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MASTER THESIS

Mesozooplankton Community Dynamics in a High Arctic Fjord

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Abstract

I studied the larger (> 10^3 µm) fraction of mesozooplankton in an Arctic coastal water community in Billefjorden, Svalbard (78°40' N) from August 2008 to May 2009 in order to describe the life histories of dominant taxa in different trophic levels. Sampling and enumeration was performed under the ArcWin project by the University Centre of Svalbard. Herbivorous *Calanus* spp. (*C. finmarchicus*, *C. glacialis*, and *C. hyperboreus*) numerically dominated the zooplankton community. *Aglantha digitale*, *Mertensia ovum*, *Beroe cucumis,* and *Parasagitta elegens* represented dominant carnivores. The copepod *Metridia longa* dominated the omnivorous community. Zooplankton of all trophic levels clearly indicated annual routines, which were related to seasonal variations of food availability. The phytoplankton food supply for herbivores showed extremely temporal variability. As a result, seasonal habitat shifts and overwintering were prominent in this group. However, herbivores spawned in the early spring, largely in the absence of their primary food source. Food availability to carnivores and omnivores was more or less stable in time, and these groups remained active year-round. However, the vertical distribution of prey varied across seasons. As a result *A. digitale*, *M. ovum*, and *B. cucumis* seasonally followed their prey across different habitats. *P. elegans* continued to occupy deep parts of the fjord, which likely sustained its year-round feeding requirements. Spawning of carnivores and omnivores occurred between spring and autumn, possibly with the peak abundance of their prey. This study suggest that in seasonal environments, annual routines of prey can be traced also in their predators.

Keywords: Arctic zooplankton · seasonality · annual routines · life history · food availability

1. Introduction

Unlike their tropical counterparts, high Arctic marine zooplankton are challenged by pronounced seasonal dynamics of abiotic and biotic environments. These include seasonal oscillations of temperature, solar radiation, sea ice, food availability, and predation pressure (Grainger, 1959; Clarke, 1983; Węsławski et al., 1988; Clarke & Peck, 1991; Conover & Siferd, 1993; Hagen, 1999; Kaartvedt, 2000; Hagen & Auel, 2001; Walsh, 2008; Varpe & Fiksen, 2010; Mackas et al., 2012; Varpe, 2012). Above all, the extreme seasonality in food availability has been documented as the most challenging demand (Clarke, 1983; Clarke & Peck, 1991; Conover & Huntley, 1991; Conover & Siferd, 1993; Hagen, 1999).

Life histories of organisms encompass strategic adaptations to face the challenging demands of their environment (Stearns, 1977, 1992). Among high latitude zooplankton, a variety of such adaptations have evolved to counteract the highly seasonal supply of food. Some of these include maintenance of energy stores (reviewed in, Hagen & Auel, 2001; Lee et al., 2006; Falk-Petersen et al., 2008b), diapause (*e.g.* Carlisle, 1961; Head & Harris, 1985; Hirche, 1996), arrested growth, development, and metabolism (reviewed in, Clarke, 1983; Clarke & Peck, 1991), seasonal vertical migrations (*e.g.* Conover, 1988; Falk-Petersen et al., 2008a), long life span (McLaren, 1966), production of resting eggs (reviewed in, Marcus, 1996), and tissue shrinkage (*e.g.* Hamner & Jenssen, 1974; Ikeda & Dixon, 1982; Falkenhaug, 1996). As environmental conditions (*e.g.* food availability) oscillate in a predictable manner within an annual cycle, the above strategic decisions are employed in a regularly scheduled manner over the year. This schedule has been termed as annual routines (McNamara & Houston, 1996, 2008). However, concurrent employment of most annual routines are often constrained with intrinsic trade-offs (McNamara & Houston, 1996, 2008; Fabian & Flatt, 2012; Varpe, 2012).

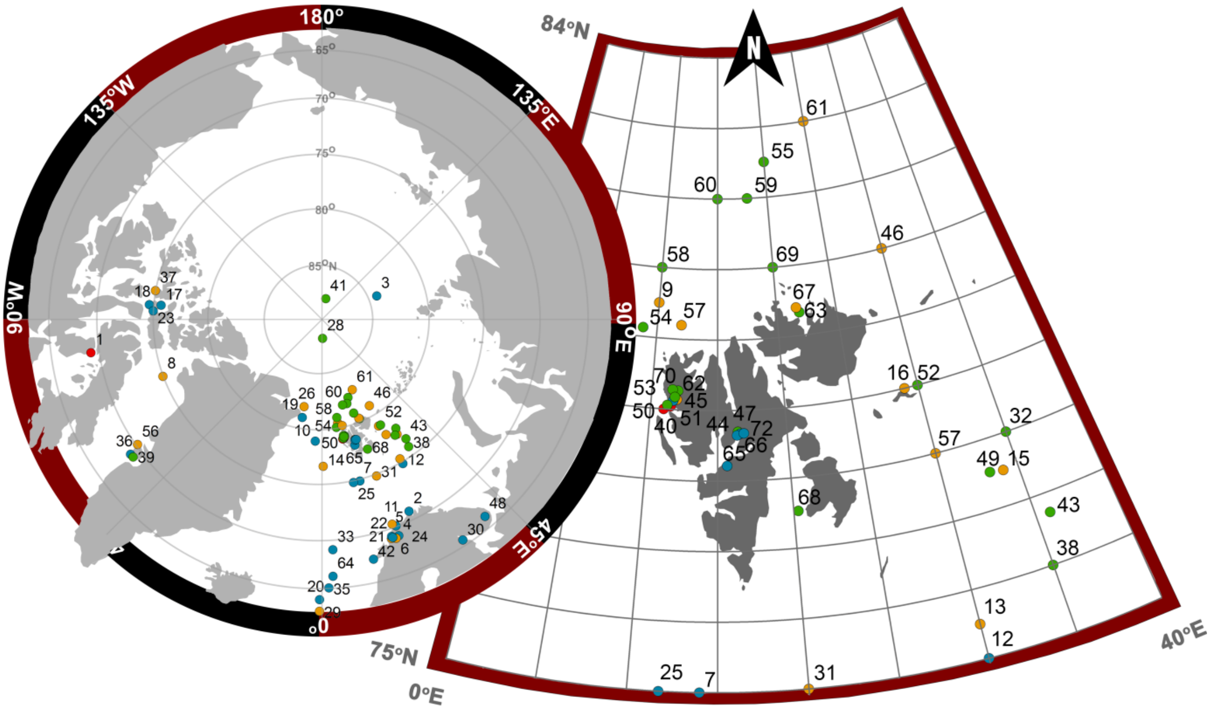

Fig.1: Some mesozooplankton life history investigations reported from high latitudes. Svalbard region is enhanced in the right figure (see coordinates for spatial reference). Literature may be biased towards the focus and location of the present study. Study locations are rough indications. ●: short-term studies on selected species, ●: long-term studies on selected species, ●: short-term community studies, ●: long-term community studies.

Fig.1 references:

[1] Grainger (1959), **[2]** Lie (1965), **[3]** Dawson (1978), **[4]** Tande and Hopkins (1981), **[5]** Tande and Grønvik (1983), **[6]** Båmstedt et al. (1985), **[7]** Tande et al. (1985), **[8]** Samemoto (1987), **[9]** Hirche and Bohrer (1987), **[10]** Smith (1990), **[11]** Diel and Tande (1991), **[12]** Tande (1991), **[13]** Unstad and Tande (1991), **[14]** Hirche (1991), **[15]** Falkenhaug (1991), **[16]** Swarnberg and Båmstedt (1991), **[17]** Sifred and Connover (1992), **[18]** Connover and Sifred (1993), **[19]** Hirche et al. (1994), **[20]** Hays (1995), **[21]** Kaartvedt (1996), **[22]** Falkenhaug (1996), **[23]** Welch (1996), **[24]** Falkenhaug et al. (1997), **[25]** Hirche (1997), **[26]** Hirche and Kwasniewski (1997), **[27]** Melle and Skjoldal (1998), **[28]** Mumm et al. (1998), **[29]** Richardson et al. (1999), **[30]** Kosobokova (1999), **[31]** Dale et al. (1999), **[32]** Falk-Petersen et al. (1999), **[33]** Kaartvedt (2000), **[34]** Scott et al. (2000), **[35]** Hirche et al. (2001), **[36]** Madsen et al. (2001), **[37]** Fortier et al. (2001), **[38]** Arashkevich et al. (2002), **[39]** Nierhoff et al. (2002), **[40]** Hop et al. (2002), **[41]** Auel and Hagen (2002), **[42]** Astthorsson and Gislason (2003), **[43]** Søreide et al. 2003, **[44]** Walkusz et al. (2003), **[45]** Kwasniewski (2003), **[46]** Hirche and Kosobokova (2003), **[47]** Arnkværn et al. (2005), **[48]** Pertzoa et al. (2006), **[49]** Blachowiak-Samolyk et al. (2006), **[50]** Hop et al. (2006), **[51]** Ludenberg et al. (2006), **[52]** Willis et al. (2006), **[53]** Cottier et al. (2006), **[54]** Blachowiak-Samolyk et al. (2007), **[55]** Daase (2007), **[56]** Madsen et al. (2008), **[57]** Daase et al. (2008), **[58]** Blachowiak-Samolyk et al. (2008), **[59]** Daase and Eiane (2008), **[60]** Falk-Petersen et al. (2008)a, **[61]** Søreide et al. (2008), **[62]** Walkusz et al. (2009), **[63]** Berge et al. (2009), **[64]** Varpe and Fiksen (2010), **[65]** Nygård et al. (2010), **[66]** Bailey (2010), **[67]** Søreide et al. (2010), **[68]** Hirche and Kosobokova (2011), **[69]** Rabindranath et al. (2011), **[70]** Berge et al. (2012), **[71]** Båtnes (2013), **[72]** Grigor et al. (2014).

Seasonality in food availability (*i.e.* primary production) likely has a profound effect on herbivore community (Clarke, 1988; Conover & Huntley, 1991). In contrast, food is more or less available year round for carnivores and omnivores (Clarke, 1988; Hagen, 1999). Therefore, it can be argued if annual routines should be more pronounced among Arctic herbivores compared to carnivores and omnivores. However, as many carnivores rely on herbivores as their main food source, the implications of herbivore annual routines on carnivores cannot also be ruled out.

As high latitude marine ecosystems are sensitive to interannual and long-term climate dynamics (Hays et al., 2005; Walsh, 2008; Wassmann, 2011; Wassmann et al., 2011), the predictability of annual environmental cycles is becoming less clear (Ji et al., 2010). This not only influences the timing of annual routines (Both et al., 2009), but can imprint different effects on different trophic levels (Stenseth & Mysterud, 2002; Edwards & Richardson, 2004; Both et al., 2009).

Describing zooplankton annual routines, associated trade-offs, and their trophic-wide implications require studying zooplankton communities and related environmental dynamics over the course of an annual cycle (Visser & Both, 2005; McNamara & Houston, 2008). However, such trophic-wide, long-term life history investigations are rare in the high Arctic (Fig. 1). Instead, most long-term (*e.g.* annual) studies have focused on life histories of one or a few selected zooplankton species (Fig. 1). In addition, zooplankton studies on the level of the community have mostly been restricted to short time intervals (*e.g.* summer, autumn) (Fig. 1) and seldom possess a life history focus.

In the summer 2008, a field data collection campaign was launched under the ArcWin project (The Arctic sea in Wintertime: ecosystem structuring due to environmental variability during the polar night), to investigate the mesozooplankton community in Billefjorden, Svalbard. Small (> 180 μm) and large (> 1000 μm) mesozooplankton were sampled separately using different sampling gears (WP2, and WP3 nets) throughout a period of approximately one year. Although analyses on *Calanus* spp. (Bailey, 2010) and *Parasagitta elegans* (Grigor et al., 2014) have been published, community-wide mesozooplankton dynamics from neither of these datasets have yet been interpreted.

This study is based on the dataset regarding the larger mesozooplankton species. Here I report the life histories of dominant zooplankton taxa in different trophic levels. I describe the seasonal and spatial (*i.e.* depth) dynamics of abundance and body size of these taxa as annual routines. Hypothesizing the seasonality of food supply as the main determinant of seasonal life history decisions, I relate the annual routines of different trophic levels to seasonal dynamics of food availability.

2. Materials and Methods

2.1 Study site

Sampling was conducted in Billefjorden (78°40'N, 16°40'E: Fig. 2A), which is a tributary fjord of Isfjorden (Baeten, 2007), located in the west coast of Spitsbergen. It is ~30 km long and 5–8 km wide (Baeten, 2007; Nilsen et al., 2008; Bailey, 2010) and spans over an area of ca. 182 km^2. Billefjorden possesses two basins which collectively encompass a volume of ca. 13 km^3 (Nilsen et al. 2008). The outer basin has a maximum depth ~230 m (Arnkværn et al. 2005, Bailey 2010) and opens to the Isfjorden. Its opening is partly chocked by the presence of a ca. 70 m deep sill (Nilsen et al., 2008; Bailey 2010) (Fig. 2B). Apart from this outer sill, the inner basin (max. depth ca. 190 m) is separated from the outer basin by another sill, which has a depth of ca. 50 m (Nilsen et al., 2008; Bailey 2010) (Fig. 2B).

The freshwater supply to Billefjorden is seasonal, and governed mainly by precipitation, river runoff, glacial, and sea ice melting. However, precipitation is limited to an annual average (1981–2010) around 191 mm (Førland et al., 2012). During the winter and spring (ca. 6 months) the inner parts of the fjord remains ice covered (Arnkværn et al., 2005).

In the summer, surface waters of Billefjorden become stratified, with a pronounced thermocline and a halocline extending down to sill depth (Walkusz et al., 2003; Daase, 2007; Bailey, 2010). However, a cold and dense water mass dominates below sill depth throughout the year. The stratification breaks down in the winter, and the water column remains homogenous until the end of spring.

Billefjorden, like many other fjords of the western Spitsbergen shelf (WSS) has the likelihood of being influenced by Atlantic Water (AW). The WSS is a convergence site for the Atlantic, Arctic, and glacial water masses (Saloranta and Svendsen 2001; Cottier et al., 2005; Nilsen et al., 2008), where AW follows its slope year-round (Cottier et al., 2005;

Nilsen et al., 2008). AW can flood Isfjorden upon relaxation of necessary geostrophic forces between the shelf and fjord (Cottier et al., 2005; Nilsen et al., 2008; Cottier et al., 2010). However, the sills of Billefjorden act as a topographical barrier against the receipt of AW through Isfjorden (Nilsen et al., 2008, Bailey 2010). Even under extreme influxes of AW into WSS (*e.g.* in 2002), Billefjorden remained free of AW signatures (Cottier et al. 2005, Nilsen et al. 2008). As a result, Ankværn et al. (2005) argued that zooplankton population dynamics of Billefjorden would be more influenced by internal processes than advection.

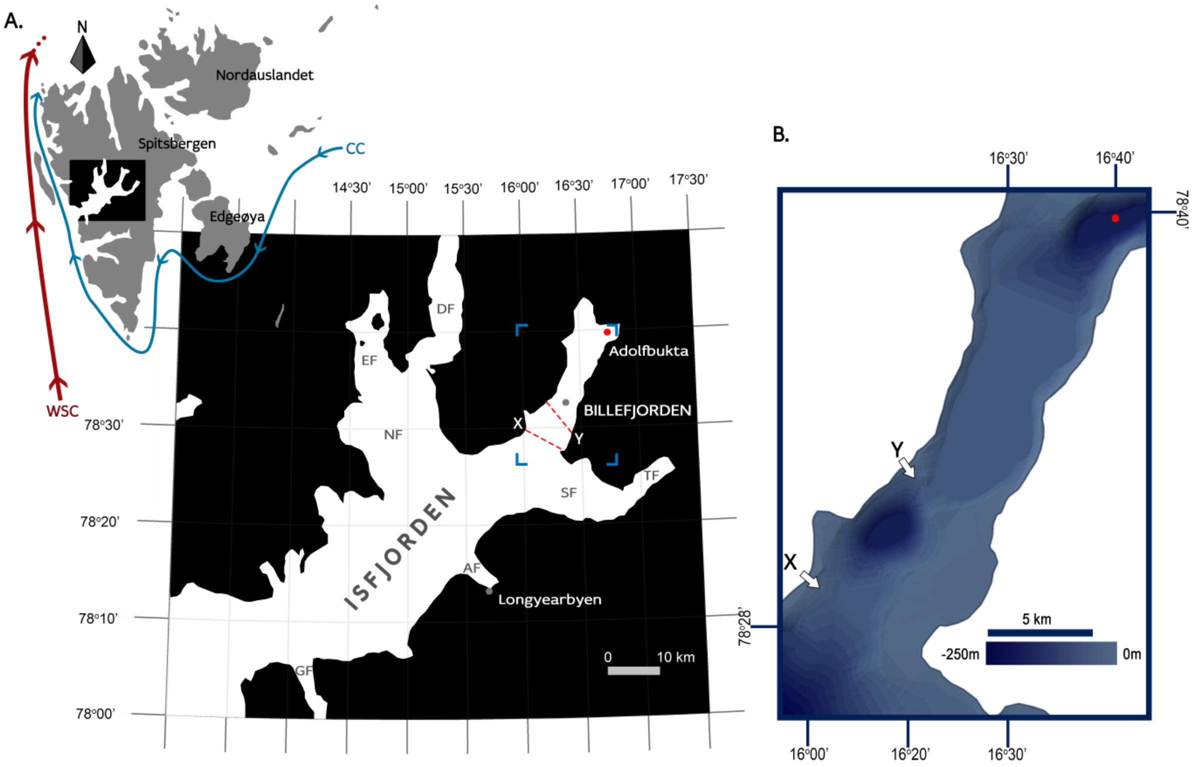

Fig. 2: Map of the study area (A) showing the location of Isfjorden system within the WSS (top left) and location of Billefjorden within Isfjorden system (bottom left). 'X' & 'Y' refer to outer and inner sills of Billefjorden respectively. A low resolution DTM (B) shows the bottom topography of Billefjorden, with 'X' & 'Y' referring to same as above (use the crosshairs, and coordinates for reference). Sampling site within Adolfbukta is represented by a red dot. **WSC**-West Spitsbergen Current, **CC**-Coastal Current, **TF**-Templefjorden, **SF**-Sassefjorden, **AF**-Adventfjorden, **EF**-Ekmanfjorden, **DF**-Dicksofjorden. Bathymetric data courtesy of MAREANO project (http://mareano.no). Positions of WSC and CC adopted from Svendsen et al. (2002).

2.2 Sampling

Sampling was carried out by the University Center of Svalbard (UNIS). It was conducted in a 189 m deep station (78º 39.72' N, 16º 44.34' E) within the inner basin (Adolfbukta) of Billefjorden (Fig. 2B). Zooplankton samples were collected from August 27th 2008 to May 4th 2009. Hydrographical samples were collected from September 22nd 2008 to July 15th 2009. Sampling was carried out monthly on board the R/V Viking Explorer (during ice free periods), or from the ice (Appendix 1, Table 1).

2.2.1 Hydrographical sampling

In-situ measurements of temperature (°C), salinity (PSU), and fluorescence ($\mu g.l^{-1}$) were profiled using a Seabird CTD (Sea-Bird Electronics, Inc.) fitted with a Turner design fluorometer. In addition, I relied on photosynthetic active radiation (PAR) measurements obtained by a QSP2300 Quantum PAR sensor (Biospherical Instruments Inc.) deployed alongside (affixed as an auxiliary sensor) a Seabird 16plus SeaCAT recorder (Sea-Bird Electronics, Inc.). This equipment setup was a part of an instrument series mounted to a mooring deployed in Adolfbukta at a depth of 29 m, covering the aforementioned time series.

Raw voltage outputs (V_i) generated by the QSP2300 quantum PAR sensor were calibrated (converted) to Irradiance (I: $\mu mol.m^{-2}.s^{-1}$) using equation 1 (Biospherical Instruments Inc.). A wet calibration factor (C) of 5.05×10^{12} and a dark voltage (V_d) of 0.0130 V were used in the calibration.

$$I = C(10^{Vi} - 10^{Vd}) \tag{1}$$

2.2.2 Zooplankton sampling

Zooplankton were sampled by a WP3 net (diameter = 1.13 m, mesh size = 1 mm) fitted with a Nansen type messenger-operated closing device, by vertical hauls (ca.1 ms^{-1}) either from the vessel or, when sampling from the ice, with the use of a tetrapod mounted cable and a snowmobile. Three depth strata were sampled (0–50 m, 50–100 m, 100–180 m).

However, due to a failure in the release mechanism of the net, two samples (N0404D and F2606N: Appendix 1, Table 1) were obtained without depth stratification. In addition, day and night replicate samples were taken in six instances between September and December 2008.

The large zooplankton were identified and their body lengths (mm) were measured on-site immediately after collection. The rest of the samples were preserved in a borax-buffered 4% formaldehyde-in-seawater solution before later enumeration in the lab.

2.3 Enumeration, identification, and morphometric estimations

All laboratory procedures described below were conducted by J. Wallenschus of the University Centre of Svalbard (UNIS).

Copepods and other small sized zooplankton (< 10 mm) were counted in random fractions of known volume until a minimum of 100 individuals were counted per sample. Large zooplankton were always counted from the entire sample.

Zooplankton taxa were identified using morphological or morphometric characters, and were classified to their respective genus or species levels. *Calanus* spp. and *Metridia longa* were separated to their respective copepodid stages.

Length measurements of counted specimen were made using a stereomicroscope (Leica microsystems). Prosome length (PL), and bell height (BH) were measured for copepods and hydromedusae respectively. Total length/body length (TL/BL) was measured for other taxa.

