estimated prey loss from guts of ~50 % when tows were longer than 2 min. Such short hauls can be unfeasible, especially when using large trawl nets such as the MIK, and when sampling populations in deeper waters. Further studies should therefore utilise new zooplankton imaging devices for observing chaetognaths in the water column without necessarily capturing them in nets. Optical methods are promising avenues (e.g. Schulz et al. 2010, Sainmont et al. 2014).

Energetics

Stable isotope and FATM analyses confirmed the position of *P. elegans* as a predator during the polar night. From its average trophic level (TL) of 2.9, it can be classified as a carnivore according to a trophic model devised for the European Arctic (Søreide et al. 2006, in which carnivores had TLs between 2.9 and 3.3). $\delta^{15}N$ (an indicator of protein content) and $\delta^{13}C$ (an indicator of organic matter content) values varied little with station or depth, and agree well with values from the Barents Sea in March (Søreide et al. 2006). $\delta^{15}N$ values were, however, lower than reported from the Bering Sea (14.7 ± 0.7 ‰, Lovvorn et al. 2005), suggesting that *P. elegans* in the sub-Arctic Pacific typically feed higher up the food chain (also see "Lipid profile" section of "Discussion"). Many factors affect the elemental composition of zooplankton species, including age, size maturity status, reproductive strategies, as well as variations in the composition and growth rates of primary producers (Ikeda 1974), yet for *P. elegans* in the Barents Sea, $\delta^{15}N$ values seem to vary little throughout the year. Søreide et al. (2006) reported $\delta^{15}N$ values ranging from 11.9 ± 0.2 ‰ in spring to 12.2 ± 0.1 ‰ in winter. $\delta^{13}C$ values varied slightly more between spring (-19.3 ± 0.8 ‰) and winter (-20.8 ± 0.3 ‰).

Lipid profile

The high levels of the FATMs 20:1(n-9) and 22:1(n-11) confirm that *P. elegans* is part of the Arctic *Calanus*-based food web (Falk-Petersen et al. 2007; Wold et al. 2011). Furthermore, the high level of 22:6(n-3) indicates that the base of the food chain is dominated by dinoflagellates, which can be very abundant in waters north of Svalbard in spring–summer (Hegseth and Sundfjord 2008). This lipid signature agrees well with previous results from the European sub-Arctic (Falk-Petersen et al. 1987). Both the presence of green detritus in *P. elegans* guts, and the surprisingly high levels of the dinoflagellate fatty acid marker docosahexaenoic acid, may suggest that some omnivory and/or detritivory occurs. Non-carnivorous feeding in chaetognaths has been suggested by Casanova et al. (2012). In the Canadian Arctic, *Eukrohnia hamata* and *Pseudosagitta maxima* have been observed ingesting green detritus under the microscope (pers. obs.). *Eukrohnia* species in Antarctica were found to contain higher amounts of 16:0, reflecting feeding on the Antarctic copepods including *Rhincalanus gigas* (Kruse et al. 2010). We suggest that winter feeding is captured in these results, following the suggestions of Graeve et al. (2005) that a new signal (source of food) will be visible relatively quickly (~4–8 days after feeding). If *P. elegans* starves during autumn and early winter, and if 22:6(n-3) undergoes little transformation or metabolism (Dalsgaard et al. 2003), it remains possible that this signal is retained from feeding on *Calanus* during a previous summer or autumn bloom (Falk-Petersen et al. 1990; Wold et al. 2011). However, this study and others (e.g. Feigenbaum 1982; Øresland 1987; Falkenhaug 1991) suggest a low likelihood of long-term fasting in *P. elegans*.

