Seasonal zooplankton dynamics in Svalbard coastal waters: The shifting dominance of mero- and holoplankton and timing of reproduction in three species of Copepoda

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Summary

Monthly sampling was conducted in the ice-free Adventfjorden in West Spitsbergen, Svalbard, from March to November 2018 to assess the seasonal development in the Arctic zooplankton community and to investigate the seasonally shifting importance of meroplankton and holoplankton. Special focus was put on the reproduction strategy of three taxa of Copepoda: *Calanus* spp. Leach, 1816, *Pseudocalanus* spp. Boeck, 1872 and *Oithona similis* Claus, 1866. Additionally, three ice-covered fjords, Van Mijenfjorden in West Spitsbergen and Inglefieldbukta and Agardhbukta in East, were sampled in March and April to investigate the impact of sea ice on zooplankton species composition and abundance. Regarding the physical and biological environment in Adventfjorden, chlorophyll *a* was found in highest concentrations in May although the water column was still unstratified. Simultaneously with the high chlorophyll *a* concentrations, Cirripedia larvae (meroplankton) greatly dominated the zooplankton community. Throughout the remaining sampling period in Adventfjorden, holoplankton dominated. Of these, Copepoda was the most dominating order whereof *Oithona similis* was found to be the most numerically important copepod, followed by *Calanus* spp. and *Pseudocalanus* spp. The stage distribution of *Calanus* spp. suggested a dominance of individuals completing their life cycle within one year, with reproduction timed so as the nauplii could take advantage of the spring bloom in May. For *Pseudocalanus* spp. however, the stage distribution indicated a continuous reproduction with hatching occurring from the end of March until the end of August. Identification of the *Pseudocalanus* spp. by species-specific PCR and Illumina sequencing suggested a dominance of *P. acuspes* (Giesbrect, 1881) and *P. moultoni* Frost, 1989 amongst the reproducing population in Adventfjorden, while older stages of *P. minutus* (Krøyer, 1845) that were found might have been advected into the fjord. Abundance of small (<150 µm) Copepoda nauplii and presence of young *Oithona* spp. Baird, 1843 in late summer suggest that the genus most likely reproduced independent of phytoplankton abundance. At the ice-covered stations in early spring, chlorophyll *a* was found in similarly low amounts as in winter in Adventfjorden, and zooplankton abundance was low. Due to the reduced light penetration through ice, it's expected that the bloom in phytoplankton might not happen before the ice melts, and thus potentially delaying a peak in both mero- and holoplankton. The abundance of CIII and adult female *Calanus* spp. in the ice-covered fjords on the east coast might suggest a mix of individuals completing their life cycle within 1 or more years here. The high abundance of small Copepoda nauplii in Van Mijenfjorden indicated that zooplankton take advantage of the ice algae to fuel reproduction.

Contents

1 Introduction

In the marine environment zooplankton (zoo- (animal) + plankton (drifter)), animals with limited swimming capabilities which drift in the pelagic realm, constitutes a key link between primary production and the higher trophic levels. Many of the species are herbivores, depending on phytoplankton abundance, which in turn depend on solar energy for growth. This way, the marine ecosystem is generally largely controlled by light. In the Arctic, there's a strong seasonality in incoming solar radiation, where the sun is below the horizon (dark period) in winter and above (midnight sun) during summer, with length of each period depending on latitude. In Svalbard, an archipelago in the High Arctic, consisting of all islands between 74-81 °N and 10-35 °E, the dark period starts in the end of October and the period with midnight sun starts around mid-April (Figure 1.1). Both periods persist about four months each. This leads to a strong seasonality in primary production (Leu et al. 2015; Kubiszyn et al. 2017) with cascading impacts on their grazers and higher trophic levels. The incoming light is further restricted by sea-ice covering the water in many coastal areas in the Arctic through parts of the year.

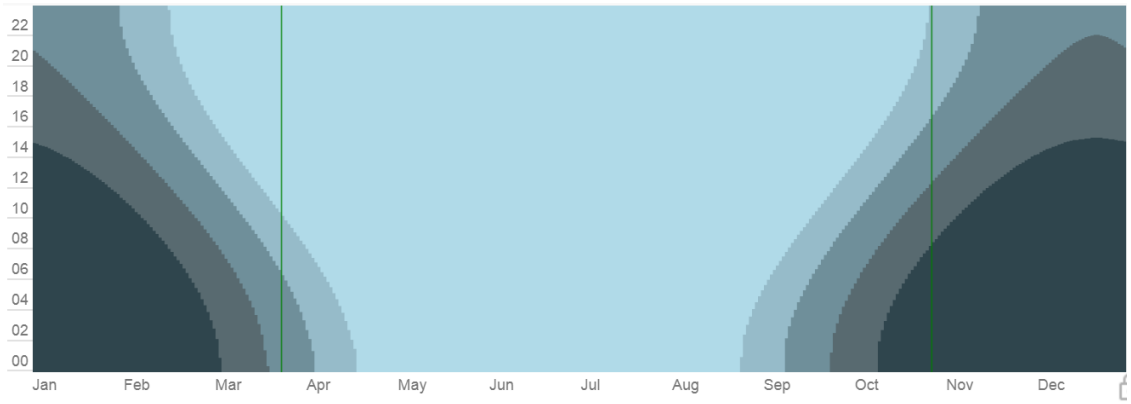

Figure 1.1. Sun graph of Longyearbyen in 2018, with day/night length (hours) as a function of date (month, x-axis) from January to December, with shading indicating light condition from dark to light: Night, sun more than 18° below horizon; Astronomical twilight, 12-18° below horizon; Nautical twilight, 6-12° below horizon; Civil twilight, 0-6° below horizon; Daylight, sun above horizon.
Illustration: timeanddate.com

Although there are many other factors affecting the marine ecosystem, as e.g. nutrient content and circulation, the seasonally shifting light plays one of the most important roles in the Arctic. In addition to the seasonality in light, the Arctic marine ecosystem in Svalbard is affected by differing hydrology, which change both seasonally and depending on location around the Archipelago. Generally, the west coast of Spitsbergen, the biggest island in Svalbard, is relatively mild, compared to other Arctic areas. This is due to the influence of the West Spitsbergen Current (WSC), a branch of the North Atlantic Current, which bring warm Atlantic

Water from the south (Figure 1.2a). The east coast of Spitsbergen however is more affected by Arctic Water (Skogseth et al. 2005) and generally has a colder climate than the west coast. Additionally, the water in the fjords of Svalbard receive fresh water from melting of snow and glaciers which cover 60 % of the land. Due to the WSC, most of West Spitsbergen remain ice-free throughout the year, while most of the ArW-influenced fjords in East Spitsbergen are covered by land fast sea ice during winter (Figure 1.2b).

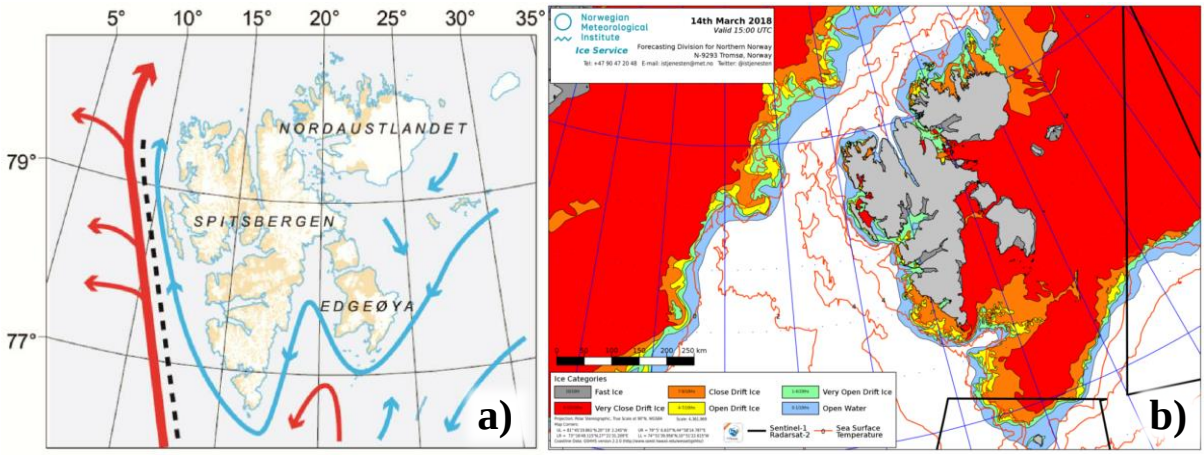

Figure 1.2. Map of Svalbard with a) the major currents, Atlantic water from the WSC (red line) and Arctic water (blue) with the frontal area between the currents (dashed black line) (From Svendsen et al. (2002)) and b) sea ice cover on 14 March 2018, with the darker grey colour representing fast ice (Illustration: the Norwegian Meteorological Institute).

When the sun rises higher on the horizon and day length increases sufficiently for providing enough light, the ice-free water experience an increase in the phytoplankton abundance (the spring bloom) after a period of low abundance in winter (Kubiszyn et al. 2017). Opposed to more temporal areas, the Arctic has most commonly only this one major peak in pelagic primary production (Daase et al. 2013). In the ice covered fjords however, the sea ice provides a limitation to the amount of light available to the phytoplankton, as the ice and overlying snow reflects and absorbs the incoming radiation. This delays the growth of pelagic phytoplankton which won't bloom before the shading sea ice melts (Hegseth 1998). A peak of primary production is however commonly found in the ice covered waters prior to this. The early peak of primary production is caused by algae growing within and at the bottom of the sea ice (ice algae) which starts to grow as soon as sufficient light is available (Leu et al. 2015) and persists until the sea ice breaks up and melts. Thus, the ice-covered waters commonly experience two blooms in primary production; an ice algal bloom followed by a phytoplankton bloom (Søreide et al. 2010).

In the zooplankton community in Svalbard, both meroplankton, organisms which only spend parts of their life cycle as plankton, and holoplankton, organisms which are plankton their whole life cycle, can be found. The meroplankton are larval stages that drift around in the pelagic realm before either settling on the sea floor as benthos or developing to actively swimming nekton. Only the meroplankton of benthic origin are studied in this thesis, and for the remainder of the thesis the use of the term meroplankton refers to these. The planktonic larval stage is advantageous for the benthic fauna as a way to increase dispersal rate and area (Scheltema 1986), and has been found in high abundances in Arctic waters (Fetzer & Arntz 2008; Stübner et al. 2016) although previously believed to be scarce at high latitudes (Thorson 1936). In Svalbard waters, meroplanktonic larvae of e.g. Crustacea, Bivalvia, Polychaeta and Echinodermata have been found to be numerous (Stübner et al. 2016). While the holoplankton are present as important prey in the water column throughout the productive summer season, the meroplankton are potentially present in high abundances in short pulses. The meroplankton also contribute to the pelagic-benthic coupling, in both directions. Organisms having a planktotrophic larval stage which feed in the pelagic realm transfers energy from the pelagic to the benthic, while working the other way around when the meroplanktonic larvae are preyed on by pelagic organisms.

Of the holoplanktonic community in Svalbard, both under sea ice and in ice-free regions, the zooplankton community is generally dominated by Copepoda, with the three Calanoida species *Calanus glacialis* Jaschnov, 1955, *C. finmarchicus* (Gunnerus, 1770) and *C. hyperboreus* Krøyer, 1838 amounting to 50-80% of the total mesozooplankton biomass in the area (Daase & Eiane 2007; Søreide et al. 2008). The zooplankton communities around the archipelago generally doesn't differ between each other in term of taxonomic distribution, but rather in species abundances where hydrography determines each species' abundance in the different areas (Søreide et al. 2003; Daase & Eiane 2007). In addition to the three previously mentioned *Calanus* species, the Cyclopoida *Oithona similis* Claus, 1866, and the calanoids *Pseudocalanus* spp. Boeck, 1872 and *Metridia longa* (Lubbock, 1854), can amongst others be found (Hop et al. 2002; Daase & Eiane 2007).

The holoplanktonic Copepoda species has a life cycle with eggs hatching into nauplius larvae (6 naupliar stages, abbreviated NI-NVI) which develop into copepodid larvae (5 copepodid stages, abbreviated CI-CV) before maturing into the sixth copepodid stage – the adult female or male (abbreviated CVIF/AF or CVIM/AM respectively). Time needed to complete the life

cycle varies between genera and species, with developmental rate much depending on location and consequent water temperature (Corkett & McLaren 1979; Corkett et al. 1986).

Studies on copepod development in the Arctic has largely been focused on the bigger copepods, and particularly on the genus *Calanus* Leach, 1816, where e.g. *Calanus glacialis* has been found to vary their reproduction strategy depending on location in the Arctic (Daase et al. 2013). Generally, they time reproduction so the offspring can take advantage of the high-quality food during the spring bloom. During summer they develop through the naupliar and copepodid stages and accumulate lipids prior to descending to the deep for diapause in autumn, mainly as CIV and CV (Søreide et al. 2010). They are capital breeders, i.e. reproduction is fuelled by internal energy storages (Daase et al. 2013). Individuals living in ice-covered water, however, has been shown to utilise both ice algae and phytoplankton, and take advantage of the delay of 1-2 months between the two primary production peaks (Søreide et al. 2010; Daase et al. 2013). The ice algae are used to fuel and speed up gonad maturation which allow reproduction to happen earlier so that the offspring can feed on the high-quality food during the pelagic phytoplankton bloom occurring once the ice has melted.

The life cycles of the smaller Copepoda in the Arctic are generally poorly studied. This is partly due to the difficulty in handling their small size, and that they are often underrepresented in samples taken by standard zooplankton nets (Gallienne & Robins 2001). In the genus *Pseudocalanus* high degree of morphological and morphometrical similarity exist between the congeners (Frost 1989), making it increasingly difficult to identify species specific differences in life history strategies and population dynamics. It was previously believed to only occur with two species, *P. minutus* (Krøyer, 1845) and *P. acuspes* (Giesbrecht, 1881), in Svalbard waters, but studies involving genetic identification showed representation of a third congener, *P. moultoni* Frost, 1989 (Aarbakke et al. 2011), which is close to morphologically identical to *P. acuspes* (Frost 1989). Of these *P. acuspes* is suggested to be a neritic species, while *P. minutus* is more oceanic (Koszteyn & Kwasniewski 1991; Lischka & Hagen 2005), and *P. moultoni* is likely to co-occur with *P. acuspes* (Frost 1989).

Small copepods are potentially important prey for fish larvae (Heath & Lough 2007), thus it is of utmost importance to have basic knowledge on their biology. With the expected rise in global temperature the coming years (Hartmann et al. 2013), where the Arctic is expected to experience higher temperature rise than the global average (Serreze & Francis 2006; Screen &

Simmonds 2010), a change in species composition and life history strategies may be expected (Wassmann et al. 2011; Kortsch et al. 2015). Additionally, the increased temperature has led to a decrease in extent of sea ice cover in the Arctic, and models predict total loss of sea ice during September with further addition of CO_2 emissions (Notz & Stroeve 2016). The reduction in sea ice extent and longevity will impact the algal bloom phenology and consequently the grazers (Søreide et al. 2010; Daase et al. 2013).

A base line knowledge of present species composition and life histories is important for detecting potential consequences of climate change on high Arctic marine ecosystems. To improve our seasonal baseline knowledge on high Arctic zooplankton communities, monthly sampling was conducted in an ice-free fjord in West Spitsbergen from March to November 2018. Special focus was put on two important genera of Calanoida: *Calanus* and *Pseudocalanus*, and the Cyclopoida *Oithona similis*. Individuals of *Pseudocalanus* were genetically identified to species to investigate this poorly known genus' species composition. Zooplankton was sampled with a fine meshed (60 µm) zooplankton net to sample the smaller Copepoda and naupliar stages. To investigate how the sea ice and different water masses in East and West Spitsbergen impact zooplankton abundance and species composition, sampling was conducted in three ice-covered fjords in early spring 2018 for comparison, two in East and one in West Spitsbergen. The following five research questions were targeted:

1. How does the seasonally changing physical and biological environment shape the zooplankton community in Adventfjorden?
2. How is the dominance of meroplankton and holoplankton shifting through the productive season in Adventfjorden, and what taxa dominates in the respective groups?
3. How does the presence of sea ice influence the zooplankton community in early spring, and how does this differ between East and West Spitsbergen?
4. What are the reproductive strategies of the dominating Copepoda genera, *Calanus*, *Pseudocalanus* and *Oithona*?
5. What species of *Pseudocalanus* can be found in Adventfjorden, and does the composition of the congeners differ through the season?

2 Materials and methods

Sampling was conducted in four fjords around Spitsbergen, the largest island of the Svalbard archipelago: Adventfjorden and Van Mijenfjorden on the west coast and Agardh- and Inglefieldbukta on the east coast (Figure 2.1). Sampling was done once a month from March to November in Adventfjorden, in March in Van Mijenfjorden, twice in winter-spring (March and April) in Inglefieldbukta and once in April in Agardhbukta (Table 2.1).

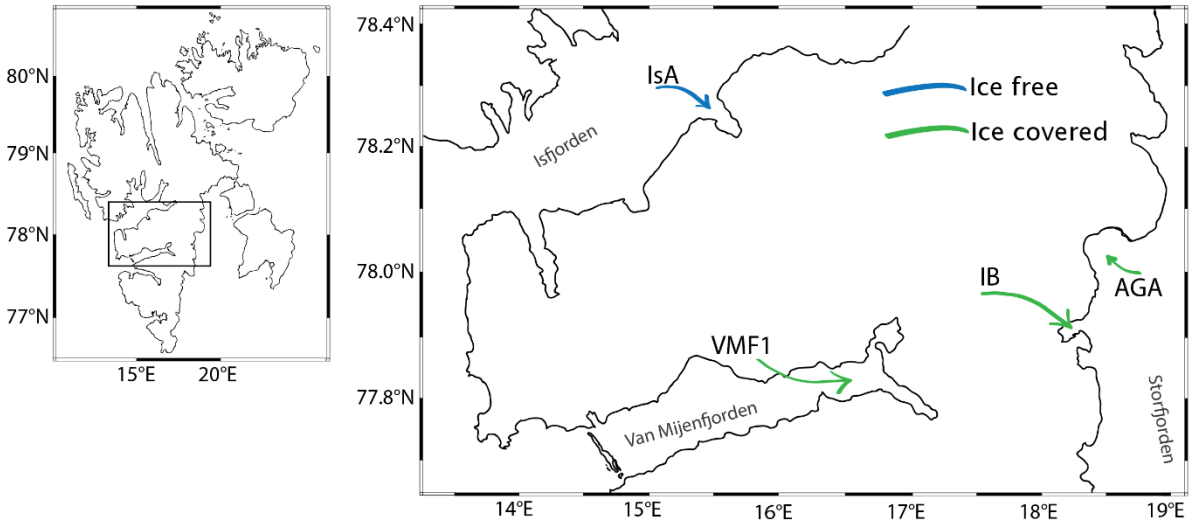

Figure 2.1. Map of Spitsbergen, Svalbard, and location of the ice free (blue) and ice covered (green) sampling stations in Adventfjorden (IsA), Van Mijenfjorden (VMF1), Inglefieldbukta (IB) and Agardhbukta (AGA).

2.1 Study area

Adventfjorden (78.3°N, 15.5°E) is an ice-free fjord on the western coast of Spitsbergen. Adventfjorden is oriented to the northwest and is a small side fjord (3.5 km wide and 8 km long) of Isfjorden, the largest fjord system in Svalbard. The fjord is 60-120 m deep and has no sill. It receives freshwater from the river Adventelva which creates a big river delta at the innermost part of the fjord. The fjord is mainly influenced by Atlantic water from the West Spitsbergen Current. Sampling was conducted at the long-term sampling station Isfjorden-Adventfjorden (IsA), situated at the fjord mouth at 78.26°N, 15.53°E, from March to November 2018. Due to logistical problems and surface drifting of the sampling vessel on sampling day, the exact position of sampling varied from month to month (Table 2.1), but all sampling was conducted around the fjord mouth.