2.4 Data processing, analysis, and interpretation

2.4.1 Hydrographical data

The Spatial Analyst extension of ArcGIS v. 9.3 (ESRI inc.) was used to analyze and represent hydrographical data. Temperature, salinity, and fluorescence profiles were interpolated in time and space (*i.e.* over the depth range) using natural neighbor interpolation technique. Sea ice charts produced by the operational sea ice service of the Norwegian Metrological Institute (http://polarview.met.no) were used to describe the sea ice dynamics of Billefjorden during this investigation.

2.4.2 Zooplankton data

2.4.2.1 Detailed classification of zooplankton taxa

Classification of all zooplankton taxa were adopted from the World Register of Marine Species (http://www.marinespecies.org/), and arranged in a phylogenical order following Maddison & Maddison (2014). I further classified the zooplankton taxa based on their feeding modes published in relevant literature. Potential predators and prey of the dominant zooplankton taxa were also adopted from published literature.

2.4.2.2 Taxonomic composition of Calanus *spp.*

Copepodid stages IV, V, and adults of *C. hyperboreus* were identified using morphological characterization (*i.e.* presence of an acute spine on the fifth thoracic segment: *e.g.* Parent et al. (2011)), and separated from the rest of the *Calanus* spp. Since younger copepodids (CI–CIII) of *C. hyperboreus* were not captured in this investigation, this method could isolate it from other *Calanus* species.

I used a length frequency analysis based on the R™ (R Core Team 2013) package 'mixdist' v.0.5-4 (Macdonald & Du, 2012) to resolve the taxonomic composition of *Calanus* spp. This program is designed to fit finite mixture distribution models to size frequency data through maximum likelihood method, following a combination of Newton-type and Expectation-maximization (EM) algorithms, based on user-defined model parameters (*i.e.* means, and standard deviations) (Macdonald & Du, 2012). The goodness of fit of the models are ultimately assessed using Chi-squared test statistics.

PL's of 5741 individuals of *Calanus* spp. were available for the length frequency analyses (Table 1). However, I discarded the PL data of CIII and CIV stages, since they were captured in low numbers, and their full size spectrum was less likely to be represented by the WP3 net due to the size selectivity of its coarse mesh width (UNESCO, 1986).

Table 1: Number of individuals *(n)* within each copepodid stage of *Calanus* spp. yielding morphometric data for length frequency analysis.

Copepodid stage	CV	Females	Males
n	3908	1409	387

PL's of each copepodid stage (CV, adult females, and males) were plotted as histograms with 0.1 mm PL bins (Fig. 7A1–C1). These histograms were trimodal for CV's and adult females, with component distributions (C_i) extending from: C_1: < 2.5 mm, C_2: 2.5 - 3.1 mm, and C_3: < 3.1 mm (Fig. 7A1 & B1). A bimodal PL histogram was evident for adult males, with C_1: 2.5 - 3.1 mm, and C_2: < 3.1 mm (Fig. 7C1). Parameters (mean and the SD) of each of these component distributions were used in the subsequent PL analyses. This analysis was based on the assumptions that each component distribution was normally distributed, and the temporal variation of PL within each copepodid stage was negligible.

The fitted component distributions were separated at their respective points of intersects (henceforth known as PL boundaries) based on the assumption that the candidate distributions would lose and gain equal numbers (Arnkværn et al., 2005). These PL boundaries were ultimately evaluated against those published in relevant literature to distinguish species.

2.4.2.3 Population composition of Parasagitta elegans

The size structure of *P. elegans* was also resolved based on TL data of 3346 individuals using a similar technique as described above. Since the variability of TL during the study period was pronounced, I performed the length frequency analysis on monthly aggregates of data. TL frequency distributions of each month (Fig. 8A) illustrated the presence of three overlapped distributions (Appendix 1, Table 2). Fitting of component distributions and the ultimate separation were done using the same methods described above.

2.4.2.4 Estimators of abundance

Zooplankton abundance was estimated assuming 100% filtration efficiency of the WP3 net. The abundance (ind.m^{-3}) of a given taxon in a given sample (*i*) was estimated from:

$$A_i = n_i F_i / \pi r^2 D_i \qquad (2)$$

Here, A_i is abundance of sample '*i*', n is the number of individuals counted in the sample, F is the fraction of the sample counted, r is the radius of the net opening, and D_i is vertical distance that the net was towed. The total abundance of a given taxon was estimated from summing the entities of A_i for the period of interest.

Due to unequal sampling effort between sampling dates, the mean total abundance was used in most instances of data presentation. This was estimated by averaging the total abundance of a given sampling date by the number of samples (*i.e.* number of entire water column sweeps) collected on that date.

2.4.2.5 Estimators of vertical distribution

The vertical distribution of zooplankton was represented by the weighted mean depth (Z_m) and the standard deviation of the mean depth (Z_s), according to Sørnes et al. (2007) and Daase et al. (2008), following the modification from Manly (1977).

$$Z_m = \frac{1}{2}\sum_{j=1}^{n} f_j d_j z_j / O \qquad (3)$$

$$Z_s = \sqrt{\frac{1}{2}\sum_{j=1}^{n} f_j d_j z_j^2 / O - Z_m^2} \tag{4}$$

$$O = \frac{1}{2}\sum_{j=1}^{n} d_j f_j \tag{5}$$

Here, n is number of depth strata, d_j is the lower sample - upper sample depth (m) of the sample interval 'j', f_j is abundance of taxon under study (ind.m^{-3}) at depth interval 'j', and O is the surface integrated abundance. The Z_m and Z_s for a given taxa at a given time was graphically illustrated as points with dispersion bars generated using the R^{TM} (R Core Team 2013) package 'Hmisc' v. 3.13–0 (Harrell et al., 2013).

2.4.2.6 Estimator of overlapping vertical distributions

The extent of overlap between the vertical distributions of two given taxa (*i.e.* potential predators, *vs*. prey) was represented by the vertical overlap (V) adopted from Williamson et al. (1989) and Williamson & Stoeckel (1990).

$$V = \sum_{z=1}^{m} (N1_z N2_z) m \Big/ \sum_{z=1}^{m} (N1_z) \sum_{z=1}^{m} (N2_z) \tag{6}$$

Here, $N1$ and $N2$ are abundances (ind.m^{-3}) of any two taxa in depth interval 'z', and m is the no. of depth intervals sampled. Given the three depth strata, V ranged between 0 (non overlapping distributions) and 3 (identical distributions), with V of 1 indicating uniform distribution of either one of the two depth distributions concerned.

The vertical overlap of potential predators and prey in the time series was represented using a linear series of pixels (with monthly resolution) generated by the R^{TM} (R Core Team 2013) package 'raster' v. 2.2–31 (Hijmans, 2014). In the series, each pixel was assigned a colour based on the value of 'V', with the minimum and maximum intensity of the colour range representing the theoretical upper and lower limit of 'V' (0 and 3).

2.4.2.7 Statistical relationships between potential food and dominant zooplankton

Relationships between seasonal vertical distributions of zooplankton taxa and those of their potential food were described using linear statistical models developed in R^{TM} software (R Core Team 2013). Monthly mean chlorophyll concentrations (*i.e.* chlorophyll-*a* fluorescence) were used to describe the monthly mean depths of dominant herbivores. Furthermore, monthly mean depths of potential prey species were used to describe those of their predators.

2.4.2.7 Zooplankton annual routines

In order to describe zooplankton annual routines I featured the annual cycle as four seasons: summer (June-July), autumn (August-October), winter (November-February), and the spring (March-May). Timing of the thermo-haline stratification, fluorescence, and PAR maxima (see results) were used to distinguish above seasons. In addition, the water column was described as two potential habitats: the surface habitat (< 100 m), and the deep habitat (> 100 m). These habitats were demarcated considering the thermo-haline stratification depths, maximum sill depth, and the vertical distribution of summer fluorescence levels (see results). I also referred to the published work of the WP2 dataset collected parallel to this investigation to make inferences about younger developmental stages of *Calanus* spp. (Bailey, 2010) and *Parasagitta elegans* (Grigor et al. 2014). Moreover, the annual routine descriptions of dominant zooplankton was based on the assumption that the spatial and temporal patterns of abundance and body size of zooplankton observed in this study were cyclic, and are repeated on an annual basis.

3. Results

3.1 The physical environment

3.1.1 Sea ice

Billefjorden was ice free at the onset of this study (Fig. 3B). Very open drift ice was first observed by early November 2008 (Fig. 3C), and developed into fast ice by January 8th 2009 (Fig. 3D). The first episode of fast ice break up was observed in the outer part of the fjord during early May (Fig. 3E). Land Fast ice prevailed in the inner basin of Billefjorden (including Adolfbukta) until late June (Fig. 3G), and the entire fjord was ice free by mid July 2009 (Fig. 3H).

3.1.2 Temperature, and salinity

Thermal stratification in surface waters (ca. down to 70 m) was observed from late September to the end of December (Fig. 4A). Thereafter the stratification broke down, and more or less homogenous temperatures (< -1.0 ^{o}C) were recorded throughout the water column until late May. During June and July, the surface waters were stratified again, but with stratification depths rarely exceeding 50 m. The most pronounced salinity stratification occurred in the upper 20 m between June and July. During this period, low salinities (< 17 PSU) were recorded in surface waters (Fig. 4B). Waters with higher salinities (> 34 PSU) spanned over a large depth range of the fjord during the rest of this investigation.

Thermo-haline properties of the study area referred to several water mass associations (Fig. 5). However, AW or transformed Atlantic water (TAW) were not detected during this investigation.

3.1.3 Solar radiation, and chlorophyll fluorescence

PAR (at 30 m depth) progressively decreased from the start of this investigation, and reached 0 μmol.m^{-2}.s^{-1} by mid November (Fig. 6A). PAR remained zero until the onset of

March, after which it gradually increased. A peak in PAR level (>20µmol.m^{-2}.s^{-1}) was observed between mid June and July.

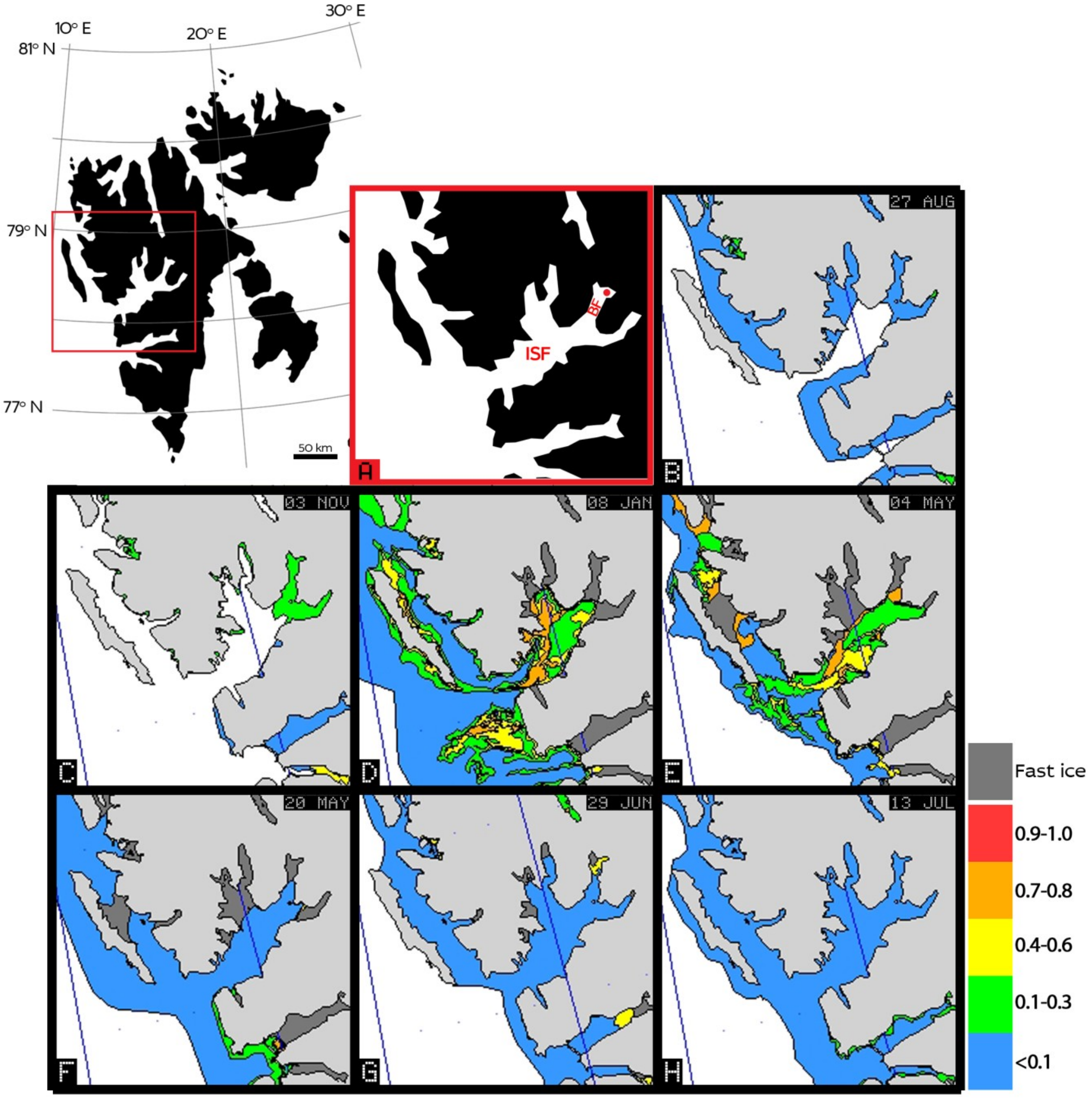

Fig. 3: Sea Ice dynamics of Billefjorden. Ice concentration is indicated by the colour gradient (see legend). **BF**: Billefjorden, **ISF:** Isfjorden. Sampling site is indicated by the red dot. (Sea Ice charts courtesy of Norwegian Meteorological Institute: www.polarview.met.no)

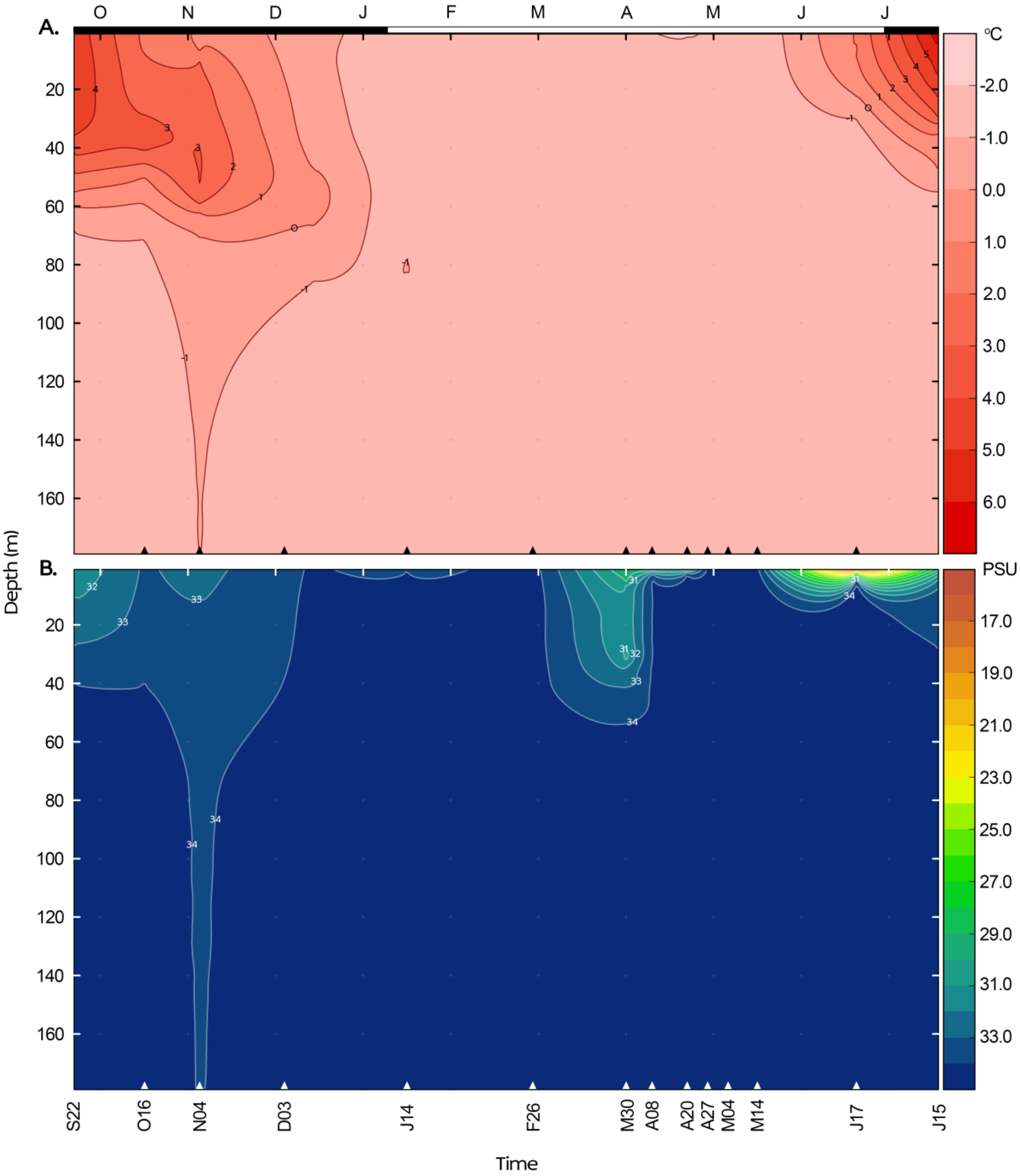

Fig. 4: Dynamics of temperature (A) °C and salinity (B) PSU during the study period. Interpolated data are presented with contour lines 1 °C and 1 PSU resolution. The Overhead white bar indicates the period with fast ice cover.

Moderate levels of fluorescence (up to 72 x 10^4 µg.l^{-1}chl-*a*) were detected in surface waters (< 40 m) during the early part of this investigation (Fig. 6B). The fluorescence gradually decreased thenceforth, and remained lower than 2 x 10^4 µg.l^{-1}chl-*a* from late November until March. Thereafter, fluorescence progressively increased to a maximum > 340 x 10^4 µg.l^{-1}chl-*a*, occupying a depth around 40 m by mid June (Fig. 6B). During the whole investigation, negligible levels of fluorescence prevailed in deep waters (> 120 m).

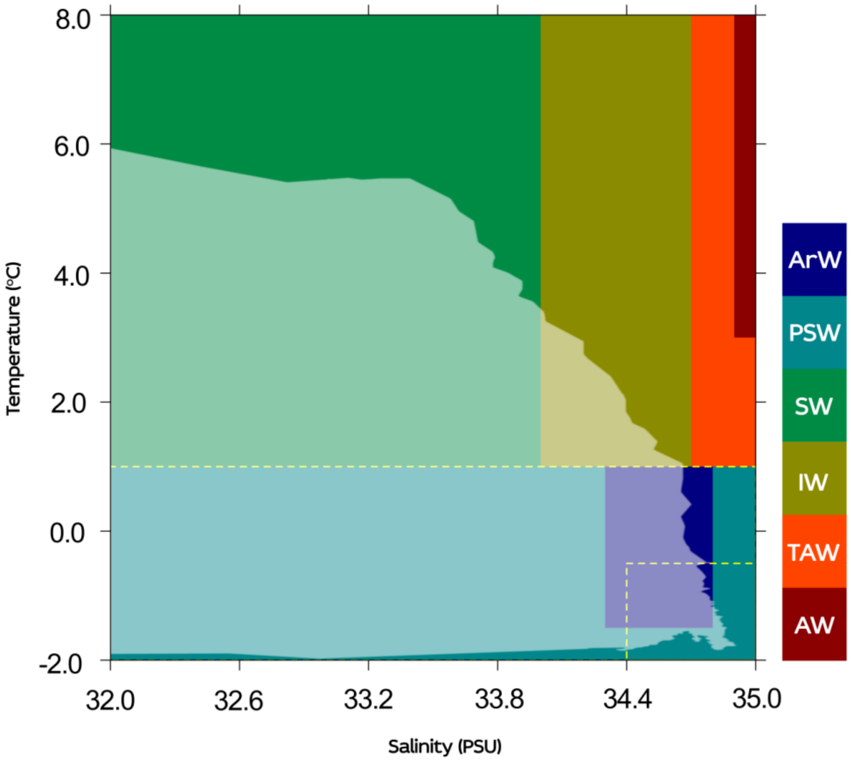

Fig. 5: The range of temperature and salinity measurements observed during this investigation (opaque white area), and their water mass associations (coloured polygons). Note that the abscissa is cropped at 32 PSU. Water mass classifications are adopted from Swift (1986), T.S.Hopkins (1991), Svendsen et al. (2002), and Nilsen et al. (2008). **ArW**: Arctic water, **PSW**: polar surface water, **SW**: surface water, **IW**: intermediate water, **TAW**: transformed Atlantic water, **AW**: Atlantic water, Dashed lines indicate local water: **LW** (above) and winter cooled water: **WCW** (bottom right).

