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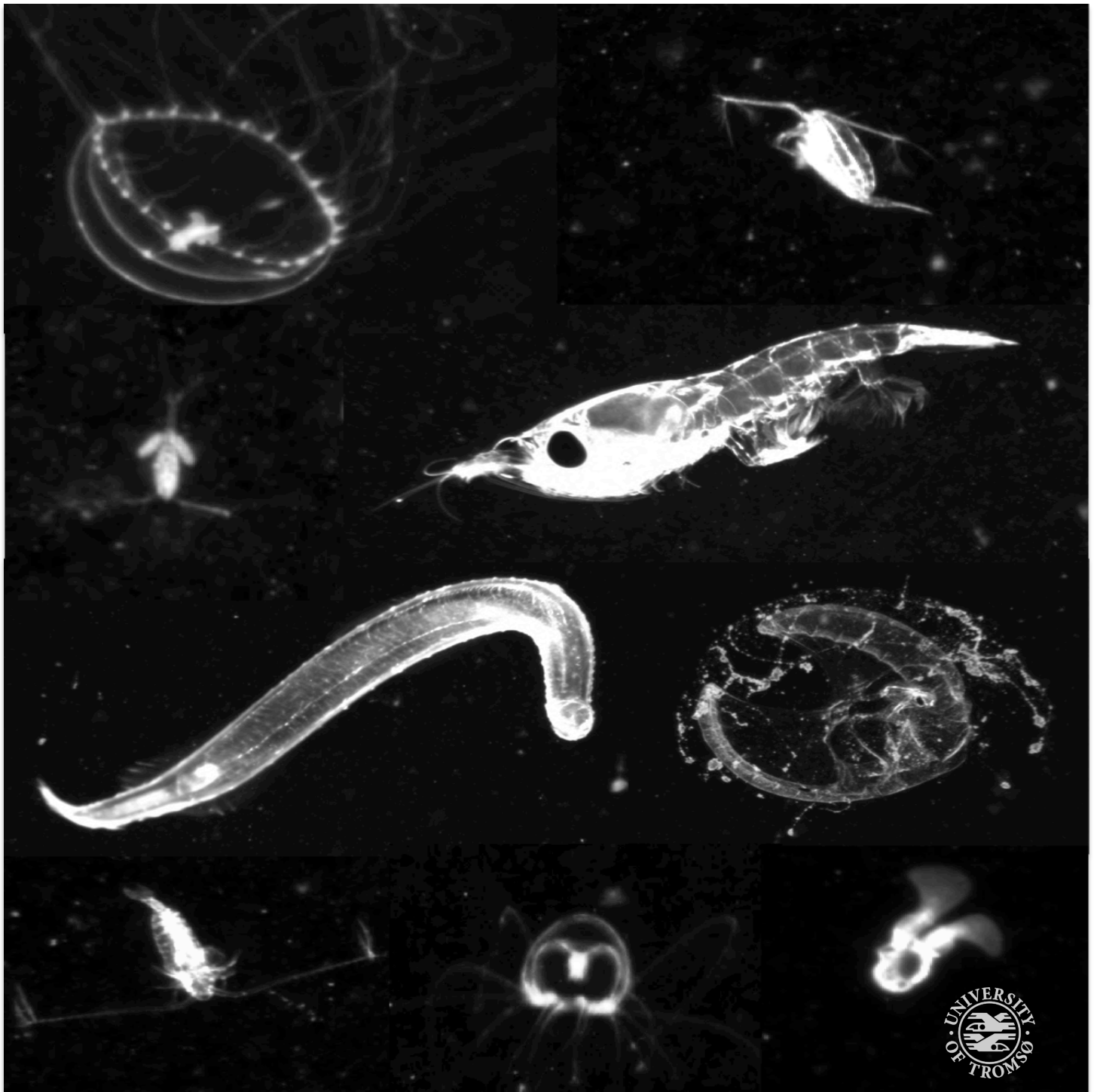
Department of Arctic and Marine Biology

## Vertical distributions of zooplankton using the Video Plankton Recorder in two high-latitude fjords

*“A case study on diel migration in Billefjorden, Svalbard, and seasonal migration in Porsangerfjord, northern Norway”*

Alejandro Prat Varela

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*Voldria donar les gràcies a la meva àvia, sempre has estat animantme en tot allò que he fet a la vida, d'aquí poc em teniu per casa baba. També, a la meva germana, que sempre estarem junts per tot allo que fagi falta. Us estimo familia.*

Tromsø, August 2015 Alejandro Prat



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## **Abstract**

Zooplankton is the link between primary producers and higher trophic levels, so it is of vital importance for the food chain. The strong seasonality in the Arctic affects the vertical distribution of zooplankton in the water column. Predators can also affect the vertical distributions of their prey in the water column due to avoidance adaptations. The importance of these differences between prey and predator vertical distributions is the main point of interest in this study.

The present study is an attempt to gain more knowledge about how the vertical distribution and interactions between prey and predator zooplankton affect the structure/their disposition throughout the water column. It is important to know the interactions and vulnerability of the species, and how they adapted to survive in this special environment. The study took place in two different arctic fjords, where diel and seasonal migrations were studied.

The diel vertical migration (DVM) of prey related to predators was studied, using a Multi Plankton Sampler (MPS), MIK nets, trawl nets and the video Plankton Recorder (VPR) in Billefjorden, Svalbard. The seasonal vertical migration (SVM) was studied along different sampling stations at Porsangerfjord, Northern Norway. The zooplankton community of Porsangerfjord has not been deeply studied. This study will try to cover the lack of information in this area.

DVM was observed for more vulnerable prey species and SVM was observed for all the species. Migration to the surface was related to the phytoplankton bloom for all the species. Also, differences in distributions between predator – prey and small – large copepods were observed some of the months.

In summer and fall, small and large copepods have different vertical distributions and predators affect on the vertical distribution of their prey. Visual predators can be in high abundance in fjords in Norway and further analysis comparing acoustic data from echo sounders with data from VPR will give a better overview on the predator – prey interactions and migrations.

## 1. Introduction

### **Zooplankton and predator prey relationships**

Zooplankton is an important part of the food web of most marine ecosystems (Frederiksen et al. 2006). Marine environment in the arctic is complex due to the strong seasonality varying greatly between summer and winter. The high-latitude zooplankton has developed some adaptations such as body lipid content, diapause and controlling the time of growth and reproduction to survive (Falk-Petersen et al. 2009, Varpe 2012) when no food is available in the water column. Diel and seasonal vertical migrations are observed in various zooplankton species (Heywood 1996, Fortier et al. 2001, Liu et al. 2003, Berge et al. 2009, van Haren & Compton 2013, Berge et al. 2014), which are determined by the presence and location of food and predators during different periods of time (Haney 1988, Liu et al. 2003, Berge et al. 2014).