Van Mijenfjorden (77.7-77.8°N, 14.8-16.8°E), in West Spitsbergen, is a sill fjord with a seasonal ice cover. The fjord faces west-southwest and is 15 km wide and over 50 km long. It has a 74 m deep inner basin and a 115 m deep outer basin, separated by a 45 m deep sill. The island Akseløya almost completely blocks the fjord's outlet, making the fjord constitute mainly of local water, which has low temperature and salinity due to winter cooling and river and glacier discharge in summer, creating favourable conditions for sea ice formation during winter. Sampling was conducted at the station VMF1 on sea ice in April 2018, in the inner basin of Van Mijenfjorden (Table 2.1)

Inglefieldbukta (77.9°N, 18.3°E) and Agardhbukta (78.0°N, 18.5°E) are two bays in East Spitsbergen with seasonal ice cover. Inglefieldbukta faces to the east, is 3 km wide and 3.8 km long. The bathymetry of the bay is currently unknown, but field investigations during March 2018 indicated that the bay consists of a basin with around 30 m depth and a 9 m deep sill at the entrance. The sea terminating glacier Inglefieldbreen is approx. 4 km wide and dominates the coastline in the west. Agardhbukta faces to the south east, is 9 km wide and 4.5 km long. The river Agardhelva flows out in the innermost part of the bay. Bottom depth is largely unknown but is most likely quite shallow. The sampling station in 2018 was located rather far out (Figure 2.1) and had a depth of 40 m. Both Inglefield and Agardhbukta are located in Storfjorden which is mainly influenced by Arctic water (Skogseth et al. 2005). Sampling was conducted in Inglefieldbukta (station IB) in March and April and in Agardhbukta (station AGA) in April 2018 (Table 2.1).

Table 2.1. Sampling dates, station names and coordinates and bottom depths in Adventfjorden, Van Mijenfjorden, Inglefieldbukta and Agardhbukta during sampling conducted in 2018.

Fjord	Station	Sampling date	Latitude (DD)	Longitude (DD)	Bottom depth (m)
Adventfjorden					
	IsA	March 14	77.25530	15.53399	78
		April 5	78.26133	15.49183	84-73
		May 1	78.25530	15.53399	72
		May 11	78.25530	15.53399	100
		June 18	78.275	15.4783	100
		July 19	78.275	15.4783	123
		August 18	78.26133	15.52757	88
		September 17	78.2545	15.53133	70-83
		October 15	78.2665	15.33167	94
		November 15	78.25556	15.53361	68
Van Mijenfjorden					
	VMF1	April 14	77.82455	16.57377	70
Inglefieldbukta					
	IB	March 23	77.8911	18.23595	34
		April 27	77.88803	18.22947	32
Agardhbukta					
	AGA	April 15	78.00967	18.57377	42

2.2 Sample collection

2.2.1 Physical properties

Hydrography

The *in situ* conductivity, temperature and density through the water column was measured using a CTD (Conductivity, Temperature and Density) at all stations and all sampling dates. A handheld SD208 CTD (SAIV, Bergen) was used at all stations and dates, except at IsA May 11 and August 18 when a SBE911+ CTD-Rosette water sampler system (Sea-Bird Electronics Inc.) was used onboard R/V Helmer Hansen. The handheld CTD, set to make a measurement every second, was lowered to around 10 m above the sea floor (Appendix 1.1, table A1.1) with a speed of maximum 0.5 m s^{-1}, after leaving it one minute just below the surface for acclimatisation, and it was raised with the same speed.

Light and turbidity

Light intensity through the water column was measured as close to noon as possible (See Appendix 1.2, Table A1.2 for measurement times) at all stations and sampling dates, except at IsA on May 11 and in August, October and November. The photosynthetic active radiation (PAR; light with wave bands between 400-700 nm) in number of photons arriving the sensor per unit time per unit area (µmol s^{-1} m^{-2}) was measured at discrete depths, between surface and 40 m (Appendix 1.2, table A1.2 for measurement depths), with a LI-192 Underwater Quantum Sensor (LiCor, USA). Simultaneously the light intensity over water surface was measured with a LI-190 Quantum Sensor (LiCor, USA). Measurements were read of a LI-1400 DataLogger (LiCor, USA) with light intensity in water (I_Z) and light intensity at surface (I_S) being noted at approximately the same time for each depth (maximum 3 seconds in between the reading of each). For IB March, only one measurement was done of I_S.

The ice thickness and snow depth was measured in the ice above where light was measured at all ice-covered stations but IB in April. Ice thickness was measured through the hole created by coring using a tape measurer. Snow depth was measured at three random points around each core hole by pushing a ruler through the snow to the top of the ice. For IB in April, data presented is average data of measurements done in the ice and snow for 12 ice cores taken the same day.

2.2.2 Chlorophyll a

Water was collected at pre-determined standardised depths (Table 2.2) by a 10L Niskin Water Sampler bottle (KC Denmark, Silkeborg) for chlorophyll *a* (chl *a*) content. Water was sampled at 15 m at all stations except at IB in March where only water at 3 m depth was sampled (Table 2.2). The water was transferred to 10 L canisters which were placed in a cooler box for as little light exposure and as stable temperatures as possible during storage and transportation back to the laboratory for further processing.

Table 2.2. Sampling depths (m) for the surface and deep water samples taken at all sampling stations during 2018, with X in the 15 m column for dates when sampling was conducted of this depth.

Fjord	Station	Sampling date	Surface (m)	15 m	Deep (m)
Adventfjorden					
	IsA	March 14		X	68
		April 5	1	X	75
		May 1		X	65
		May 11	1	X	80
		June 18	1	X	
		July 19	1	X	
		August 18	1	X	
		September 17		X	50
		October 15		X	80
		November 15		X	60
Van Mijenfjorden					
	VMF1	April 14	1	X	65
Inglefieldbukta					
	IB	March 23	3		
		April 27	1	X	
Agardhbukta					
	AGA	April 15	1	X	37

2.2.3 Zooplankton

Mesozooplankton was sampled using a WP2 net (Hydro-Bios, Kiel) with a mesh of 60 µm and a cod end with 60 or 64 µm mesh size. A 200 µm mesh size net and cup was used at IsA in May to avoid clogging by phytoplankton. The net was lowered to approx. 10 m above the seafloor (Table 2.3) and raised vertically at a slow speed (0.5 m s^{-1}) to surface. After gently rinsing the net, the sample was transferred to a bucket using seawater from the surface and stored in a cooling box until concentration. Minimum two hauls were taken at all stations, one for formalin and one for ethanol fixation. Most stations had additional hauls, but not all were processed. Metadata are only presented for the processed hauls (Table 2.3).

Table 2.3. Overview of zooplankton net samples conducted by vertical WP2 net (0.25 m^2) hauls in 2018. Processed hauls are presented with bottom (B) and sample (S) depth (m), fixative (formalin (F) or ethanol (E)) is given in addition to number of haul. For station coordinates, see table 2.1.

Station	Sampling date	Replicate and fixative	Mesh size (µm)	B. depth (m)	S. depth (m)
IsA	March 14	F1	60	78	65
	April 5	F1	60	84	75
		F2	60	83	75
	May 1	F1	60	72	60
		F2	200	72	60
		E1	200	72	60
	May 11	F1	200	100	70
		E1	200	103	70
	June 18	F1	60	100	90
	July 19	F1	60	123	115
		E1	60	123	115
	August 18	F1	60	88	75
		F2	60	82	75
		E1	60	79	75
	September 17	F1	60	83	70
	October 15	F1	60	94	75
	November 15	F1	60	68	58
VMF1	April 14	F1	60	70	70
IB	March 23	F1	60	34	29
	April 27	F1	60	32	26
AGA	April 15	F1	60	42	35

The samples were concentrated over a sieve with mesh size 60 µm and transferred to 250 mL sample bottles within 6-12 hours after capture. For formalin fixed samples 36 % borax buffered formalin was added to ensure a final concentration of 4 % formalin. Ethanol was added to as high concentration as possible (70-80 %) for the ethanol fixed samples, and the ethanol was changed after 24 hours to ensure sufficiently high concentration. Ethanol fixed samples were stored in 4 °C.

2.3 Sample analyses

2.3.1 Chlorophyll a

The water samples for chl *a* concentration was filtered with a vacuum pump filtration system, in as dark conditions as possible. A set volume, based on particle density in the water sample (Appendix 1.3, table A1.3), was filtered through GF/F grade glass microfiber filters (GE Whatman, UK) of pore size 0.7 µm. The filters were placed in 10 mL methanol and kept in darkness at 4 °C for 24 hours for chl *a* extraction. Some filters were frozen at -80 °C for up to six months prior to extraction (see Appendix 1.3, Table A1.3).

After extraction in methanol, the content was poured into a 13 mm cuvette, through a 0.22 µm glass filter when particles from possible dissolved filters were observed in the sample. After cleaning the cuvette with soft paper, the cuvette was placed in a 10-AU Fluorometer (Turner Designs, California) and measured. Uncorrected raw chl *a* content was recorded (*chl* a_{RAW}). Two droplets of 10 % HCl was added to break down active chl *a* into phaeophytin *a*. The cuvette was placed back into the fluorimeter after some turning of the cuvette to mix the HCl, and phaeophytin *a* content was recorded (*phaeo* a). The final corrected chl *a* (excluding the phaeophytin *a* proportion) content in the water in µg L^{-1} was calculated using the formula

(F 1)

$$chl\ \mathrm{a} = ((chl\ \mathrm{a}_{RAW} - Blank) - (phaeo\ \mathrm{a} - Blank)) \times \frac{1.7 \times Vol_{MetOH}}{Vol_{filtered}}$$

Where *Blank* is the fluorometer reading of a cuvette filled with methanol only, Vol_{MetOH} is the volume (mL) of methanol used for extraction and $Vol_{filtered}$ is the volume (mL) of water filtered.

2.3.2 Zooplankton community composition

Samples preserved in 4 % formalin were poured over a 60 µm sieve to get rid the fixative and rinsed twice with 20 µm filtered seawater to remove the formalin. For samples with high concentrations of zooplankton, the sample was split in 2 or 4 using a Motoda plankton splitter (Motoda 1959; Van Guelpen et al. 1982). Macrozooplankton, defined as everything longer than 10 mm (e.g. chaetognaths), and rare individuals easily distinguishable with the naked eye (e.g. Decapoda zoea larvae and hydrozoans), were picked out from the sample before taking subsamples. These were picked out from the total sample for all but IsA May 11 when macrozooplankton was picked out from one of two parts of a split sample. The macrozooplankton fraction was identified to the taxonomic level given in the species list in Appendix 6 and counted.

The sample was diluted with 20 µm filtered seawater to a suitable volume and subsamples were taken using a 1-5 mL Finnpipette (ThermoFisher Scientific). All individuals in each subsample were identified to the lowest distinguishable taxonomic level possible (Appendix 6) using a Leica MZ16 stereomicroscope (Leica Microsystems, Meyer Instruments, Houston) and suitable literature (Koszteyn & Kwasniewski 1991; Conway 2006; Larink & Westheide 2011; Daase & Kwasniewski 2016), and counted. Subsamples were taken until at least 300 specimens had been identified and counted for total community composition.

Prosome lengths was measured of *Calanus* spp. copepodids after the length class definition from Daase and Eiane (2007) for species identification. Data is however only shown at genus level due to the questionable reliability of this method (e.g. Gabrielsen et al. (2012) found significant overlap in prosome lengths between the species in Svalbard waters). *Pseudocalanus* and *Microcalanus* Sars 1903 were separated based on *Pseudocalanus* lengths from Ershova et al. (2016). Copepoda nauplii were categorised after developmental stage and size: NI-III < or > 150 µm, NIV-VI < or > 500 µm, after the length distribution of *Calanus* spp. nauplii in Daase et al. (2011). The copepod nauplii were counted in subsamples until totally 100 nauplii had been counted, and subsamples for *Pseudocalanus* spp. stage composition were taken until at least a total of 100 *Pseudocalanus* spp. individuals were counted (see Appendix 1.4, Table A1.4 for size of fractions counted for each sample).

2.3.3 Pseudocalanus *molecular identification*

Molecular identification was attempted for *Pseudocalanus* spp. by species-specific Polymerase Chain Reaction (ssPCR, methods provided in Appendix 2). This did not prove successful, most likely due to degradation of the DNA after extraction.

Successful molecular identification of *Pseudocalanus* spp. was done by Dr Elizaveta Ershova (Post-doctoral researcher, UiT) at UiT, the Arctic University of Norway, using the following methods. Results will be presented and discussed with permission from Dr Ershova. A total of 120 *Pseudocalanus* spp. of different copepodid stages were picked out at random from subsamples of four ethanol preserved samples from Adventfjorden (Table 2.4). The *Pseudocalanus* DNA was extracted by HotSHOT extraction. The individuals were placed in PCR-tubes filled with 25 µL Alkaline Lysis Reagent (ALR) which were heated at 95 °C for 30 mins. 25 µL neutralisation buffer was added directly after.

Table 2.4. Number of *Pseudocalanus* spp. individuals of each copepodid stage (CI-AM) picked out from a subsample (proportion of total sample given in Fraction) of ethanol preserved samples from four sampling dates (Date) in Adventfjorden 2018, for molecular species identification, with total number of individuals picked from each sample (Total) and method for species identification (Method): Illumina sequencing (Illumina) and species specific PCR (ssPCR). 8 individuals from August 18 were identified using both ssPCR and Illumina.

Date	**Fraction**	**C1**	**C2**	**C3**	**C4**	**C5**	**AF**	**AM**	**Total**	**Method**
May 1	0.2					2	3	4	**9**	Illumina
May 11	0.0375			1		4	7	3	**15**	Illumina
July 19	0.15	4	11	18	8	6		1	**48**	Illumina
August 18	0.15	9	12	11	6	8	2		**48**	ssPCR(+Illumina)

The HotSHOT extracted DNA was used for species identification by Illumina sequencing and ssPCR. The individuals from May and July and 8 from August were identified by Illumina sequencing (Table 2.4), following methods described in Ershova et al. (subm.), while all individuals from August were identified using ssPCR. For the ssPCR, species specific reverse primers designed for each of the three congeners (*P. minutus, P. acuspes* and *P. moultoni*) designed by Dr Elizaveta Ershova (Ershova et al. 2016) were used together with a general *Pseudocalanus* forward primer (Table 2.5).

Table 2.5. Primer names and sequences used in ssPCR on *Pseudocalanus* spp. from Adventfjorden.

Primer name	Sequence
Minutus 398R	CGCAAACARAGGTATTTGGTCT
Acuspes 238R	AGAGGAGGGTATACAGTTCACC
Moultoni 520R	ACAATATTGTAATTGCMCCAGC
PseudoFmod	TTCGAATASARYTRGGHMVRGY

The primers were used in a 10 µL reaction including 5 µL Accustart II PCR ToughMix (Quantabio), 0.5 µL of each reverse primer, 1 µL forward primer, 0.2 µL GreenMix loading dye, 0.8 µL MilliQ water and 1.5 µL HotSHOT-extracted *Pseudocalanus* spp. DNA. Three positive controls, containing DNA of each species confirmed by sequencing, and one negative control containing MilliQ water were run for each PCR. The amplification protocol was 94 °C 3 min, 35 cycles of 94 °C 40 sec, 58 °C 40 sec and 72 °C 50 sec, and 72 °C 7 min. 4 µL of the resulting amplified DNA product was run on a 2 % agarose gel, containing 100 mL 1X TAE-buffer, 2 g agarose and 5 µL Etidium bromide, together with 4 µL Quick load 1kb DNA ladder (New England BioLabs) at 120 V until the DNA had run a sufficient distance on the gel. The gel was visualised under UV light and the *Pseudocalanus* species were determined by the length on the resulting amplified DNA (Figure 2.2).

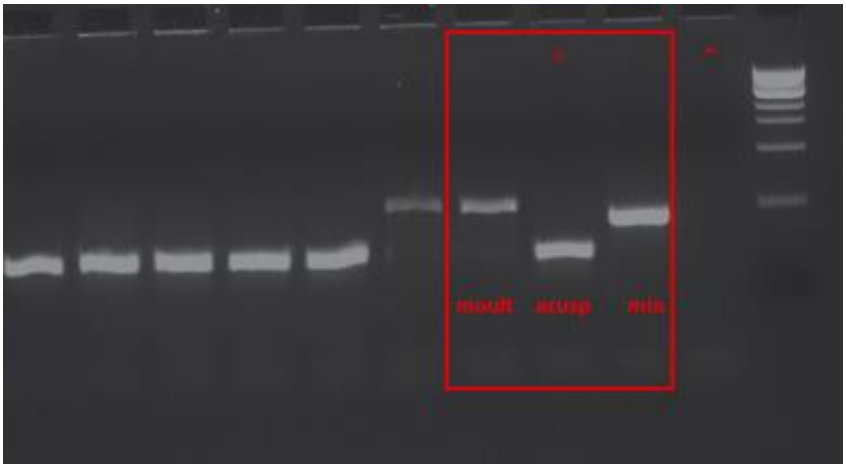

Figure 2.2. Illustration of UV visualization of DNA on agarose gel of DNA amplified by ssPCR where the species specific primers results in DNA of different length. Picture taken by Dr Elizabeta Ershova (UiT) showing a test run with DNA from 6 *Pseudocalanus* individuals, 3 positive controls (+, in red square) with *P. moultoni* (moult), *P. acuspes* (acusp) and *P. minutus* (min) DNA and 1 negative control (red - to the right of the red square).

2.4 Data analysis

2.4.1. Physical properties

2.4.1.1 Hydrography

Salinity at each depth was calculated from conductivity and temperature using the command gsw_SP_from_C() from the package "oce" (Kelley et al. 2018) in RStudio (R version 3.4.1). CTD data measured when lowering the CTD was processed in Ocean Data View (version 5.1.2), where plots of temperature and salinity as a function of depth and TS-plot were made. Water mass definitions were added in Adobe Illustrator following definitions by Svendsen et al. (2002) and Nilsen et al. (2008).

2.4.1.2 Light attenuation

Due to change in incoming solar radiation during lowering of the light meter, the fraction of light penetrating to depth *z* (f_z) was calculated by equation

(F 2)

$$f_z = {}^{I_Z}/_{I_S}$$

Where I_z is light intensity at depth *z* and I_S is light intensity (µmol s^{-1} m^{-2}) over surface (either measured from a boat or on the sea ice) when I_Z was measured. For Inglefieldbukta in March, when only one measurement was done of I_S, all I_Z-measurements were divided with this one value, assuming little change in surface light intensity.

Beer-Lamberts law for intensity of an electromagnetic wave through a material can be put as

(F 3)

$$I_z = aI_S\, e^{-kz}$$

where the product aI_S is an expression for light just below water surface. Here, *a* is a coefficient describing light lost when passing through the water surface, or sea ice when present, and *k* is the light attenuation coefficient (m^{-1}). Combining equation F2 and F3 gives

(F 4)

$$f_z = {}^{I_Z}/_{I_S} = ae^{-kz}$$

The natural logarithm of f_z found by F2 was plotted against depth *z* in Windows Excel. Linear regression was applied to the resulting plots, giving a linear regression line following the formula for the natural logarithm of F4:

(*F 5)*

$$ln(f_Z) = ln\left({}^{I_Z}/_{I_S}\right) = lna - kz$$

where *a* describes amount of light lost when passing through the water surface and *k* is the amount of light absorbed per m depth, as described for F3.

2.4.2 Chlorophyll a

Point plot for Chlorophyll *a* concentration (µg L^{-1}) per depth was made in RStudio (R version 3.5.2) using the function ggplot() from the package "tidyverse" (Wickham 2017).

2.4.3 Zooplankton community

Counts of individuals per subsample was converted to individuals per sample by dividing each count with the number for Fraction Counted (Appendix 1.4, table A1.4), and n individuals m^{-2} were found by dividing individuals per sample with 0.255, the area (m^2) of the WP2 net opening.

Taxa from the raw data sheet were pooled together, either manually in Microsoft Excel or by the command rowSums() in RStudio (R version 3.5.2). Frequency of each species or taxa (individuals m^{-2}) was averaged for the two net hauls sorted for three sampling dates at IsA (May 1, April 5, August 18). Plots were made in RStudio using the function ggplot().

To investigate similarities in species composition between the sampling stations and dates, a Principal Components Analysis (PCA) was performed in Rstudio (R-version 3.5.2), using the package "vegan" (Oksanen et al. 2019), on square root transformed species data from all sampled stations. Prior to analysis the following species and taxa in the species data were grouped by summing: All stages of each species (providing one species count per species (e.g. for *Calanus* and *Pseudocalanus* spp.)), each larval stage of Euphauciacea, the two unidentified Harpacticoida spp., unidentified male and young of *Oithona* spp., *Parasagitta elegans* macro and small, *Themisto abyssorum* and *Themisto* sp., *Triconia borealis* and *Triconia* sp. male (See Appendix 3, script 1 for grouping variables). Thereafter frequency of each species or taxa (individuals m^{-2}) was averaged for the two net hauls sorted for three sampling dates at IsA (May 1, April 5, August 18) (See Appendix 3, script 2). By performing a Detrended Correspondence Analysis (DCA) on the grouped species data using the function decorana() it was found that the first axis was 2.69 SD (Standard Deviation) long. Being longer than 2 SD, suggesting a slightly unimodal response curve, the following PCA was performed on square root transformed data (having an axis length of 2.01 SD). The PCA was done by function rda(). Plotting a scree plot of the ordination with a broken stick indicated that the two first axes were interpretable (the inertia of Ordination and Broken stick crossed just after PC2). The PCA ordination results were therefore plotted, using base R-function plot(), displaying the first two axes (see Appendix 3, Script 3, for full script).