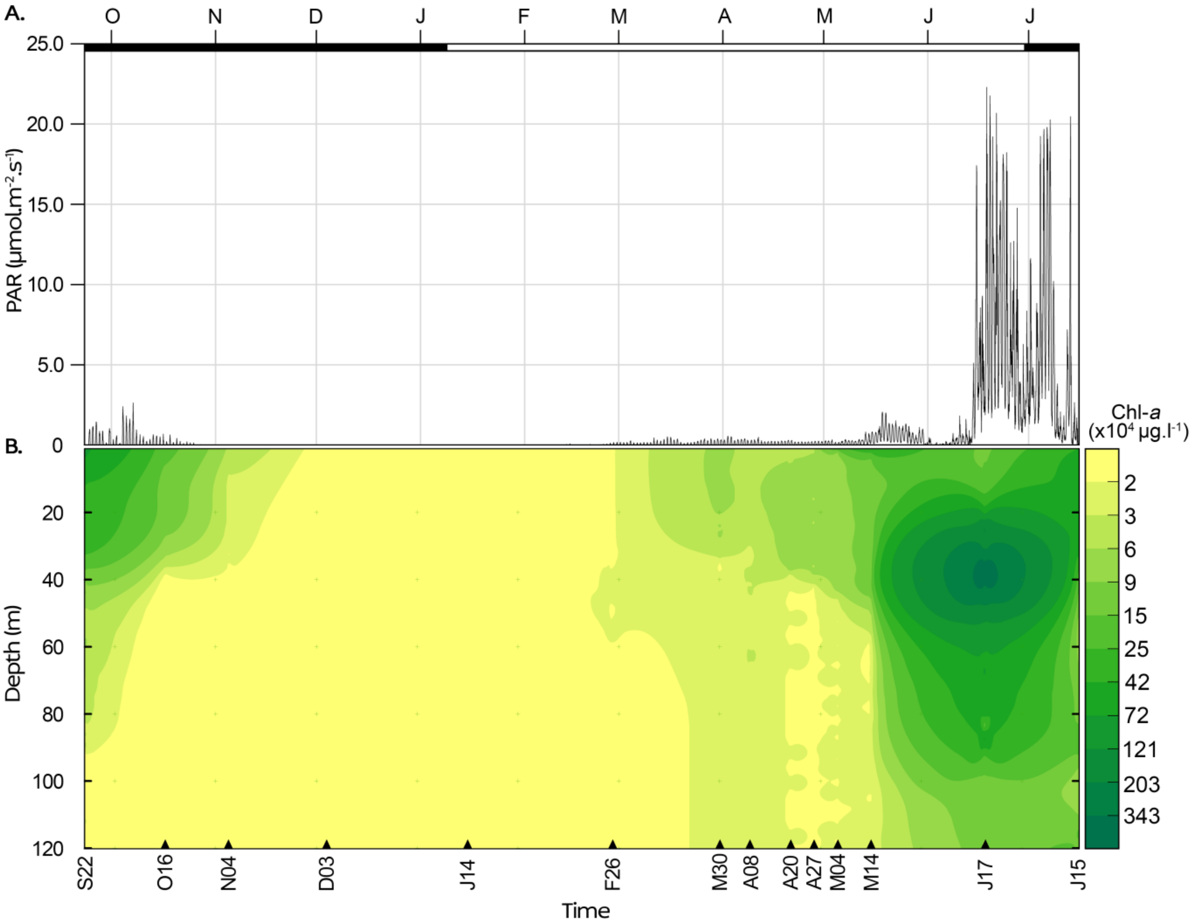

Fig. 6: Dynamics of Photosynthetic Active Radiation (PAR) (A), µmol.m^{-2}.s^{-1} and fluorescence (B), µg.l^{-1}chl-*a* during the study period. The overhead white bar indicates the periods with fast-ice cover. PAR measurements are those estimated from the mooring setup (section 2.2.1), which can be accessed from the Martech^{TM} server of Scottish Marine Institute (http://martech.sams.ac.uk/arctictimeseries).

3.2 Taxonomic composition

37 mesozooplankton taxa were captured during this investigation (Table 2). Pelagic arthropods (22 taxa) dominated the taxonomic composition. These included amphipods, isopods, mysids, euphausiids, decapods and copepods. Ctenophores, hydrozoans, mollusks and chaetognaths were the other major taxa. Eight species of herbivores, 16 species of carnivores, eight species of omnivores, and two species of detritivores represented the trophic diversity of this study (Table 2).

Table 2: Zooplankton taxa captured during this investigation, their respective feeding modes, and abundances

Category	Taxon	Feeding mode [References]	Relative abundance (%)
Hydrozoans	Order: Anthoathecata		
	Suborder: Filifera		
	Bougainvillia spp. Lesson, 1830	Carnivore [60]	0.02
	Halitholus spp. Hartlaub, 1914	Carnivore [60]	0.01
	Suborder: Capitata		
	Sarsia spp. Lesson, 1843	Carnivore [24,39]	<0.01
	Order: Trachymedusae		
	Aglantha digitale (O.F. Müller, 1776)	Carnivore [5,24,39,40,45,47]	0.21
Ctenophores	Class: Tentaculata		
	Mertensia ovum (Fabricius, 1780)	Carnivore [25,46,50]	0.45
	Class: Nuda		
	Beroe cucumis Fabricius, 1780	Carnivore [25,27,37]	0.36
Annelids	*Brada* spp. Stimpson, 1854	Detritivore [55]	<0.01
Mollusks	Class: Gastropoda		
	Order: Gymnosomata		
	Clione limacina (Phipps, 1774)	Carnivore [3,4,26,44]	0.02
	Order: Thecosomata		
	Limacina helicina (Phipps, 1774)	Omnivore [16,23,42,53]	0.03

Table 2 contd.

	Limacina retroversa (Fleming, 1823)	Herbivore [51,60]	<0.01
	Unidentified species - 1	-	0.01
Chaetognaths	Order: Aphragmophora		
	Parasagitta elegans (Verrill, 1873)	Carnivore [6,7,17,19,22,32,33,36,52,28]	1.18
	Order: Phragmophora		
	Eukrohnia hamata (Möbius, 1875)	Carnivore [7, 19,30,31]	0.08
Amphipods	Order Amphipoda		
	Suborder: Gammaridea		
	Anonyx nugax (Phipps, 1774)	Carnivore [14,21]	<0.01
	Suborder: Hyperiidea		
	Themisto abyssorum Boeck, 1870	Carnivore [18,36,38]	<0.01
	Themisto libellula (Lichtenstein in Mandt, 1822)	Carnivore [18,36,38]	0.01
	Unidentified species - 2	-	<0.01
Isopods	Order: Isopoda		
	Suborder: Asellota		
	Munnopsis spp. M. Sars, 1861	Herbivore/Detritivore [59]	<0.01
	Unidentified species - 3	-	<0.01
Mysids	*Mysis* spp. Latreille, 1802	Omnivore [60]	0.03
Euphausiids	Family: Euphausiacea		
	Meganyctiphanes norvegica (M. Sars, 1857)	Omnivore [2,9]	<0.01

Table 2 contd.

	Thysanoessa inermis (Krøyer, 1846)	Herbivore [2,8,11]	0.11
	Thysanoessa longicaudata (Krøyer, 1846)	Omnivore [60]	<0.01
	Thysanoessa raschii (M. Sars, 1864)	Omnivore [9,12]	<0.01
Decapods	Infraorder: Caridea		
	Superfamily: Alpheoidea		
	Eualus gaimardii (H. Milne Edwards, 1837)	Carnivore [49]	<0.01
	Superfamily: Pandaloidea		
	Pandalus borealis Krøyer, 1838	Omnivore [15]	<0.01
	Infraorder: Brachyura		
	Superfamily: Portunoidea		
	Necora puber (Linnaeus, 1767)	Carnivore [29,54]	<0.01
	Superfamily: Majoidea		
	Hyas spp. Leach, 1814	Omnivore [60]	<0.01
Copepods	Family: Calanidae		
	Calanus finmarchicus (Gunnerus, 1770)	Herbivore [57,60]‡	16.92
	Calanus glacialis Jaschnov, 1955	Herbivore [57,60]‡	77.56
	Unidentified taxonomic group (G_x)†		0.11
	Calanus hyperboreus Krøyer, 1838	Herbivore [60]‡	2.02
	Family: Clausocalanidae		

Table 2 contd.

	Microcalanus spp. Sars G.O., 1903	Detritivore [13]	<0.01
	Pseudocalanus spp. Boeck, 1872	Herbivore [43,60]	<0.01
	Family: Euchaetidae		
	Paraeuchaeta norvegica (Boeck, 1872)	Carnivore [34,41,53]	<0.01
	Family: Metridinidae		
	Metridia longa (Lubbock, 1854)	Omnivore [1,10,12,20,48]	0.86
Chordates	Subphylum: Tunicata		
	Oikopleura spp. Mertens, 1830	Herbivore/Particle feeder [56]	<0.01
	Subphylum: Vertebrata		
	Leptoclinus spp. Gill, 1861	Carnivore [58]	<0.01
Unclassified	Unidentified species -4	-	<0.01
	Eggs and larvae	-	-

[†] Taxon resolved by the length frequency analysis of *Calanus* spp. (see section 3.2.1)

[‡] See the references in Table 8

[1] Haq (1967), **[2]** Ackman et al. (1970), **[3]** Lalli (1970), **[4]** Conover & Lalli (1972), **[5]** Arai & Fulton (1973), **[6]** Pearre (1973, 1980), **[7]** Sullivan (1980), **[8]** Sargent & Falk-Petersen (1981), **[9]** Falk-Petersen et al. (1982), **[10]** Båmstedt & Ervik (1984), **[11]** C. C. E. Hopkins et al. (1984), **[12]** Båmstedt et al. (1985), **[13]** T. L. Hopkins (1985), **[14]** Sainte-Marie & Lamarche (1985), **[15]** Shumway et al. (1985), **[16]** Gilmer & Harbison (1986), **[17]** Greene (1986), **[18]** Falk-Petersen et al. (1987), **[19]** Samemoto (1987), **[20]** Båmstedt & Tande (1988), **[21]** Sainte-Marie et al. (1989), **[22]** Falkenhaug (1991), **[23]** Gilmer & Harbison (1991), **[24]** Matsakis & Conover (1991), **[25]** Swanberg & Båmstedt (1991), **[26]** Hermans & Satterlie (1992), **[27]** Siferd & Conover (1992), **[28]** Alvarez-Cadena (1993), **[29]** Freire & Gonzalez-Gurriaran (1995), **[30]** Øresland (1995), **[31]** Froneman et al. (1998), **[32]** Brodeur & Terazaki (1999), **[33]** Dale et al. (1999), **[34]** Olsen et al. (2000), **[35]** Fleddum et al. (2001), **[36]** Saito & Kiørboe (2001), **[36]** Auel et al. (2002), **[37]** Falk-Petersen et al. (2002), **[38]** Auel & Werner (2003), **[39]** Colin et al. (2003), **[40]** Mackie et al. (2003), **[41]** Skarra & Kaartvedt (2003), **[42]** Gannefors et al. (2005), **[43]** Lischka & Hagen (2005), **[44]** Böer et al. (2006), **[45]** Ikeda & Imamura (2006), **[46]** Lundberg et al. (2006), **[47]** Pertsova et al. (2006), **[48]** Blachowiak-Samolyk et al. (2007), **[49]** Nygård et al. (2007), **[50]** Graeve et al. (2008), **[51]** Bernard & Froneman (2009), **[52]** Sakshaug et al. (2009), **[53]** Comeau et al. (2010), **[54]** Silva et al. (2010), **[55]** World Register of Marine Species, **[56**] Encyclopedia of Life, **[57]** Centre Of Ecotoxicology And Experimental Biology, **[58]** Fish Base, **[59**] Maddison & Maddison (2014), **[60]** Sirenko et al. (2014).

3.2.1 Taxonomic composition of **Calanus** *spp.*

PL boundaries derived by the length frequency analysis regarding the large size distributions (Fig. 7A2, B2, & C2) matched those published for *C. finmarchicus* and *C. glacialis* in previous investigations (Table 3). However, identity of the smallest size distribution (G_x: Fig. 7A2 & B2) remained unclear. The relative compositions of these *Calanus* taxa are presented in Table 4.

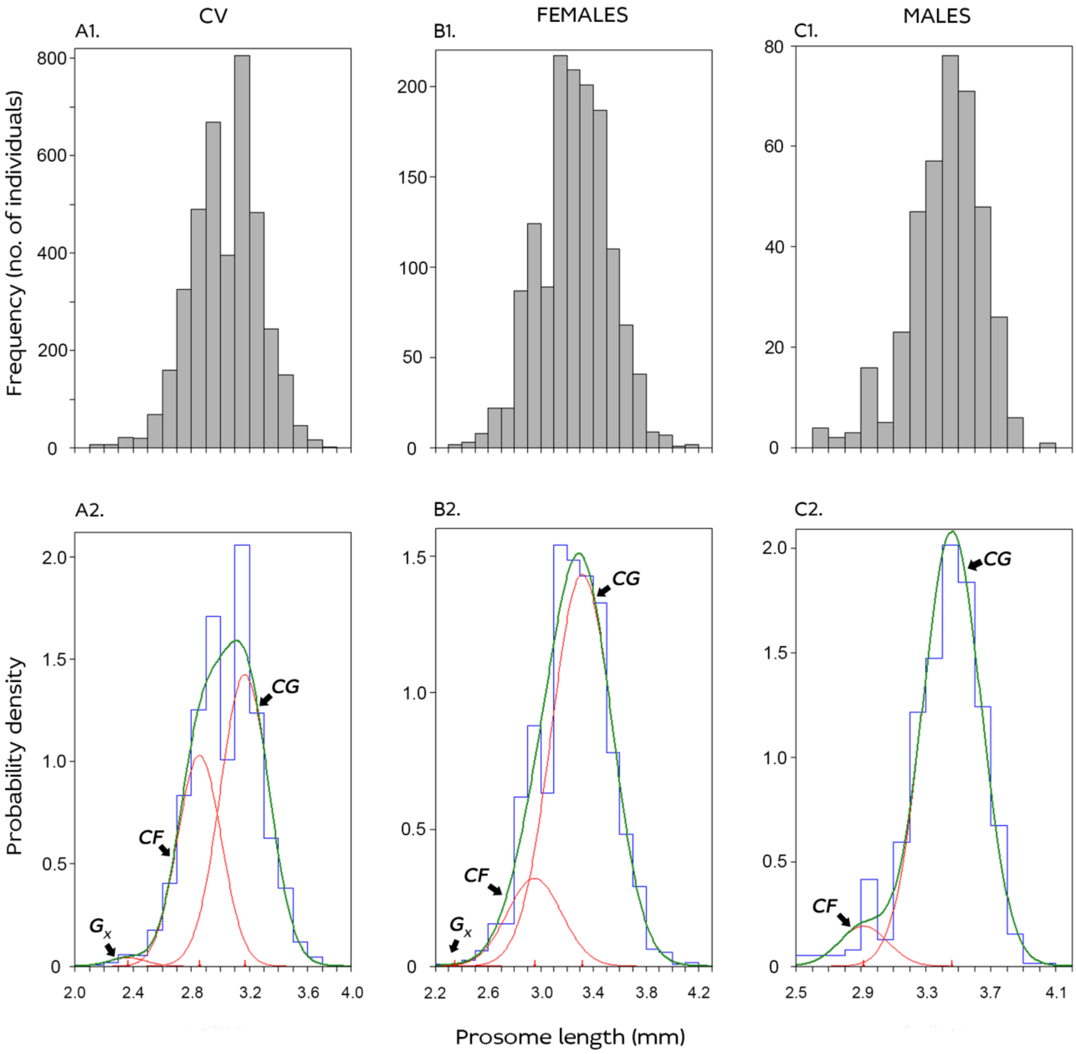

Fig. 7: Multimodal PL distributions of *Calanus* spp. (A1, B1 & C1), and the taxonomic groups identified by fitting normal distributions using the length frequency technique mentioned in section 2.4.2.2 for each developmental stage (A2, B2 & C2) **Gx**: Unidentified taxonomic group, **CF**: *C. finmarchicus*, **CG**: *C. glacialis*

Table 3: Prosome length (mm) boundaries of this study and those published in previous studies for the separation of *C. finmarchicus*, and *C. glacialis* (CV and adult females)

Reference	CV		Adult females		Location	Remarks
	CF	CG	CF	CG		
Jaschnov (1972)	-	-	$2.20 - 3.00^{A}$	$3.60 - 4.50^{B}$	A: Norwegian Sea, B: White Sea	Fore-body length
Hirche (1991)	< 3.10	> 3.10	<3.20	> 3.20	Greenland Sea	MPS (Hydrobios,Kiel) 150 µm mesh
Unstad and Tande (1991)	< 3.00	3.00 - 3.40	< 3.20	3.20 - 4.50	Northern Barents Sea	Pump system strained at 180 µm mesh
Hirche et al. (1994)	1.95 - 3.05	2.95 - 3.90	2.35 - 3.20	3.20 - 4.60	Northern water polynya, Greenland Sea	Bongo net 200 and 300 µm mesh
	< 3.05	3.05 - 3.95	2.85 - 3.00	3.50 - 3.95	Tikhaia Bay, (Franz Josef Land)	Cited in Hirche et al. (1994)
Madsen et al. (2001)	1.75 - 2.70	2.725 - 3.90	< 3.00	> 3.00	Disco bay, Greenland	Pump system strained at 50 µm mesh
Kwasniewski et al. (2003)	< 2.90	≥ 2.90	< 3.20	≥ 3.20	Kongsfjorden, Svalbard	MPS (Hydrobios, Kiel) 180 µm mesh
Daase and Eiane (2007)	< 2.937	> 2.937	< 3.240	> 3.240	North of Svalbard	MPS (Hydrobios, Kiel), and WP2 180 µm mesh
Bailey (2010)	≤ 2.40	2.40 - 4.10	≤ 2.60	≥ 2.61	Billefjorden, Svalbard	WP2 180 µm mesh
Hirche and Kosobokova (2011)	1.70 - 2.85	2.90 - 3.50	2.90 - 3.15	3.20 - 4.60	Storfjorden and Northern Barents Sea	MPS (Hydrobios, Kiel) 55 µm mesh CF: 1.85 - 2.90 (males) CG: 2.95 - 3.60 (males)
Present study	2.45 - 2.98	≥ 2.98	2.38 - 2.92	≥ 2.92	Billefjorden	WP3 (1000 µm mesh) CF: 1.85 - 2.90 (males) CG: 2.95 - 3.60 (males) G_x: ≤ 2.45 (CV) G_x: ≤ 2.38 (females)

CF: *C. finmarchicus*, **CG:** *C. glacialis*, **AF:** Adult females, **AM:** Adult males, **G_x:** 'Group-X', **MPS:** Multiple Plankton Sampler

Calanus glacialis was the dominant *Calanus* species, which comprised more than 80% of the adult male and female populations, and nearly 60% of copepodid stage V. *C. finmarchicus* also comprised a considerable fraction within this group (Table 4). However, the relative composition of unidentified taxonomic group (G_x) remained extremely low, occupying only ~1% of CV and ~0.1% adult female populations, and was not detected among adult males. Therefore, I did not elaborate its population dynamics in detail.

Table 4: PL boundaries (mm) (with % composition of each developmental stage in parentheses) used to separate the three taxonomic groups of *Calanus* spp. Model fitting criteria (Chi-square value, and the degrees of freedom in parentheses) are given in the rightmost column.

Stage	G_x	*C. finmarchicus*	*C. glacialis*	Model fits
CV	≤ 2.45 (1.30%)	2.45–2.98 (38.96%)	≥ 2.98 (59.74%)	187.97^{**} (11)
Adult females	≤ 2.38 (0.12%)	2.38–2.92 (16.64%)	≥ 2.92 (83.24%)	54.47^{**} (13)
Adult males	-	≤ 3.04 (7.20%)	> 3.04 (92.80%)	19.55^{*} (10)

Note: Chi-square value is the test statistic of the goodness of fit of each of the fitted models
$^{*}p < .05$, $^{**}p < .01$

3.2.2 Population composition of **Parasagitta elegans**

The population of *P. elegans* was composed of three different size groups, labeled, G_0, G_1, and G_2 (Fig. 8B). The mean TL (± SD) of the three groups were 14.53 ± 1.70, 23.76 ± 2.67, and 33.96 ± 3.27 mm respectively. Although the three size groups were more or less abundant throughout the study, the mean relative proportion of G_0 (~4%) was significantly smaller than those of G_1 (~46%), and G_2 (~52%) (Appendix 1, Table 2).

3.3 Numerical abundance

3.3.1 Herbivores

Herbivores numerically dominated the zooplankton community, accounting for more than 96.6% of the total abundance (Table 2). *Calanus glacialis* was the most abundant species (relative abundance ~76%). *C. finmarchicus* and *C. hyperboreus* were among the other dominant herbivores, with a collective contribution around 19% to the total abundance.

The euphausiid *Thysanoessa inermis* was the most abundant non-copepod herbivore (relative abundance ~0.1%).