Arctic copepods are rich in lipids and represent an important food source for other zooplankton species (Larson & Harbison 1989, Noyon et al. 2011), pelagic fishes such as polar cod (*Boreogadus saida*) (Ajiad 1990, Jensen et al. 1991), herring (Dalpadado 2000), capelin (*Mallotus villosus*) (Karamushko & Reshetnikov 1994, Orlova et al. 2005), and some seabird species (Hovinen et al. 2014). The species composition, density and distribution of zooplankton have a direct relation in fishery resources. The production of zooplankton is important due to its ability to support the higher trophic levels in the marine ecosystems. Zooplankton is an important food source for juvenile and pelagic fish and the abundance on available zooplankton may affect on recruitment, fish production, growth rates and survival (Bradstreet & Cross 1982, Kristiansen et al. 2011).

Seasonal migration is related to the food availability in the water column and therefore to the phytoplankton bloom, which starts in the high arctic between spring and summer. The spawning season of herbivorous zooplankton is coupled with the beginning of the phytoplankton bloom, in which nauplii can graze directly on rich food compounds to grow fast. Therefore is crucial for zooplankton to couple with the phytoplankton bloom for survival of the next generations, mismatch between zooplankton and phytoplankton peaks have negative consequences for the entire ecosystem (Søreide et al. 2010).

The availability of resources concentrates zooplankton and therefore predators. The ideal free distribution (IFD) (Fretwell & Lucas 1969) say that in absence of predators, herbivorous zooplankton will occupy the layers with highest resources. But In accordance to the habitat



choice theory predators may hunt in the habitat in which the prey have more resources (Sih 1998), being this habitats riskier for prey (Brown 1998). Some species have adapted to survive in layers with less food resources not following the IFD, avoiding the hunting areas of some predators.

Resistant and non-resistant zooplankton need different amount of energy to survive, being distributed in rich or poor resources patches (Brown 1998). Small zooplankton will normally use food resources better than larger zooplankton when food becomes limited (Brown 1998).

Habitat choice is determinate by body size of predator and prey (Persoon et al. 1996, Baier & Purcell 1997). The abundance of predators in some layers may affect the distributions of zooplankton, which are avoided by some zooplankton species. Zooplankton have evolved to perform migrations due to mechanoreception, which responds to hydrodynamic disturbances created when approaching predators (Bollens et al. 1994), or chemoreception of kairomones released by fish (Cohen & Forward 2009). Light is also an important factor controlling the daily migration of zooplankton. Some zooplankton species perform DVM in periods of time when the presence of food and light levels are enough to allow visual predators to hunt effectively (Pearre 2003). DVM is a beneficial strategy for zooplankton only when lost of food can be accepted to reduce predation risk (Sainmont et al. 2014). Zooplankton DVM occurs in the High Arctic during late summer/early autumn (Sainmont et al. 2014).

## **Fjord environments**

### **A. Hydrography and external forces.**

The data was collected in a fjord in northern Norway (Porsangerfjord) and in an Arctic-fjord in the Svalbard Archipelago (Billefjorden). The current system in these areas is influenced by different water masses (Figure 1). The North Atlantic Current (NAC) is warm and saline water coming from the Atlantic Gulf Stream that break in two branches while arriving into the Barents Sea, which are going towards north to the western coast of Svalbard and to the coast of Nova Zemlya.



**Figure 1** Circulation of the different water masses in the Barents Sea. Source: The main features of the circulation and bathymetry of the Barents Sea (PINRO/IMR report).

The West Spitsbergen Current (WSC) and the Coastal Current are the two major water currents affecting the Svalbard fjords. The WSC flows along the western side of Svalbard and is an extension of the NAC bringing warm and saline Atlantic water to the Arctic. The CC is coming from the eastern part of Svalbard and brings towards north Arctic Water (AW). This different water properties and the inflow of each stream in the fjords affects directly into the species composition.

The NAC and the Norwegian coastal current (NCC) affect the North Norwegian fjords. The NCC is a continuation of the Baltic current flowing along the Norwegian coast into the Barents Sea. It is colder and less salty than the NAC (Mork 1981) because is affected by water from the Baltic Sea, Norwegian fjords and rivers. But it is also much warmer and saltier than the Arctic Sea.

The environment in the fjords are affected by other external forces like wind, tides, air-sea exchange and freshwater input (Inall & Gillibrand 2010). Different external forces, because of their location properties, affect the fjords used in this study. The inner part of Porsangerfjord (Østerbotn) is considered to be the only arctic fjord system found in mainland Norway today (Soot-Ryen 1951). A comparison between species composition and distribution between

Østerbotn and Billefjorden is an important aim for the Fram centre flagship project (“Pelagic ecosystems in ice-covered and ice-free fjords under climate change”) in which my study took part. Various factors can affect the distributions of zooplankton in these two fjords, such as a glacier in Billefjorden, and wind stress producing upwelling/downwelling events in Porsangerfjord (Svendsen & Thompson 1978, Cushman-Roisin et al. 1994).

The physical properties in the water column play an important role between phytoplankton, prey and predator interactions and their survival. The stratification of the water column provides a necessary condition for the formation of prey or predator aggregations (Norrbín et al. 1996).

### **B. Biological environment in fjords**

Different phytoplankton blooms are observed in the fjords where this study took place. In Billefjorden, two blooms are represented by two different categories of primary producers (Søreide et al. 2010). The bloom starts with algae underneath the ice, which covers the fjord during winter, having special compounds important for reproduction, growth and development of the arctic herbivorous zooplankton species. The ice melts at the surface, then phytoplankton from the offshore region will bloom in the fjord giving more resources for grazers to survive the overwintering period (Søreide et al. 2010).

The spring bloom in the north norwegian fjords consist in phytoplankton. The bloom occurs between late march to May, with the peak in April (Eilertsen & Degerlund 2010), but in Porsangerfjord the spring bloom continues until summer (Eilertsen & Frantzen 2007). It might be possible that a second bloom happen in fall due to re-suspension of nutrients. In high latitudes herbivorous species feed heavily on phytoplankton during the period of time in which storing lipids in their bodies is still available to survive the winter at depth.