3 Results

3.1 The physical and biological environment

3.1.1 Hydrography

The water masses in Adventfjorden (Stn. IsA) from March throughout May were rather stable in terms of temperature and salinity, and a mixture of local water (LW), locally formed winter cold water (WCW) and Arctic water (ArW) persisted (Figure 3.1.1, see Appendix 4.1 for temperature and salinity as a function of depth). In June the water masses changed, when warmer (1-2°C) and more saline transformed Atlantic water (TAW) dominated the upper 30 m. Snow melt and increased river run off combined with solar heating led to an upper fresher and warmer surface water (SW) layer from July to September, which reached max temperature (7 °C) in July. Below the SW, a mixture of SW and TAW led to an Intermediate Water (IW) mass. The IW dominated in the whole water column in October and November.

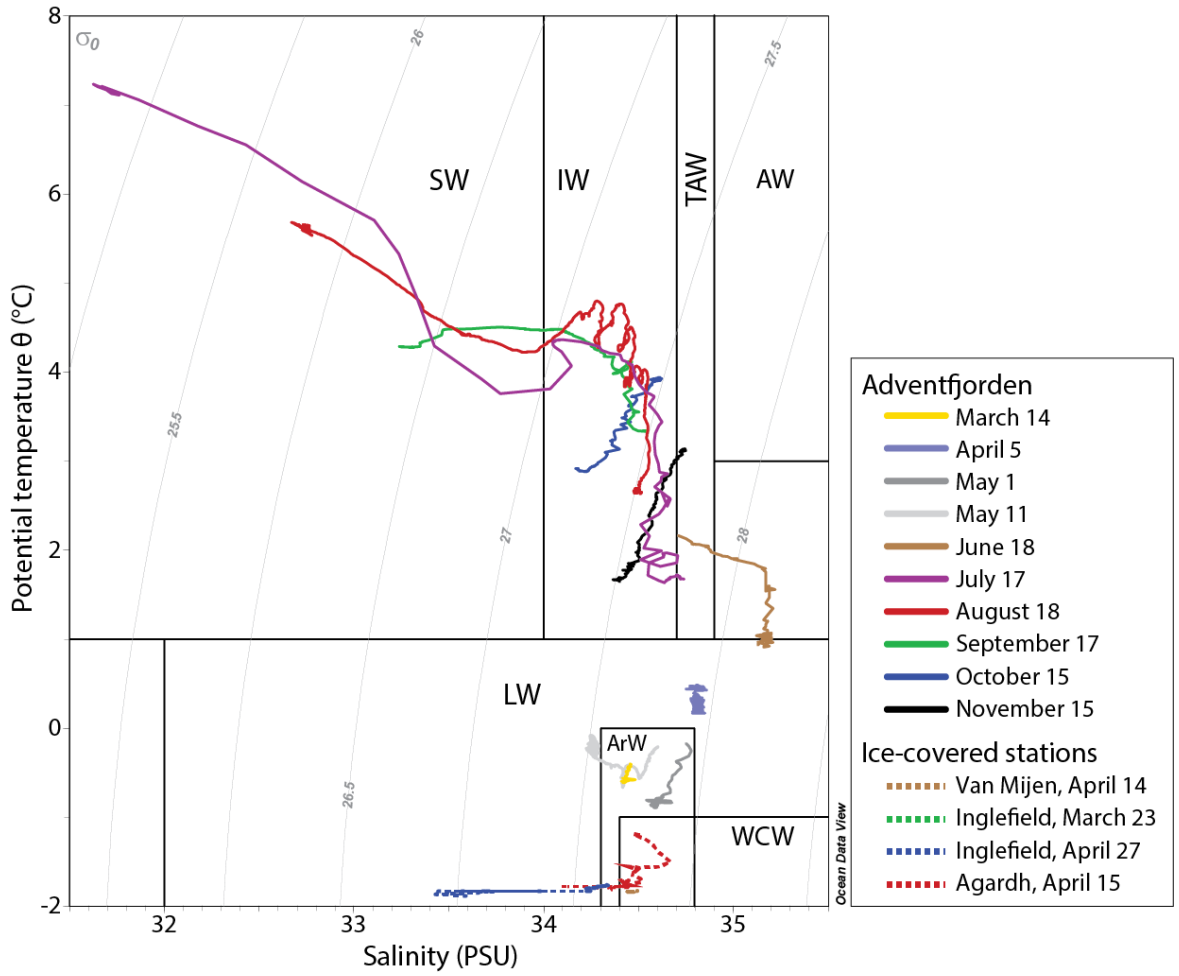

Figure 3.1.1. TS-plot of CTD data from all stations sampled from March to November 2018: those in Adventfjorden with solid lines and those from the ice-covered with dashed lines (Van Mijenfjorden, Inglefieldbukta and Agardhbukta), with water mass definitions following Nilsen et al. (2008). Data from Inglefieldbukta in March and upper water column from Van Mijenfjorden not included due to erroneously low salinity (see figure A4.1b in Appendix 4.1).

The water masses at the ice-covered stations were dominated by LW, ArW and WCW with lower temperatures than in Adventfjorden (Figure 3.1.1). The temperature profiles remained mostly stable through the water column at each station (temperatures around -1.75°C). Inglefieldbukta had low salinity (<25 PSU) throughout the water column in March, and salinities below 30 PSU was found in Van Mijenfjorden above 5 m depth (Figure A4.1b in Appendix 4.1). These measurements were erroneously low and are not included in Figure 3.1.1.

3.1.2 Light penetration and ice and snow thickness

The water column in Adventfjorden had a high light attenuation in July (K-value 0.288 m^{-1}, Table 3.1). A bigger fraction of the incoming light was reflected/absorbed before reaching the water at the ice-covered stations, compared with the ice free Adventfjorden (ln(*a*), Table 3.1). Of the ice-covered stations, lowest fraction of light (*a*) reached the water in Van Mijenfjorden and Inglefieldbukta in April (0.05% and 0.06%, respectively). See Appendix 4.2 for plot of relative light (f_Z) as function of depth.

Table 3.1. Proportion of light lost when passing through water surface or ice in logarithmic scale (ln(a)), and light attenuation coefficients (K, m^{-1}) for all locations and dates when light was measured, with coefficient of determination (R^2) and number of light measurements (n) used to calculate K (See Appendix 1.2). Percent of light passing through the water surface or sea ice ($a \times 100$) given in %light.

Location	Date	ln(a)	K	R^2	n	%light
Adventfjorden	March 14	-0.918	0.115	0.916	18	39.93
	April 5	-0.879	0.081	0.937	18	41.52
	May 1	-0.386	0.184	0.989	18	67.98
	June 18	-0.353	0.183	0.946	14	70.26
	July 19	0.151	0.288	0.930	15	116.30
	September 17	-0.672	0.152	0.938	16	51.07
Van Mijenfjorden	April 14	-7.614	0.164	0.996	12	0.05
Inglefieldbukta	March 23*	-4.222	0.170	0.981	28	1.47
	April 27	-7.410	0.192	0.959	20	0.06
Agardhbukta	April 15	-4.060	0.175	0.735	16	1.73

*Erroneous measurements for Inglefieldbukta in March, see Materials and Methods

Of the ice-covered stations sampled in March and April, the sea ice was thickest in Inglefieldbukta in April, followed by Van Mijenfjorden, and thinnest in Inglefieldbukta in March. Snow cover was thickest in Inglefield in April, followed by Van Mijenfjorden (Table 3.2).

Table 3.2. Ice physics data for the four ice-covered stations sampled in spring 2018, with ice thickness (cm) and mean snow depth (cm) ±standard deviation, in the ice above the water column where light intensity was measured

Station	Sampling day	Ice thickness (cm)	Mean snow depths (cm)
VMF1	April 14	81	12.83 (±0.24)
IB	March 23	44	6.17 (±1.25)
	April 27	89.33* (±8.12)	39.96* (±1.62)
AGA	April 15	50.5	10.33 (±5.34)

*Measurements from IB in April are not from ice directly over where light measurements were conducted, but averaged values from measurements done for 12 ice cores taken approximately 4 m away.

3.1.3 Phytoplankton

During winter (March and April) chlorophyll *a* (chl *a*) was low in Adventfjorden (Figure 3.1.3), with the ice-covered stations having similar low chl *a* concentrations in the water column (all mentioned stations had chl *a* ≤ 0.149 µg L^{-1}, mean 0.077 ±0.012 µg L^{-1}). Chl *a* concentrations in Adventfjorden increased in spring (May and June), with May 1 having the highest, followed by June (maximum values of 3.59 ±0.14 and 2.99 µg L^{-1} respectively). During the summer months (July to September) chl *a* concentrations were stable around 1 µg chl *a* L^{-1}.

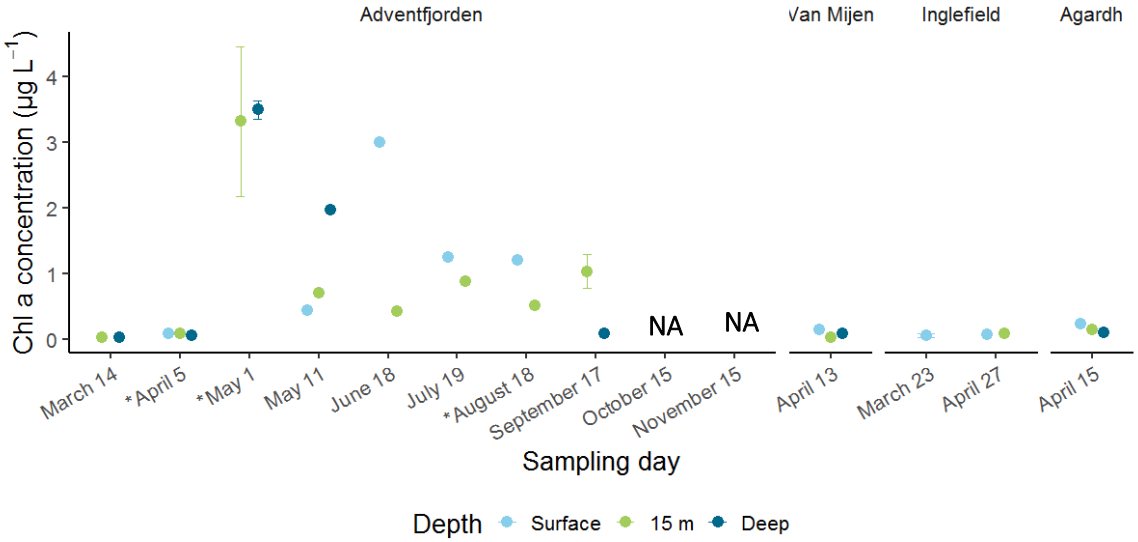

Figure 3.1.3. Mean chlorophyll *a* (Chl a) concentration (µg L^{-1}) with error bars, as found in the GF/F grade) filters, colour coded for sampling depth (see Table 2.2 for depths of Deep sample), from Adventfjorden (Stn. IsA) from March to September and Van Mijenfjorden (Stn. VMF1), Inglefieldbukta (Stn. IB) and Agardhbukta (Stn. AGA) from March and April 2018.

3.2 Zooplankton community

Highest zooplankton abundance (2.55×10^6 ind. m^{-2}) was found in Adventfjorden in May. This was due to high Cirripedia nauplii and cypris abundances which exceeded 2×10^6 ind. m^{-2} on both May 1 and 11 (Figure 3.2.1). Holoplankton dominated the zooplankton community in Adventfjorden for all months except in May. Holoplankton occurred in low numbers in winter (March and April), but gradually increased in numbers during the summer and autumn months (July-October), before declining in numbers in November (Figure 3.2.1). Excluding the Cirripedia larvae in May, July and October had the highest zooplankton abundances (4.25×10^5 and 4.24×10^5 ind. m^{-2}, respectively). Amongst the ice-covered stations, highest total zooplankton abundance was found in Van Mijenfjorden (7.8×10^4 ind. m^{-2}) (Figure 3.2.1), almost twice as high (1.7 times higher) than found in Adventfjorden in April (4.6×10^4 ind. m^{-2}) and eight times higher than the ice-covered station having second highest abundance (AGA April 15, 9.6×10^3 ind. m^{-2}). Inglefieldbukta had the lowest total amount of zooplankton of all stations for both sampling dates (1.7×10^3 and 5.6×10^3 ind. m^{-2} for March and April respectively), where the abundance on April 27 was 2.8×10^{-3} times lower than in Adventfjorden on May 1.

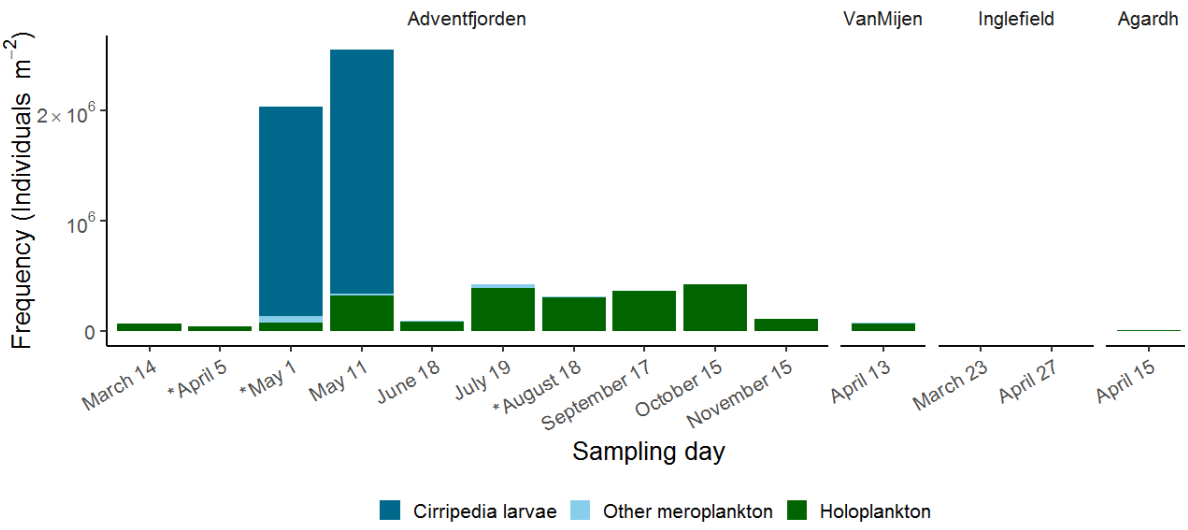

Figure 3.2.1. Total zooplankton abundance (ind. m^{-2}) found in Adventfjorden from March to November 2018 and at the ice covered stations (VanMijen, Inglefield and Agardh) in March and April 2018. Inglefield with lowest zooplankton abundance (1.7×10^3-5.6×10^3 ind. m^{-2}).
*In x-axis text: zooplankton abundance is mean value of sorting of two hauls

The Principal Components Analysis (PCA) indicate that, based on the square root transformed species data, the sampling stations cluster together in three or four clusters (Figure 3.2.2). The first cluster, Adventfjorden May, includes the two sampling dates in May in Adventfjorden,

affected by Cirripedia nauplii and on the positive end of the added Chl *a* gradient (chla15mGFF). The second cluster (Adventfjorden Summer) includes the sampling dates in Adventfjorden from July-October. The third cluster (Inglefield-Agardhbukta) include Agardhbukta and the two Inglefieldbukta sampling dates clustered in the positive end of the "sea ice" environmental scale (presence/absence of sea ice). The fourth cluster, including Adventfjorden from November and June, Van Mijenfjorden, and Adventfjorden from March and April (given in order of appearance along the axis PC2 from 0 and down in Figure 3.2.2), is in between cluster two and three along the PC2 axis where it is closer to the "Agardh-Inglefieldbukta"-cluster than the "Adventfjorden summer"-cluster.

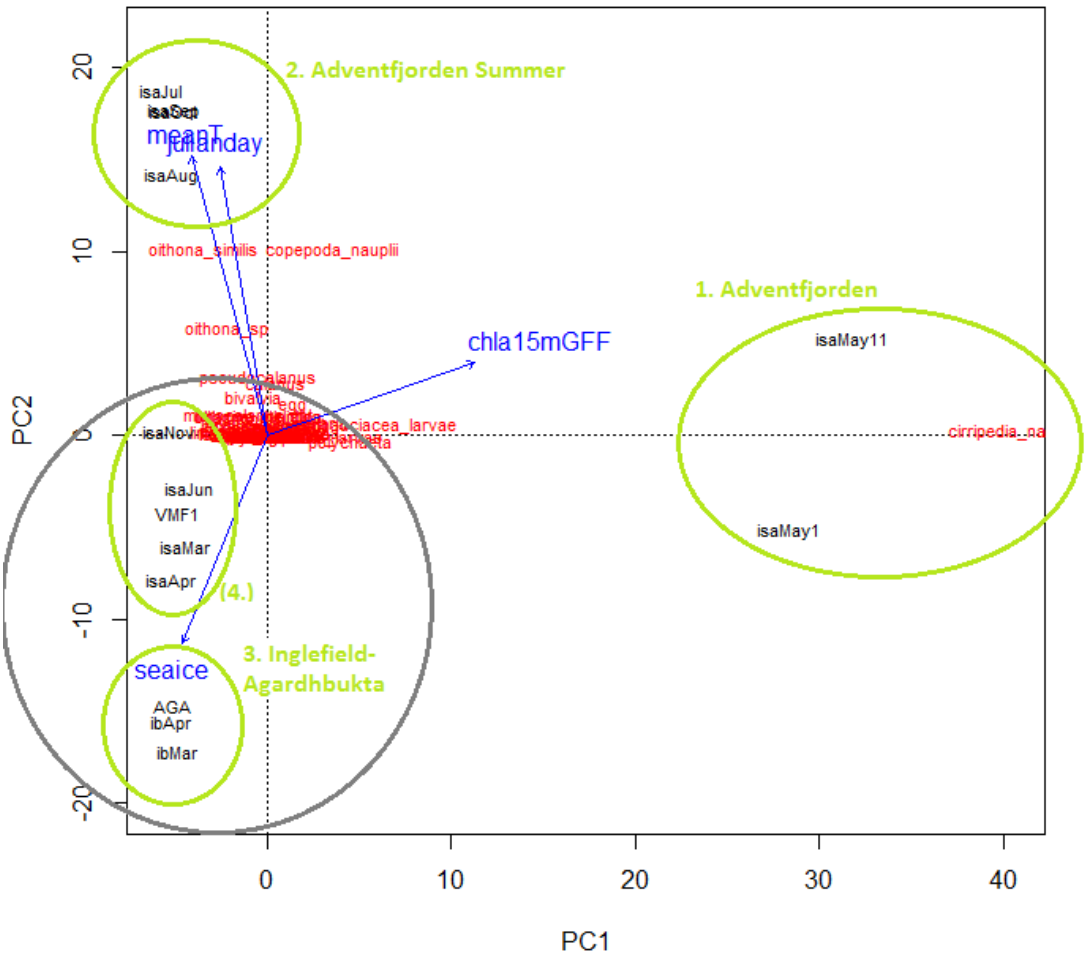

Figure 3.2.2. Plot of the two interpretable axes resulting from the Principal Components Analysis (PCA) on square root transformed species data (red text) from all stations and dates (black text) sampled in Adventfjorden from March to November (isaMar-isaNov) and at the ice covered stations sampled in March and April 2018 (ibMar, ibApr, AGA, VMF1). With significantly correlating environmental variables added (blue arrows): mean temperature (°C) of main water mass (meanT(***)), sampling date in Dublin Julian Day (julianday(**)), mean chlorophyll *a* concentration (µg L^{-1}) at 15 m depth found in GF/F grade filter (chla15mGFF(.)) and presence/absence (presence=1, absence=0) of ice at the station (seaice(*)). Green circles, suggesting clustering scheme with green text giving cluster number and name, added for illustration purposes. Grey line around cluster 3 and 4 indicates uncertainty with clustering scheme.
Significance codes: p<0.001 (***), 0.001 (**), 0.01 (*), 0.05 (.)

3.2.1 Meroplankton abundance and composition

Total meroplankton abundance in Adventfjorden was highest in May, dominated by Cirripedia nauplii, followed by Polychaeta and trochophore larvae (Figure 3.2.3). In July, Bivalvia veliger larvae was found in high abundances and totally dominated the meroplankton fraction. Low (<6.1×10^3 ind. m^{-2}) abundance of meroplankton was found in the remaining months amongst which Echinodermata and Decapoda larvae were found (See Appendix 5 for meroplanktonic abundances through the sampling period). At the ice-covered stations in April, meroplankton abundance was overall low (<350 ind. m^{-2}), especially in Agardh- and Inglefieldbukta in East Spitsbergen (39.2 and 27.5 ind. m^{-2} respectively).