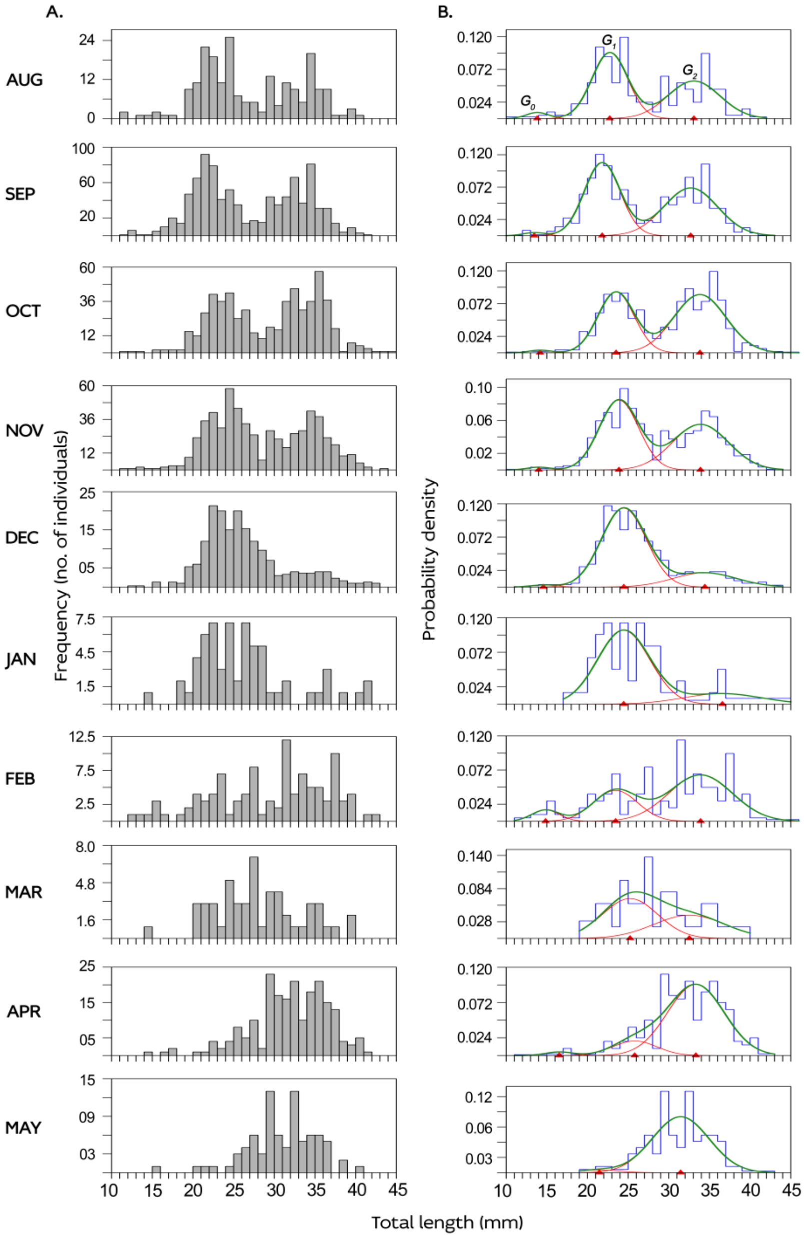

Fig. 8: Monthly total length distributions of *Parasagitta elegans* (A), and the three size groups (G_0, G_1, and G_2) identified by fitting normal distributions using the length frequency technique mentioned in section 2.4.2.3 (B). Note that some extreme TL values were considered as outliers during model fitting.

3.3.2 Carnivores

Carnivores collectively comprised ~2.4% of the total zooplankton abundance (Table 2). Chaetognaths *Parasagitta elegans* (relative abundance of all size groups: ~1.2%) and *Eukrohnia hamata* (~0.1%), ctenophores *Mertensia ovum* (~0.5%) and *Beroe cucumis* (~0.4%) along with the hydromedusae *Aglantha digitale* (~0.2%) were the numerically dominant carnivorous taxa. Other carnivorous zooplankton had relatively little contribution to the numerical abundance (Table 2).

3.3.3 Omnivores, and detritivores

Omnivorous zooplankton only accounted for ~1% of the total zooplankton abundance (Table 2). The copepod *Metridia longa* (relative abundance: ~0.9%) was the most dominant omnivorous species. Compared to other functional groups, abundance of detritivores were relatively insignificant, and did not exceed 0.01% of total zooplankton abundance (Table 2).

3.4 Population dynamics of dominant taxa

3.4.1 Herbivores

The mean total abundance of *C. finmarchicus* increased from 30 ind.m^{-3} at the onset of this investigation to a peak at ca. 80 ind.m^{-3} by November. Its abundance decreased thence, never to exceed 8 ind.m^{-3} from late February onwards (Fig. 9A1). From late August to mid January, > 98% of the recorded *C. finmarchicus* population was composed of stage V copepodids (Fig. 9A2). Thereafter, this figure dropped sharply to 40% by late February, and remained below 65% for the rest of the time series. The proportion of adult females steadily increased in the population from early November (4%), and reached a maximum on February 26th (57%) (Fig. 9A2). Adult males were first observed in the samples collected in early December. Since then they on average comprised ~3% of the *C. finmarchicus* population for the rest of the time series (Fig. 9A2).

C. glacialis peaked in abundance (mean total abundance: 524 ind.m^{-3}) on September 7th (Fig. 9A2). Thereafter, its total abundance was low (< 310 ind.m^{-3}), and reached a minimum of ~6 ind.m^{-3} at the end of this investigation. Until early November, more than 97% of the *C. glacialis* population was composed of stage V copepodids (Fig. 9B2). However, their relative proportions decreased thenceforth to < 20% for the rest of the investigation. Adult females only comprised a low proportion (~2% on average) of this population up to early December (Fig. 9B2). Afterwards, their proportions increased up to > 80% at the end of this study. After their first capture on September 7th, the relative proportions of adult males increased, and peaked (~25%) in December (Fig. 9B2), but declined thereafter and barely exceeded 1% after the end of March.

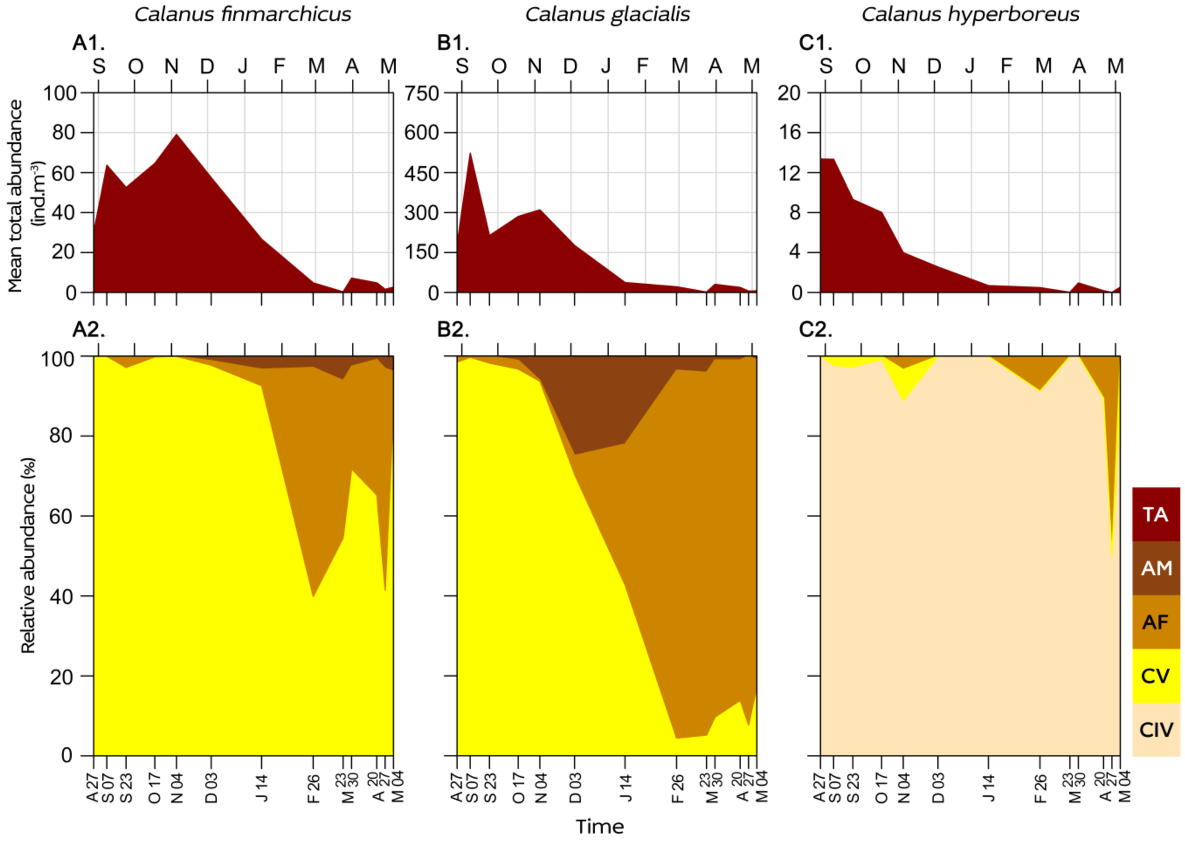

Fig. 9: Temporal dynamics of mean total abundance (A1, B1 & C1), and population composition (A2, B2, & C2) of *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus*. **TA**: mean total abundance, **AM**: adult males, **AF**: adult females

The mean total abundance of *C. hyperboreus* was highest (~13.3 ind.m^{-3}) at the onset of this investigation, and decreased steadily thenceforth (Fig. 9C1). Throughout this study, the largest fraction (92.5% on average) of the *C. hyperboreus* population was composed of stage IV copepodids (Fig. 9C2). Stage V copepodids comprised ~3% of the population from early September to December, and ~11% on early May (Fig. 9C2). After October, adult females were also observed discontinuously in the time series. Adult males were not encountered in this study.

3.4.2 Carnivores

Aglantha digitale expressed a single distinct peak in abundance (mean total abundance: 4.2 ind.m^{-3}) on October 17th (Fig. 10A1). It was found only in low densities thenceforth (0.08 ind.m^{-3} on average). Relatively smaller individuals (5–8 mm BH) dominated the mid October population peak (Fig. 10B1). The mean size (BH) of this species increased steadily thereafter, and reached a plateau from February onwards.

Mertensia ovum was captured in growing numbers from the start of this investigation, until it reached its peak abundance (mean total abundance: 4.1 ind.m^{-3}) in October (Fig. 10A2). Thereafter, its mean total abundance dropped, and remained < 1 ind.m^{-3} for the remainder of the study. Although there was a nett increase of body length of *M. ovum* during the time series, both small (< 15 mm), and large (> 50 mm) individuals were found throughout this investigation (Fig. 10B2). However, the minimum mean body length ± SD (6.41 ± 5.65 mm) was recorded in October (at its population peak).

Two distinct abundance peaks were noted in *Beroe cucumis*: the first between September and October (mean total abundance ~2.1 ind.m^{-3}), and the second in May (~2.5 ind.m^{-3}) (Fig. 10A3). Its abundance between these two periods did not exceed 0.5 ind.m^{-3}. Relatively larger individuals (ca. up to 70 mm) of *B. cucumis* were predominantly captured during the early part of this study (Fig. 10B3). After November, its mean body length progressively decreased, and individuals lesser than 2 mm predominated the May population peak.

The mean total abundance of *Parasagitta elegans* showed three distinct peaks (Fig. 10A4). The most prominent peak occurred in September (~ 5.5 ind.m^{-3}), the second peak in December (4.4 ind.m^{-3}), and was followed by a less prominent third peak in April-May (~1.3 ind.m^{-3}). Between August and November, *P. elegans* population was composed of more or less equal proportions of G_1 and G_2 size groups (Fig. 10B4). Thenceforward, the population composition of G_1 increased steadily, and peaked between December and January (comprised ~80% of total abundance). By this time, the relative abundance of G_2 remained at its lowest. From January onwards, the population proportion of G_1 decreased, and reached a minimum (~4%) by the end of this study. In the meantime, G_2 increased in numbers and proportions (occupied ~96% of total abundance by May), and predominantly comprised the third peak (Fig. 10A4 & B4). Moreover, numbers, and proportions of G_0 remained low throughout this study.

The mean total abundance of *Eukrohnia hamata* increased from the start of this investigation to November, and remained constant at 0.5 ind.m^{-3} till the onset of December (data not presented). Only a few individuals (0.02 ind.m^{-3} on average) of *E. hamata* were captured after December.

3.4.3 Omnivores

The mean total abundance of *Metridia longa* decreased from the onset of this investigation (2.7 ind.m^{-3}) to early November (0.5 ind.m^{-3}) (Fig. 11A1). Afterwards, its abundance increased, and remained constant at 4.7 ind.m^{-3} between December and mid January. Despite *M. longa* was captured in decreasing numbers thenceforward, its abundance reached a peak (7.3 ind.m^{-3}) on April 20th. During most part of this study the population of-

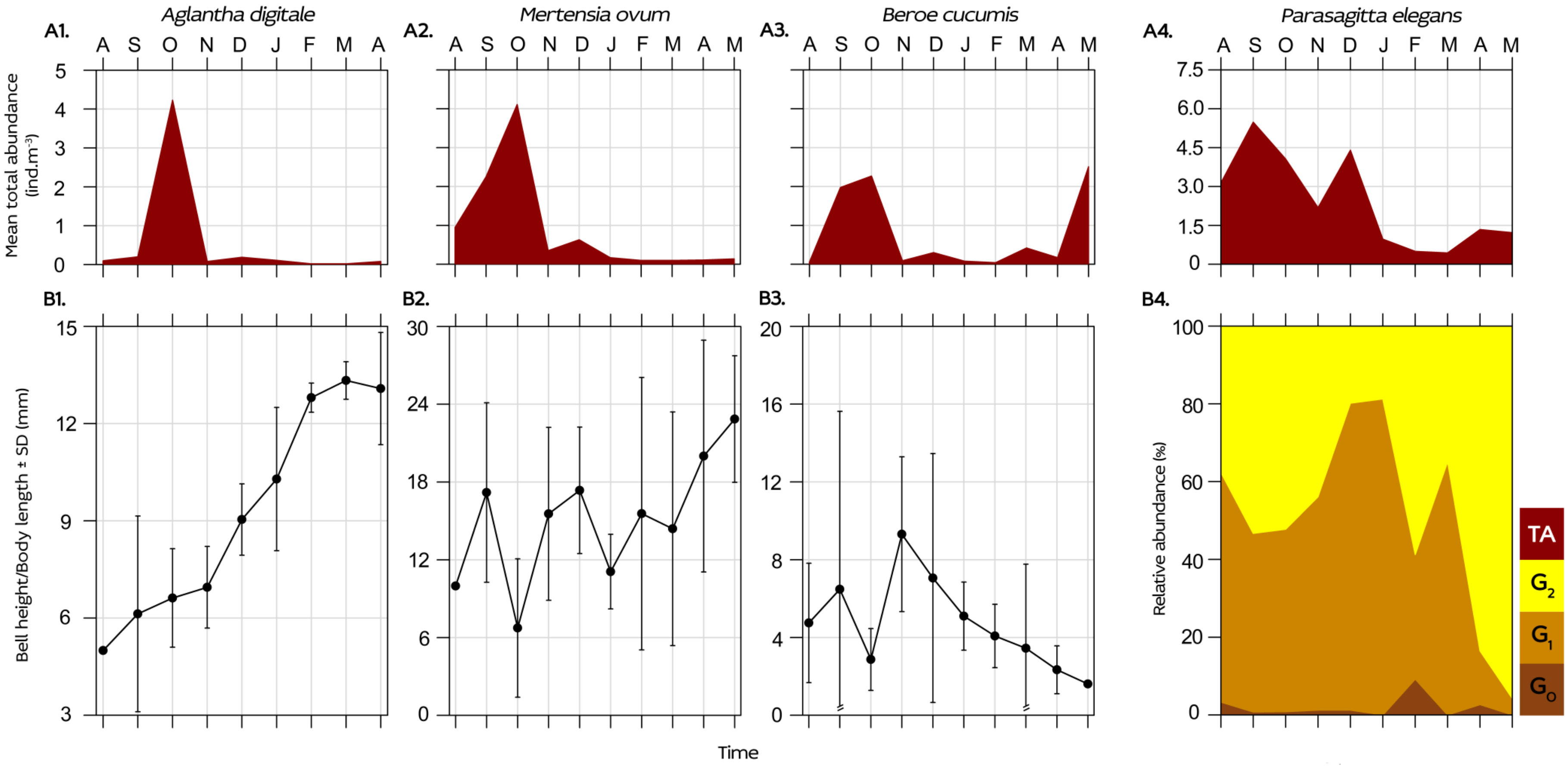

Fig. 10: Temporal dynamics of mean total abundance (A1–A4), and population compositions of some dominant carnivorous species (B1–B4). Population compositions of *A. digitale* is represented as mean bell heights (BH), and those of *M. ovum*, and *B. cucumis* are expressed as mean body lengths (BL). Population dynamics of *P. elegans* are presented as relative abundances (%) of its size groups. Dispersion bars represent standard deviations (SD). **TA**: mean total abundance

-*M. longa* was dominated by adult females (occupied ~87% of the total abundance on average) (Fig. 11A2).The copepodid stage V comprised > 50% of the population between mid October and early November. Although adult males were more or less abundant throughout this investigation, their contribution to the total abundance did not exceed 15% at any given time.

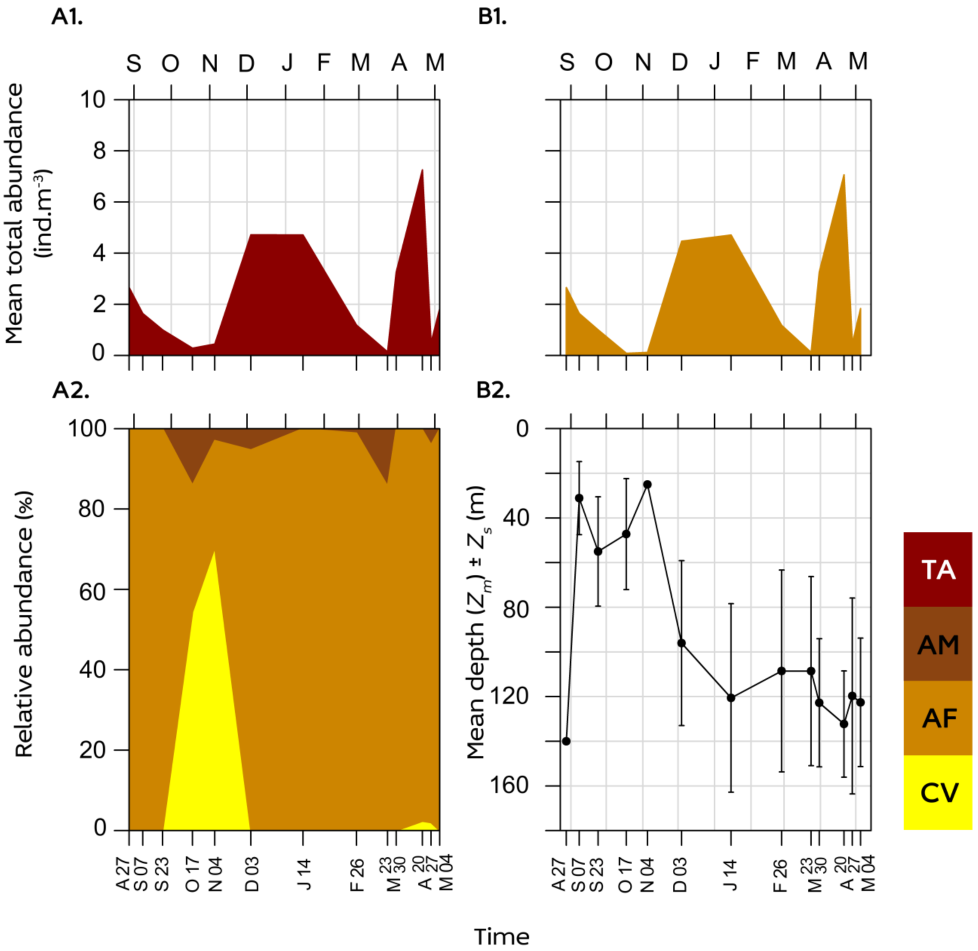

Fig. 11: Temporal dynamics of total abundance (A1 & B1), the population composition (A2), and the seasonal vertical behaviour (B2) of *Metridia longa*. Vertical distribution data corresponds only to adult females. Depth distribution is presented as the mean depth (Z_m), with the Z_s, which is denoted by the dispersion bars.**TA**: mean total abundance, **AM**: adult males, **AF**: adult females.

3.5 Seasonal vertical behaviour of dominant taxa

3.5.1 Herbivores

The mean depth ($Z_m \pm Z_s$) of *C. finmarchicus* CV's increased from the onset of this investigation, and remained constant ~137 m with little variation (Z_s not exceeding 16 m) between mid October and November (Fig. 12B2). Thereafter, these stage V copepodids were found more or less dispersed throughout the water column, with an increasing mean depth up to mid January. Adult females of *C. finmarchicus* were captured at progressively shallower depths from late September onwards (Fig. 12B3). Since then, their mean depth remained ca. < 80 m for the rest of the time series. At the time of their peak abundance (*i.e.* December-January: Fig. 12A4), the mean depth of adult males remained shallower (Z_m < 75 m: Fig. 12B4). Thereafter, an extremely few number of males (< 0.2 ind.m^{-3}: Fig.12A4) were found at varying depths.

C. glacialis CV's were captured deeper (Z_m ~137 m) in the water column with little variation (Z_s not exceeding 20 m) up to early November (Fig. 12C2). The mean depth of these CV's became relatively shallower thereafter, with their population remained spread throughout the water column. Adult females of *C. glacialis* were found in the deeper parts of the water column (Z_m > 133 m and Z_s < 20 m) until mid October (Fig. 12C3). Their mean depth became progressively shallower thereafter, and remained above 80 m during most part this investigation thence. Adult males were continued to be captured in shallower depths from mid October to the onset of December (Fig. 12C4). Until April, they were distributed throughout the water column, with relatively shallower mean depths (< 80 m). Afterwards, a fewer number of males (0.03 ind.m^{-3} on average: Fig. 12A4) were captured at increasing depths.