### **C. Environmental changes**

The warming of the climate has changed species composition in some areas in the arctic in the last decades in the sub-arctic and Arctic marine ecosystems. The increase of temperature and loose of ice in the Arctic is clear if we take into consideration some Svalbard fjords, which in the past were covered by ice during several months of the year and currently free of ice the whole year. This change in the water masses properties, are affecting directly the marine species composition in these areas. Arctic zooplankton species are richer in lipids than warm water zooplankton species, which are poor in lipids. That negatively affects into the food chain and higher trophic levels such as fish, birds and marine mammals. Other problem is the

introduction of species from other parts of the world, like is the case of the King crab in Porsangerfjord, where the invasion is extended through all Northern Norway (Falk-Petersen et al. 2011), affecting on the benthic ecosystem with the subsequent affection to fish populations (SunnSet 2008).

The predation influence on the zooplankton communities is under-studied due to the variety of larval fish predators and the sampling with net-based systems that do not allow collecting properly some of the predatory species (e.g. Ctenophores and hydromedusae). Other methods are starting to being used currently to improve the understanding of the predator/prey interactions.

### **This study**

For this study was used the Video Plankton Recorder (VPR) to observe the different species in their environment through the water column and see the vertical distributions. The use of the VPR makes possible to study the fine-scale spatial position of individuals, which is not possible with many traditional net-sampling systems used. Also, is possible to have the sizes of individuals of the good quality images. One important characteristic is the ability to study the environmental data (fluorescence, salinity, temperature and depth) at the same time you are registering the different organisms. To obtain the species composition in the fjords different nets were used to compare the results with the VPR.

The main subject of this thesis was to study the vertical distribution of zooplankton in relation to predators over the season. During this year, it was not possible to take samples during the seasons where highest abundances of predators can be found in the water. Acoustic data was recorded during all the VPR samplings, but problems while processing the data did not allow us to present the results in this thesis.

### ***Hypotheses:***

- H<sub>1</sub>. Prey and predator species had different depth distributions
- H<sub>2</sub> More vulnerable prey species had different distributions than less vulnerable species
- H<sub>3</sub>. Higher predator presence leads to a change in the vertical distribution of prey specie

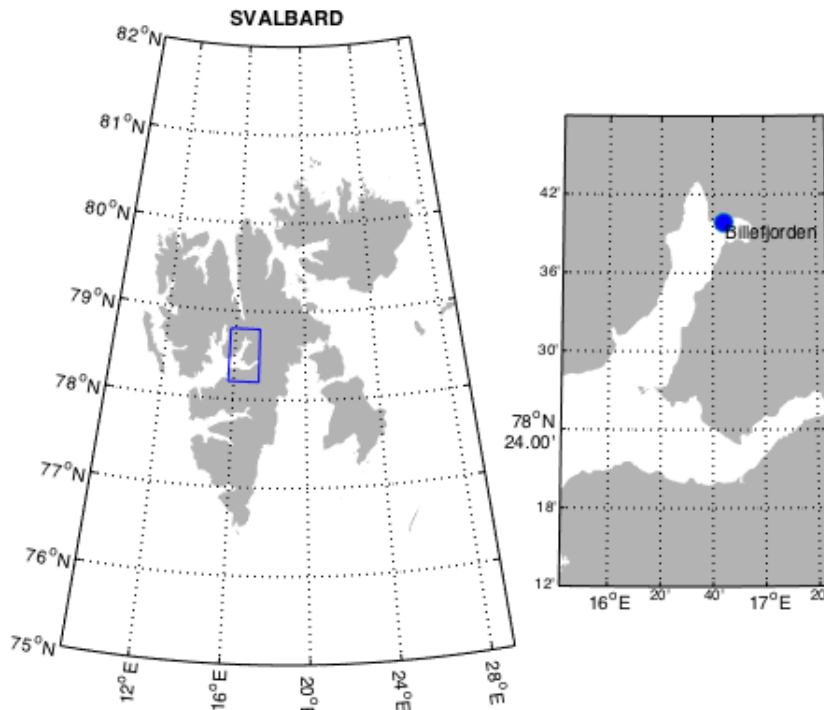
## 2. Materials and Methods

### 2.1. Study Areas.

The data used in this thesis was collected in Billefjorden in Svalbard and in Porsangerfjorden in the north of Norway.

#### 2.1.1. Svalbard

During the cruise of the UNIS course AB-320 (Arctic marine zooplankton) from September 22 to October 6 2014, I was able to take samples in the Svalbard Archipelago. Samples were collected with R/V Helmer Hanssen in Billefjorden (Figure 2 and table 1).



**Figure 2** Billefjorden (blue) map in Svalbard.

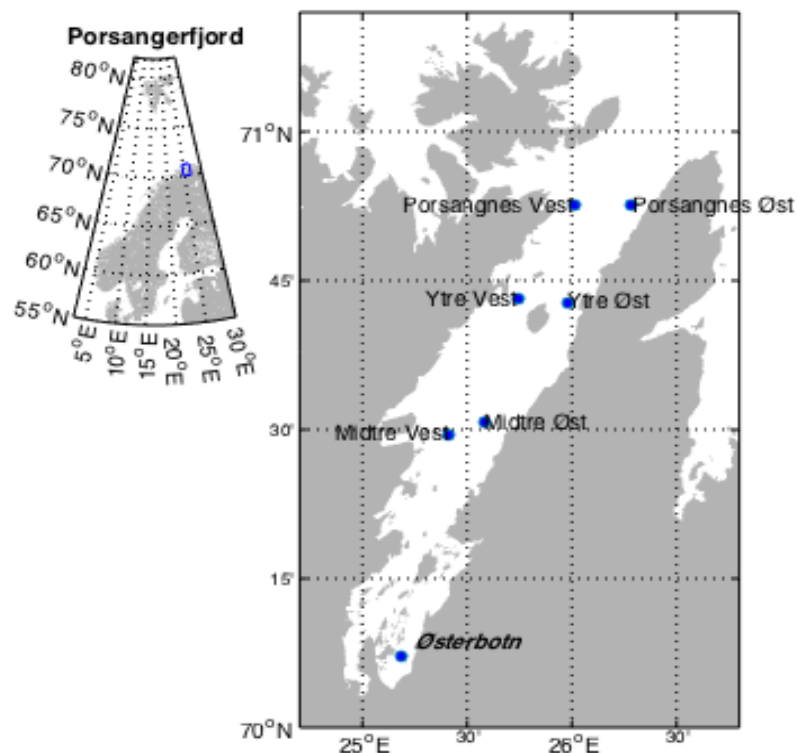
The expedition started in Longyearbyen where we sailed to different stations around Svalbard, which are not shown in this study. Billefjorden is the innermost fjord in the Isfjorden complex. The fjord is about 30 km long and 5-8 km wide with an outer sill of 70 m and an inner sill of 50 m. The inner sill divides Billefjorden into outer and inner basins, which are 230 m and 200 m in size, respectively. The average depth in the main basin of the fjord is 160 m deep (Nilsen et al. 2008). The fjord is covered with ice during most of the winter and spring each year. Winter cooled waters and reduced influence of warm Atlantic water from Isfjorden system (Berge et al. 2014) predominates. Arctic species dominate the zooplankton communities in Billefjorden.