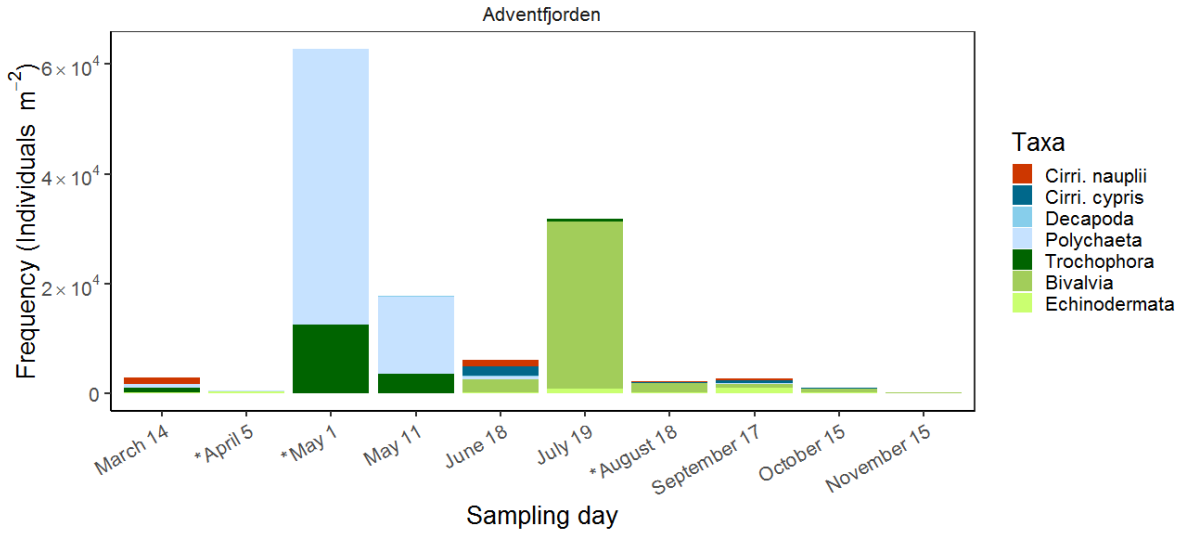

Figure 3.2.3. Meroplankton abundance (ind. m^{-2}) in Adventfjorden from March to November 2018 (Cirripedia nauplii in May excluded).
*In x-axis text: value for date is mean value of sorting of two hauls

3.2.2 Holoplankton abundance and composition

Except in May, holoplankton dominated the zooplankton community of which Copepoda dominated (relative abundance between 68-99.5 %, mean 95.8 ±3.8 %)) in all months (Figure 3.2.4). The two holoplankton taxa with second highest abundance, Euphauciacea and Appendicularia, had their highest abundance in May. Highest Copepoda abundance was found during the summer and autumn months, where October had the highest abundance (4.2×10^5 ind. m^{-2}). For May 11 and October, the Copepoda composition mainly comprised of Copepoda nauplii (Figure 3.2.4).

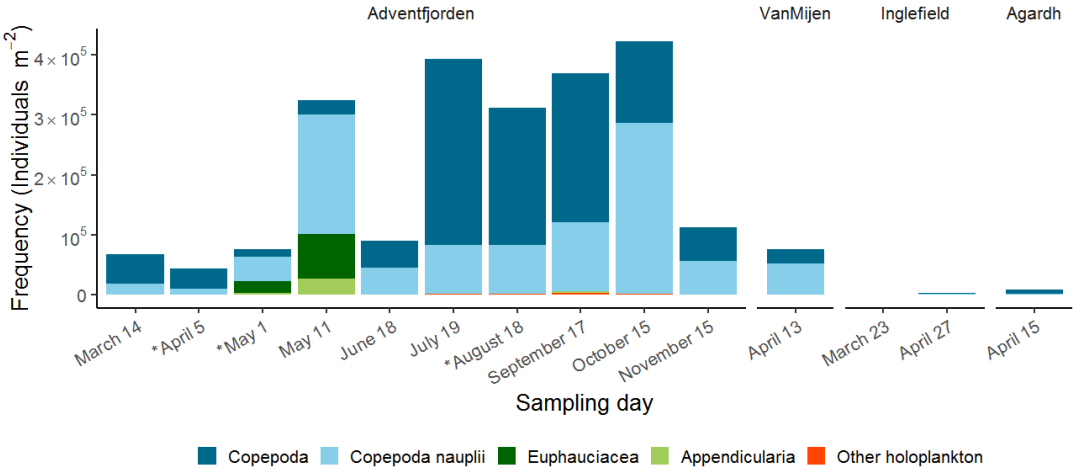

Figure 3.2.4. Holoplankton abundance (ind. m^{-2}) in Adventfjorden from March to November 2018 and at the ice covered stations (VanMijen, Inglefield and Agardh) in March and April 2018.
*In x-axis text: zooplankton abundance for date is mean value of sorting of two hauls

Excluding the Copepoda nauplii, July had the highest abundance (3.1×10^5 ind. m^{-2}) of Copepoda, followed by September and August (Figure 3.2.5). The small cyclopoid copepod *Oithona* spp. dominated numerically during all months, comprising between 48 % (March) and 88 % (October) of all copepods, except on May 11 and in June (<34%). For both these sampling dates the bigger copepods of the order Calanoida, genus *Calanus*, comprised more than 50 % of the copepod abundance. Of the other copepods (Figure 3.2.5, "Other Copepoda"), the small Cyclopoida *Triconia* Böttger-Schnack, 1999 spp. and the Harpacticoida *Microsetella norvegica* (Boeck 1865) were found in highest numbers, followed by the Calanoida *Acartia longiremis* (Liljeborg 1853) (See Appendix 6 for full species list).

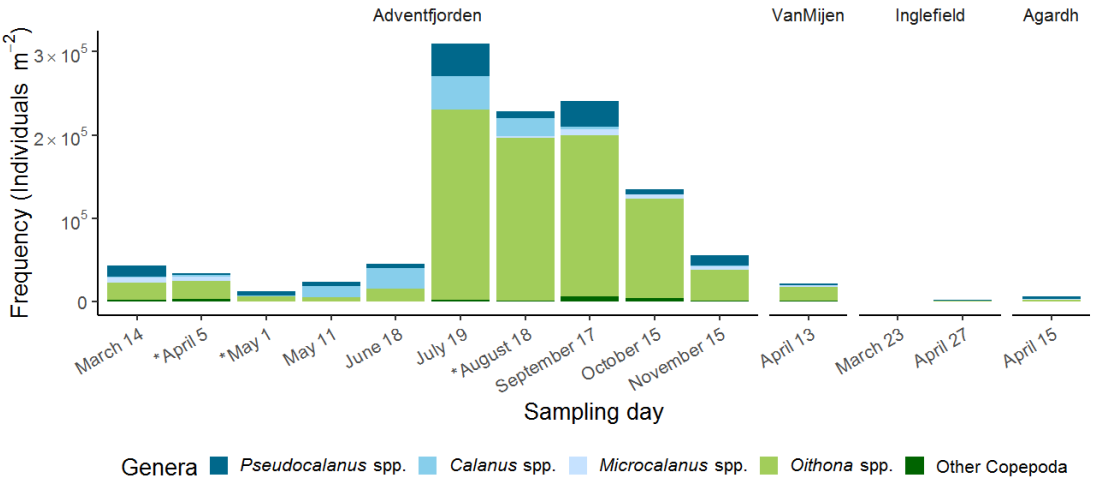

Figure 3.2.5. Copepoda abundance (ind. m^{-2}) at IsA (Adventfjorden) from March to November and at the ice covered stations (VanMijen, Inglefield and Agardh) in March and April 2018. *In x-axis text: abundance for date is mean value of sorting of two hauls.

At the ice-covered stations, holoplankton dominated the zooplankton community. Copepod nauplii numerically dominated (67%) the zooplankton composition in Van Mijenfjorden, while older Copepoda dominated the ice-covered stations on the east coast (relative abundance of 48, 43 and 75 % for Inglefieldbukta March and April and Agardhbukta respectively). The total number of copepods (excluding nauplii) followed the same pattern as total zooplankton, with Van Mijenfjorden having the highest total amount, followed by Agardhbukta and then Inglefield (Figure 3.2.5). Among the Copepoda, *Oithona* was the most numerical genus at all ice-covered stations (relative abundance between 46-73 %) except AGA April 15 where 56 % of the copepod individuals comprised of *Pseudocalanus* spp.

3.3 Population development of dominant copepods

3.3.1 Copepoda nauplii abundance and size composition

In Adventfjorden, highest number of copepod nauplii was found in October, followed by May 11 (Figure 3.3.1). In October the small nauplii of stage NI-III (< 150 µm) amounted to 89 % of the total nauplii composition, while older and bigger nauplii NIV-VI (> 500 µm) dominated among the nauplii (99 %) on May 11. Amongst the ice-covered stations, highest abundance of copepod nauplii was found at Van Mijenfjorden where small nauplii of stage NI-III had a relative abundance of 90 %. Egg abundance at the sampling stations included in Appendix 7.

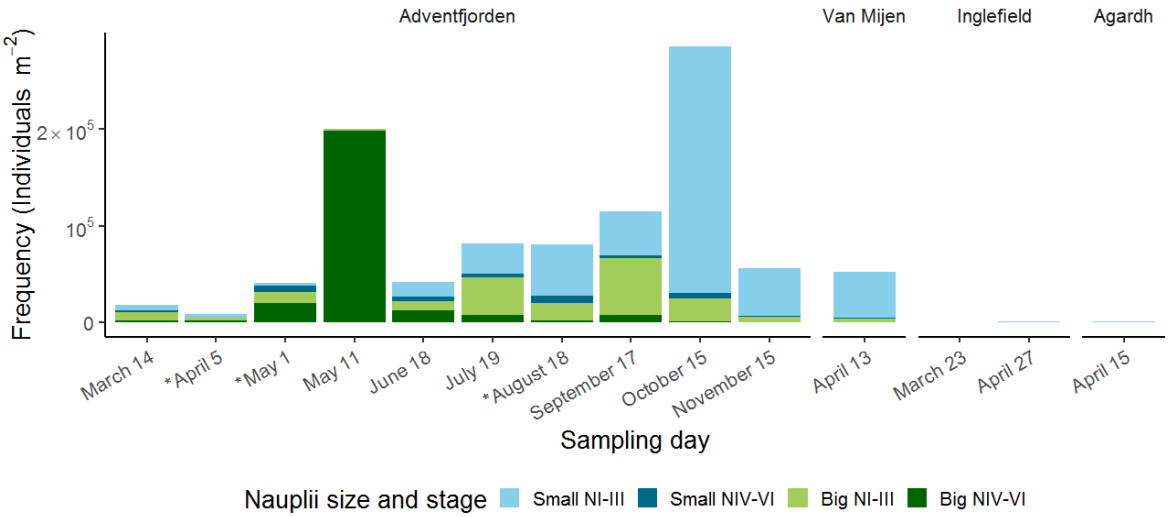

Figure 3.3.1. Abundance of Copepoda nauplii (ind. m^{-2}) in Adventfjorden from March to November and at the ice covered stations (VanMijen, Inglefield, Agardh) in March and April 2018, given in composition of each size and stage group (498, 1.58×10^3 and 1.63×10^3 ind. m^{-2} in Inglefieldbukta March, Inglefieldbukta April and Agardbukta respectively).
*In x-axis text: zooplankton abundance for date is mean value of sorting of two hauls.

3.3.2 Calanus *abundance and stage composition*

In Adventfjorden, total *Calanus* spp. abundance was highest (4.0×10^4 ind. m^{-2}) in July, followed by June and August (Figure 3.3.2a). The winter and spring months (March – May 1) had a generally low abundance of *Calanus* spp. (322 and 2.7×10^3 ind. m^{-2} for March and April respectively), similar to that of late summer and fall (September-November). At the ice-covered stations, *Calanus* spp. was found in low abundances (59-412 ind. m^{-2}), all lower than in Adventfjorden in April. Van Mijenfjorden was dominated by the earlier copepodite stages (CI-CIV), while adult females (AF) dominated (>54%) the stage composition in Inglefieldbukta and Agardhbukta almost exclusively consisted of CV and AF (Figure 3.3.2b).

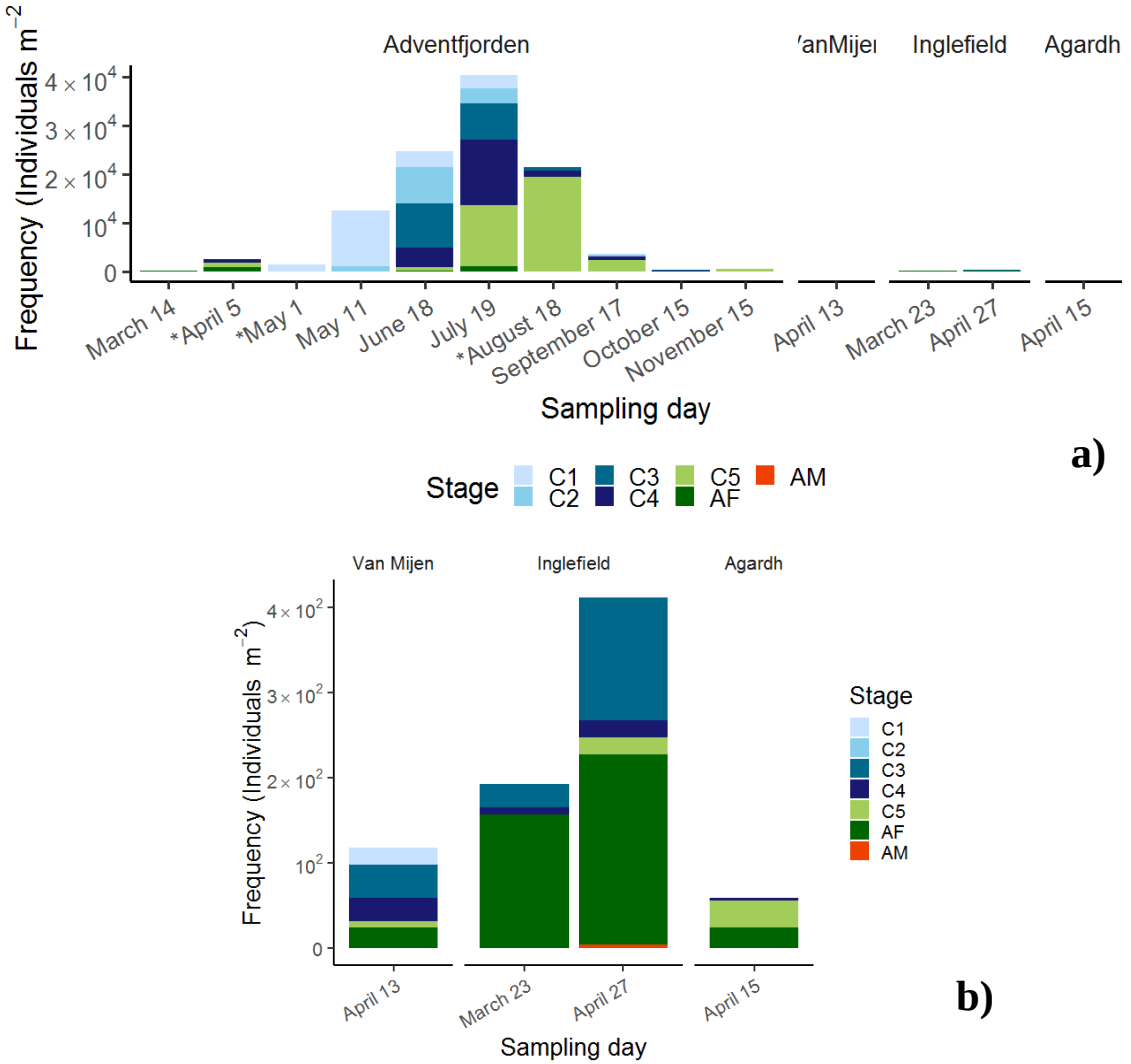

Figure 3.3.2. Total abundance (ind. m^{-2}) of *Calanus* spp. in Adventfjorden for each sampling date sampled from March to November and at the ice covered stations (VanMijen, Inglefield, Agardh) in March and April 2018, with composition of each developmental stage (C1 to AM), at (a) all stations and (b) same as above but only the ice covered stations.
*In x-axis text: mean value of sorting of two hauls

In Adventfjorden, the AF peaked in abundance in April (866 ±278 ind. m^{-2}) and July (1.2×10^3 ind. m^{-2}). Abundance of CI peaked on May 11 (1.1×10^4 ind. m^{-2}), C2 and C3 in June (7.3×10^3 and 9.2×10^3 ind. m^{-2} for C2 and C3 respectively), C4 in July (1.3×10^4 ind. m^{-2}) and C5 in August ($1.99\times10^4\pm2.2\times10^3$ ind. m^{-2}) (Figure 3.3.3).

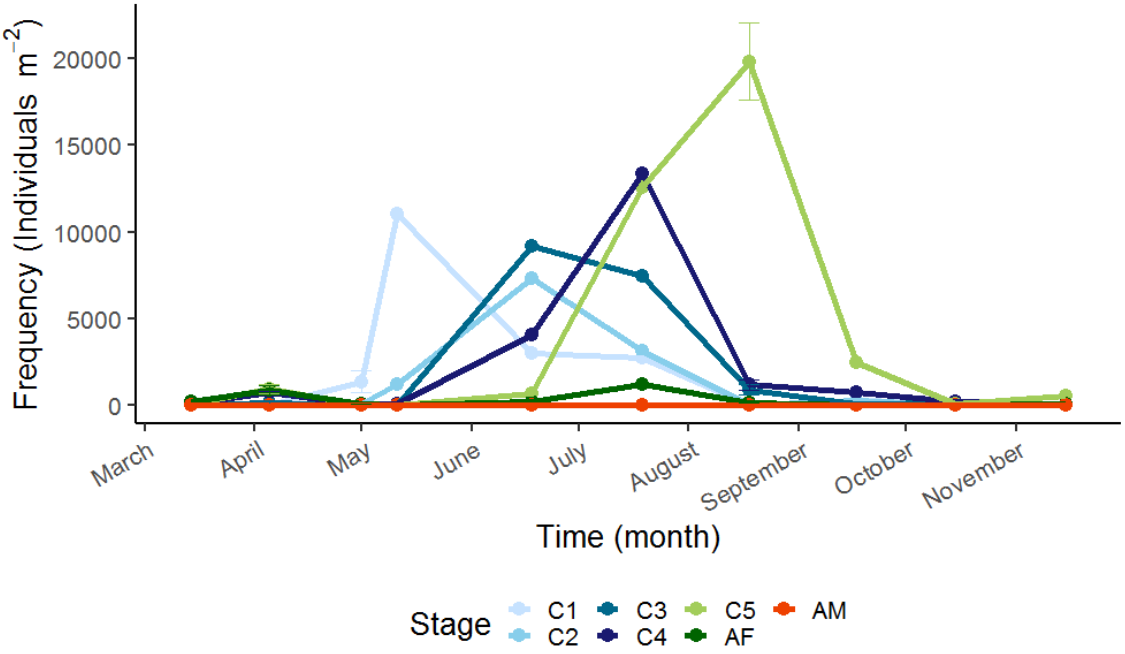

Figure 3.3.3. Abundance (ind. m^{-2}) of each *Calanus* spp. stage in Adventfjorden from March to November 2018 with Time (month) given on a continuous date scale and the coloured (colour coded for copepodid stage) dots indicating time of sampling, with line given by function geom_line. Error bars are given when value is mean of sorting of two hauls.

3.3.3 Pseudocalanus *abundance and stage composition*

Total abundance of *Pseudocalanus* spp. in Adventfjorden ranged between 1.5×10^3 and 3.8×10^4 ind. m^{-2} (Figure 3.3.4a). The lowest abundance was found in April while July had the highest, followed by September (3.1×10^4 ind. m^{-2}). The ice-covered stations had low abundances of *Pseudocalanus* spp. ($<4\times10^3$ ind. m^{-2}), whereof Agardhbukta had the highest abundance (3.98×10^3 ind. m^{-2}) followed by Van Mijenfjorden (2.8×10^3 ind. m^{-2}), both higher than that found in Adventfjorden in April.

In Adventfjorden, the earliest copepodite stages CI-CIII dominated the *Pseudocalanus* stage composition (having a relative abundance of over 50 %) for all months but April and May when CIV-CV and CV-CVI dominated (Figure 3.3.4b). From June to November the relative abundance of each stage kept relatively stable, with similar relative abundances of stages CI-CIV in each month. The adult stage CVI were in generally low numbers throughout the

sampling season, but abundance peaked in May and July. At the ice-covered stations stage compositions varied. (Figure 3.3.4b).