The mean depth of stage IV copepodids of *C. hyperboreus* remained below 125 m until late September, and continued to decrease thenceforward. It become shallowest (~37 m)

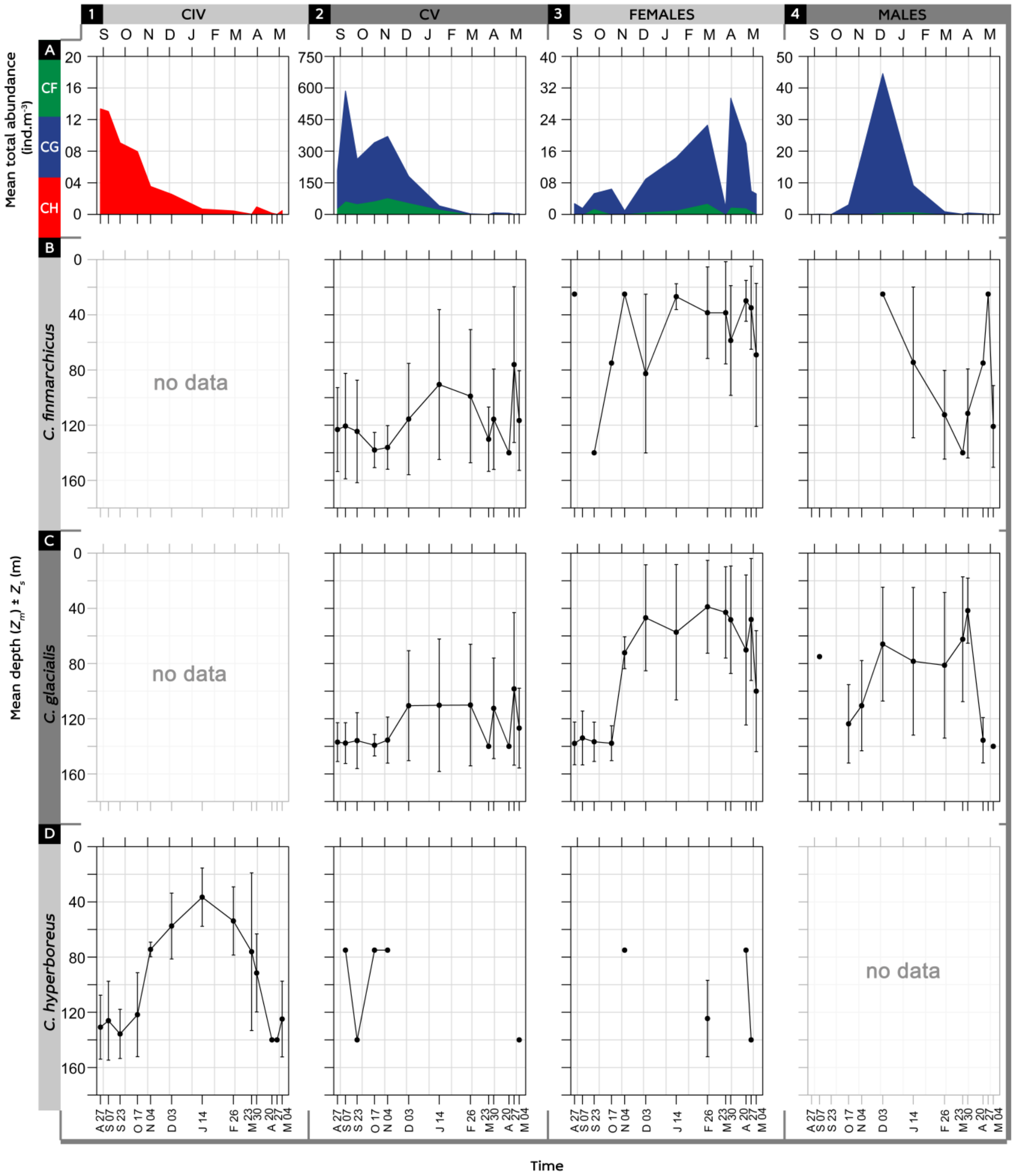

Fig. 12: The seasonal vertical behaviour of different copepodid stages of *Calanus* spp. The top panels (A1-A4) represent mean total abundance. Data are presented as the mean depth (Z_m), with the SD (Z_s) denoted by the dispersion bars. **CF:** *C. finmarchicus,* **CG:** *C. glacialis*, **CH:** *C. hyperboreus*

-on January 14th. (Fig. 12D1). Afterwards, its mean depth progressively increased and remained below 120 m from mid April onwards. CV's and adult females were captured discontinuously and in low numbers (mean total abundance ~1.9 and 0.6 ind.m^{-3} respectively): hence, their seasonal vertical dynamics are not elaborated herein.

3.5.2 Carnivores

The mean depth of *Aglantha digitale* progressively deepened from the start of this investigation to October (Fig. 13A2). The deepest mean depth (~137 m) and the peak population size of this species coincided in October (Fig. 13A1 & A2). Thereafter, a few individuals (mean total abundance < 0.5 ind.m^{-3}) *A. digitale* were found more or less dispersed in the water column, with shallower mean depths (< 100 m) up to February.

The ctenophores *Metensia ovum* and *Beroe cucumis* were captured at progressively increasing depths during the early part of this investigation (Fig. 13B2). *B. cucumis* was found in deep waters with little vertical dispersion (Z_m ~139 m and Z_s < 9 m) from late September to mid October. A similar deep depth distribution was observed for *M. ovum* (Z_m ~139 m and Z_s < 8 m), but only in October. Thereafter, the mean depth of both species became progressively shallower, with marked similarities in its dynamics .

The three size groups of *Parasagitta elegans* showed distinct depth distributions. The smallest size group (G_0) was found at shallowest depths, while the two larger size groups (G_1, and G_2) were found at progressively increasing depth ranges (data not presented). Since the G_0 was present in extremely low abundances, and there was a high degree of overlap between the depth distributions of larger size groups throughout the study, I presented the seasonal vertical dynamics of G_1 and G_2 size groups *P. elegans* collectively (Fig. 13C2). Despite the progressive increase of its mean depth from early September to November, and the reversing trend observed up to mid January, *P. elegans* population remained well dispersed within the intermediate to deep waters (mean depth > 95 m) throughout this investigation.

The mean depth of *Eukrohnia hamata* became shallower from the start of the study (Z_m ± Z_s: 140 ± 0 m) to December (34 ± 25 m) (Fig. 13C2). Thereafter, it was captured in relatively shallow waters ($Z_m < 65$ m).

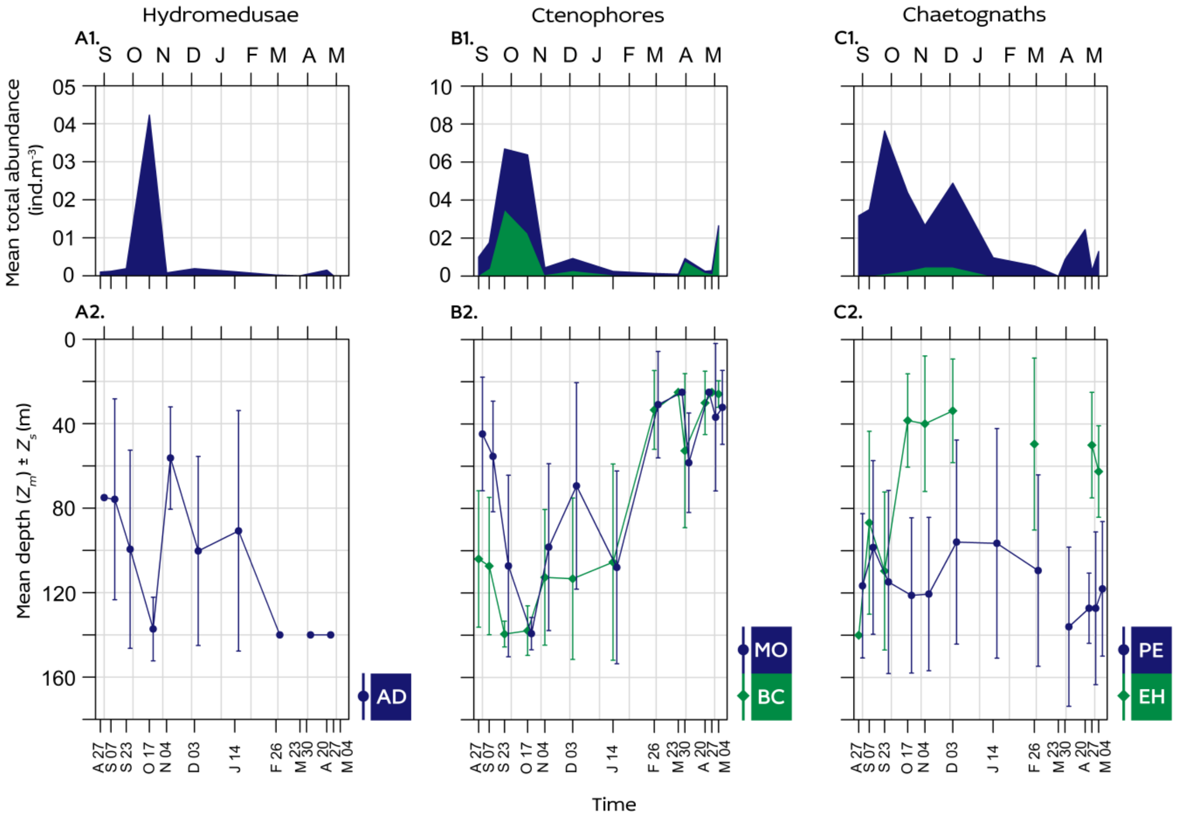

Fig. 13: The seasonal vertical behaviour (A2–C2) of dominant carnivorous species. The top panels (A1–C1) indicate mean total abundance. Data are presented as the mean depth (Z_m), and (Z_s) denoted by the dispersion bars. **AD**: *A. digitale*, **MO**: *M. ovum*, **BC**: *B. cucumis*, **PE**: *Parasagitta elegans*, **EH**: *Eukrohnia hamata*.

3.5.3 Omnivores

The mean depth (Z_m ± Z_s) of adult females of *Metridia longa* became shallower from the start of the study (140 ± 0 m) to the onset of November (25 ± 0 m) (Fig. 11B2). Thereafter, its mean depth progressively deepened (> 108 m), with individuals dispersed over the deep parts of the water column. Vertical dynamics of stage V and adult male copepodids are not elaborated here due to their low and inconsistent abundances.

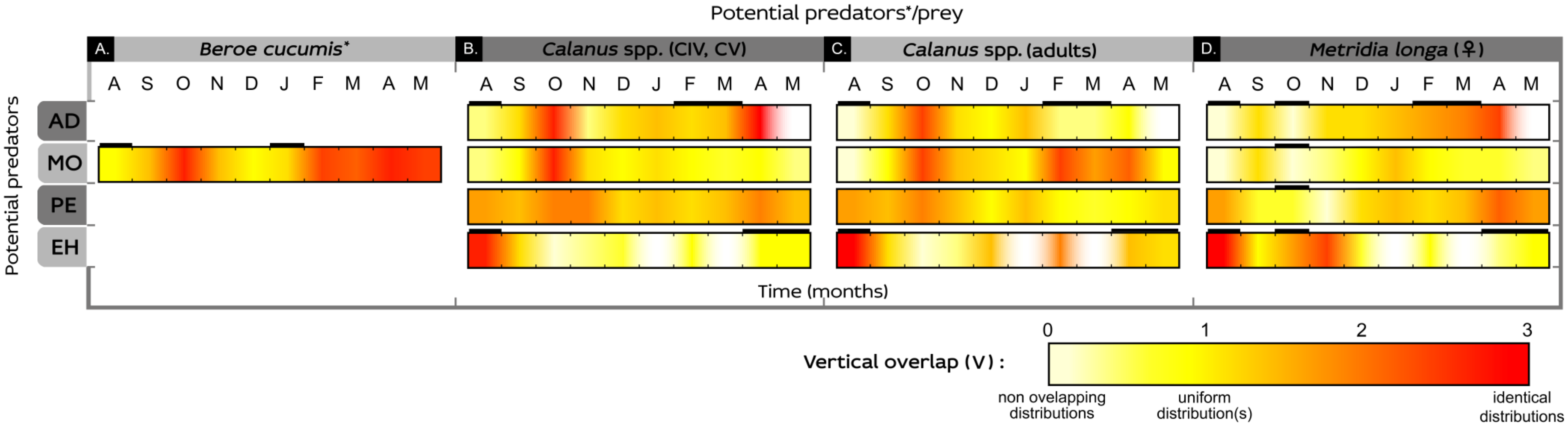

Fig. 14: The overlap of vertical distributions (V) of potential prey and predator species (see legend to the bottom right). Overhead black bars indicate cases with extremely low abundance (< 0.1 ind.m^{-3}) of either prey or predatory species considered. **AD:** *Aglantha digitale*, **MO:** *Mertensia ovum*, **PE:** *Parasagitta elegans*, **EH:** *Eukrohnia hamata*.

3.6 Overlapping vertical distributions of potential prey, and predatory taxa

Throughout the time series, vertical distributions of stage IV and V copepodids of *Calanus* spp. showed a considerable overlap with that of *Parasagitta elegans*, but showed a little overlap with *Eukrohnia hamata* (Fig. 14B). Furthermore, *Aglantha digitale* and *Mertensia ovum* also showed high degree of vertical overlap (V ~3) with the above developmental stages of deep dwelling *Calanus* (see above: section 3.5.1) especially in October (Fig. 14B).

The vertical distribution of adult *Calanus* copepodids also overlapped considerably with that of *P. elegans* between August to November (Fig. 14C). After November, their depth distribution showed a substantial overlap with that of *M. ovum* ($V > 2.2$), and *A. digitale* ($V > 1.5$) (Fig. 14C). However, *A. digitale* showed extremely low abundances (< 0.1 ind.m^{-3}) after January onwards.

From the start of this study to the onset of November, the vertical distribution of *Metridia longa* only overlapped with that of *Eukrohnia hamata* (Fig. 14D). However, this period was characterized by low numbers of both species (total abundance < 0.1 ind.m^{-3}). During the latter part of the study, *M. longa* showed a significant vertical overlap ($V > 2$) with the vertical distribution of *P. elegans* (Fig. 14D).

Throughout this study, vertical distributions of *Mertensia ovum* and *Beroe cucumis* overlapped considerably (Fig. 14A). Furthermore, this vertical overlap was most prominent (V > 2.5) in October, and February onwards.

3.7 Statistical relationships between potential food, and dominant zooplankton

Statistical relationships between the vertical distributions of dominant zooplankton and those of their food in different parts of the time series (Fig. 15) are presented in Table 5.

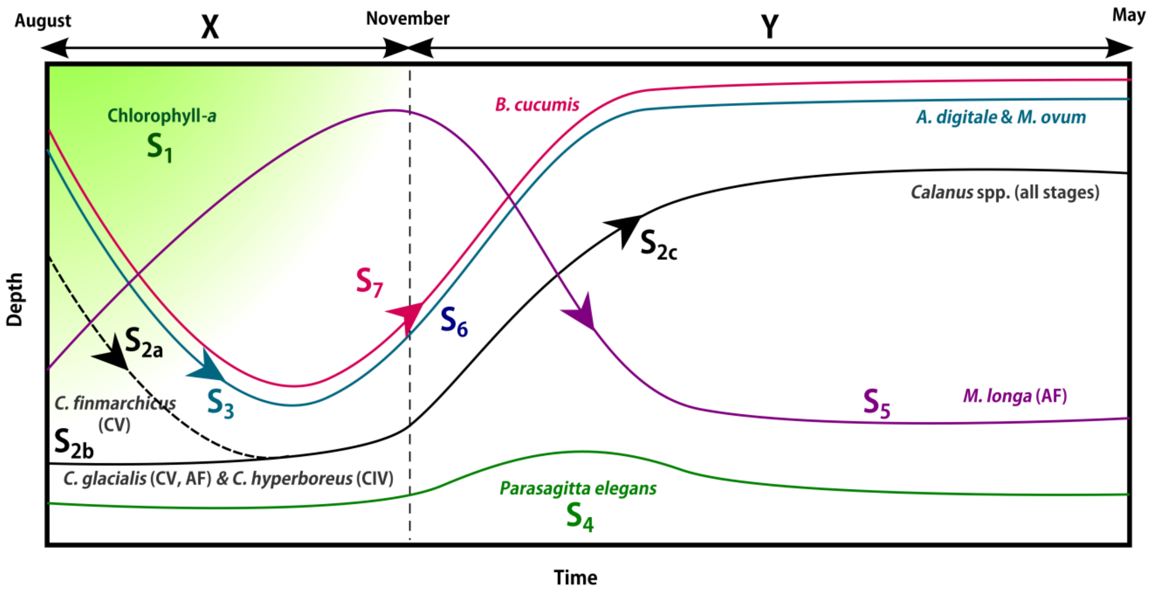

Fig. 15: Generalized[1] vertical distributions of dominant taxa (S_2–S_7), and chlorophyll fluorescence (S_1) in the autumn (X) and winter-spring (Y) in Billefjorden. S_6 is the generalized vertical distribution of *M. ovum*, and identical to S_3. Statistical relationships between these seasonal vertical distribution data are given in Table 5. Depth axis is not to scale, and does not represent neither absolute, nor relative vertical distributions of any taxa/parameter.

Table 5: The coefficients of determination (R^2) of the fitted linear models for relating seasonal vertical distributions of food and feeders. *W* and *BP* are test statistics of Shapiro-Wilk and Breusch-Pagan tests for normality and homoscedasticity of the residuals. *n* is the no. of data points used in each model.

Food (V_E) *vs.* feeder (V_R)	R^2	*W*	*BP*	*n*
XS_1 *vs.* XS_2a	0.79*	0.87	0.94	4
XS_1 *vs.* XS_2b	-0.02	0.98	3.40	4
YS_1 *vs.* YS_2c	-0.02	0.95	0.08	7
XS_2a *vs.* XS_3	0.89*	0.97	0.62	4
XS_2b *vs.* XS_3	-0.06	0.86	3.31	4
YS_2c *vs.* YS_3	0.52*	0.97	0.81	7
(XS_2a + XS_2b) *vs.* XS_4	0.42*	0.83	0.51	4
YS_5 *vs.* YS_4	0.33	0.91	0.37	7
$(X+Y)S_7$ *vs.* $(X+Y)S_6$	0.70***	0.84*	0.26	10
$(X+Y)S_1$ vs. $(X+Y)S_5$	-0.07	0.77**	0.82	10

V_E: Explanatory variable, V_R: Response variable
*p<.05, **p < .01, ***p < .001
Significant W and BP statistics denote residuals with non-normality and heteroscedasticity. Breusch-Pagan statistic was estimated using R™ package lmtest (Zeileis and Hothorn, 2012)

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[1] Vertical distribution lines presented in Fig. 15 were modified from mean depths (section 3.5), and presented with applying smoothing functions in R™ (R core team, 2013).

The Vertical distribution of *C. finmarchicus* CV's in the autumn (XS_2a) showed a statistically significant relationship to the mean chlorophyll-*a* fluorescence during this period (XS_1). The chlorophyll-*a* fluorescence explained nearly 80% of the vertical distribution of the above species. However, it did not adequately describe the vertical distributions of *C. glacialis* (CV, adult females) and *C. hyperboreus* (CIV) (S_2b), or that of *Calanus* spp. (S_2C)in the winter-spring season (Y) (Fig. 15, Table 5).

Autumn vertical distributions of *A. digitale* and *M. ovum* (XS_3), and *P. elegans* (XS_4) showed statistically significant relationships with those of *C. finmarchicus* (R^2: 0.89), and *Calanus* spp. (R^2: 0.42) respectively (Fig. 15, Table 5). In the winter-spring season, vertical distribution of *Calanus* spp. (YS_2c) was significantly related (R^2: 0.52) to that of *A. digitale* and *M. ovum* (YS_3). Furthermore, the vertical distribution of *M. ovum* (S_6) explained 70% ($p < 0.001$) of that of *B. cucumis* (S_7) throughout the study period (X+Y).

4. Discussion

Results of this investigation illustrated spatial and temporal variations of abundance and body size of dominant zooplankton taxa. Most species seasonally occupied different parts of the water column. Distinct abundance peaks were observed in all investigated dominant species. However, timing and the population composition of these abundance peaks varied species-specifically. Henceforth I describe the life histories of dominant zooplankton species by presenting the aforementioned dynamics as annual routines. Moreover, I discuss these annual routines in relation to seasonal dynamics of food availability.

4.1 Life histories of dominant herbivores

4.1.1 Potential sources of food, and their dynamics

Phytoplankton and ice algae are the two main sources of food available to high-latitude herbivorous zooplankton (Cota & Horne, 1989; Sakshaug & Slagstad, 1991; Falk-Petersen et al., 2000; Lizotte, 2001; Sakshaug, 2004; Falk-Petersen et al., 2008a; Søreide et al., 2010; Slagstad et al., 2011). In Billefjorden, the pelagic phytoplankton bloom developed around mid June as a combined effect of water mass stratification, melting sea ice, and increasing PAR (Fig. 3, 4 & 6). According to Bailey (2010) and Grigor et al. (2014), the ice algal bloom developed in early May. These findings suggest that the productive period in Billefjorden was short (May-July), and food supply to herbivores remained limited for most part of the year. Moreover, the primary production was restricted to the surface habitat (Fig. 6), and the deep habitat remained largely unproductive throughout the year.

4.1.2 Annual routines

4.1.2.1 Habitat shifts, and overwintering

During the unproductive part of the year, the dominant herbivorous zooplankton (*i.e. Calanus* spp.) were located in the deep habitat. According to Bailey (2010), *C. glacialis*

(CV), and *C. hyperboreus* (CIV) descent to deep waters between July and August. My findings indicate that *C. finmarchicus* (CV) completed its descent by mid October (Fig. 12B2). Positive scaling of its autumn vertical distribution with the chlorophyll-*a* fluorescence (R^2: 0.79, $p < 0.05$) suggest that *C. finmarchicus* foraged in the surface habitat, and descended with the depletion of phytoplankton food in the autumn.