Arctic species dominates the zooplankton communities in Billefjorden.

### ***2.1.2. Porsangerfjord***

Data was collected with the research vessel R/V Johan Ruud in connection to the Fram centre flagship project (“Pelagic ecosystems in ice-covered and ice-free fjords under climate change”), in the months of March, April, May and November 2014 in Porsangerfjord. This fjord has a length of 100 km approximately and a width of 15–20 km, making it the third largest fjord in Norway and the largest in Northern Norway. Porsangerfjord is a semi-enclosed fjord system with an area of 1800 km<sup>2</sup>, with a 60 m deep sill, 30 km from the head of the fjord that is divided into an inner and outer basin (Eilertsen & Degerlund 2010). The middle part is from the 60 m sill, which is separated from the outer part by an island (Tamsøya) 70 km from the head. The outer part has a 180 m deep sill. Most of runoff to Porsangerfjord comes from the Lakselv and Børselv rivers, both situated in the inner part (Eilertsen & Frantzen 2007). The outer basin has a maximum depth of 285 m, and is affected by the Norwegian Coastal Current (NCC) with a frequent exchange of deep water (Wassmann et al. 1996, Eilertsen & Skarðhamar 2006). Subzero temperatures are found below the pycnocline in the inner part of the fjord, considered an arctic environment with a diverse arctic fauna (Christiansen & Fevolden 2000). The inner part of the fjord in Østerbotn is covered with ice during some winters. Several stations were sampled in the months of March, April, May and November along the fjord to get an overview of the zooplankton and predator communities in the different basins of Porsangerfjord. Samples were taken from the inner part to the outer part with samples at the East and West sites of the fjord when possible (Figure 3 and Table 1).

The main purpose was to sample the inner, middle and outer part of the fjord each month. In March, Østerbotn was not sampled with the Video Plankton Recorder (VPR) because the light ring broke in the middle of the fjord. In April, the expedition faced bad weather conditions and were all busy with a course, not allowing enough time to sample the outer part of the fjord. In November, it was not possible to sample in the outermost part of the fjord because of the weather but the sampling was carried at two stations, which are similar in hydrography and zooplankton.



**Figure 3** Map of Porsangerfjord and its location in Norway. Stations sampled during the four expeditions in 2014

## 2.2. Biological Sampling.

### 2.2.1. Multinets (MPS)

In Billefjorden, zooplankton was collected with a Multiple Plankton Sampler Multinet (MPS; Hydro-Bios, Kiel) with a mesh size of 200  $\mu\text{m}$  and an opening of 0.25  $\text{m}^2$ . All samples were immediately placed in 4% formaldehyde for later identification and enumeration of species. All plankton from the MPS (table 1) was sorted during the expedition for AB-320.

### 2.2.2. MIK nets

In addition, a MIK net, with a diameter of 2 m, an opening area of 3.14  $\text{m}^2$  and a mesh size of 500  $\mu\text{m}$ , was used to collect macro-zooplankton in Billefjorden. The MIK net was towed for 5 min at the chosen depth (table 1). All plankton from the MIK nets was sorted during the course expedition. Sampling depths were determined by the location of the main sound scattering layers (SSL) during the day and night as identified from the long-term mooring (ADCP) data used for the course.

### **2.2.3. WP-2 nets**

In Porsangerfjord, the zooplankton was collected using a WP-2 net with different mesh sizes, depending on the expedition (table 1). For March and November we used an 85  $\mu\text{m}$  net and for April and May samples were collected with a 180  $\mu\text{m}$  mesh size, because the same net size was not available for all the expeditions. For a proper identification and enumeration of species, samples were placed immediately in a fixative mixture of 4% formaldehyde and 10% 1,2-propanediol (propylene glycol), except during the November expedition, where 70% ethanol was used for the fixation because we forgot to bring formaldehyde.

### **2.2.4. Trawling nets**

Pelagic trawl nets were used to sample nekton communities that can be preying on zooplankton. The trawling was only carried out in Billefjorden in October. To choose the depth where the trawl had to sample, we decided to use the SSL seen by the echo sounder of the vessel (table 1).

## **2.3. Video Plankton Recorder.**

A Video Plankton Recorder (VPR; Seascan, Inc.) was used to study the zooplankton in situ. The VPR is an optical underwater instrument, consisting of a tow body with two arms, on which a video camera and a Xenon strobe are mounted to illuminate the imaged volume. High-resolution images (1.4-MPixel) of in situ zooplankton and other particles are obtained. Images were taken at a rate of 21 frames  $\text{s}^{-1}$  approximately. In addition to the camera, a CTD (Seabird SBE49) and a turbidity and fluorescence instrument (Wetlabs Ecopuck) were also mounted on the VPR body. The images and physical data were saved internally, on a detachable flash drive, on the VPR. After the March 2014 expedition, the ring illuminator of the VPR had to be replaced. We calibrated the new setup in the lab to determine the volume sampled using the camera 2 setting, i.e. using an image window of 22x32.5 mm this was 28 mL for the station taken in March at Porsangerfjord and 35,2 mL for all other sampling months.

The VPR was attached to the hydrography wire on the side of the ship, and was run vertically through the water column from the surface to 10 m above the bottom depth, with a tow speed between 0.8 and 1  $\text{ms}^{-1}$ . This method was used for all the stations sampled in this thesis. The number of legs of each tow changed depending on the depth



of each station and the sampling time we were able to use.

**Table 1.** Billefjorden, Svalbard, station position and depth at each site, deployment time and depth layers for MPS, MIK and trawl, and number, deployment time and depth of sampling for the VPR. Porsangerfjord, Northern Norway, station positions and depth at each site, the number, deployment time and depth of sampling for the VPR and WP-2.