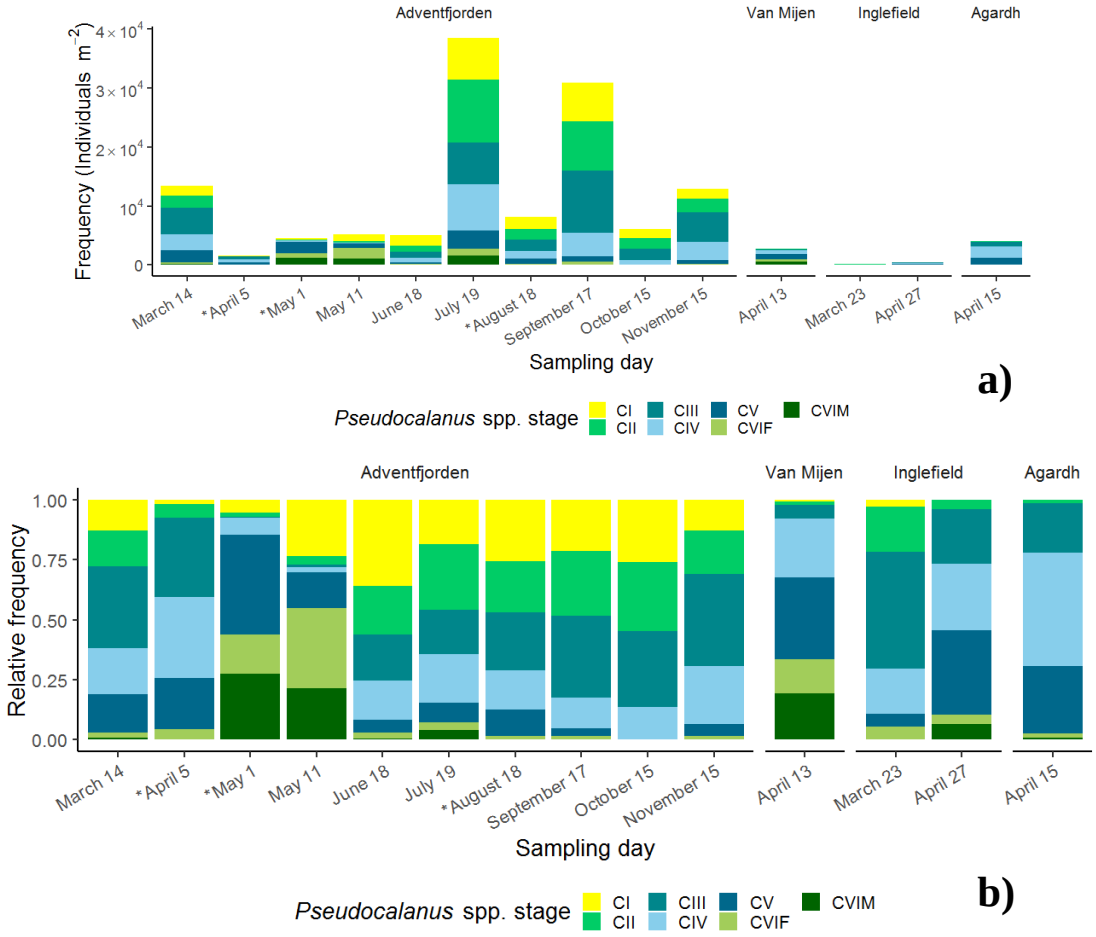

Figure 3.3.4. Abundance of *Pseudocalanus* spp. in Adventfjorden for each sampling date from March to November and at the ice covered stations (VanMijen, Inglefield, Agardh) in March and April 2018, with composition of each stage with females and males from CIV and CV grouped, in (a) total abundance (ind. m^{-2}) and (b) relative abundance (n ind. of each stage/total *Pseudocalanus* abundance). *In x-axis text: value for date is mean value of sorting of two hauls.

Pseudocalanus species composition

Of the 120 *Pseudocalanus* spp. copepodids picked for molecular identification, 119 were identified (1 AF from May 11 gave no result, possibly lost in transfer to PCR-tube). All but two from the May samples (n= 23) were identified to *P. acuspes* (Figure 3.3.5). The remaining two were of *P. moultoni*. *Pseudocalanus minutus* was found among the older stages (CIII-CV) in July and August. Most (59 out of 65) of the younger stages (CI-CIII) from the same dates were identified to *P. acuspes* and *P. moultoni*.

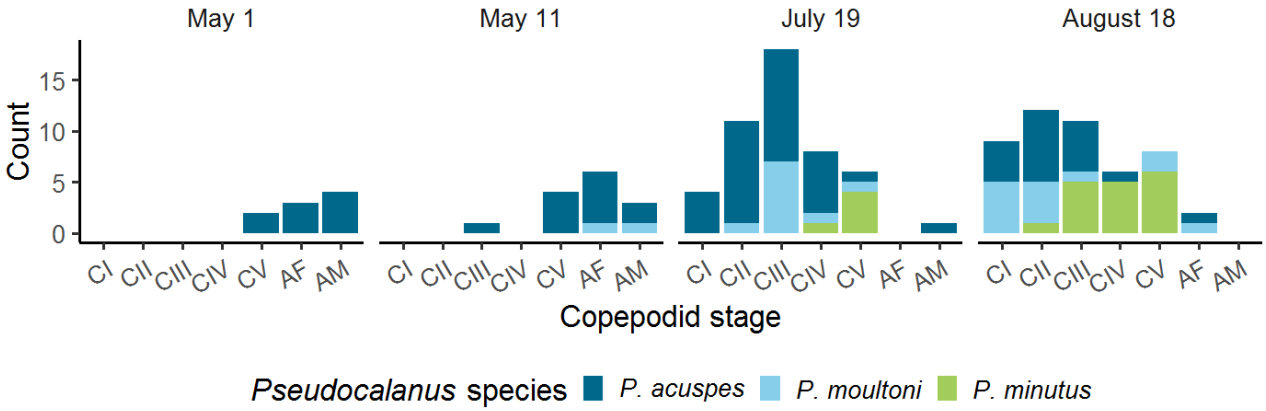

Figure 3.3.5. Distribution of the three *Pseudocalanus* congeners (*P. acuspes*, *P. minutus* and *P. moultoni*) amongst 119 randomly selected copepodids (Table 2.4) from four sampling dates in Adventfjorden 2018, identified by ssPCR and Illumina sequencing. One individual gave no results.

3.3.4 Oithona *spp. abundance*

As mentioned previously, the composition of copepods was numerically dominated by *Oithona* spp. most months, whereof *O. similis* was the most abundant species (Figure 3.3.7). In Adventfjorden, highest abundance of *Oithona* spp. was found in July (2.3×10^5 ind. m^{-2}). *Oithona atlantica* Farran 1908 was present in low numbers in Adventfjorden, with abundances below 300 ind. m^{-2} between March and June, and highest abundance (1.7×10^3 ind. m^{-2}) in October. Unidentifiable *Oithona* (young and males) were present from June to November, with July and September having the highest numbers (7.3×10^4 and 4.4×10^4 ind. m^{-2}, respectively).

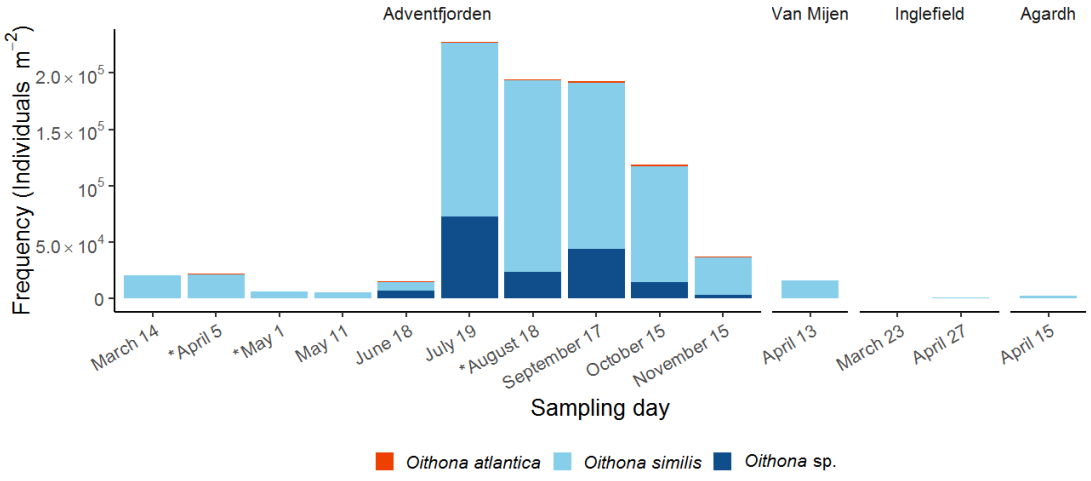

Figure 3.3.6. Abundance (ind. m^{-2}) of *Oithona* spp. in Adventfjorden for each sampling date from March to November and at the ice covered stations (VanMijen, Inglefield, Agardh) in March and April 2018, with undistinguishable young and male individuals grouped in *Oithona* sp.
*In x-axis text: value for date is mean value of sorting of two hauls.

4 Discussion

How does the seasonally changing physical and biological environment shape the zooplankton community in Adventfjorden?

Three seasonal regimes were found in Adventfjorden: winter/autumn with low primary and secondary production, spring with a bloom of phytoplankton and high meroplankton abundance and summer with high abundance of holoplankton.

The seasonal regimes are suggested based on the seasonal change in water mass distribution, chlorophyll *a* (chl *a*) concentration and zooplankton species composition as indicated by the PCA. The winter months (March and April) had both a quite stable and unstratified water column, although the dominant water masses differed between the months. Both had a low abundance of zooplankton and similar species composition. Increased chl *a* concentrations were found in the spring months (May and June), timed with increased day length and sun altitude, and the consequent increase in photosynthetic active radiation (PAR). Although the water masses were as unstratified and cold as the winter months, May marks the start of the productive season by the high chl *a* concentration and high abundances of Cirripedia larvae. The spring bloom appeared to have started shortly before the first sampling in May, as high abundance of diatom chains and some colonies of *Phaeocystis pouchettii* (Hariot) Lagerheim 1896 were observed in the zooplankton sample from May 1 (personal observation) (Kubiszyn et al. 2017). June, on the other hand, had much lower zooplankton abundance and a composition more similar to that of the winter months. This might be explained by the high rate of settlement of Cirripedia nauplii (Kuklinski et al. 2013), which is supported by the presence of Cirripedia cyprid larvae in June. Alternatively, parts of the community might have been transported out from the fjord by currents, based on the change in water mass composition found in June and the general high water exchange between Adventfjorden and Isfjorden.

The summer months (July-October) started with a dominance of warm and fresh surface water (SW) due to the increased river runoff from snow and glacial melt caused by increased mean air temperatures from end of June in Longyearbyen (Appendix 8) (MET 2019). Chl *a* was found in lower concentrations than in May but higher than in winter, and holoplankton was dominating. Although the hydrography differed, October had similar zooplankton abundance and species composition and is therefore included as a summer month. Autumn included November, when the water mass was dominated by colder Intermediate Water (IW) and zooplankton abundance was again low.

How does the dominance of meroplankton and holoplankton shift through the productive season in Adventfjorden, and what taxa dominates in the respective groups?

Meroplankton was found to be more abundant than holoplankton in May, coinciding with the chl *a* peak. The amount of zooplankton was then five times higher than found in other months, due to an outburst of Cirripedia larvae. A second much smaller meroplankton peak dominated by Bivalvia larvae was found in July. The holoplankton dominated in all months but May, whereof Copepoda was the most numerous taxa.

The short period of high meroplankton abundance, with dominance of meroplankton over holoplankton in a short period, agrees with previous reports from coastal areas in the Arctic and sub-Arctic (Węsławski et al. 1988; Coyle & Paul 1990; Arendt et al. 2012; Kuklinski et al. 2013). The duration of meroplankton dominance does however differ from what Stübner et al. (2016) found in Adventfjorden in 2012, when meroplankton was found to dominate in the zooplankton community for a much longer period. The 2012 meroplankton dominance was mainly caused by a much higher abundance of Bivalvia larvae than found in 2018 (over 7.5×10^4 ind. m^{-3} in 2012, compared to just over 250 ind. m^{-3} in July 2018). Additionally, a second peak in Cirripedia larvae abundance was found in 2012. One reason for finding meroplankton to be dominating only in May in 2018 could be that sampling occurred too infrequently compared to in 2012, and peak occurrence of Bivalvia might have happened prior to or after sampling. More than 30 days separated the May and June samples in 2018, and as meroplankton commonly occurs in short bursts, any additional peaks in meroplankton abundance might have been missed.

Finding high amounts of Cirripedia larvae to coincide with high chl *a* concentration agrees with current knowledge on their biology. Many Cirripedia species are capital breeders which respond quickly to high abundance of phytoplankton by releasing larvae in the water (Crisp & Spencer 1958). This enables the larvae to take advantage of the energy available in the spring bloom. In spite of the high numbers of Cirripedia, the chl *a* concentrations still remained fairly high early in May. Stübner (2016) suggested, based on her feeding experiments, that the Cirripedia alone cannot control the phytoplankton abundance in the spring bloom. The Cirripedia appeared to not have outcompeted other zooplanktonic taxa by grazing down the phytoplankton in Adventfjorden. The relatively low abundance of holoplankton might rather be explained by the longer time needed to respond to phytoplankton abundance by the pelagic residents, where an overwintering stock of adults needed for reproduction in spring did not appear in big numbers

in Adventfjorden. Holoplankton, mostly represented by Copepoda nauplii, had an increased abundance later in May. A similar spring succession of Cirripedia nauplii preceding those of Copepoda has been recorded previously in Arctic and sub-Arctic water (Arendt et al. 2012). Potentially the combined high presence of Cirripedia and Copepoda nauplii had a top down impact on the phytoplankton biomass, explaining the lower chl *a* concentration in mid-May, but more knowledge on these taxa's grazing rates are needed before a conclusion can be drawn.

The pattern of high abundance of Cirripedia during high primary production and Bivalvia later in the season is similar to previous observations in fjords around Svalbard (Węsławski et al. 1988; Kuklinski et al. 2013; Stübner et al. 2016). This is most likely explained by the fact that many of the Bivalvia species reproduce by income breeding, spawning after they have assimilated energy from the spring bloom (Ockelmann (1958) in Stübner et al. (2016)). Additionally, Bivalvia larvae can be expected to appear later than Cirripedia larvae due to most of the Bivalvia release gametes into the water where fertilisation occur.

Not surprisingly did Copepoda dominate among the holoplankton (Hop et al. 2002; Daase & Eiane 2007). Of the developed copepods (copepodids and adults), highest abundance was found in July, followed by August and September, similar to previously found patterns (Węsławski et al. 1988; Stübner et al. 2016). *Oithona* spp., mainly represented by the cosmopolitan *O. similis* which is one of the most numerically important copepod in Arctic water (Kosobokova et al. 1997; Hop et al. 2002; Daase & Eiane 2007; Darnis et al. 2012), was also the most numerically important copepod in Adventfjorden. The low presence of the Atlantic water associated *O. atlantica* (Koszteyn & Kwasniewski 1991), support the minor influence of AW and TAW in Adventfjorden 2018, with the exception of June. Finding low abundance of *O. atlantica* in June was unexpected.

The calanoid genera *Calanus* and *Pseudocalanus* were also found in high numbers in Adventfjorden. This is also as expected as both genera include Arctic associated species, especially the Arctic *C. glacialis* and *C. hyperboreus* (Kwasniewski et al. 2003), and boreal/Arctic *P. acuspes* and *P. minutus* (Frost 1989; Koszteyn & Kwasniewski 1991). Additionally, the more deep-water dwelling genus *Microcalanus* was found in surprisingly high numbers in Adventfjorden, especially in March and September. As Adventfjorden generally is shallower than the genus' resident depths of below 100 m (Sars 1903; Koszteyn & Kwasniewski 1991; Conway 2006), it's unlikely that these species have a population in Adventfjorden but

has most likely been advected from deeper waters outside. In addition to the copepods, the orders Euphausiacea were found in high numbers in May. The Euphausiacea were present in larval stages only, while few more developed individuals were found, most likely due to them avoiding the slowly moving WP2. The Copelata were also absent for all months but May.

How does the presence of sea ice influence the zooplankton community in early spring, and how does this differ between East and West Spitsbergen?

The sea-ice was found to greatly reduce the amount of light reaching the water column and is thus expected to delay the bloom in phytoplankton and consequent increase in zooplankton abundance, compared to ice-free water. Inglefieldbukta having such lower zooplankton abundance in April compared to what found in Adventfjorden sampled four days later illustrates this. It might appear that the differences in location around the archipelago and consequent differing affecting water masses were just as important as the sea-ice conditions for shaping the pelagic community, as Van Mijenfjorden in East Spitsbergen was more similar to Adventfjorden in terms of zooplankton abundance and species composition. Van Mijenfjorden also had a higher abundance of small Copepoda nauplii than the winter months in Adventfjorden, despite the low chl *a* content in water, which might suggest sufficient ice algae was present in the area to start reproduction and thus that the spring had advanced further here.

The water masses at the ice-covered stations were mostly unstratified, as for Adventfjorden in winter, although all had colder temperatures. All stations had similar low chl *a* concentrations as in Adventfjorden, although the ice-covered stations had lower light intensity in the water column. Consequently, as for Adventfjorden in winter, zooplankton was found in low abundances. The holoplanktonic Copepoda was dominating in the zooplankton composition in all fjords. The abundance of developed Copepoda was lower in the ice-covered fjords than in Adventfjorden, suggesting that the sea-ice affect abundance of copepods in winter.

The presence of sea ice was found to greatly reduce the amount of light reaching the underlying water masses, compared with the ice-free Adventfjorden. Highest attenuation by ice and snow was found in Van Mijenfjorden and Inglefield in April where the thickest sea ice and/or deepest overlying snow was found. Hence, phytoplankton will most likely not bloom before the sea ice has melted, whereof Van Mijenfjorden and Inglefield in April might be expected to experience a later melt and phytoplankton bloom compared to Agardhbukta. The sea-ice delaying the pelagic spring bloom has previously been found to occur in ice-covered waters in the Arctic

(Søreide et al. 2010). Based on this, even though later seasonal data is unavailable for the ice-covered stations, assuming pelagic primary production will be delayed by the sea-ice, a later peak in zooplankton abundance compared to ice-free Adventfjorden may expected. Sampling later in spring and summer is however needed to investigate whether this would lead to a reduced zooplankton abundance through the productive summer season and remaining year in seasonally ice-covered waters compared to the ice-free areas.

In the ice-covered marine ecosystems, a bloom in primary production by ice algae is commonly found as soon as sufficient light is available (Søreide et al. 2010; Leu et al. 2015). Previous studies have found specialised zooplankton (e.g. *Calanus glacialis* (Søreide et al. 2010; Daase et al. 2013)) to utilise to fuel early maturation and reproduction. When sampling in April, ice algae was observed to grow under the sea ice in the outer parts of Van Mijenfjorden where thinner ice was found (personal observation), in greater abundance than the sampled station in Van Mijenfjorden (VMF1) and the other ice-covered stations. Van Mijenfjorden had a higher abundance of small Copepoda nauplii than the winter months in Adventfjorden, despite the low chl *a* content in water, which might suggest sufficient ice algae was present in the area to start reproduction and thus that the spring had advanced further here.

Interestingly, the two fjords on the east coast of Spitsbergen (Inglefield- and Agardhbukta) both had lower zooplankton abundances than Van Mijenfjorden on the west coast, which had a much higher abundance of both Copepoda nauplii and *Oithona* spp. This might partly be explained by the deeper sampling depth in Van Mijenfjorden, being twice as deep as both Inglefield- and Agardhbukta. The east coast stations did however still have lower zooplankton abundance than Van Mijenfjorden when adjusting for sampling depth by calculating abundance in individuals m^{-3} (See Appendix 9). Alternatively, it could have been related to the different light conditions of the fjords, and consequent potentially different primary production, but as Agardhbukta had the lowest loss of light through snow and sea ice of the ice-covered stations, this is not supported by the presented results.

The variations in zooplankton abundances might rather be due to the differing hydrology between east and west of Spitsbergen, as described in introduction, where the west coast is generally affected by Atlantic Water (AtW) and the east by Arctic Water (ArW). A study of zooplankton distribution in northern Svalbard indicated that zooplankton abundance was largely correlated with temperature, where areas associated with inflow of AtW had highest

abundance (Daase & Eiane 2007). Lower zooplankton abundances were found in the ArW-influenced fjords in East Spitsbergen, and the species composition placed Van Mijenfjorden in a cluster together with the spring/fall samples from Adventfjorden, rather than with the other ice-covered stations. However, as data of zooplankton abundance in the coastal areas in East Spitsbergen are scarce, both under sea-ice and after the sea-ice has melted, further studies with sampling later in the season after the ice has melted is needed to establish whether there is a lower productivity here.