Calanus spp. are known to migrate to deeper waters for 'overwintering' (reviewed in Conover, 1988). I argue the occupation of deep habitat by *Calanus* spp. in Billefjorden during autumn and early winter (Fig. 12) as a part of their overwintering strategy. I suggest that *C. finmarchicus* CV's overwintered for ca. two months (Fig. 12B2), whilst *C. glacialis* CV's, and adult females (Fig. 12C2 & C3), and *C. hyperboreus* CIV's (Fig. 12 D1) overwintered for ca. 4–5 months. The overwintering adult females of *C. glacialis* might have been descendants of the previous generation (*e.g.* Hirche, 1989; Kosobokova, 1999). A thorough review of affiliated literature confirms the overwintering stage structure of *Calanus* spp. documented above (Table 6).

The wintertime ascent of copepodid stages from the deep habitat marked the termination of the overwintering period. By January, almost entire *Calanus* community were found in the surface habitat. My results show that the ascent of *Calanus* spp. occurred independent from the availability phytoplankton food (Fig. 15, Table 5). The subsequent emergence of adult copepodids (Fig. 9A2–C2) suggests that moulting occurred parallel to the habitat shift. According to Bailey (2010) these adult copepodids and their subsequent generation (G_1) co-occurred in the surface habitat until the end of the forthcoming productive season.

Table 6: Overwintering stage compositions of *Calanus* spp. documented from high latitudes. Some additional literature are also available in the review of Falk-Petersen et al. (2008b). Within each species, most commonly cited stage(s) are given the priority in arrangement.

Species	Overwintering stage(s)	Reference(s)
C. finmarchicus	CV	Fish (1936), Matthews et al. (1978), Aksnes & Magnesen (1983), Hirche (1991)[B], Diel & Tande (1992), Hirche & Kwasniewski (1997), Melle & Skjoldal (1998)[C], Arashkevich et al. (2002), Niehoff et al. (2002), Hirche & Kosobokova (2003)
	CIV and CV	Lie (1965), Tande & Hopkins (1981), Hirche (1991)A, Hirche et al. (1994), Falk-Petersen et al. (1999), Scott et al. (2000), Hirche et al. (2001), Madsen et al. (2008), Hirche & Kosobokova (2011)
	CV and females	Melle & Skjoldal (1998)[D], Arnkværn et al. (2005)
	CIII CIV and CV	Madsen et al. (2001)[†]
C. glacialis	CIV, CV and females	Tande et al. (1985), Hirche & Bohrer (1987), Falk-Petersen et al. (1999), Kosobokova (1999), Arnkværn et al. (2005)
	CIV and CV	Hirche (1989), Hirche (1991)[A], Scott et al. (2000), Madsen et al. (2001), Søreide et al. (2010)
	CIII and CIV	Melle & Skjoldal (1998)[D2], Hirche & Kosobokova (2011)
	CIV	Hirche et al. (1994), Hirche & Kosobokova (2003)
	CV and females	Hirche & Kwasniewski (1997), Melle & Skjoldal (1998)[C,D1]
	CIII, CIV and females	Arashkevich et al. (2002)
	CIV and females	Hirche (1991)[B]
C. hyperboreus	CIV and CV	Matthews et al. (1978), Hirche (1991)[B], Hirche et al. (1994)[E], Hirche (1997)[H], Madsen et al. (2001)
	CIII, CIV, CV and females	Falk-Petersen et al. (1999), Scott et al. (2000)
	CIII, CIV and CV	Conover (1988), Astthorsson & Gislason (2003)
	CIII and CIV	Matthews et al. (1978), Hirche & Kosobokova (2011)
	CII, CIII and CIV	Dawson (1978)
	CIII, CIV and females	Hirche (1997)[G]
	CIII and females	Hirche (1991)[A]
	CIII	Hirche et al. (1994)[F]
	CIV	Arnkværn et al. (2005)
	CIV, CV and females	Hirche & Kosobokova (2003)
	CV and females	Hirche & Kwasniewski (1997)

A: Greenland Sea Gyre, **B:** South of Arctic front in Greenland Sea, **C:** Atlantic water region of Barents Sea, **D1:** Polar front region of Barents Sea (single year life cycle), **D2:** Same as D1 (two year life cycle), **E:** Greenland Sea, **F:** Fram Strait, **G:** Greenland Sea Gyre, **H:** West Spitsbergen Current, [†]For late spawners.

4.1.2.2 Reproduction

I estimated the peak spawning periods of the three *Calanus* species with the aid of their respective new generation (G_1) emergence times (adopted from (Bailey, 2010)), and appropriate life stage development functions (Table 7). Results indicate that all three species spawned prior to the pelagic phytoplankton bloom (Table 7).

Table 7: Estimated development times (DT) for *Calanus* spp. Spawning periods are back-calculated from the peak CI abundance data (Bailey, 2010) using Belehrádek's temperature function: DT = $a(T - \alpha)^b$. 'T' represent the mean temperature of the surface habitat (-0.17 ± 2.25 ^{o}C), and 'b' was assumed to be -2.05.

Parameter	*C. finmarchicus*	*C. glacialis*	*C. hyperboreus*
Peak abundance of CI	July 23rd	June 10th	June 10th
DT (days)	59.08	47.19	58.52
Peak spawning period	May 25th	April 24th	April 12th
a	5267[†]	8882[‡]	13532[‡]
α	9.11[†]	13.04[‡]	14.40[‡]

[†]Campbell et al. (2001), [‡] Corkett et al. (1986)

Pre bloom spawning has been documented for these species, but appears more common among *C. glacialis* and *C. hyperboreus* than *C. finmarchicus* (Table 8). Capital breeding (Stearns, 1992) is a well documented reproductive strategy among *C. hyperboreus* (Table 8), which is accredited to its well developed lipid economy (Hagen & Auel, 2001; Lee et al., 2006; Falk-Petersen et al., 2008b). However, none of the up-to-date literature (Table 8) have mentioned *C. finmarchicus*, or *C. glacialis* as predominantly capital breeders. Therefore, I suggest that income breeding must have played a central role in the reproductive strategy of these two species. Ice algae (*e.g.* Runge & Ingram, 1991; Tourangeau & Runge, 1991; Hirche & Kwasniewski, 1997; Hirche & Kosobokova, 2003; Søreide et al., 2010), microzooplankton (*e.g.* Ohman & Runge, 1994; Hirche & Kwasniewski, 1997), and their own eggs/naupliar stages (*e.g.* Ohman & Hirche, 2001; Basedow & Tande, 2006; Neuheimer et al., 2009) might have served as likely food sources to fuel the pre-bloom spawning of *C. finmarchicus*, and *C. glacialis*.

The early spawning might have allowed the offspring of the three *Calanus* spp. to utilize the pelagic phytoplankton bloom that developed in mid June as a food source. Søreide et al. (2010) argued that high-quality food of Arctic phytoplankton blooms can aid development of the younger stages once their occurrences coincide. These findings revisit the match-mismatch hypothesis (Cushing, 1990), where peak energetic demands of the offspring match peak food availability (Both et al., 2009). In addition, spawning prior to the phytoplankton bloom yields numerous advantages that enhances the reproductive, and survival traits (*i.e.* fitness) of newborns (Varpe et al., 2007).

Table 8: The spawning timing of *Calanus* spp. in relation to phytoplankton bloom or laboratory manipulated food availability.

Species	Timing of spawning	Reference
C. finmarchicus	Pre-bloom	Diel & Tande (1992), Melle & Skjoldal (1998)^{A,B,C}, Richardson et al. (1999), Arnkværn et al.(2005)
	Bloom and post-bloom	Tande & Hopkins (1981), Aksnes & Magnesen (1983), Tande et al. (1985), Plourde & Runge (1993), Scott et al. (2000), Madsen et al. (2001), Arashkevich et al. (2002)^{D}, Niehoff et al. (2002), Astthorsson & Gislason (2003), Hirche & Kosobokova (2003), Madsen et al. (2008)
C. glacialis	Pre-bloom	Smith (1990), Tourangeau & Runge (1991), Hirche et al. (1994), Hirche & Kwasniewski (1997), Melle & Skjoldal (1998)^{A,B,C}, Falk-Petersen et al. (1999), Kosobokova (1999), Scott et al. (2000), Madsen et al. (2001), Arashkevich et al. (2002)^{D,E}, Niehoff et al. (2002), Hirche & Kosobokova (2003), Arnkværn et al. (2005), Madsen et al. (2008), Søreide et al. (2010), Hirche & Kosobokova (2011)
	Bloom/food availability	Tande et al. (1985), Hirche & Bohrer (1987), Hirche (1989)
C. hyperboreus	Pre-bloom/winter	Conover (1965) & (1967), Dawson, (1978), Matthews et al. (1978), Conover (1988), Smith (1990), Hirche (1991)^{F}, Hirche et al. (1994), Hirche (1997), Hirche & Kwasniewski (1997), Melle & Skjoldal (1998), Falk-Petersen et al. (1999), Scott et al. (2000), Madsen et al. (2001), Niehoff et al. (2002), Astthorsson & Gislason (2003), Hirche & Kosobokova (2003), Arnkværn et al. (2005), Hirche & Kosobokova (2011)

A: Atlantic water region of Barents Sea, **B:** Polar front region, **C:** Arctic water region of Barents Sea, **D:** South of ice edge (open water) Barents Sea, **E:** North of Polar front (ice covered), **F:** Greenland Sea Gyre.

Note: Ankværn et al. (2005) did not estimate the onset of the phytoplankton bloom. Considering the sea ice conditions of Billefjorden 2002, I hypothesized that bloom occurred sometime in June.

Although the three *Calanus* species spawned ahead of the phytoplankton bloom, my results suggest a possible mismatch between the spawning of *C. finmarchicus*, and the food source. Varpe et al. (2007) suggested that eggs produced early in the season have adequate time to develop into overwintering CV's at the end of the feeding season. The spawning of *C. glacialis* in this study likely resembles the above scenario. I argue that the early peak abundance of CV's (Fig. 9B1 & B2), and their dominance in the overwintering population of this species occurred as a result of early spawning. In contrast, *C. finmarchicus* CV's peaked late (*i.e.* winter) (Fig. 9A1 & A2), and a large number of CIV's overwintered alongside CV's (Bailey, 2010). The estimated ca. one month delay in *C. finmarchicus* spawning compared to *C. glacialis* (Table 7) might have caused the development of its life stages to be time-constrained (Varpe et al., 2007), and possibly hampered by the food shortage (Vidal, 1980a, 1980b) later in the season.

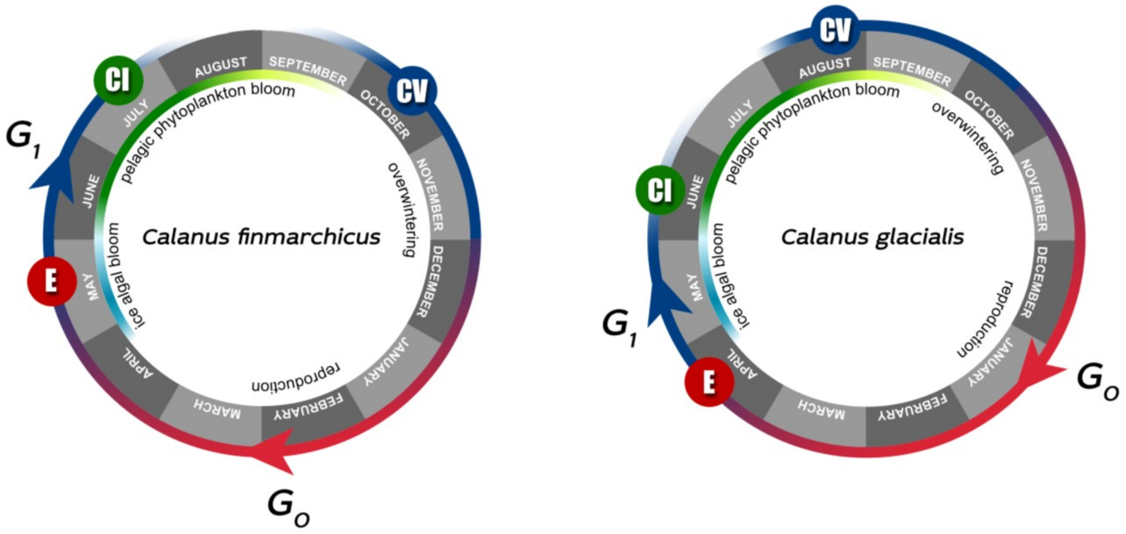

Fig. 16: Reconstructed life histories of *Calanus finmarchicus* and *C. glacialis*. **'CV'** refers to the time at which stage V copepodids of each species were found overwintering depths. Potential reproductive period is represented by the reddish outer ring. The onset of reproduction was estimated from the time at which male and female copepodids coexisted in their respective populations. **'E'** refers to the estimated peak emergence of eggs (*i.e.* peak spawning). Timing of the ice algal bloom, and the emergence of CI's are from Bailey (2010).

Results of this study suggest that *C. finmarchicus*, and *C. glacialis* completed its life cycles within a single year (Fig. 16). Since the ability of *C. hyperboreus* CIII's to overwinter in Billefjorden is not known, I suggest 1, or 2 year life cycle for the above species. A review of different life cycle lengths suggested for these species from both low, and high latitudes is available in Table 9.

Table 9: Different life cycle lengths of *Calanus* spp. documented in previous literature. Some additional literature are also available in the review of Falk-Petersen et al. (2008b).

Species	Life cycle length	References
C. finmarchicus	2 - 3 generations per year	Fish (1936), Lie (1965), Matthews et al. (1978)
	1 year	Lie (1965), Tande & Hopkins (1981), Aksnes & Magnesen (1983), Tande et al. (1985), Hirche (1991)[A,B], Hirche & Kwasniewski (1997), Melle & Skjoldal (1998)[C,D], Falk-Petersen et al. (1999), Scott et al. (2000); Hirche et al. (2001), Madsen et al. (2001), Arashkevich et al. (2002)[E], Niehoff et al. (2002), Astthorsson & Gislason (2003), Arnkværn et al. (2005)
C. glacialis	1 year	Smith (1990), Hirche (1991)[B], Hirche & Kwasniewski (1997), Melle & Skjoldal (1998)[C,D], Arashkevich et al. (2002)[E]
	More than 1 year	Hirche & Kwasniewski (1997)[†]
	1 - 2 years	Falk-Petersen et al. (1999), Scott et al. (2000), Arnkværn et al. (2005), Søreide et al. (2010)
	2 years	Tande et al. (1985), Hirche (1991)[A,B], Melle & Skjoldal (1998)[D], Arashkevich et al. (2002)[F]
	2 or more years	Madsen et al. (2001), Astthorsson & Gislason (2003)
	3 years	Kosobokova (1999)
C. hyperboreus	1 year	Conover (1965), & 1967, Matthews et al. (1978), Smith (1990), Hirche (1991)[B], Hirche & Kwasniewski (1997) Arnkværn et al. (2005)
	2 years	Hirche (1991)[A,B]
	2 - 3 years	Hirche (1997)[H]
	2 or more years	Madsen et al. (2001)
	3 years	Dawson (1978), Hirche (1997)[G♀]
	3 - 4 years	Conover (1988)
	3 - 5 years	Falk-Petersen et al. (1999)
	3 or more years	Scott et al. (2000)
	4 years	Hirche (1997)[G♂]

A: Greenland Sea Gyre, **B:** South of Arctic front in Greenland Sea, **C:** Atlantic water region of Barents Sea, **D:** Polar front region of Barents Sea, **E:** South of ice edge (open water) Barents Sea, **F:** North of Polar front (Ice covered) Barents Sea, **G♂:** Greenland Sea Gyre (for males), **G♀:** same as above (females), **H:** West Spitsbergen Current,

[†] For late spawners

4.2 Life histories of dominant carnivores

4.2.1 Potential sources of food, and their dynamics

4.2.1.1 Potential prey of predatory species

The dominant carnivores (predators) of Billefjorden are known to feed on a number of other zooplankton species (prey). The hydromedusa *Aglantha digitale*, ctenophore *Mertensia ovum*, and the two chaetognath species feed primarily on copepods (Table 10). *Beroe cucumis* feed on other ctenophores (Greve, 1970; Anderson, 1974; Swanberg, 1974), and especially on *Mertensia ovum* (Table 10).

Table 10: Main food (prey) sources of dominant carnivorous zooplankton in Billefjorden

Species	Main prey	References
Aglantha digitale	Copepods	Arai & Fulton (1973), Mackie et al. (2003), Ikeda & Imamura (2006) and references therein, Pertsova et al. (2006)
Mertensia ovum		Swanberg & Båmstedt (1991), Lundberg et al. (2006) and references therein, Larson & Harbison (1989)
Parasagitta elegans		Pearre (1973, & 1980), Sullivan (1980), Greene (1986), Samemoto (1987), Falkenhaug (1991), Alvarez-Cadena (1993), Brodeur & Terazaki (1999), Dale et al. (1999), Saito & Kiørboe (2001), Sakshaug et al. (2009)
Eukrohnia hamata†		Sullivan (1980), Samemoto (1987), Øresland (1995), Froneman et al. (1998)
Beroe cucumis	*M. ovum*	Swanberg & Båmstedt (1991), Siferd & Conover (1992), Falk-Petersen et al. (2002)

†Life history of *E. hamata* is not discussed due to its comparatively low abundances

4.2.1.2 Predator-prey size ranges

As the prey size is a main factor affecting predation (Brooks & Dodson, 1965), it can be argued if the size ranges of prey species matched those of their predators in this study. Greene (1986) and Swanberg and Båmstedt (1991) mentioned that cydippid ctenophores and chaetognaths can feed on older (hence larger) developmental stages of *Calanus* spp. Furthermore, Saito and Kiørboe (2001) noted that the northern North Sea *P. elegans* could ingest copepods with lengths of approximately up to 20% of its total length. Adopting the above estimate to my data suggests that the entire *Calanus,* and *M. longa* community sampled in this study (range: 0.3–6.4 mm PL, mean: ~3.0 mm PL) act as potential prey of chaetognaths (range: 15–45 mm TL, mean: ~28 mm TL).

Since *B. cucumis*, and *M. ovum* showed an inverse body length relationship (predator smaller than its prey: Fig. 10B2 & B3), it can be argued if smaller *B. cucumis* could feed on larger *M. ovum*. Size interpretations of gelatinous zooplankton should be done with caution, given their ability to shrink (*e.g.* Hamner & Jenssen, 1974; Falkenhaug, 1996). It is also likely that large, sparsely located *B. cucumis* individuals might not have sampled by the net. However, Swanberg, (1974), and Tamm & Tamm (1991) noted that beroid ctenophores can engulf larger prey with the aid of their voluminous stomodaea. Moreover, Swanberg (1974) observed beroid ctenophores feeding on body parts of other ctenophores. Therefore I argue that *M. ovum* in Billefjorden might have been a source of prey for *B. cucumis* despite their contrasting size ranges.

4.2.1.3 Temporal dynamics of food availability

I assume the abundance of *Calanus* spp. and *M. longa* as a rough estimate[1] of food availability for *A. digitale*, *M. ovum*, *P. elegans*, and *E. hamata*. Similarly, the abundance of *M. ovum* can be assumed to reflect the food availability to *B. cucumis*. The predator-prey ratio (V/P) between copepods and their predators illustrate a near-constant predator-prey ratio between the above groups (Fig. 17). A similar pattern in predator-prey ratio[2] (V/P: ~0.4) was also observed between *B. cucumis* and *M. ovum* for most part of this study (data not presented). This suggest that the dominant invertebrate predators of Billefjorden had a

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[1] Here I only considered the older developmental stages (*i.e.* CIV, CV, and adults) of *Calanus* spp. and *M. longa*. Younger developmental stages of above species and other copepod species should also be considered to derive an accurate prey density estimate.

[2] This estimate might not be accurate due to the potential sampling bias caused by patchy, and sparse distribution of ctenophores (*e.g.* Swanberg & Båmstedt, 1991; Siferd & Conover, 1992; Falkenhaug, 1996; Lundberg et al., 2006).

substantial abundance of prey for most part of this investigation. Clarke (1988) and Hagen (1999) also argued that carnivores sustain a more or less year round availability of food.

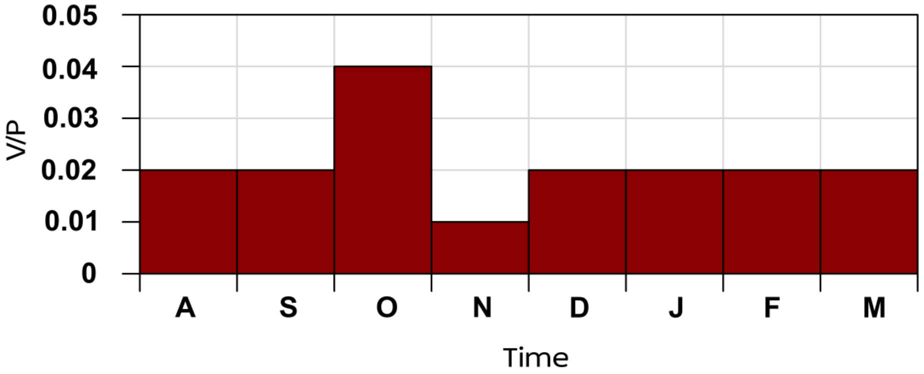

Fig. 17: Monthly ratio of total abundance between copepod prey (**P**: *Calanus* spp., and *Metridia longa*), and their potential predators (**V**: *Aglantha digitale*, *Mertensia ovum*, *Parasagitta elegans*, and *Eukrohnia hamata*). Data beyond March (during the potential spawning season of *Calanus* spp.) are not presented since the total abundances of eggs, and naupliar stages were not estimated.