<b>Svalbard</b>													
Station	Date	Latitude	Longitude	Multinets		MIK		Pelagic Trawl		VPR			
				Depth (m)	Time (UTC)	Depth (m)	Time(UTC)	Depth SSL (m)	Time (UTC)	Time (s)	n°	Time (UTC)	
<i>Billefjorden</i>	4 - 5/10/14	78,39	16,44	0-30, 30-60, 60-100, 100-182	21:28	40,60,120	23:05/23:29/23:50	30	8:13	900	6	21:55	
						40,60,120	03:12/03:25/03:40					7	4:06
					9:18	40,60,120	10:20/10:40/11:00	50	20:05	900	8	11:23	
						40,60,120	14:43/14:55/15:11					9	15:53
<b>Porsanger</b>													
Station	Date	Latitude	Longitude	VPR		WP-2							
				n°	Time (UTC)	Depth (m)	Mesh size (µm)	n°	Time (UTC)	Depth (m)	Mesh size (µm)		
<i>Østerbotn</i>	4/3/14	70,07	25,11	5	15:27	100	85						
<i>Midtre Øst</i>	4/3/14	70,31	25,35	3	14:10	190	85						
<i>Midtre Vest</i>	4/3/14	70,3	25,25	4	15:27	120	85						
<i>Porsanges Øst</i>	4/3/14	70,53	26,17	2	9:13	210	85						
<i>Porsanges Vest</i>	4/3/14	70,52	26,01	1	7:40	200	85						
<i>Østerbotn</i>	2/4/14	70,07	25,11	2	21:38	100	180						
<i>Midtre Øst</i>	3/4/14	70,31	25,35	5	5:13	190	180						
<i>Midtre Vest</i>	3/4/14	70,3	25,25	4	3:16	120	180						
<i>Østerbotn</i>	21/5/14	70,07	25,11	7	8:13	105	180						
<i>Midtre Øst</i>	21/5/14	70,31	25,35	5	21:44	190	180						
<i>Midtre Vest</i>	21/5/14	70,3	25,25	10	18:05	112	180						
<i>Porsanges Øst</i>	20/5/14	70,53	26,17	3	12:15	215	180						
<i>Porsanges Vest</i>	20/5/14	70,52	26,01	2	9:38	200	180						
<i>Østerbotn</i>	19/11/14	70,07	25,11	5	8:32	100	85						
<i>Midtre Øst</i>	19/11/14	70,31	25,35	9	20:16	185	85						
<i>Midtre Vest</i>	18/11/14	70,3	25,25	2	16:30	110	85						
<i>Yre Øst</i>	20/11/14	70,43	25,57	10	14:17	243	85						
<i>Yre Vest</i>	18/11/14	70,43	25,45	1	12:50	200	85						
<i>Østerbotn</i>	17/8/12	70,11	25,14	8	15:00	-	-						
<i>Porsanges Vest</i>	23/8/12	70,87	26,02	16	20:00	-	-						

## **2.4. Processing of biological samples.**

### **2.4.1. MPS and WP-2 sorting**

Samples were rinsed and placed into a bath of seawater to extract the formaldehyde. After approximately 1 h, samples were diluted into different volumes, depending on the density of species found for each sample. All macro-zooplankton were removed prior to subsampling. Different subsampling volumes were used for the different samples. Each sample was then sorted so that at least 300 individuals of the most abundant species were counted. The length of all chaetognats, euphausiids, amphipods and 100 *Calanus sp.* were measured for each of the net samples from Porsangerfjord.

### **2.4.2. MIK nets sorting**

When the net was collected, the cod end of the MIK net was emptied and rinsed in big buckets. Samples that were too dense to count were then split in half using a sample splitter. They were split repeatedly when necessary. The samples were then sorted into the lowest taxonomic groups without using a microscope (groups: copepods, chaetognaths, jellyfish, pteropods, amphipods, euphausiids and decapods). The numbers of individuals in each group were counted, except for copepods due to high abundance, and total wet weight was measured.

### **2.4.3. Trawl net sorting**

Trawls were sorted just after net was collected with no help of microscope. At Billefjorden, the fraction of samples counted was different in the morning and night sampling. In the morning, the whole catch was sorted, weighed, and classified into species of fish and in groups for krill, amphipods, shrimps and jellyfish. For the night sampling, all the cod (*Gadus morhua*) was counted and weighted, 1/3 of the *Liparis* (larvae), herring and flat fish, and 1/18 of the remaining taxa (small fish, krill, jellyfish and amphipods). At Porsangerfjord, the entire sample was sorted into species of fish and groups of krill and jellyfish, and then counted and weighed.

## 2.5. Net sample analysis.

Abundance and biomass were calculated to obtain the composition of species or taxa in the water column at the different stations. For MPS, MIK and trawl nets, the abundance was calculated by dividing the number of organisms of the same species counted in the sample by the volume of water sampled in  $\text{ind}\cdot\text{m}^{-3}$ . Biomass was calculated for the MIK and trawls nets by dividing the wet weight of the sample by the volume sampled in  $\text{mg}\cdot\text{m}^{-3}$ . The Microsoft Excel 2011 software for Mac was used to calculate and plot the biomass and abundances for each of the species or groups found in the nets.

The diversity for each station and month of sampling at Porsangerfjord was calculated using the Shannon-Wiener index ( $H'$ ) (Eq.1).

**Equation 1** Shanon-Wiener diversity index.

$$H' = - \sum_{i=1}^R p_i \ln p_i = - \sum_{i=1}^R \ln p_i^{p_i}$$

## 2.6. VPR images: Analysis and classification.

### 2.6.1. Extraction

From each of the frames recorded by the VPR, the plankton and other particles (e.g. fecopellets and marine snow) were extracted as regions of interest (ROIs) using the Autodeck image analysis software (Seascan). ROIs were saved to a computer hard drive as TIFF files for post-processing analysis. The name of each ROI is the ms time of the day, which allows it to be time-matched with the CTD data, to know the depth and environmental data for each image.

### 2.6.2. Image classification

An automatic classification of the images was done using the Visual Plankton software (VP/ Woods Hole Oceanographic Institution, USA). VP is an application written mainly in MATLAB (Mathworks) for image processing and visualization of VPR data.