An important difference between the two main chaetognath species in Arctic waters, *Eukrohnia hamata* and *P. elegans*, is that the former typically possess oil vacuoles in the centre of their bodies, whilst the latter do not (Øresland 1990; Pond 2012, pers. obs.). Previous studies that considered the presence of oil vacuoles in this species to reflect recent feeding may therefore have overestimated feeding rates (e.g. Samemoto 1978; Froneman and Pakhomov 1998). The role of these vacuoles in *E. hamata* (e.g. buoyancy, storage) is not yet clear (Pond 2012), but unlike *P. elegans*, *E. hamata* has a cosmopolitan range. In the Arctic, both species commonly occur at epipelagic depths (Bieri 1959), but in the North Pacific, *E. hamata* populations are commonly found residing deeper, and throughout a wider depth range than *P. elegans* (e.g. Bieri 1959; Alvarino 1964). Maintaining such wide vertical distributions would certainly require a strong control of buoyancy, which could be offered by having centrally positioned oil vacuoles (Pond 2012). Lipid reserves form a central component of the life history of polar zooplankton species (Falk-Petersen et al. 2009; Varpe et al. 2009). In Antarctica, 34 % of examined *Eukrohnia bathyantarctica* individuals were found to contain oil droplets in summer compared to 57 % of individuals in winter. This species also contained relatively high amounts of the fatty acid 18:1(n-9), which is found in storage lipids (Kruse et al. 2010). If the primary role of oil vacuoles is storage, this could suggest that survival and possibly reproduction in *E.*

hamata is less dependent on concurrent food intake than in *P. elegans*. Studies of the extent of capital breeding (Varpe et al. 2009) in *E. hamata* are therefore needed.

Reproduction

Small *P. elegans* <10 mm were absent from MPS samples from January, and whilst many individuals above 20 mm had synthesised high sperm loads, many of the largest *P. elegans* specimens in the nets (40–51 mm) still lacked well-developed seminal receptacles, suggesting that they were not fully mature (Russell 1932; Choe et al. 2003). Grigor et al. (2014) frequently observed pronounced receptacles in individuals ≥20 mm from February to May, after which they disappeared. In the Arctic, breeding of *P. elegans* generally takes place in spring and summer (Kramp 1939; Ussing 1939; Bogorov 1940; Grigor et al. 2014); this is in contrast to *Eukrohnia hamata*, which may also reproduce in winter (pers. obs.). Saito and Kiørboe (2001) showed that *P. elegans* <5 mm in the North Sea fed almost exclusively on prey <350 µm in length. In Svalbard, the prey in this size range is represented by small cyclopoids such as *O. similis*, as well as *Calanus* nauplii and the young *Calanus* stages. In winter, individuals may be waiting for increased food input before they reproduce or for suitable food for the young and newborns to feed on (in terms of size and availability). By investing energy into maturation during winter, egg hatching can be scheduled to coincide with the reproduction of a wide range of copepod prey in spring and summer, and the buoyancy of chaetognath eggs may also allow them to hatch in shallow waters (Hagen 1999 and references therein) amongst their grazing prey. In another fjord on Svalbard, large numbers of *P. elegans* eggs became visible in the water column in March 2003, suggesting that conditions for reproduction begin to improve at this time of year (Hirche and Kosobokova 2011).

Concluding remarks

Knowledge of an organism's activity level and foraging ecology outside of the windows of the main primary production period (spring–summer) is key to establishing an understanding of the full annual routine (Varpe 2012). Here, we have focused on the polar night feeding ecology of a predatory zooplankter, adding to recent work on the life history and vertical distribution (Grigor et al. 2014). We found the chaetognath *P. elegans* to feed during the polar night, but with feeding rates lower in winter than have been reported from other seasons. As growth rates (e.g. Dunbar 1962; Grigor et al. 2014) may also decrease at this time and reproduction does not seem to occur, individuals should have lower-energy requirements and require less food. Although several copepod taxa may rest at depth in an unalert state during the Arctic winter, our study shows that mortality on copepods caused by *P. elegans* in the water column is low at this time of year. This study did, however, not sample the zone immediately above the seafloor, the hyperbenthic zone, where high densities of chaetognaths are known to aggregate during winter (Choe and Deibel 2000), and where abundances of resting copepods may also peak. The activities of *P. elegans* in this zone, as well as those of the other Arctic species *Eukrohnia hamata* and *Pseudosagitta maxima*, require more attention.

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