4.2.1.4 Spatial dynamics of food availability (i.e. the vertical distribution of prey)

My results show that vertical distribution of copepod prey varied significantly during the year. The spring, and summer seasons were characterized by high abundance of adult, and younger copepodids, nauplii, and eggs in the surface habitat (Bailey, 2010). During this period the deep habitat remained low in prey density, but low numbers of *M. longa* adult copepodids were found (Fig. 11B1 & B2). In the autumn, the prey density gradually shifted to the deep habitat, following the seasonal descent of *Calanus* spp. (Fig. 12). Except the adult copepodids of *M. longa* (Fig. 11B2), the prey abundance of the surface habitat remained low during the winter.

Similarly, the vertical distribution of *M. ovum* varied throughout the time series (Fig. 13B2). It descended to the deep habitat in the autumn, and gradually ascended back to the surface habitat in the spring.

4.2.2 Annual routines

4.2.2.1 Habitat shifts

In the autumn *A. digitale* and *M. ovum* descended from the surface habitat to the deep habitat (Fig. 13A2 & B2). Grigor et al. (2014) also documented an autumn descent by surface dwelling *P. elegans* juveniles. Vertical distributions of *A. digitale*, and *M. ovum* considerably overlapped with that of *Calanus* spp. during the descent (Fig. 14B). In addition, autumn mean depths of above predators were statistically related to those of *C. finmarchicus*. (R^2: 0.89, $p < 0.05$). Therefore, I argue that the autumn habitat shift of above carnivores was governed by the seasonal descent of their copepod (*i.e. Calanus*) prey. This corroborates the findings of David (1958) and Torres et al. (1994) that invertebrate predators follow their prey into deeper waters during the autumn and winter.

From November onwards *A. digitale* and *M. ovum* gradually ascended back to the surface habitat (Fig. 13A2 & B2). Vertical distributions of these predators considerably overlapped with those of *Calanus* overwintering stages during this ascent (Fig. 14B & C). Moreover, the winter-spring mean depths of *A. digitale*, and *M. ovum* were statistically related to those of *Calanus* copepodid stages (R^2: 0.52, $P < 0.05$). In the spring, *M. ovum*, occupied the surface habitat with co-occurring adult and young (Bailey, 2010) developmental stages of *Calanus* spp., with nearly identical vertical distributions (Fig. 14C). These findings link the seasonal ascent of these predators (especially *M. ovum*) with that of their prey. Siferd and Conover (1992), and Lundberg et al. (2006) also related the shallow seasonal vertical distribution of *M. ovum* to summertime abundance of copepod prey.

Unlike *M. ovum*, large size groups of *P. elegans* (G_1, and G_2) continuously occupied the deep habitat without pronounced seasonal migration (Fig. 13C2). Occupation of deep habitats by larger size groups of *P. elegans* are also documented in Pearre (1973), King, (1979), Sullivan (1980), Terazaki & Miller (1986), Samemoto (1987), and Choe & Deibel, (2000). Moreover, despite low feeding rates (Øresland, 1990), chaetognaths can feed under winter conditions (Pearre, 1973; Øresland, 1995; Grigor et al., 2014). Therefore, I argue that the deep habitat possessed an adequate food supply to sustain its year-round feeding requirements. Vertical distributions of *P. elegans* considerably overlapped with those of overwintering *Calanus* copepodids in the autumn (Fig. 14B), and showed positive statistical relationship (R^2: 0.42, $p < 0.05$). After the seasonal ascent of *Calanus* prey (November onwards), vertical distributions of *P. elegans* and *M. longa* adult females noticeably overlapped (Fig. 14D). However, relationship between the mean depths of above species was not statistically significant (Fig. 15, Table 5). Nonetheless, it can be argued if *M. longa* acted as an alternative source of prey, upon the depletion of *Calanus* stocks in the deep habitat in the winter-spring period. Dale et al. (1999) documented overlapping depth distributions of overwintering *Calanus*, and chaetognaths in Norwegian, and Greenland Seas. Vertical distribution patterns of chaetognaths in the Southern Ocean (David, 1958) also corroborate this view.

Apart from the above predators, *B. cucumis* showed a marked similarity in vertical distribution to its main prey *M. ovum*. This was characterized by an autumn descent to deep habitat, followed up by a subsequent ascent to surface habitat in the spring (Fig. 13B2). Moreover, a strong overlap (Fig. 14A), and a statistically significant relationship in the mean depths of these two species (R2: 0.70, $p < 0.001$) throughout this investigation suggest that *B. cucumis* might have followed its prey across different habitats. Swanberg and Båmstedt (1991), and Siferd and Conover (1992) also interpreted the similarities between the vertical distributions of these two species to their feeding relationship.

4.2.2.2 Overwintering

Occupation of deep waters (*e.g.* Siferd & Conover, 1992; Falkenhaug, 1996; Hosia & Båmstedt, 2007), tissue shrinkage (*e.g.* Falkenhaug, 1996), and high total lipid content (*e.g.*

Percy 1988; Larson & Harbison 1989; Lundberg et al., 2006) have been considered as main overwintering characteristics of *A. digitale*, *M. ovum*, and *B. cucumis*. Therefore, it can be argued if these three species occupying the deep habitat in late September and/or November (Fig. 13A2 & B2) had overwintered.

Two sample t-tests show no significant decrease in mean BH of *A. digitale* in October (t: 4.28, $p > 0.05$), and mean BL of *B. cucumis* (t: 1.57, $p > 0.05$) in late September, and October, compared to rest of the time-series (see Fig. 10B1 & B3). This suggest that tissue shrinkage was not pronounced during the their occupation of the deep habitat. In contrast, the mean BL of *M. ovum* in October was significantly smaller (t: 4.28, $p < 0.001$) compared to rest of the year (see Fig. 10B2). Therefore, possibility of tissue shrinkage of this species cannot be ruled out. Since the tissue shrinkage is indicative of poor food availability (Larson & Harbison, 1989; Sifred & Connover, 1992; Falkenhaug, 1996), it can be argued if deep dwelling *M. ovum* starved in late autumn.

During the above period, *M.* ovum and other gelatinous predators co-occurred the deep habitat with substantial abundance of prey (mean total abundance of *Calanus* spp. > 350 $ind.m^{-3}$, and *M. ovum* > 3 $ind.m^{-3}$), with nearly identical vertical distributions (Fig. 14A & B). Larson and Harbison (1989) argued that *M. ovum* can feed prolonged on copepod patches upon detection. In addition, this species possesses digestive enzymes that can operate in low temperatures, that enable wintertime feeding (Siferd & Conover, 1992). Therefore, it is likely that deep dwelling *M. ovum* in October have utilized overwintering *Calanus* copepodids as food. The wintertime increase in total lipid content of *M. ovum* (*e.g.* Lundberg et al., 2006) is also argued to be due to the consumption of lipid rich *Calanus* spp. (Percy, 1988; Larson & Harbison, 1989). Although this species is known to reduce its activity, and switch to a lipid-based metabolism under poor wintertime feeding conditions (Percy, 1988), there is little evidence to suggest that *M. ovum* in Billefjorden overwintered under reasonable food conditions.

Based on these findings I suggest that the occupation of the deep habitat by above hydromedusan, and ctenophore predators in the autumn was likely governed by their deep dwelling prey, rather than a part of their overwintering strategy.

4.2.2.3 Reproduction

Aglantha digitale

An autumn population peak of *A. digitale* comprising of smaller individuals (Fig. 10 A1 & B1) have also been documented by Arai and Fulton (1973), Williams and Conway (1981), Ikeda and Imamura (2006), Pertsova et al. (2006), and Hosia and Båmstedt (2007). It is likely that this species spawned in the summer or autumn (references as above), with the succeeding new generation peaking in late autumn (*i.e.* October). The continuous increment of bell height (Fig. 10B1), and lack of multimodality in their size distribution (data not presented) indicate the possible development of a single cohort throughout the year. Furthermore, lack of a secondary abundance peak within the year (*e.g.* Russell, 1938; Hosia & Båmstedt, 2007) suggest an annual life cycle for *A. digitale* in Billefjorden. Single year life cycles for this species have been recorded from the northeast Pacific (Arai & Fulton, 1973), northeast Atlantic (Williams & Conway, 1981), northwest Pacific (Ikeda & Imamura, 2006), and White Sea (Pertsova et al., 2006). Multi-generation cycles have been documented from the English Channel (Russell, 1938), and western Norwegian fjords (Hosia & Båmstedt, 2007).

Mertensia ovum

The late autumn abundance peak of *M. ovum* comprising relatively small (< 15 mm) individuals (Fig. 10 A2 & B2) resembles the population composition of this species in

Kongsfjorden, Svalbard (Lundberg et al., 2006). Similar peak abundance episodes have also been documented in the summer (Percy, 1989; Siferd & Conover, 1992), and spring (Siferd & Conover, 1992). It can be argued that this species spawned in the summer or autumn (*e.g.* Percy, 1989; Siferd & Conover, 1992; Lundberg et al., 2006), and the new generation continued to develop thenceforward. The increasing trend of their body length during the course of this investigation (Fig. 10B2) supports this argument. However, the coexistence of small and large individuals throughout this study possibly indicate the presence of multiple cohorts in its population (*e.g.* Lundberg et al., 2006). Due to low abundance of *M. ovum* I could not follow its cohort dynamics. This hampers an accurate interpretation of its life cycle in Billefjorden.

Beroe cucumis

Predominance of smaller individuals (juveniles: ~1.6 mm BL) in the early May population peak of *B. cucumis* (Fig. 10A3 & B3) possibly indicates the springtime development of their new generation. Similar population structure was documented by Falkenhaug (1996) from a northern Norwegian fjord. It is likely that this species spawned in the early spring (*e.g.* Siferd & Conover, 1992; Falkenhaug, 1996). Despite this generalization, coexistence of small and large (as large as 70 mm BL) individuals in autumn *B. cucumis* population (Fig. 10B3) may indicate the presence of multiple cohorts in this population. However, detailed cohort dynamics of this species could not be interpreted due to low abundance.

Parasagitta elegans

I considered the three size groups (G_0, G_1, and G_2) of *P. elegans* as three distinct cohorts (0, 1, and 2) in order to describe its life history. Considering the coarse mesh width of the sampling gear, it is unlikely that cohort–0 was fully represented in this study. Therefore, I refer to the dynamics of the smallest cohort of Grigor et al. (2014) to describe those of cohort–0.

Grigor et al. (2014) argued that *P. elegans* in Billefjorden spawned during the spring (May), and the subsequent new generation (cohort–0) peaked in July. I found relatively high abundances of cohorts–1, and 2 by late August (Fig. 10A4 & B4). A typical 0–cohort individual with a mean TL of 8.6 ± 2.8 mm (Grigor et al., 2014) should grow at a rate of 0.49 mm $TL.d^{-1}$, and 0.83 mm $TL.d^{-1}$ to be recruited respectively to cohort–1 (23.2 ± 2.0 mm) and cohort–2 (33.6 ± 3.0 mm) respectively from July to August (within ca. one month). Above rates are unusually high compared to those suggested by Grigor et al. (2014), Welch et al. (1996), Kotori (1999), and Choe and Deibel, (2000). Therefore, it can be suggested that cohorts–1, and 2 were spawned in previous year(s).

The peak abundance of cohort–2 in September (Fig. 10B4) suggest that it received recruits from cohort–1. Despite recruitment, the size of cohort–1 increased untill December: possibly due to the continuation of recruitment from cohort–0. However, cohort–1 began to shrink in size from January onwards with a parallel swell in cohort–2 (Fig. 10B4). Furthermore, the near extinction of cohort–1 at the end of this investigation (Fig. 8B) possibly indicate total recruitment of cohort–0 into cohort–2 within a period of approximately one year. According to Grigor et al. (2014), larger individuals (cohort–2) attained sexual maturity, and spawned in the following spring.

The three cohort population structure, coupled with the ability of mature individuals to spawn in consecutive years (Russell, 1932) point to a more than 1 year life cycle (possibly 2, or 3 years) for *P. elegans* inhabiting Billefjorden. This is in agreement with the life cycle lengths documented from Arctic and subarctic seas (Dunbar, 1962), Resolute passage (Welch et al., 1996), northern North Pacific (Kotori, 1999), Conception Bay (Choe & Deibel, 2000), and Billefjorden (Grigor et al., 2014). Longer life cycle of *P. elegans* is viewed as an adaptation to the life in high latitudes (McLaren, 1966), compared to annual, and multi-generation life cycles observed elsewhere (*e.g.* English Channel (Russell, 1932, 1933), Dabob Bay (King, 1979), and subarctic Pacific (Terazaki & Miller, 1986)).

Relation of spawning to food availability

Arnkværn et al. (2005), and Bailey (2010) found large numbers of young copepod, and nauplii stages occupying surface waters of Billefjorden in the spring, and summer. The spring-summer spawning of dominant carnivores in Billefjorden might likely be due to the above 'bloom' in prey abundance (Grigor et al. 2014). Similar findings have been documented in numerous studies (Table 11).

Table 11: Studies that coupled the spawning of carnivorous zooplankton to annual (*i.e.* spring-summer) population peak of copepods

Species	References
Aglantha digitale	Russell (1938), Arai & Fulton (1973), Williams & Conway (1981), Ikeda & Imamura (2006), Pertsova et al. (2006)
Mertensia ovum	Siferd & Conover (1992), Lundberg et al. (2006), Percy (1989)
Parasagitta elegans	King (1979), Welch et al. (1996), Choe and Deibel (2000), Grigor et al. (submitted)

The peak spawning of species of *Beroe* is known to occur with or after that of its prey (Greve & Reiners, 1988; Siferd & Conover, 1992; Falkenhaug, 1996). The spawning times I estimated for *B. cucumis* occurred earlier than *M. ovum* (spring *vs.* the summer-autumn), and does not corroborate the above literature. Moreover, the estimated spawning period of *B. cucumis* coincided with low abundances of its prey (Fig. 10B2 & B3). Despite stable predator-prey ratios between these two species prevailing earlier in the time series (section 4.2.1.3), it largely increased (V/P > 1) from March onwards (data not presented). Therefore it is unclear how *B. cucumis* fulfilled energy requirements to fuel its (estimated) springtime spawning. Feeding on alternative food sources (Greve & Reiners, 1988; Siferd & Conover, 1992), such as on the pteropod *Limacina helicina* (Larson & Harbison, 1989), which has been reported as one of the most numerous mesozooplankon species in this fjord (Walkusz et al., 2003) can be suggested as a possible explanation.

4.3 The life history of the dominant omnivore

4.3.1 Potential sources of food, and their dynamics

The omnivorous feeding strategy of *M. longa* allows it to feed on the phytoplankton bloom, as well as other food sources such as microzooplankton, naturally occurring particles (Haq, 1967, Båmstedt & Ervik, 1984; Båmstedt et al., 1985; Båmstedt & Tande, 1988, Blachowiak-Samolyk et al., 2007), eggs, nauplii, and smaller copepodid stages of *Calanus* spp. (Haq, 1967). Apart from the phytoplankton food, the spatio-temporal dynamics of its main food sources during remain unknown in this investigation.

4.3.2 Seasonal life history strategies

4.3.2.1 Habitat shifts

Occupation of surface habitat in the autumn by adult females of *M. longa* (Fig. 11B2) possibly indicate its prolonged foraging in a late phase of the phytoplankton bloom (*e.g.* Tande & Grønvik, 1983; Båmstedt & Tande, 1988). Dasse et al. (2008) also found shallower depth distribution of adult stages in September. However, I did not obtain any statistical relationship between the vertical distribution of this species with the chlorophyll-*a* concentrations (Fig. 15, Table 5). As large copepods migrate to deep waters in the autumn, the surface layers are mainly occupied by peak abundance of smaller copepods and protozooplankton (Blachowiak-Samolyk et al., 2007). These smaller zooplankton might also have been potential food for surface dwelling *M. longa* in the autumn. The wintertime migration of these adult copepodids to the deep habitat resembles the findings of Grønvik and Hopkins (1984), and Falkenhaug et al. (1997). However, Hays (1995) and Hirche and Mumm (1992) found that older stages of *M. longa* spend closer to surface waters during the winter. Although the factor(s) causing the above wintertime habitat shift of *M. longa* remains unclear, it might have been governed by food, predator avoidance (*e.g.* Falkenhaug, 1997), or hydrographic preferences (*e.g.* Hirche & Mumm, 1992) (see Appendix IV).

Despite the wintertime migration to deep habitat, the vertical dispersion of *M. longa* remained pronounced (Fig. 11B2), and showed no sign of physical inactivity. Overwintering seems not to be an important life strategy for this omnivore, which does not rely on internal lipid reserves to spend the winter (Hagen & Auel, 2001). Furthermore, the opportunistic feeding behaviour allows *M. longa* to exhibit year-round physical (*i.e.* feeding) and behavioral (*i.e.* swimming) activity (Båmstedt & Ervik, 1984; Båmstedt et al., 1985; Båmstedt & Tande, 1988).

4.3.2.2 Reproduction

Lack of younger developmental stages in my samples hampers an accurate description of reproductive timing of *M. longa*. However, the presence of CV's in mid October, and November, and the subsequent augmentation of the adult female populations (Fig. 11B1) indicate wintertime recruitment to adult stages. This late recruitment might possibly be due to prolonged feeding on the phytoplankton bloom, and delayed spawning (late summer, or autumn) of adult females (*e.g.* Tande & Grønvik, 1983; Båmstedt & Tande, 1988, and the references therein).

4.4 Potential sources of error

The coarse mesh width of the WP3 net might not have captured certain taxa, eggs, and developmental stages. As a result some of the most numerically abundant taxa of this fjord such as *Limacina helicina*, *Oithona similis* (Walkusz et al., 2003) were not represented in my samples. Community interactions of some species with low abundances were also not discussed in detail (*i.e. Eukrohia hamata*). In addition, I did not consider the population dynamics of the euphausiid *Thysanoessa inermis*, and opossum shrimp *Mysis* spp. given their renowned ability to avoid nets (*e.g.* Fleminger & Clutter, 1965; Brinton & Townsend, 1967; Land, 1980; Mauchline, 1980; Wiebe et al., 1982; UNESCO, 1986; Brinton et al., 1987; Bowers, 1988; Ohman, 1988). Furthermore, organisms in higher trophic levels such as visual predators (*e.g.* fish) were not sampled. Although the diurnal vertical migration (DVM) is indication of visual predation (Lampert, 1989; Hays et al., 2001), diurnal replicate samples did not cover the full time series (Appendix II summarizes the findings on DVM). However, roles played by these species in the community can nonetheless be ruled out.

Net samples did not cover the bottom ca. 8 meters, and likely undersampled the zooplankton occupying the hyperbenthic zone (*e.g.* Choe & Deibel, 2000; Auel et al., 2003). Patchiness might also have hampered accurate interpretation of the population dynamics of gelatinous zooplankton (*e.g.* Swanberg & Båmstedt, 1991; Siferd & Conover, 1992; Falkenhaug, 1996; Lundberg et al., 2006) Potential misidentification of species (such as the Arctic *Calanus* spp.: see Appendix III) might also have been a likely source of error. Complex predator-prey interactions (other than those discussed here) might also add complications the relationships I described.

The lack of summertime zooplankton data hampered accurate life history descriptions of several species. Fewer temporal data points can blur the accuracy of my linear models. Coarse spatial (*i.e.* depth) resolution also likely have affected the accuracy of mean depth, and vertical overlap estimations. Although the advective impact on the present study seemed to be insignificant, implications of deepwater renewal was not quantified. Furthermore, I did not address the influence of physical parameters on annual routines in detail. However, there was little evidence to suggest that physical parameters (temperature, salinity, and day length) governed the seasonal habitat choice of dominant taxa (Appendix IV). In addition, instrumental, personal, and statistical errors might also have played minor roles in this study.

5. Conclusions

The focus of this investigation was to study the community dynamics of large size mesozooplankton using spatio-temporal variations of their numerical abundance, and body size. I described the life histories of dominant species in different trophic levels, and linked their annual routines to seasonal variations in food availability.

Zooplankton life histories investigated in this study reveal several annual routines (McNamara & Houston, 1996, 2008). Seasonal habitat shifts were common to all trophic levels: which were driven by temporal, and spatial dynamics of food availability. Overwintering was most pronounced in herbivores (ca. 2-5 months), but was not prominent in carnivores, and omnivores. This indicate that carnivores, and omnivores were active year-round compared to herbivores (*e.g.* Hagen, 1999). The reproduction was seasonal, and species of neither trophic level could spawn year-round. Spawning was the earliest in herbivores, which was largely decoupled from their main food source. In the contrary, carnivores, and omnivores spawned relatively late, (*i.e.* late spring, or summer) possibly with the annual development of food sources in surface waters.

The absence of year-round reproduction likely signify the trade-offs in energy allocation between survival (*e.g.* overwintering, seasonal migration) and reproductive strategies (*e.g*. McNamara & Houston, 1996, 2008; Zera & Harshman, 2001; Nygård et al., 2010; Fabian & Flatt, 2012; Varpe et al., 2009; Varpe, 2012). My findings suggest that annual energy budgets of neither trophic levels (with reference to investigated taxa) were efficient enough to counter the tradeoff between survival, and reproduction.

Results of this study indicate that the seasonal habitat occupation of predators was governed by those of their prey. In addition, I suggested possible links between the seasonal reproduction timing of most carnivores to those of their prey species. Therefore, I could trace the annual routines of prey species (i.e. lower trophic levels) in the life histories of their predators (higher trophic levels).

My findings also indicate that all the investigated dominant species were active in the winter. Inactivity (*i.e.* overwintering) of herbivores was restricted to autumn, but showed physical activity such as seasonal migrations and spawning under winter conditions (see also Arnkværn et al. 2005). This agrees with the recent findings of (Berge et al., 2009; Berge et al., 2013; Båtnes, 2013; Båtnes et al., 2013) that biological activity in Arctic ecosystems do not cease in the winter.