Before classification, a certain number of ROIs (depending on the number of organisms found) were manually copied into different taxa or category folders (approximately 200 ROIs is the proper number of ROIs needed for each training folder (Hu & Davis 2006) using the software Irfanview (I. Skiljan, Austria). These, called training ROIs (trROIs),

were later used to train the computer for the automatic classification. To train the computer, the software uses feature extraction algorithms to detect, isolate and measure features of each of the images. Two classifiers are then created from the same trROIs in parallel. The origin of each of the classifiers is different; the first one is built from shape-based features and called ‘learning vector quantization neural network’ (LVQ-NN); and the second one is built on texture-based features and called ‘support vector machine’ (SVM) (Hu & Davis 2006). For the classification of the ROIs in this thesis we only used the LVQ-NN, because the DUAL classifier did not work properly on the laptops used.

After using VP, manual sorting was done with the software Irfanview to correct possible errors done by the automatic classification and to classify the results into more groups and species.

### **2.6.3. *Estimating plankton distribution and abundance.***

By using special MATLAB scripts created by Fredrika Norrbin I was able to plot the vertical distribution and abundance of the organisms sorted.

## **2.7. CTD analysis.**

The data from the CTD was extracted in a MAT file using VP. The software MATLAB was used to plot and create the graphics of the hydrography in each of the stations sampled.

## **2.8. Statistical analysis.**

Patchiness of zooplankton may invalidate standard statistical methods used to compare vertical distributions (Venrick 1986). A robust method to patchiness was used based on a modified Kolmogorov-Smirnov test and the Solow *et al* test (Solow *et al.* 2000). In this study the most abundant zooplankton species observed with the VPR were analyzed using B statistics (Paul & Banerjee 1998) and the approach of Beet *et al.* (Beet *et al.* 2003). The method developed by Solow *et al.* (2000) is used for single samples, while the Beet *et al.* (2003) test is used when replicates are available to compare vertical distributions.

The aim of the analysis was to see if the distributions for one specie at different times of the day or the distributions of two different species were different. Zooplankton distributions were analyzed using the number of individuals observed at each leg of the VPR sample as replicates. The bin depth used was 25 m at Billefjorden and the outer station in Porsanger, and 10 m at Porsanger Østerbotn.

### 3. Results

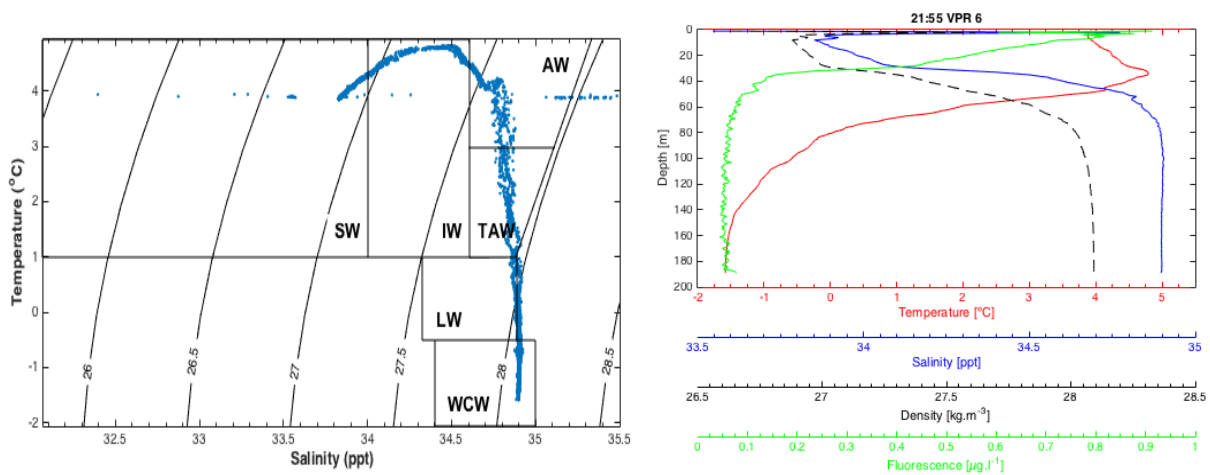
The first part of this section will give the results for the 24h station sample at Billefjorden. In this case, the diel vertical distributions of different zooplankton species are shown. The second part is the focus on the seasonal and regional distribution of zooplankton in Porsangerfjord, showing the differences between the stations in terms of hydrography, species composition and vertical distributions. The last part will try to demonstrate, with statistical methods, if the different distribution of species is significant, which can be due to avoidance of some species.

#### 3.1. Billefjorden.

##### 3.1.1. Hydrography.

The CTD profiles (Appendix I) showed no difference of temperature, salinity and Fluorescence for the four times of sampling.

Different water masses were observed in Billefjorden (figure 4). The CTD profiles showed warm and fresh SW in the upper 20 m. From 20 - 60 m, three different water masses were observed: IW, AW and TAW. Between 60 and 95 m was a layer of LW. Below, the entire fjord basin was filled with WCW. The highest temperature was 4.8 °C, registered at 30 m, and the minimum was -1.6 °C at 186 m. Salinity had its maximum concentration at 104 m with 34.9 ppt and its minimum at 10 m with 32,87 ppt.



**Figure 4** T-S diagram and CTD profile at Billefjorden vpr6 at midnight. The water masses describe, are related to Cottier et. Al 2005. Surface Water (SW); Intermediate Water (IW); Atlantic Water (AW); Transformed Atlantic Water (TAW); Local Water (LW); Winter Cooled Water (WCW).

From the fluorometer, the maximum Chl *a* was 1,2  $\mu\text{g}\cdot\text{l}^{-1}$  at 4 m depth, being the highest concentrations between the surface and 20 m of depth. A sharp decline was observed between 20 and 40 m of depth.

### 3.1.2. Zooplankton

#### 3.1.2.1. General Overview.

A total of 28 taxa were found in Billefjorden for day and night together (appendix II).