The reproductive strategy of *Calanus* spp. in Adventfjorden and in ice-covered water

The abundance of *Calanus* spp. copepodite stage CV in mid-August, and absence of high amounts of the same stage in the beginning of the season, suggests a dominance of individuals having a one-year life cycle in Adventfjorden. The same might occur in the ice-covered waters, where AF was found in abundance in Inglefieldbukta in early spring.

Previous studies have established a potential difference between the *Calanus* congeners in terms of life cycle duration in the Arctic. *Calanus finmarchicus* mostly has a 1 year life-cycle and *C. glacialis* commonly needs two years to fulfil its life cycle (Tande et al. 1985; Conover 1988; Kosobokova 1999; Kwasniewski et al. 2003) due to investing much energy in developing from CIV to CV as an adaption to the fluctuating Arctic climate (Scott et al. 2000). *Calanus glacialis* can however achieve this within one year under favourable conditions. As this has been reported to occur in the Arctic (Maclellan 1967; Daase et al. 2013), it's likely that the life cycle lengths are more dependent on location and e.g. water temperature and food availability, rather than species specific life history strategies. Daase et al. (2013) found *C. glacialis* completing their life-cycle within one year to occur in both ice-free and ice-covered waters, where spawning and maturation of nauplii was timed to the phytoplankton bloom. Using the length class definitions from Daase and Eiane (2007) for the *Calanus* spp. copepodid stages in August, indicated an almost equal distribution of the two species amongst the CV (Appendix 10), which is an overwintering stage for both species. Hence, a 1-year life cycle appeared to have occurred for both *C. glacialis* and *C. finmarchicus*. However, this method for species identification has been questioned the last years, as e.g. Gabrielsen et al. (2012) and Choquet et al. (2018) found significant overlap in prosome lengths between the species in Svalbard waters. Hence, only data at genus level has been presented in this thesis.

Additionally, regarding the life cycle of *Calanus* spp., the concentrations of CI and nauplii indicate that they mainly produced eggs using existing energy reserves (capital breeding). The high abundance of CI on May 11, and assuming a developmental time of 46 days from egg to CI at 0 °C (Corkett et al. 1986), would indicate a start of spawning towards the end of March. The abundance of late naupliar stages at the same time as CI would indicate a continued reproduction from the end of March. As these estimates place start of reproduction before the peak in chl *a*, it appears that *Calanus* spp. mainly conducted capital breeding in Adventfjorden 2018. This assumption agrees with studies done on *C. glacialis* in Kongsfjorden (Kwasniewski et al. 2003; Daase et al. 2013).

Calanus spp. completing its life cycle within one year might also have occurred for the individuals in the ice-covered fjords. Especially both Inglefieldbukta and Agardhbukta had a high presence of AF in APril, relative to total *Calanus* spp. abundance. Later stage composition is unknown, but previous studies has shown that at least *Calanus glacialis* can utilise the ice algae to fuel spawning by income breeding (Søreide et al. 2010; Daase et al. 2013), where Daase et al. found *C. glacialis* in ice-covered water to complete the life cycle in the same time frame as those in ice-free environments. The presence of CIII in Inglefield in April and Van Mijenfjorden might suggest some individuals spend multiple years on completing the life cycle.

The reproductive strategy and species composition of *Pseudocalanus* spp. in Adventfjorden

Opposed to the single-event reproduction in *Calanus*, the stage composition of *Pseudocalanus* in Adventfjorden, with the continuous high proportion of early copepodid stages (CI-CIII) from June to October, indicate a continuous reproduction throughout the summer months in 2018. The molecular identification of *Pseudocalanus* spp. indicated that the early copepodids in July and August mainly were of *P. acuspes* and *P. moultoni*, suggesting that these might have spawned around the same time in Adventfjorden. The absence of early copepodids and adult females of *P. minutus* in all analysed months might suggest that this species did not spawn in Adventfjorden.

Pseudocalanus spp. has been found to spend approx. 45 days to develop to CI from hatching at 0 °C by Corkett and McLaren (1979) where they used Belehrádek's temperature function for individuals from Halifax, Nova Scotia. Back calculating the estimated 45 days of development for the first and last major (≥25%) CI presence (May 11 and October) indicates that the

Pseudocalanus spp. in Adventfjorden hatched from the end of March until the end of August. The hatching possibly lasted longer as the time needed to develop from hatching to CI decrease to approx. 25 days when water temperature increase to 4 °C, which was the water temperature above 50 m depth in July-September. The similar distribution of *P. acuspes* and *P. moultoni* amongst stages CI and CII in August might suggest that both species reproduced simultaneously in Adventfjorden.

The abundance of *P. acuspes* and *P. moultoni* amongst the identified animals is as expected based on both being found to have a more neritic distribution (Frost 1989; Koszteyn & Kwasniewski 1991; Lischka & Hagen 2005). The high proportion of *P. acuspes* amongst the identified animals might suggest this to be the most dominant congener in Adventfjorden. This is similar to what was found in the Chukchi Sea, a shallow Arctic shelf sea, where *P. acuspes* was found to dominate in all years sampled (Ershova et al. 2016). *Pseudocalanus minutus* however was mostly found amongst the later copepodid stages (CIII-CV). From this it might appear that *P. minutus* did not reproduce in Adventfjorden but might rather have been advected into Adventfjorden from more oceanic areas. This could be expected from the assumption of *P. minutus* being more oceanic than its congeners (Wiborg 1955; Koszteyn & Kwasniewski 1991). Alternatively, *P. minutus* may spawn later and the sampling was too sporadic to have gotten a representative sample of the species. Moreover, only a few *Pseudocalanus* individuals (n= 48 for July and for August) were analysed genetically, and further studies with molecular identification of more individuals are needed to establish how the *Pseudocalanus* congeners reproduce in Adventfjorden.

Although previous studies on *Pseudocalanus* in the Arctic indicate that this genus mainly reproduces in late May/June (Conover 1988; Lischka & Hagen 2005), *Pseudocalanus* spp. in more temperate areas has been found to reproduce continuously or have multiple successive generations (Corkett & McLaren 1979). The same strategy may be viable in Arctic water, as both *P. acuspes* and *P. minutus* has been found to overwinter already as CIII and CIV respectively (Norrbin 1991). Having the ability to overwinter at an early stage might make it feasible to reproduce late in the productive season. *Pseudocalanus acuspes* can feed more efficiently on heterotrophic flagellates than *P. minutus* (Cleary et al. 2015). Heterotrophic flagellates have previously been found to be present in low numbers through most of the year in Adventfjorden (Kubiszyn et al. 2017). Thus, *P. acuspes* may have a higher chance of

accumulating enough energy for a viable overwintering stage in spite of the lack of phytoplankton outside the time spring bloom.

The relatively high abundance of adults found in May might suggest that a main reproductive event occurred. This spring reproduction may mainly have been done by *P. acuspes*, as most of the identified adults from this month were identified to this species. However, further sampling involving genetic identification on more individuals are needed for this to be stated with certainty. Additionally, the two peaks of total abundance of *Pseudocalanus* spp. in July and September might suggest two main reproductive events occurred prior to this. Alternatively, abundance was generally high during July-September, and the low abundance found in August was due to circulation patterns advected more individuals out of the fjord. Also, patchiness in zooplankton distribution could have caused the lower abundance, illustrated by the difference in e.g. *Oithona* spp. abundance between the two processed hauls from August (see Appendix 11).

The reproductive strategy of *Oithona* spp. in Adventfjorden

Oithona spp. also appear to have had a rather continuous reproduction throughout the summer season, with a reproduction peak in late summer. The late peak is indicated by a high presence of small (< 150 µm) nauplii found in October which most likely were nauplii of *Oithona* spp. This assumption is based on the nauplii fitting the size range of *O. similis* (Gibbons & Ogilvie 1933), the numerically dominant *Oithona* species in Svalbard waters. Additionally, earlier studies on *O. similis*, e.g. Digby (1954) and Ussing (1938) in Eastern and Western Greenland, found abundance of *O. similis* nauplii to peak in September-November. Lischka and Hagen (2005) found the same to occur in November in Kongsfjorden.

The fairly high presence of young *Oithona* spp. (most likely *O. similis*, although undistinguishable from *O. atlantica* as young) found in Adventfjorden from June to October, suggest that a reproduction had taken place prior to this. Hence, it appears that *Oithona* spp. had a continuous reproduction, with the nauplii abundance in October indicating a reproduction peak in late summer, as found by Lischka and Hagen (2005) in Kongsfjorden. This is likely possible due to their omnivorous feeding mode and consequent independence of the phytoplankton bloom (Lischka et al. 2007). As *P. acuspes*, *O. similis* feed on heterotrophic dinoflagellates (Nakamura & Turner 1997), and has also been found to feed on sinking faecal matter from calanoid copepods (Gonzalez & Smetacek 1994). The assumed all-time presence

of flagellates and dinoflagellates in Adventfjorden (Kubiszyn et al. 2017), and the abundance of the calanoid genera *Calanus* and *Pseudocalanus* found in the summer months, likely made this opportunistic life strategy of *O. similis* viable in Adventfjorden.

The earlier studies all found signs of increased reproductivity in spring in addition to that towards the end of the productive season (Ussing 1938; Digby 1954; Lischka & Hagen 2005). In Adventfjorden, *Calanus* spp. had a higher relative abundance than *Oithona* spp. in both May and June. The coinciding lack of small nauplii in spring might be due to high predation pressure by *Calanus*, as suggested in the previously mentioned studies. Alternatively, the course net (200 µm) used for the sampling on May 11 might have let through the smaller nauplii of *Oithona* spp.

Concluding remarks

The present results provide data on the productive season in Adventfjorden in 2018 and gives an insight into the state of the zooplankton community here. Meroplankton was found to be dominant in the zooplankton community during the period of high primary production, while holoplankton was important in the remaining year. Although present for a short time only, the abundance of meroplankton found in May is likely making them an important part of the marine ecosystem in Adventfjorden. The shorter time of dominance found in 2018 compared to 2012 might have been caused by too infrequent sampling. Seasonal sampling with high temporal resolution might therefore be important to establish the length of period of high meroplanktonic presence.

Amongst the three most abundant Copepoda, the dominating holoplanktonic order, different reproductive strategies were found. *Calanus* spp. appeared to predominantly complete their life cycle within one year in Adventfjorden, with reproduction timed with the peak abundance of phytoplankton. *Pseudocalanus* spp. was most likely reproducing continuously throughout the productive season, with spawning taking place between March and August. All three expected congeners (*P. acuspes*, *P. moultoni* and *P. minutus*) was found. From the molecular identification it appeared that both *P. acuspes* and *P. moultoni* reproduced simultaneously, while *P. minutus* might not have reproduced in Adventfjorden. Further studies with genetical identification of more individuals is however needed to establish this. *Oithona similis* appear to also have had a continuous reproduction in Adventfjorden, with a peak in spawning in late summer indicated by the high abundance of small nauplii in October. It's however uncertain whether these nauplii were of *Oithona* spp. or another small Copepoda, and further studies including identification of nauplii would be needed.

Additionally, a glimpse of the situation in ice-covered coastal areas in the Arctic during early spring is given. The ice-covered fjords had lower abundance of adult Copepoda compared to the ice-free Adventfjorden and might be expected to experience a later peak in primary and secondary production due to the ice shading the underlying water masses. The lower zooplankton abundance found in the fjords in East Spitsbergen, compared to that of Van Mijenfjorden, suggest that the differing hydrology between east and west contribute to shaping the pelagic community. This illustrates the importance of considering impact of hydrology and circulation in future studies of how the sea-ice affect the pelagic ecosystem.

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Appendix 1 – Metadata

Appendix 1.1 – Metadata for CTD-measurements

Table A1.1. Sampling depths for CTD-casts taken in Adventfjorden, Van Mijenfjorden, Inglefieldbukta and Agardhbukta during sampling conducted in 2018.

Fjord	Station	Sampling date	Bottom depth (m)	Sampling depth (m)
Adventfjorden				
	IsA	March 14	78	70
		April 5	84-73	76
		May 1	72	70
		May 11	100	97
		June 18	100	85
		July 19	123	107
		August 18	88	78
		September 17	70-83	63
		October 15	94	82
		November 15	68	64
Van Mijenfjorden				
	VMF1	April 14	70	71
Inglefieldbukta				
	IB	March 23	34	32
		April 27	32	31
Agardhbukta				
	AGA	April 15	42	41

Appendix 1.2 – Metadata for light measurements

Table A1.2. Sampling Time (LT) and depths (m) of light measurements taken at each sampling station for each date, with X indicating that light intensity was measured at this depth for that date. Depth= 0+ is just above the sea surface and depth= 0- is just below. Measurements were conducted for each meter at depths given in intervals (e.g. 16-19).

	IsA								IB		VMF1	AGA
	Mar 14	**Apr. 5**	**May 1**	**May 11**	**Jun. 18**	**Jul. 19**	**Aug 18**	**Sep. 17**	**Mar 23**	**Apr 27**	**Apr 13**	**Apr 15**
Time / Depth	**12:37-12:47**	**12:30**	**~12:00**	**NA**	**10:55**	**NA**	**NA**	**14:25-14:55**	**~12:00**	**~12:00**	**14:00**	**13:06-13:16**
0+	X	X	X		X	X						
0-	X	X	X		X	X		X				
0.5	X	X	X									
1-10	X	X	X		X	X		X	X	X	X	X
11						X		X	X	X	X	X
12						X		X	X	X		X
13						X			X	X		X
14						X			X	X		X
15	X	X	X		X			X	X	X	X	X
16-19									X	X		
20	X	X	X		X			X	X	X		X
21-28									X			
25	X	X	X		X							
30	X	X	X					X				
35	X	X	X									
40	X	X	X									

Appendix 1.3 – Metadata for Chlorophyll a filtration

Table A1.3. Sampling depths (m) (S. depth(s) (m)), number of replicate GF/F grade filters for each depth (n rep), volume (mL) of water filtered through each filter replicate ($V_{filtered}$), date of filtration and times for extraction of Chlorophyll *a* (Extract. start, Extract. end) in water sampled at all sampling stations sampled during 2018.

Station	Sampling date	S. depth(s) (m)	n rep	$V_{filtered}$ (mL)	Extract. start	Extract. end
IsA	March 14	15, 68	3	300	15/5/18; 16:30-17:00	16/5/18; 11:00-14:00
	April 5	15, 75	3	300	15/5/18; 16:30-17:00	16/5/18; 11:00-14:00
		1, 15	1	300	28/10/18; 13:00	29/10/18; 11:00
	May 1	15	3	50	15/5/18; 16:30-17:00	16/5/18; 11:00-14:00
		65	3	100	15/5/18; 16:30-17:00	16/5/18; 11:00-14:00
	May 11	15, 80	3	250	15/5/18; 16:30-17:00	16/5/18; 11:00-14:00
		1	1	300	25/10/18; 19:00	26/10/18; 16:00
		15	1	300	16/10/18; 16:00	17/10/18; 13:00
	June 18	1	1	100	15/10/18; 11:10	16/10/18; 10:00
		15	1	300	15/10/18; 10:30	16/10/18; 10:00
	July 19	1, 15	1	300	28/10/18; 13:00	29/10/18; 11:00
	August 18	1	1	650	24/10/18; 16:00	25/10/18; 17:00
		15	1	750	24/10/18; 16:00	25/10/18; 17:00
	September 17	15, 50	3	500*	NA	NA
VMF1	April 14	1, 5, 15, 20, 40, 65	3**	500	NA	NA
		1, 5, 15, 20, 40, 65	1**	1000	19/4/18; 14:15	20/4/18; 13:45
IB	March 23	3	3	500	5/11/18; 11:14	5/11/18; 10:15
	April 27	1, 5, 15	3	500	28/4/18; 16:00	29/4/18
AGA	April 15	1, 5, 15, 37	3	1000	NA	15/4/18; 21:30

*IsA 17/9: One 15 m-replicate had 300 mL water filtered

**VMF1 14/4: Measurements done on the 3 500 mL filtered replicates were done in polluted methanol, values for the 1000 mL filtered replicates used

Appendix 1.4 – Metadata for zooplankton sample processing

Table A1.4. Fraction of each replicate sample (Rep. nr), taken at each sampling date (S. date) at the stations sampled during 2018, sorted for each subsample type (Subs. type), including sample volume (V_{sample} (mL)), subsample volume (V_{subs} (mL)), number of subsamples taken (n subs) and Split factor (equal to 1 if sample was not split, 0.5 when split once with a zooplankton splitter and 0,.25 when split twice). Fraction counted gives what fraction of the total was counted for each subsample type, given by ((n subs x V_{subs}) / V_{sample}) x Split factor).

Station	S. date	Rep. nr	Subs. type	Split factor	V_{sample} (mL)	V_{subs} (mL)	n subs	Fraction counted
IsA	Mar. 14	1	Community 1 (*Oithona*, Copepod nauplii)	1	100	2	2	0.04
			Community 2	1	100	2	3	0.06
			Calanus	1	100	100	1	1
	Apr. 5	1	Community	1	100	2	3	0.06
			Pseudocalanus, Calanus	1	100	2	4	0.08
		2	Copepod nauplii	1	100	2	2	0.04
			Community	1	100	2	3	0.06
			Calanus	1	100	2	6	0.12
			Pseudocalanus	1	100	2	11	0.22
	May 1	1	Cirripedia	0.5	400	2	1	0.003
			Community 1 (excl. Cirripedia)	0.5	400	2	3	0.008
			Community 2 (excl nauplii, other larvae)	0.5	400	2	20	0.05
			Pseudocalanus	0.5	400	2	40	0.1
		2	Cirripedia	0.25	200	1	1	0.001
			Community 1	0.25	200	2	4	0.01
			Community 2 (Copepods, others)	0.25	200	2	20	0.05
			Copepod nauplii	0.25	200	2	8	0.02
			Pseudocalanus	0.25	200	2	28	0.07
	May 11	1	Community 1	0.5	300	2	1	0.003
			Community 2	0.5	300	2	10	0.033
			Pseudocalanus	0.5	300	2	20	0.067
	Jun. 18	1	Community	1	100	3	1	0.03
			Pseudocalanus	1	100	5	2	0.1
			Calanus CV, AF	1	100	5	4	0.2
	Jul. 19	1	Community	1	400	2	1	0.005
			Community (excl *Oithona*, Copepod nauplii, Bivalvia)	1	400	2	2	0.01

	Aug. 18	1	Community 1 (*Oithona* spp.)	1	300	2	2	0.013
			Community 2 *(Oithona atlantica*, Copepod nauplii)	1	300	2	3	0.02
			Community 3 (*Calanus*, rest)	1	300	2	4	0.027
			Pseudocalanus	1	300	2	10	0.067
		2	*Oithona* spp., Copepod nauplii	1	300	2	2	0.013
			Comunity	1	300	2	4	0.027
			Pseudocalans	1	300	2	7	0.047
	Sep. 17	1	Community 1 (*Oithona*, Copepod nauplii)	1	200	2	1	0.01
			Community 2 (excl. *Oithona*, Copepod nauplii)	1	200	2	2	0.02
			Calanus, Pseudocalanus	1	200	9	1	0.045
	Oct. 15	1	Community 1 (*Oithona* spp., Copepod nauplii)	1	200	2	1	0.01
			Community 2 (*Oithona atlantica*)	1	200	2	3	0.03
			Community 3 (rest)	1	200	2	5	0.05
			Calanus, Pseudocalanus	1	200	2	8	0.08
	Nov. 15	1	Copepod nauplii	1	200	2	2	0.02
			Community	1	200	2	4	0.04
			Pseudocalanus CI-CV	1	200	2	5	0.05
			Calanus, Pseudocalanus CVI	1	200	2	10	0.1
VMF1	Apr. 13	1	Copepod nauplii	1	100	2	2	0.04
			Community	1	100	2	5	0.1
			Calanus, Pseudocalanus	1	100	2	10	0.2
			Calanus CIV-AF	1	100	100	1	1
IB	Mar. 23	1	Whole sample sorted	1	100	100	1	1
	Apr. 27	1	Whole sample sorted	1	100	100	1	1
AGA	Apr. 15	1	Community	1	100	4	5	0.2
			Calanus, Pseudocalanus CVI	1	100	100	1	1

Appendix 2 – Unsuccessful methods for molecular identification of *Pseudocalanus*

Pseudocalanus spp. females were picked out from samples conserved in ethanol, from dates when females were found abundant in the formalin preserved samples (samples from IsA May 11, July 19 and September 17). The ethanol was removed by sieving the sample through a 60 µm sieve and the sample was diluted in a beaker using 20 µm filtered seawater. Subsamples were taken using a 1-5 mL Finnpipete after getting the sample to a suitable volume using 20 µm filtered seawater. All *Pseudocalanus* of stage CVIF found in the subsamples were picked and placed in a petri dish filled with MilliQ water to rinse of any residue ethanol. When too few *Pseudocalanus* of stage CVIF were present (less than one CVIF per 2 mL subsample), CVF and CIVF were also picked (Table A2.1). Subsamples were taken until 45 female *Pseudocalanus* spp. of stage CIV-CVI had been found.