Although this investigation emphasized the seasonal variation of food availability, the environmental dynamics of high latitudes should be approached in both seasonal, and interannual perspectives. Year to year and long term variations of environmental conditions (*e.g.* ACIA, 2004; Hays et al., 2005; Mackas & Beaugrand, 2010; Wassmann, 2011; Wassmann et al., 2011; Mackas et al., 2012) are pronounced in the Arctic, and can bring about interannual variations in food conditions (Ji et al., 2010, Søreide et al., 2010, Leu et al., 2011). Such conditions may greatly hamper specialized feeders, such as predominantly herbivorous zooplankton (*e.g.* Søreide et al., 2010, Leu et al., 2011), causing mismatches between their seasonal life history decisions and the environment (Stenseth & Mysterud, 2002; Edwards & Richardson, 2004; Visser & Both, 2005; Both et al., 2009; Ji et al., 2010; Søreide et al., 2010; Leu et al., 2011). However, opportunistic feeders (*i.e.* omnivores) may suffer less from above challenges. According to my findings, the success of the omnivory was such that some dominant herbivores stragecally switched to omnivory during their spawning season (see also: Ohman & Runge, 1994; Hirche & Kwasniewski, 1997; Ohman & Hirche, 2001; Basedow & Tande, 2006). These results collectively indicate that versatile feeding strategy might arguably hold the 'key' for adapting to the seasonal, and interannual extremities of the high Arctic.

Some limitations of this investigation include the coarse spatial (*i.e.* depth), biological, and to a certain extent temporal resolution. Zooplankton community dynamics of the WP2 dataset collected under this project can potentially be interpreted parallel to the findings of this study. This can not only address the aforementioned resolution concerns, but also might yield confirmations to the speculations/projections (*e.g.* spawning timing) I made in this study. In general, studying zooplankton as communities rather than few selected species should be encouraged. In such studies adequate sampling techniques should be adopted to describe both small (small taxa, eggs, nauplii etc.) and larger (predators in higher trophic levels) elements of the community. Although my descriptions on zooplankton annual routines mainly based on the bottom-up influences of trophic interactions (*i.e.* food availability), the influences of top-down regulation (*i.e.* predatory impact) should also be focused in future studies.

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Appendix I - Additional tables

Table 1: Information on zooplankton (Z) and hydrographical (H) samples collected during this investigation. Time is given as local time (UTC+1).

Date (code)	Transport	Type	ID	Time	Depth range (m)	Remarks
27.08.2008 (A27)	Viking Explorer	Z	A2701	0319	0-50	
			A2702	0325	50-100	
			A2703	0338	100-180	
06.09.2008 (S06)	Viking Explorer	Z	S0601D	1400	0-50	Diurnal replicate (Day)
			S0602D	1410	50-100	
			S0603D	1425	100-180	
07.09.2008 (S07)	Viking Explorer	Z	S0701N	0120	0-50	Diurnal replicate (Night)
			S0702N	0130	50-100	
			S0703N	0220	100-180	
22.09.2008 (S22)	Viking Explorer	H	S22H	-	0-180	Downcast
23.09.2008 (S23)	Viking Explorer	Z	S2301D	1330	0-50	Diurnal replicate (Day)
			S2302D	1400	50-100	
			S2303D	1310	100-180	
			S2304N	0130	0-50	Diurnal replicate (Night)
			S2305N	0145	50-100	
			S2305N	0230	100-180	
16.10.2008 (O16)	Viking Explorer	Z	O1601D	1530	50-0	Diurnal replicate (Day)
			O1602D	1530	50-100	
			O1603D	1645	100-180	
			O1603N	N	0-50	Diurnal replicate (Night)
		H	O16H	-	0-180	Downcast
17.10.2008 (O17)	Viking Explorer	Z	O1701N	N	50-100	Diurnal replicate (Night) (along with O1603N)
			O1702N	N	100-180	
04.11.2008 (N04)	Viking Explorer	Z	N0401D	1425	0-50	Diurnal replicate (Day) : (excluding N0404D)
			N0402D	1450	50-100	
			N0403D	1540	100-180	

Table 1 contd.

			N0404D	D	0-180	
			N0405N	0025	0-50	Diurnal replicate (Night)
			N0406N	0035	50-100	
			N0407N	0045	100-180	
		H	N04H	-	0-180	Downcast
02.12.2008 (D02)	Viking Explorer	Z	D0201N	0050	0-50	Diurnal replicate (Night)
			D0202N	0109	50-100	
			D0203N	0130	100-180	
03.12.2008 (D03)	Viking Explorer	Z	D0301D	1315	0-50	Diurnal replicate (Day)
			D0302D	1338	50-100	
			D0303D	1400	100-180	
		H	DO3H	-	0-180	Downcast
14.01.2009 (J01)	Snowmobile	Z	J1401	2020	0-50	
			J1402	2010	50-100	
			J1403	1955	100-180	
		H	J14H	-	0-180	Upcast
26.02.2009 (F26)	Snowmobile	Z	F2601D	1145	0-50	Diurnal replicate (Day)
			F2602D	1133	50-100	
			F2603D	1117	100-180	
			F2604N	0024	0-50	Diurnal replicate (Night) : (excluding F2606N)
			F2605N	0034	50-100	
			F2606N	0055	0-180	
		H	F26H	-	0-180	Downcast
23.03.2009 (M23)	Snowmobile	Z	M2301	1910	0-50	
			M2302	1925	50-100	
			M2303	1940	100-180	
		H	M23H	-	0-20	Downcast (Excluded)
30.03.2009 (M30)	Snowmobile	Z	M3001	1615	0-50	
			M3002	1645	50-100	
			M3003	1658	100-180	
		H	M30H	-	0-180	Downcast
20.04.2009 (A20)	Snowmobile	Z	A2001	1600	0-50	

Table 1 contd.

			A2002	1750	50-100	
			A2003	1740	100-180	
		H	A20H	-	0-180	Downcast
27.04.2009 (A27)	Snowmobile	Z	A2701	1550	50-0	
			A2702	1600	50-100	
			A2703	1620	100-180	
		H	A27H	-	0-180	Downcast
04.05.2009 (M04)	Snowmobile	Z	M0401	1600	0-50	
			M0402	1615	50-100	
			M0403	1640	100-180	
		H	M04H	-	0-180	Downcast
14.05.2009 (M14)	-	H	M14H	-	0-180	Downcast
17.06.2009 (J17)	-	H	J17H	-	0-143	Downcast
15.07.2009 (J15)	-	H	J15H	-	0-172	Downcast

Time of some zooplankton samples were not available (only mentioned as day and night). **D:** Day, **N:** Night, **Z:** Zooplankton sample, **H:** Hydrographical sample

Table 2: Component distribution parameters (C_i), and length frequency analysis outputs of the three size groups (G_0, G_1, and G_2) of the chaetognath *Parasagitta elegans* (Verrill, 1873). All length measurements are in millimeters.

Month	G_0				G_1				G_2			
	C_i	Mean	SD	Pi (%)	C_i	Mean	SD	Pi (%)	C_i	Mean	SD	Pi (%)
August	< 19	13.81	1.33	3	19-29	22.73	2.19	53	≥ 29	33.08	3.19	44
September	< 19	13.45	1.36	1	19-29	21.80	2.20	50	≥ 29	32.69	3.30	49
October	< 19	14.16	1.35	1	19-29	23.51	2.24	42	≥ 29	33.82	3.22	57
November	< 16	13.99	1.42	1.1	16-29	23.87	2.42	51	≥ 29	33.89	3.44	48
December	< 19	14.58	1.65	0.1	19-31	24.46	2.77	79	≥ 31	34.43	3.89	20
January	< 18	-	-	-	18-32	24.44	3.21	82	≥ 32	36.59	4.80	18
February	< 18	14.84	1.71	0.7	18-29	23.45	2.70	29	≥ 29	33.90	3.91	64
March	< 20	-	-	-	20-29	25.23	3.38	57	≥ 29	32.52	4.36	43
April	< 20	16.53	1.73	0.2	20-29	25.80	2.70	13	≥ 29	33.32	3.49	85
May	< 20	-	-	-	20-29	21.45	2.39	3	≥ 29	31.45	3.50	97

Pi: relative proportion of size group *i*

Appendix II - Diurnal habitat shifts of dominant zooplankton

In this study diurnal replicate samples were obtained during the autumn to winter transition period (September to December: Appendix I, Table 1). During the first two months, there was a clear distinction in the diurnal light (PAR) regime (data not presented). In the contrary, during November, and December, the quantum PAR sensor could not perceive any level of radiation.

I found little evidence to support the existence of diurnal habitat shifts (as indicative of DVM) among overwintering stages of *Calanus* spp. (Appendix II, Fig. 1). However, adult females of *Calanus* showed shallower nighttime habitat preference compared to daytime between September, and October (*C. glacialis*), and early December (*C. finmarchicus*) (Appendix II, Fig. 1B3 & C3). The day and night samples of October, and December were obtained with no detectable PAR. Since light is considered as the proximal cue for the diurnal vertical migration (DVM) (Hays et al., 2001; Cottier et al., 2006), it is unclear what triggered the diurnal habitat shifts of above females. This finding evokes the recent theory that copepods are sensitive to low levels of light (*i.e.* background levels of radiation), which might not be perceived by most conventional light sensors (Berge et al., 2009; Båtnes, 2013; Båtnes et al., 2013). Furthermore, theory that proximal cue for DVM is an in-vivo process, which is driven by a pre-programmed, internal clock (van Haren & Compton, 2013) cannot also be ruled out. However, due to low abundances of adult females during the investigated period (Fig. 1A3) and the coarse spatio-temporal resolution (Cottier et al., 2006) of sampling, these diurnal habitat shifts needs careful interpretation.

In addition to above, none of the other dominant carnivore or omnivore species showed a rhythmical, reproducible, or synchronized (Cottier et al., 2006) pattern of diurnal habitat shifts (data not presented).

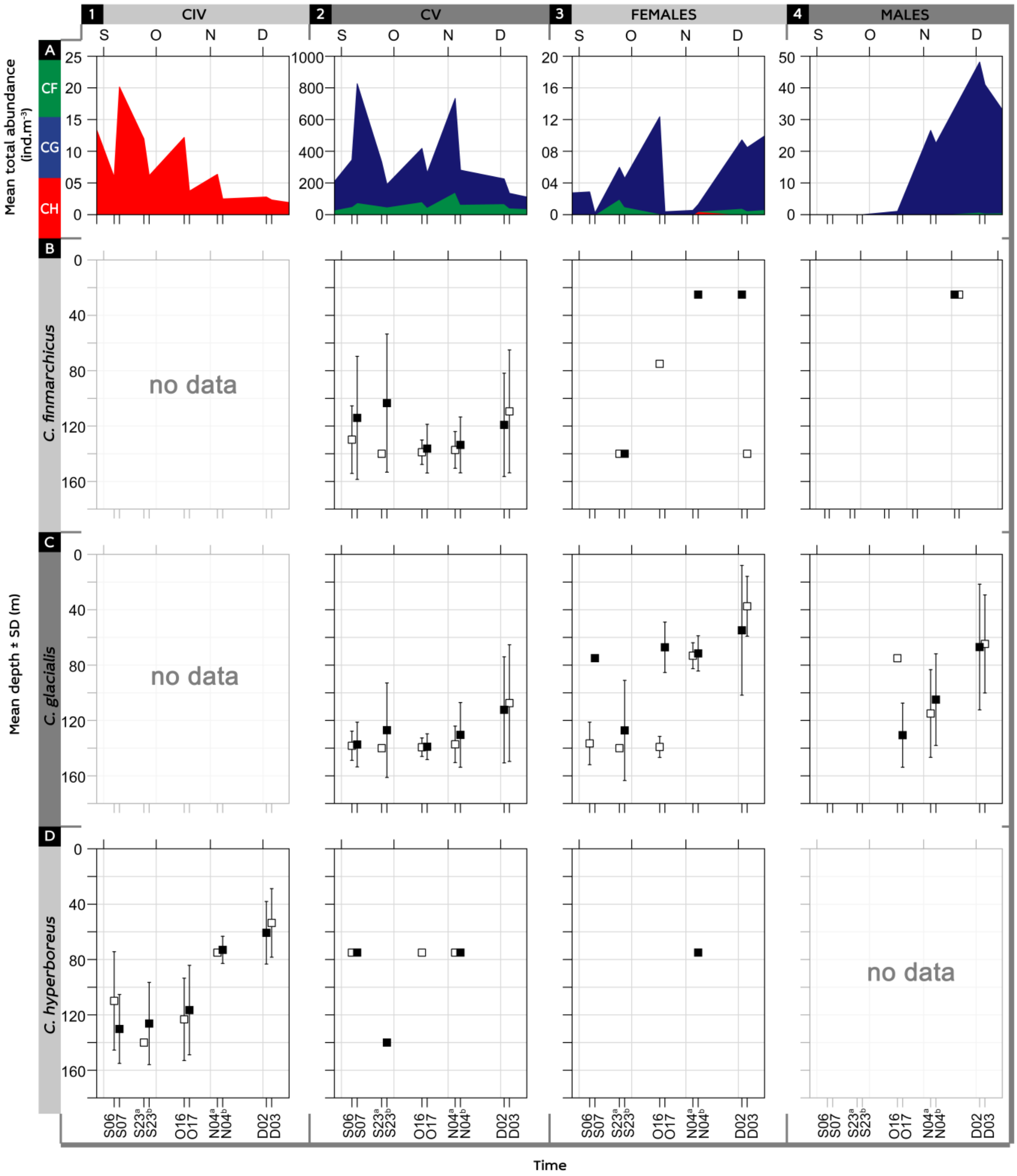

Fig. 1: The diurnal vertical behaviour (habitat shifts) of different developmental stages of *Calanus* spp. Top panels (A1-A4) indicate the mean total abundance. Data are presented as the mean depth (Z_m), with the SD (Z_s) denoted by the dispersion bars. Day (□) and night (■) are expressed according to the local time (UTC+1). **CF:** *C. finmarchicus*, **CG**: *C. glacialis*, **CH**: *C. hyperboreus*

Appendix III - Complexities in morphometric resolving of *Calanus* spp.

Among a few morphology-based traditional techniques (*e.g.* Jaschnov, 1972; Frost, 1974; Arashkevich et al., 2002), the use of morphometric characters have been widely emphasized in resolving Arctic congeners of Calanus (*e.g.* Jaschnov, 1972; Hirche, 1991; Unstad & Tande, 1991; Hirche et al., 1994; Madsen et al., 2001; Arashkevich et al., 2002; Auel & Hagen, 2002; Kwasniewski et al., 2003; Walkusz et al., 2003; Arnkværn et al., 2005; Daase & Eiane, 2007; Blachowiak-Samolyk et al., 2008; Daase et al., 2008; Søreide et al., 2008; Hirche & Kosobokova, 2011; Rabindranath et al., 2011; Bailey, 2010).

Substantial sample sizes and manageable degrees of overlap (< 40%) between their respective PL distributions (Appendix III, Table 1) allowed me to perform the length frequency analyses and derive unique PL boundaries to separate all the existing developmental stages (CV, adult females, and males) of the two *Calanus* species. The PL boundaries I obtained were comparable with those published in an array of previous literature (Table 3). However, since there are a number of spatial, temporal, and technical (*i.e.* the utility of different sampling gears) differences between studies, direct trans-study comparisons of PL boundaries should be done with caution.

Table 1: Percentage overlap (estimated by numerical integration) of the fitted normal distributions for each developmental stage of G_x, *C. finmarchicus, and C. glacialis*

Distribution (n)	G_x and CF	CF and CG	G_x and CG
CV (3908)	6.36%	33.17%	1.26%
Adult females (1409)	12.20%	39.97%	0.00%
Adult males (387)	-	10.12%	-

CF: *C. finmarchicus*, **CG:** *C. glacialis*, **G_x:** unidentified taxonomic group, **n**: sample size

Although its identity is not resolved, G_x might most likely have represented a smaller, undersized size group of *Calanus*. Also, accounting for possible instrumental, personal, and statistical errors of the morphometric analysis, it could have been possible that G_x represented mis-staged smaller developmental stages (stage IV, and V copepodids as CV's and adult females respectively).

With the development of molecular ecological tools, and techniques to distinguish sympatric populations of sibling species of Calanus (Bucklin et al., 1992, 1995; Lindeque et al., 1999; Hill et al., 2001; Parent et al., 2011; Gabrielsen et al., 2012), the use of traditional morphological, and morphometric methods have received a barrage of critique. Parent et al. (2011), and Gabrielsen et al. (2012) found out that misidentification of these species due to the lack of reliability of traditional identification methods can cause drastic errors in their subsequent numerical estimates (*i.e.* abundance). Although I basically agree with these recent views, a number of technical (*i.e.* number, and frequency of samples), and financial (cost of processing large no. of samples) challenges need to be overcome before fully implementing these advanced protocols into long term studies.

In the present study, there can be cases where individuals of *C. finmarchicus* were identified as *C. glacialis*, and vice versa. However, with substantial sample sizes, manageable levels of overlap between PL distributions, and fulfillment of other underlying assumptions of the length frequency analysis, I hypothesize that potential erroneous estimates of misidentified *Calanus* species, were minor compared to their actual population estimates.

Appendix IV - Statistical relations of physical variables and seasonal habitat choice

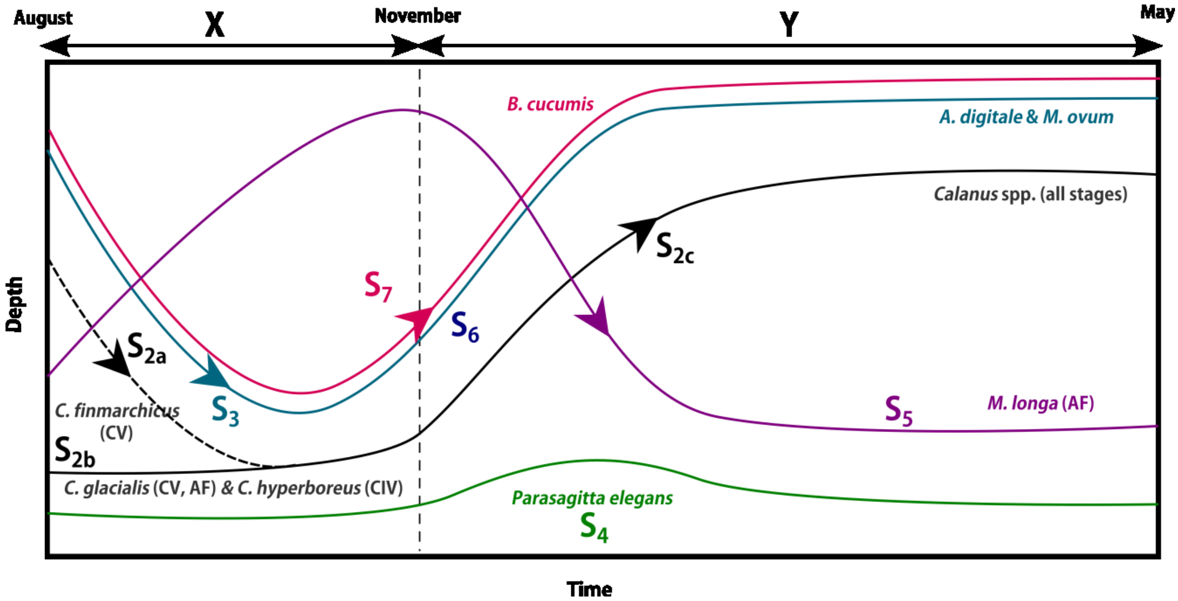

Fig. 1: Generalized vertical distributions of dominant taxa (S_2–S_7) in the autumn (X), and winter-spring (Y) in Billefjorden. S_6 is the generalized vertical distribution of *M. ovum*, and identical to S_3. Statistical relationships between these seasonal vertical distributions and physical data are given in Appendix IV, Table 1 (see below). Depth axis is not to scale, and does not represent neither absolute, nor relative vertical distributions of any taxa/parameter.

Table 1: The coefficients of determination (R^2) of the fitted linear models for relating seasonal vertical distributions with physical parameters. *W*, and *BP* are test statistics of Shapiro-Wilk, and Breusch-Pagan tests for normality, and homoscedasticity of the residuals.

V_R vs. V_E (T/S/DL)	Temperature (T)			Salinity (S)			Day length (DL)		
	R^2	*W*	*BP*	R^2	*W*	*BP*	R^2	*W*	*BP*
XS_2a vs. X	-0.50	0.77	2.67	-0.16	0.88	1.44	0.73	0.88	0.83
XS_2b vs. X	0.21	0.96	1.83	-0.37	0.87	1.50	-0.31	0.86	1.60
YS_2c vs. Y	0.46	0.80	1.25	-0.16	0.96	0.14	-0.09	0.88	0.84
XS_3 vs. X	-0.07	0.96	1.57	-0.46	0.96	1.57	-0.15	0.61	1.53
YS_3 vs. Y	0.14	0.74**	0.85	-0.18	0.19	0.85	0.65*	0.95	1.28
$(X+Y)S_4$ vs.(X+Y)	-0.12	0.96	2.25	0.38	0.96	1.47	0.17	0.91	0.47
$(X+Y)S_6$ vs. (X+Y)	0.50*	0.83*	1.98	-0.05	0.86	1.60	0.13	0.91	2.54
$(X+Y)S_5$ vs.(X+Y)	0.44*	0.75**	2.14	-0.12	0.86	0.002	0.21	0.86	0.76

V_R: Response variable, V_E: Explanatory variable
*p<.05, **p < .01, ***p < .001
Significant W and BP statistics denote residuals with non-normality, and heteroscedasticity. Breusch-Pagan statistic was estimated using R^{TM} package lmtest (Zeileis and Hothorn, 2012)