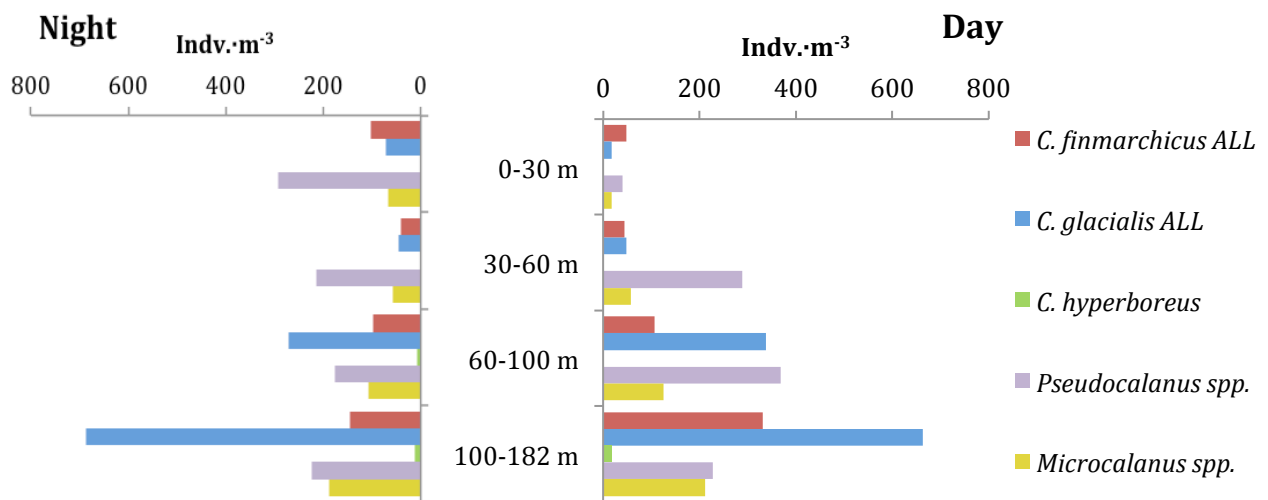
#### 3.1.2.2. Zooplankton composition using the multineets (MPS).

*Oithona similis* dominated at all depths, both at night and during the day, with no presence of strong DVM with a total abundance of 7188  $\text{ind}\cdot\text{m}^{-3}/\text{night}$  and 6297  $\text{ind}\cdot\text{m}^{-3}/\text{day}$ . The population was distributed with 69% at night and 57% during the day, over a 30 m depth. Lower abundances of *Oithona similis* were found deeper in the water column (appendix II).

The second most dominant group was the calanoid copepods: *Calanus glacialis* (1072  $\text{ind}\cdot\text{m}^{-3}/\text{night}$ ; 1068  $\text{ind}\cdot\text{m}^{-3}/\text{day}$ ), *Pseudocalanus spp.* (908  $\text{ind}\cdot\text{m}^{-3}/\text{night}$ ; 925  $\text{ind}\cdot\text{m}^{-3}/\text{day}$ ), *C. finmarchicus* (385  $\text{ind}\cdot\text{m}^{-3}/\text{night}$ ; 531  $\text{ind}\cdot\text{m}^{-3}/\text{day}$ ) and *Microcalanus spp.* (420  $\text{ind}\cdot\text{m}^{-3}/\text{night}$ ; 412  $\text{ind}\cdot\text{m}^{-3}/\text{day}$ ).

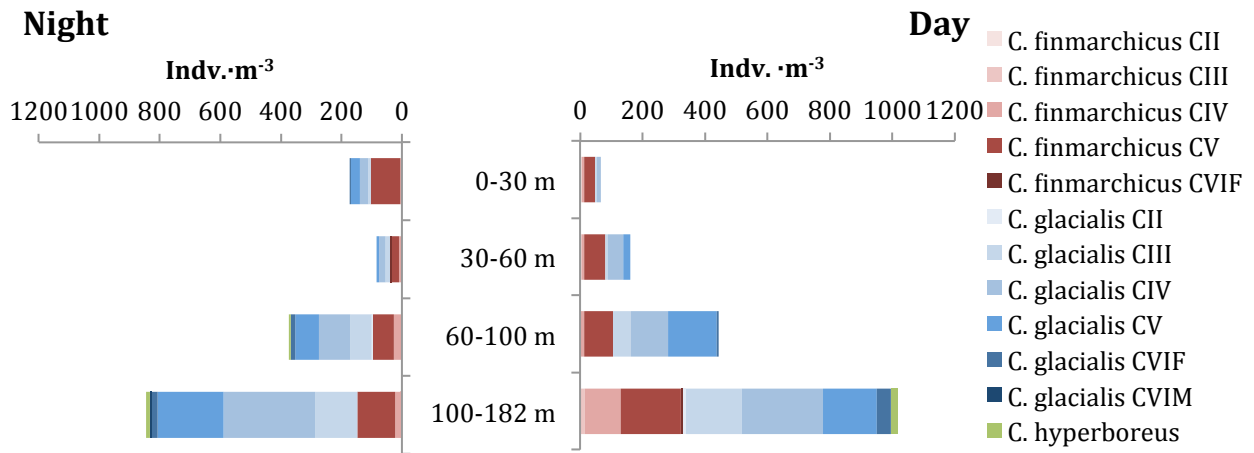
*C. glacialis*, *C. finmarchicus* and *Microcalanus spp.* were found in higher abundances in deep waters where the WCW was found. *Pseudocalanus spp.* was distributed throughout the entire water column.

DVM was observed for all the calanoid copepods (figure 5).



**Figure 5** Billefjorden. Diel abundance and vertical distribution of calanoid copepods.

For *Calanus spp.* the responsible for the majority of this migration was the copepodite stage V for *C. finmarchicus* and copepodite stage IV for *C. glacialis* (figure 6). Adult stages were mostly found in the deepest layer not presenting a DVM pattern.



**Figure 6** Billefjorden. Diel abundance and vertical distribution of *Calanus spp.* stages.

For *Microcalanus spp.* a weak DVM was observed with more organisms between 0 - 30 m at night (figure 5). A strong DVM was observed for *Pseudocalanus spp.* During the day, the population was distributed below 30 m with its highest aggregation from 60 - 100 m in depth. At night, the population had a strong migration to the surface. The abundance during the day, on the surface, was 40 ind.·m<sup>-3</sup> and 293 ind.·m<sup>-3</sup> at night. A low abundance of *C. hyperboreus* (20 ind.·m<sup>-3</sup> both day and night) was found below 60 m, being all the population in the WCW mostly concentrated.

The abundance of chaetognats observed was 8 ind.·m<sup>-3</sup>/night and 10 ind.·m<sup>-3</sup>/day. Two species were found: *Parasagitta elegans* and *Eukrohnia hamata*; being *Parasagitta elegans* the dominant one, representing more than 96%.

The total abundance, for the entire water column of all the other taxa found together was 490 ind.·m<sup>-3</sup>/night and 412 ind.·m<sup>-3</sup>/day.



### 3.1.2.3. Macrozooplankton using MIK nets.

A total of 22 taxa were observed for all the MIK nets together (appendix II).