Table A2.1 Number of *Pseudocalanus* spp. females of stage CVI-CIV picked from samples taken at IsA on three dates in 2018

Sampling date	**CVI**	**CV**	**CIV**
May 11	44	1	
July 19	17	23	5
September 17	27	18	

Each individual was photographed using a camera with a stereomicroscope adaptor, before placed in an individual PCR-tube filled with 25 µL Alkaline Lysis Reagent (ALR, table A2.2) for HotSHOT extraction. Eight individuals were placed in tubes filled with ALR at the time, and the tubes were stored in 4 °C in between. Placing of the individuals was done with tweezers to ensure as little transfer of water as possible, and the tweezer was rinsed with ethanol and MilliQ water between transfer of each individual to prevent contamination.

The *Pseudocalanus* DNA was extracted by HotSHOT extraction after each day of picking, heating the PCR tubes with *Pseudocalanus* individuals in ALR at 95 °C for 30 mins, using a GeneAmp PCR System 9700 (Applied Biosystems, ThermoFisher Scientific). 25 µL neutralisation buffer (Table 2.5) was added to each tube and the extracted DNA was stored at -20 °C until further analysis.

Table A2.2. Content in the Alkaline Lysis reagent (ALR) and Neutralisation Buffer (NB) used for HotSHOT extraction of *Pseudocalanus* spp. DNA.

Alkaline Lysis Reagent	Neutralisation Buffer
125λ 10N 25mM NaOH	324 mg 40 mM Tris-HCL
20λ 0.5M 0.2mM EDTA	50 mL ddH_2O
50 mL ddH_2O	

The HotSHOT extracted DNA from *Pseudocalanus* spp. from IsA May 11 and 15 individuals from IsA September 17 were attempted identified to species by species specific Polymrase Chain Reaction (ssPCR). Species specific reverse primers were designed for each of the three species (*P. minutus, P, acuspes* and *P. moultoni*) by Dr. Elizaveta Ershova (Post-doctoral researcher, UiT) (Ershova et al. 2016) and were used together with a general *Pseudocalanus* forward primer (Table A2.3) in analyses performed at UiT, the Arctic University of Norway. The species-specific primers ensured resulting amplified DNA of different lengths for each species.

Table A2.3. Primer names and sequences used in ssPCR on *Pseudocalanus* from Adventfjorden.

Primer name	Sequence
Minutus 398R	CGCAAACARAGGTATTTGGTCT
Acuspes 238R	AGAGGAGGGTATACAGTTCACC
Moultoni 520R	ACAATATTGTAATTGCMCCAGC
PseudoFmod	TTCGAATASARYTRGGHMVRGY

The primers were used in a 10 µL reaction including 5 µL Accustart II PCR ToughMix (Quantabio), 0.5 µL of each reverse primer, 1 µL forward primer, 0.2 µL GreenMix loading dye, 0.8 µL MilliQ water and 1.5 µL HotSHOT-extracted *Pseudocalanus* spp. DNA. Three positive controls, containing DNA of each species confirmed by sequencing, and one negative control containing MilliQ water were run for each PCR. The amplification protocol was 94 °C 3 min, 35 cycles of 94 °C 40 sec, 58 °C 40 sec and 72 °C 50 sec, and 72 °C 7 min. 4 µL of the resulting amplified DNA product was run on a 2 % agarose gel, containing 100 mL 1X TAE-buffer, 2 g agarose and 5 µL Etidium bromide, together with 4 µL Quick load 1kb DNA ladder (New England BioLabs) at 120 V until the DNA had run a sufficient distance on the gel. The gel was visualised under UV light and the *Pseudocalanus* species were determined by the length on the resulting amplified DNA. Few PCR resulted in succeful product.

Appendix 3 – Scripts

Script 1. Addition of column for species levels for grouping performed in Script 2.

```
library(tidyverse)
df.long$species <- factor(df.long$species)
df.long.fix <- df.long %>% mutate(speciesgrouped= recode(species,
       "Acartia_longiremis"="acartia","Aglantha_digitale"="aglantha",
       "Aglantha_digitale_macro"="aglantha","Beroe_cucumis"="beroe",
       "Bivalvia_veliger"="bivalvia","Bryozoa_larvae"="bryozoa",
       "Calanus_AF"="calanus","Calanus_AM"="calanus",
       "Calanus_C1"="calanus","Calanus_C2"="calanus",
       "Calanus_C3"="calanus","Calanus_C4"="calanus",
       "Calanus_C5"="calanus","Calanus_hyperboreus"="calanus",
       "Chaetognata_juv."="chaetognatha",
       "Cirripede_cypris"="cirripedia_cypris","Cirripede_nauplii"="cirripedia_nauplii",
       "Clione_limacina"="clione_limacina","Clione_limacina_juvenile"="clione_limacina",
       "Copepod_nauplii_tot"="copepoda_nauplii","Decapoda_young"="decapoda",
       "Decapoda_zoea"="decapoda","Decapoda_zoea_macro"="decapoda",
       "Echinodermata_larvae"="echinodermata","Egg"="egg",
       "Eukrohnia_hamata"="eukrohnia", "Euphauciacea_calyptopis"="euphauciacea_larvae",
       "Euphauciacea_furcilia"="euphauciacea_larvae","Euphausiacea_furcilia"="euphauciacea_larvae",
       "Euphausiacea_nauplii"="euphauciacea_larvae","Fritellaria_borealis"="fritillaria",
       "Harpacticoid_unident"="harpacticoida_sp","Harpacticoid_unident2"="harpacticoida_sp",
       "Hydrozoa_unident"="hydrozoa","Isopod_parasitic"="isopoda_parasite",
       "Limacina_helicina"="limacina_helicina","Limacina_retroversa"="limacina_retroversa",
       "Mertensia_ovum"="mertensia","Metridia_longa_AF"="metridia",
       "Metridia_longa_AM"="metridia","Metridia_longa_C1"="metridia",
       "Metridia_longa_C2"="metridia","Metridia_longa_C3"="metridia",
       "Metridia_longa_C4"="metridia","Metridia_longa_C5"="metridia",
       "Microcalanus_C1"="microcalanus","Microcalanus_C2"="microcalanus",
       "Microcalanus_C3"="microcalanus","Microcalanus_C4.Adult"="microcalanus",
       "Microcalanus_spp_tot"="microcalanus_tot",
       "Microsetella_norvegica"="microsetella","Oikopleura_sp"="oikopleura",
       "Oikopleura_sp_macro"="oikopleura","Oithona_atlantica"="oithona_atlantica",
       "Oithona_similis"="oithona_similis","Oithona_sp_male"="oithona_sp",
       "Oithona_sp_young"="oithona_sp","Ostracoda_juv"="ostracoda",
       "Parasagitta_elegans_macro"="parasagitta",
       "Parasagitta_elegans_small"="parasagitta",
       "Polychaeta_juv"="polychaeta","Polychaeta_macro"="polychaeta",
       "Pseudocalanus_C1"="pseudocalanus","Pseudocalanus_C2"="pseudocalanus",
       "Pseudocalanus_C3"="pseudocalanus","Pseudocalanus_C4F"="pseudocalanus",
       "Pseudocalanus_C4M"="pseudocalanus","Pseudocalanus_C5F"="pseudocalanus",
       "Pseudocalanus_C5M"="pseudocalanus","Pseudocalanus_C6F"="pseudocalanus",
       "Pseudocalanus_C6M"="pseudocalanus",
       "Siphonophora_polyp"="siphonophora","Themisto_abyssorum"="themisto",
       "Themisto_sp"="themisto","Thysanoessa_inermis"="thysanoessa",
       "Triconia_borealis"="triconia","Triconia_sp_male"="triconia",
       "Trochophore_larvae"="trochophore_larvae",
       "Unident_hydrozoa_larvae."="hydrozoa",
       "Unident1_parasite."="parasite_unident"))
```

Script 2. Grouping species by column added in Script 1 (speciesgrouped), averaging individuals m^{-2} for when two hauls were sorted and converting the long data frame into a wide data frame where the stationmonth variable (unique for each sampling date) is row names.

```
df.wide.mean <- df.long.fix %>%
  filter(station!= "VMFMN") %>%
  filter(speciesgrouped!="microcalanus") %>% # count of microcalanus included in microcalanus_tot
  group_by(location, station,  sampling_date, stationmonth,sample_depth, replicate, julianday,
           dayofyear, freeice, surfT, surfS, meanT, meanS, fluomax, chla15mGFF,chla15m10um, K,
           speciesgrouped) %>%
  summarise(indivspersquare= sum(indivspersquare)) %>% # Summing indivspersquare for grouping vars in
speciesgrouped
  group_by(location, station, sampling_date,stationmonth,  sample_depth,julianday, dayofyear,freeice,
           surfT, surfS, meanT, meanS, fluomax, chla15mGFF, chla15m10um, K, speciesgrouped) %>%
  summarise(mean= mean(indivspersquare)) %>% #Averaging for when 2xReplicates
  spread(key= speciesgrouped, value= mean) %>%
  column_to_rownames("stationmonth") # Makes stationmonth (unique for each samplingdate) rownames
```

Script 3. Plotting results from PCA (function rda()) on square root transformed data, including significant environmental variables

```
library(vegan)
library(cluster)
ord <- rda(sqrt(spp.df))

plot(ord,
     display= c("species","sites"), # Adding the sites and species data to the plot
     type= "text",
     choices=c(1,2), # deciding which axes to plot
     scaling= "species")
plot(envfit(ord=ord, # Adding significant env variables
            env= select(env.df, julianday, meanT, chla15mGFF, freeice),
            permutation=999, choices= c(1,2), na.rm=TRUE))
```

Appendix 4 – Environmental properties

Appendix 4.1 – Temperature (°C) and salinity (PSU) as a function of depth (m)

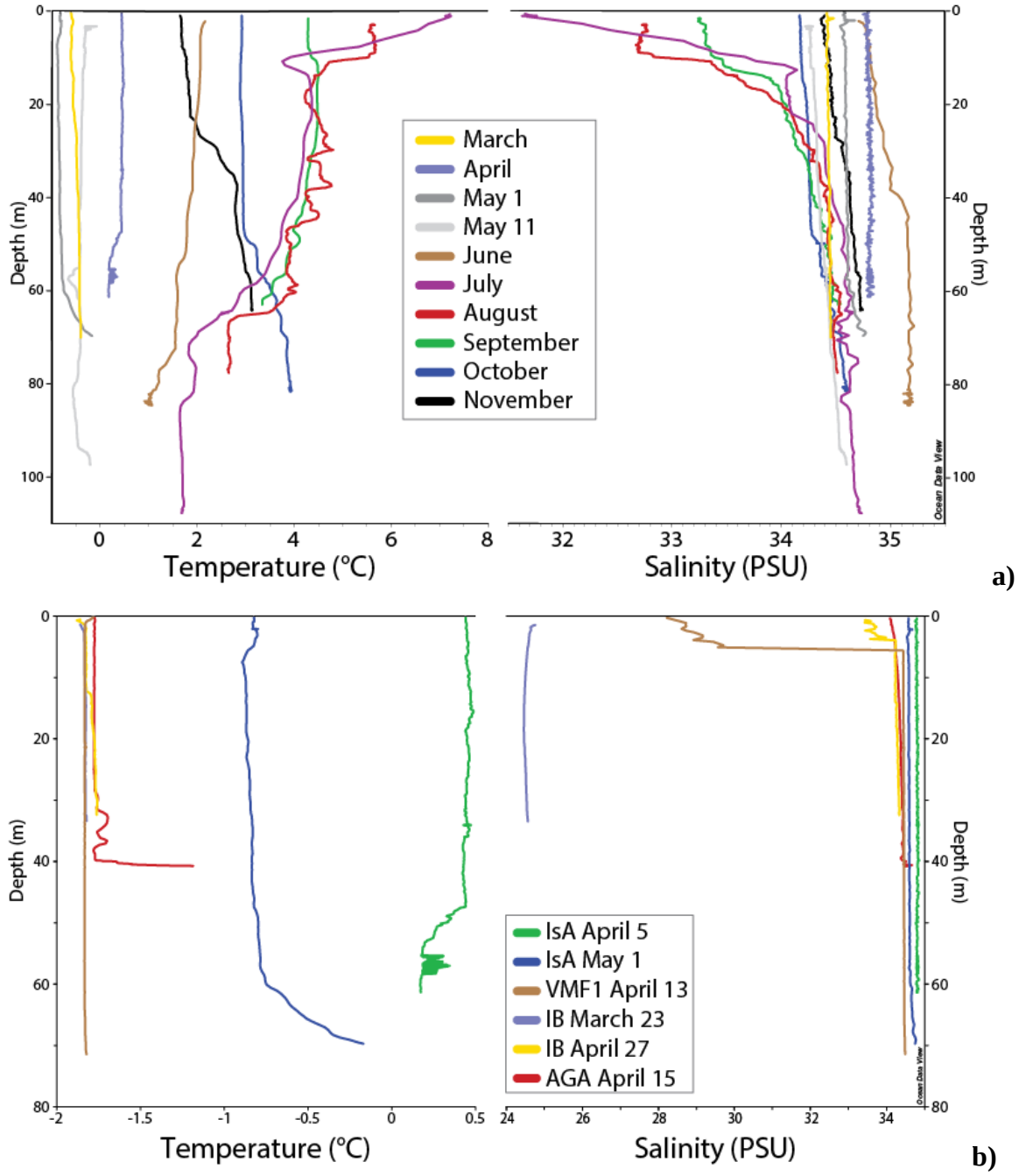


Figure A4.1. Temperature (°C) and salinity (PSU) through the water column at a) IsA from March to November 2018 and b) the ice covered stations in March and April (also including IsA April 5 and May 1 for comparisons).

Appendix 4.2 – Light penetration

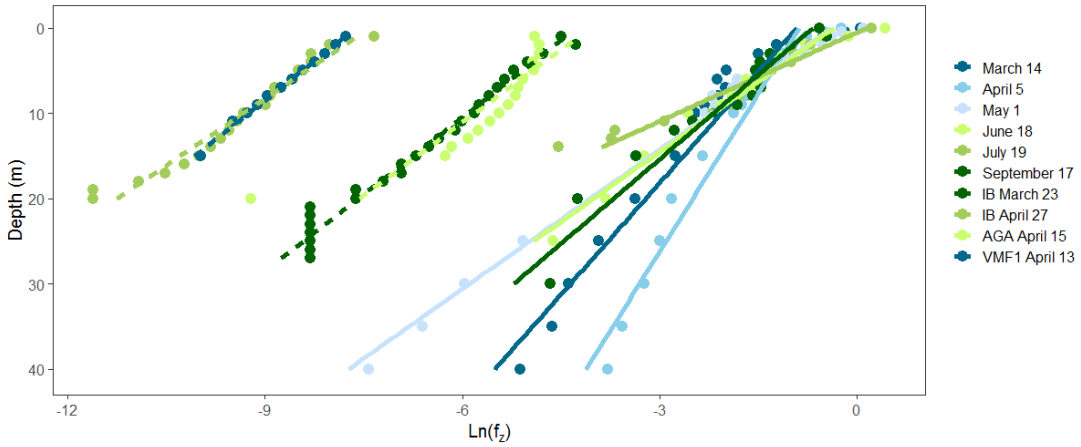


Figure A4.2. ln of relative light f_z (I_z (light intensity at depth (m)) divided by I_S (light intensity above surface when I_z was measured), as a function of depth (m) for each sampling date when light intensity through the water column was measured in Advenfjorden from March to September (solid line) and at the ice-covered stations (Van Mijenfjorden, Inglefieldbukta and Agardbukta; dashed line) in March and April 2018, with added linear regression line (geom_smooth(method="lm", formula=y~x)

Appendix 5 – Meroplanktonic abundance in Adventfjorden

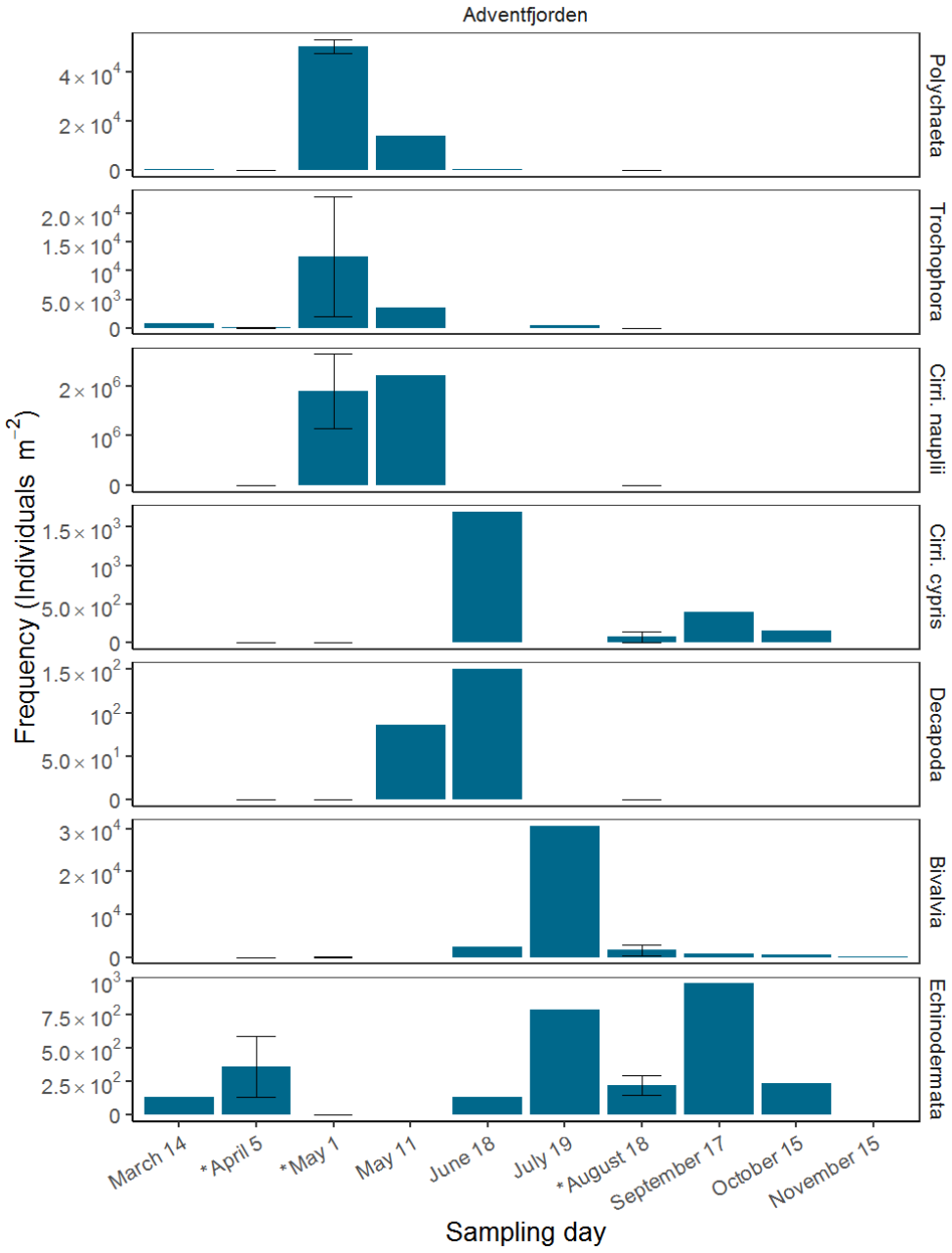


Figure A5. Meroplankton abundance (individuals m^{-2}) in Adventfjorden from March to November 2018 with bars for abundance of each taxonomic group separated with error bars for confidence intervals given for dates when two hauls were processed. Note the different scales on the y-axis for each taxonomic group.

Appendix 6 – Full list of zooplankton taxa identified

Table A6. Full list of taxa found at all dates sampled in Adventfjorden from March to November and in Van Mijenfjorden, Inglefieldbukta and Agardhbukta March and April 2018, sorted after life strategy (holo-/meroplankton or parasitic) and given by lowest taxonomic level identified. Life stage given for nauplii and larval stages.*Picked out as macro

Life strategy	Phylum	Class	Subclass	Order	Taxa
Holo	Arthropoda				
		Hexanauplia			
			Copepoda		
					Nauplii
				Calanoida	
					Acartia longiremis (Liljeborg, 1853)
					Calanus hyperboreus Krøyer, 1838 (big *)
					Calanus spp. Leach, 1816
					Metridia longa (Lubbock, 1854)
					Microcalanus spp. Sars, 1903
					Pseudocalanus spp. Boeck, 1872
				Cyclopoida	
					Oithona atlantica Farran, 1908
					Oithona similis Claus, 1866
					Oithona sp. Baird, 1843
					Triconia borealis (Sars, 1918)
					Triconia sp. Bötther-Schnak, 1999
				Harpacticoida	
					Microsetella norvegica (Boeck, 1865)
					2 unidentified spp.
		Malacostraca			
			Eumalacostraca		
				Amphipoda	
					Themisto abyssorum (Boeck, 1871) *
					Themisto sp. Guérin, 1825 *
				Euphausiacea	
					Unidentified larval stages (furcilia larvae *)
					Thysanoessa inermis (Krøyer, 1846)*
	Chaetognatha				
					Unidentified juveniles
		Sagittoidea			
				Aphragmophora	
					Parasagitta elegans (Verrill, 1873) *
				Phragmophora	
					Eukrohnia hamata (Möbius, 1875) *
	Chordata				
		Appendicularia			
				Copepolata	
					Fritillaria borealis Lohmann, 1896
					Oikopleura sp. Mertens, 1830 (big *)

	Cnidaria				
		Hydrozoa			
					Unidentified *
			Hydroidolina		
				Siphonophorae	
					Unidentified polypps *
			Trachylinae		
				Trachymedusae	
					Aglantha digitale (Müller, 1776) *
	Ctenophora				
		Nuda			
				Beroida	
					Beroe cucumis Fabricius, 1780 *
		Tentaculata			
				Cydippida	
					Mertensia ovum (Fabricius 1780) *
	Mollusca				
		Gastropoda			
			Heterobranchia		
				Pteropoda	
					Clione limacina (Phipps 1774) *
					Limacina helicina (Phipps 1774) *
Mero	Annelida				
		Polychaeta			
					Larval stages (big *)
	Arthropoda				
		Hexanauplia			
			Thecostraca		
					Cirripedia (infraclass), larval stages
		Malacostraca			
			Eumalacostraca		
				Decapoda	
					Larval stages*
	Bryozoa				
					Larval stages
	Echinodermata				
					Larval stages
	Mollusca				
		Bivalvia			
					Veliger larvae
Parasitic	Arthropoda				
		Malacostraca			
			Eumalacostraca		
				Isopoda	
					Unidentified sp.

Appendix 7 – Egg abundance in Adventfjorden and the ice-covered stations

Singular free floating eggs were found in low abundance in early spring in Adventfjorden (Stn. IsA) but increased in numbers in May and again in September (Figure A11). In October and November, close to none eggs were found in the water column. At the ice-covered stations in March and April, the egg abundance was on level with that found in Adventfjorden in April.

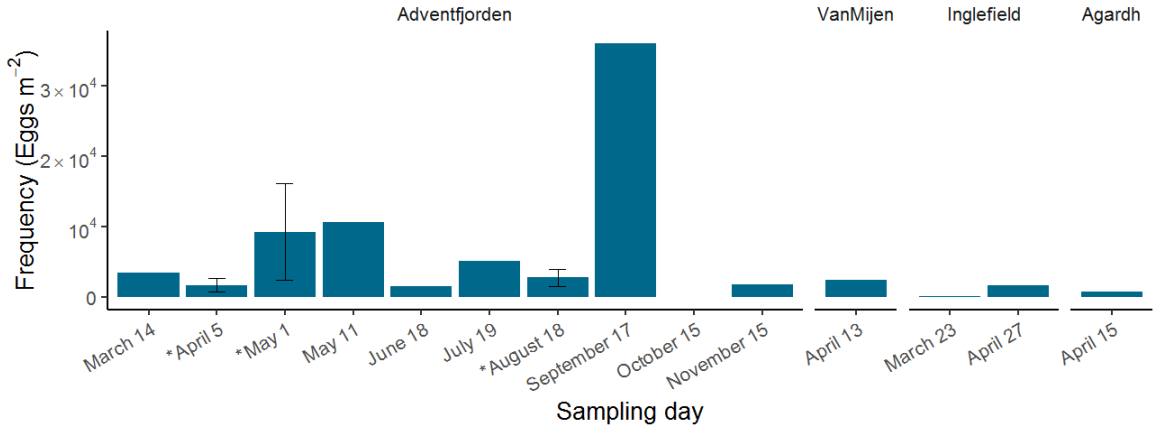


Figure A7. Abundance of singular free eggs (eggs m^{-2}) in Adventfjorden from March to November and at the ice covered stations (VanMijen, Inglefield, Agardh) in March and April 2018, with error bars for confidence intervals given for dates when two hauls were sorted.

Appendix 8 – Weather data from Longyearbyen Airport April 2018-April 2019

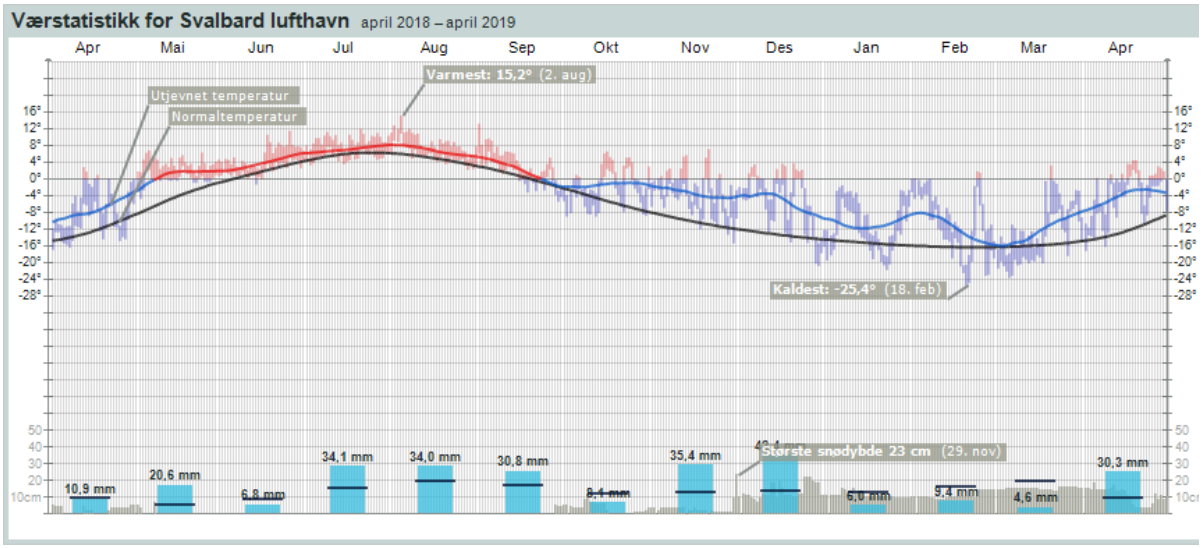


Figure A8.1. Weather statistics from Longyearbyen Airport April 2018 – April 2019, showing normal values for temperature and precipitation (black lines), daily mean temperatures (blue (<0°C) or red (>0°C) line), temperature variations through the day in maximum and minimum values (blue (<0°C) or red (>0°C) fields), total precipitation (cm) for each month (blue bars) and measured snow depth (cm) for each day (grey fields behind precipitation bars), from the Norwegian Meteorological institute (MET 2019)

Appendix 9 – Abundance per cubic for ice-covered stations

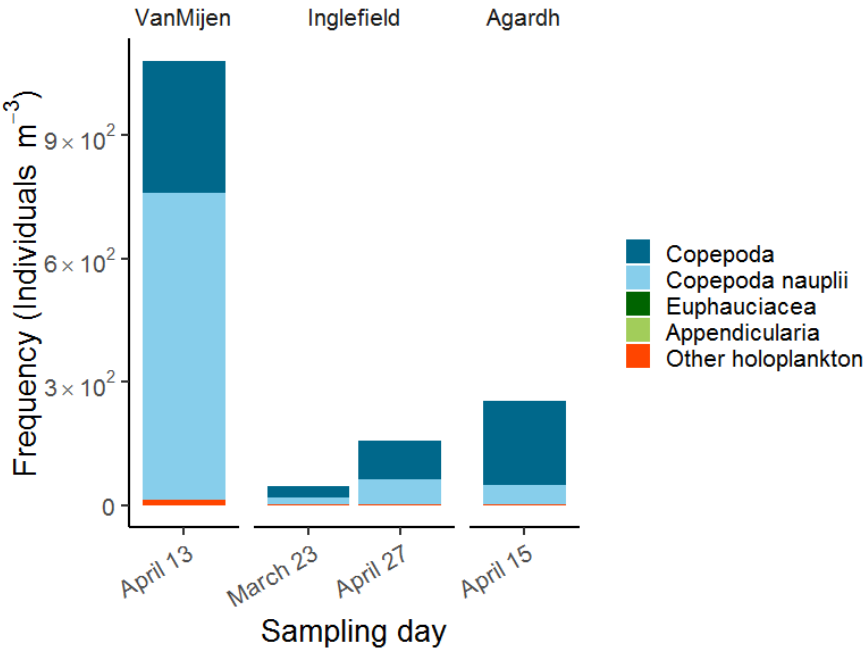


Figure A9.1. Holoplankton abundance (individuals m^{-3}) on the ice covered stations sampled in March and April 2018, given in individuals per cubic meter and colour coded for taxa.

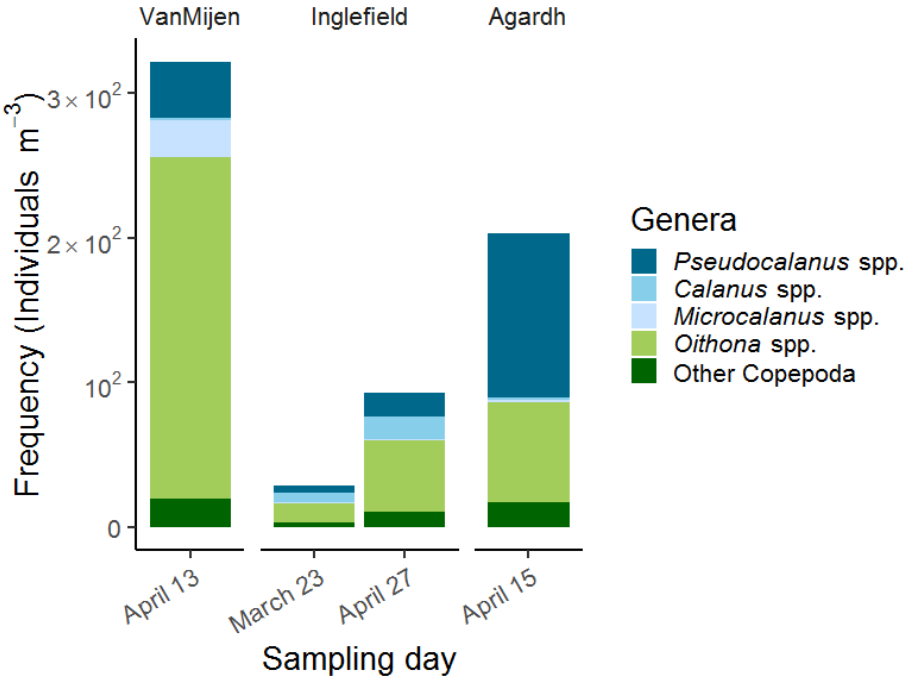
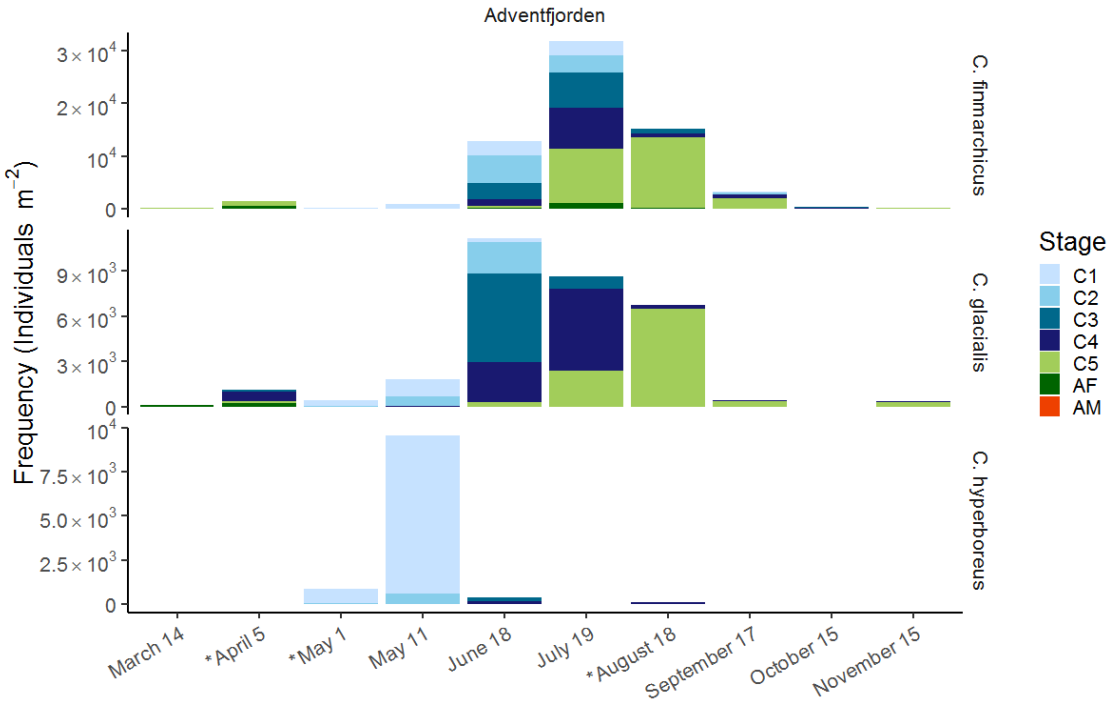


Figure A9.2. Copepoda abundance (individuals m^{-3}) on the ice covered stations sampled in March and April 2018, given in individuals per cubic meter and colour coded for taxa.

Appendix 10 – *Calanus* species composition based on prosome lengths



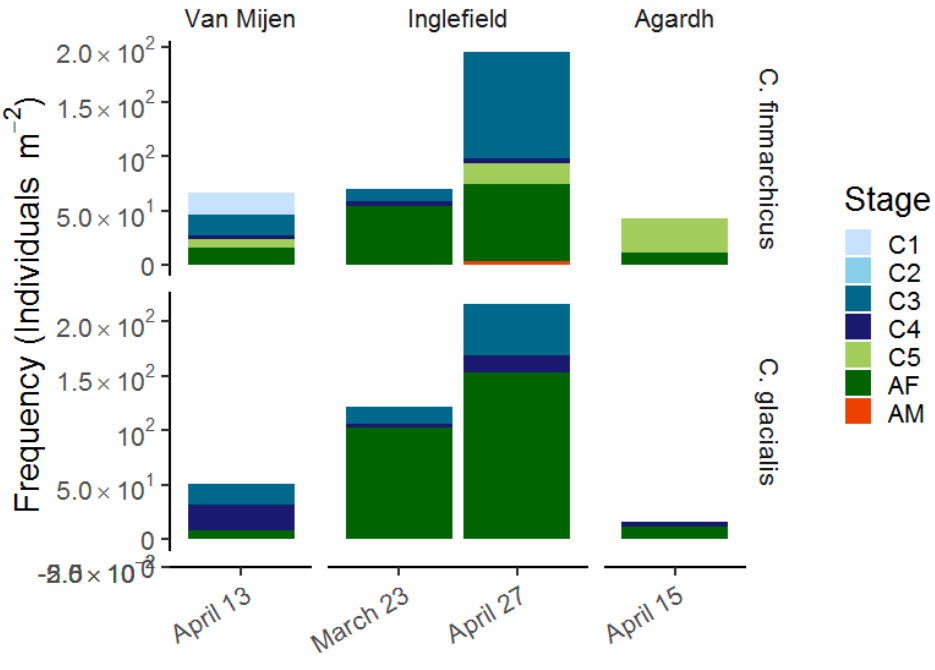


Figure A10. Composition of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*, identified based on prosome length class definitions from Daase and Eiane (2007), in a) Adventfjorden from March to November 2018 and b) the ice-covered stations (Van Mijenfjorden, Ingelfieldbukta and Agardhbukta) in March and April 2018.

Appendix 11 – Zooplankton abundance in each processed haul

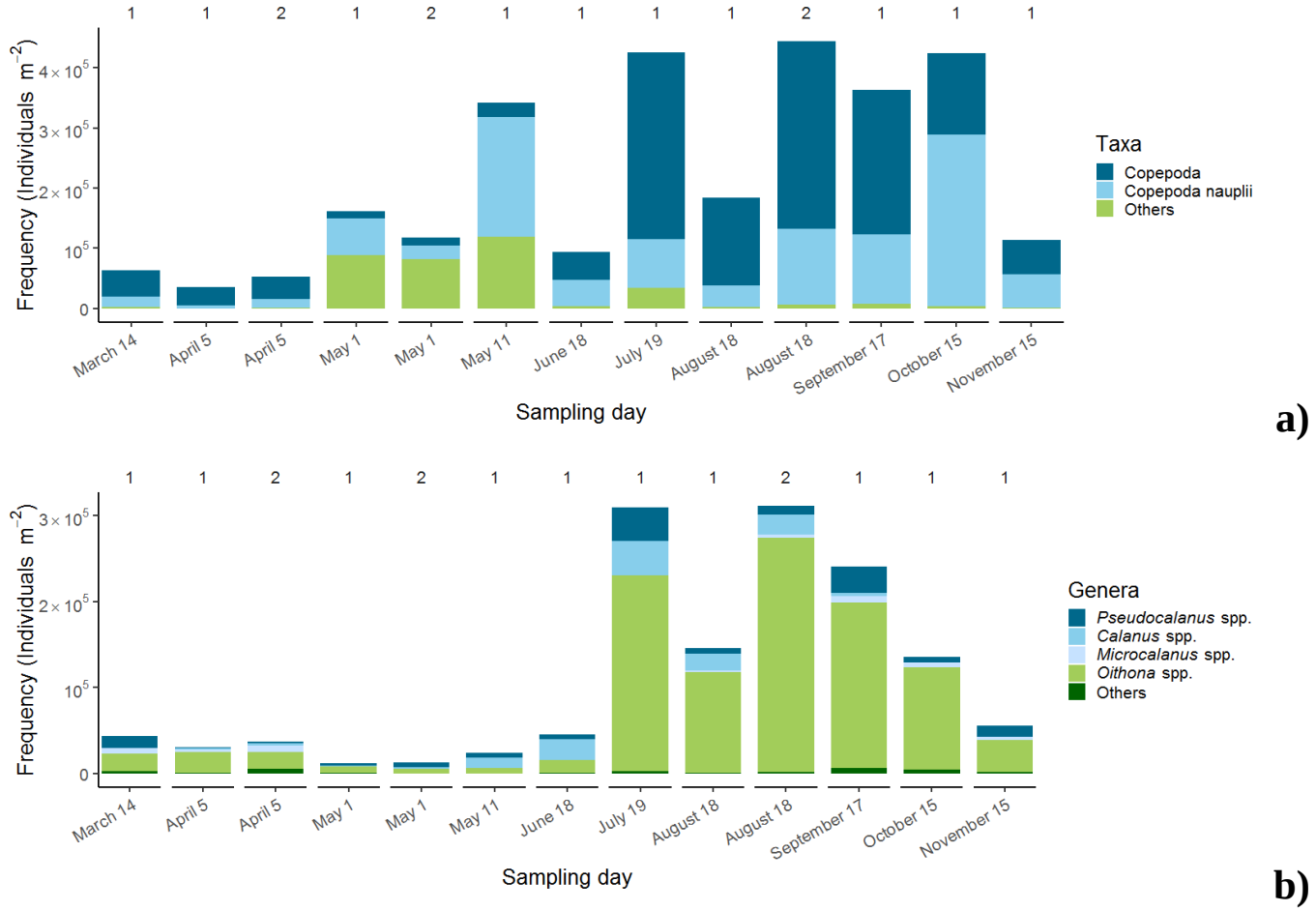


Figure A11. Zooplankton abundance (ind. m^{-2}) in Adventfjorden from March to November 2018, with each processed haul separated for April, May 1 and August (haul number above bars), in (a) total (excluding Cirripedia larvae) zooplankton abundance, and (b) Copepoda abundance.