For the morning and midnight MIK samples, the euphasiid and chaetognath species were dominating at 40 - 60 m in terms of biomass and abundance, whereas, at 120 m copepod biomass was higher with  $874 \text{ mg} \cdot \text{m}^{-3}$  at midnight and  $1080 \text{ mg} \cdot \text{m}^{-3}$  in the morning. At midday, the abundance of chaetognats at all depths was higher than for all other species, being only comparable at 120 m with the abundance of euphausiids. At 120 m, the biomass was higher for copepods being  $745 \text{ mg} \cdot \text{m}^{-3}$ . During the evening, the abundance and biomass of chaetognats was higher at 40 and 60 m depth, with a higher biomass of copepods ( $529 \text{ mg} \cdot \text{m}^{-3}$ ) at 120 m.

At 120 m there was higher abundances of euphausiids at the midnight, morning and midday sampling. The abundance was highest at 40 or 60 m at midnight and in the morning and low at all depths during the evening.

The highest abundance of chaetognats was observed at 40 m at midday and evening sampling and low abundance at 60 and 120 m during the whole day, being the lowest abundance at 120m in the evening. At all sampling times, smaller individuals at 40 m and larger individuals were found at 120 m (table 2).

Low abundances of *Themisto spp.*, planktivorous fish and jellies were observed during all the sampling times and at all depths.

**Table 2** Mean size and standard deviation of chaetognats. Local time: at midnight (23:55), in the morning (06:06), at midday (13:23) and evening (17:53). (a) Chaetognats; (b) Euphausiids.

(a)	Mean length $\pm$ SD (mm)			
	Midnight	Morning	Midday	Evening
Depth (m)				
40	26 $\pm$ 4,9	24,5 $\pm$ 4,1	22,4 $\pm$ 4,8	24,1 $\pm$ 5
60	29,7 $\pm$ 6,4	25,4 $\pm$ 6,5	23,6 $\pm$ 3,7	24,5 $\pm$ 4,7
120	28,5 $\pm$ 5,9	30,3 $\pm$ 8,4	26,7 $\pm$ 9,3	27,3 $\pm$ 7,7

(b)	Mean length $\pm$ SD (mm)			
	Midnight	Morning	Midday	Evening
Depth (m)				
40	19,4 $\pm$ 4,2	16,4 $\pm$ 4,2	15,3 $\pm$ 5,1	14,9 $\pm$ 4,9
60	19,2 $\pm$ 4,3	18,1 $\pm$ 4,1	13,5 $\pm$ 5,5	17,1 $\pm$ 4,2
120	19,1 $\pm$ 3,5	19,5 $\pm$ 4,1	22,1 $\pm$ 4	22 $\pm$ 4,1

### 3.1.3. Pelagic trawl.

The trawl taken on the evening had higher abundance and biomasses compared to the morning trawl. Krill dominated in both trawls. It also displayed the strongest increase between sampling times with an abundance of  $0.013 \text{ ind} \cdot \text{m}^{-3}/\text{day}$  and  $6.58 \text{ ind} \cdot \text{m}^{-3}/\text{night}$  and a biomass of  $0.86$

mg·m<sup>-3</sup>/day and 615 mg·m<sup>-3</sup>/night.

Other important species in the evening trawl were *Leptoclinus maculatus*, *Anisarchus medius* and *Themisto spp.* in terms of abundance. However, the species *Gadus morhua*, *Anisarchus medius*, *Boreogadus sadia* and *Themisto spp.* dominated in biomass.

During the morning, *Themisto spp.*, *Leptoclinus maculatus* and *Mallotus villosus* dominated in abundance, while for biomass, the gelatinous organisms were the most important, followed by *Themisto spp.* and *Gadus morhua*.

### 3.1.4. Vertical distribution and abundance using the VPR.

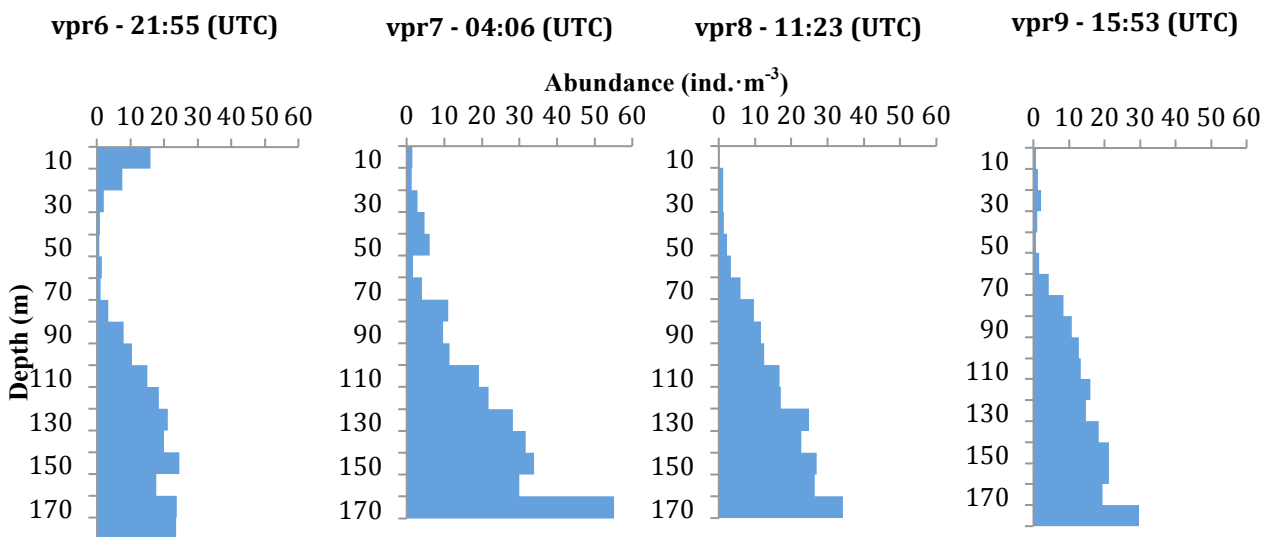
*Calanus sp.* was the dominant species at all sampling times, matching up to >87% of the total abundance, but also other copepods were observed (Table 3). The main predators were the chaetognats (< 2,4%), but there was also a notable presence of gelatinous organisms (<0,3%) comprising small hydromedusae and ctenophores.

The total abundances were different between the times of sampling at the same station due to patchy distributions.

**Table 3** Billefjorden abundance (ind.·m<sup>-2</sup>) of the different taxa observed using the VPR.

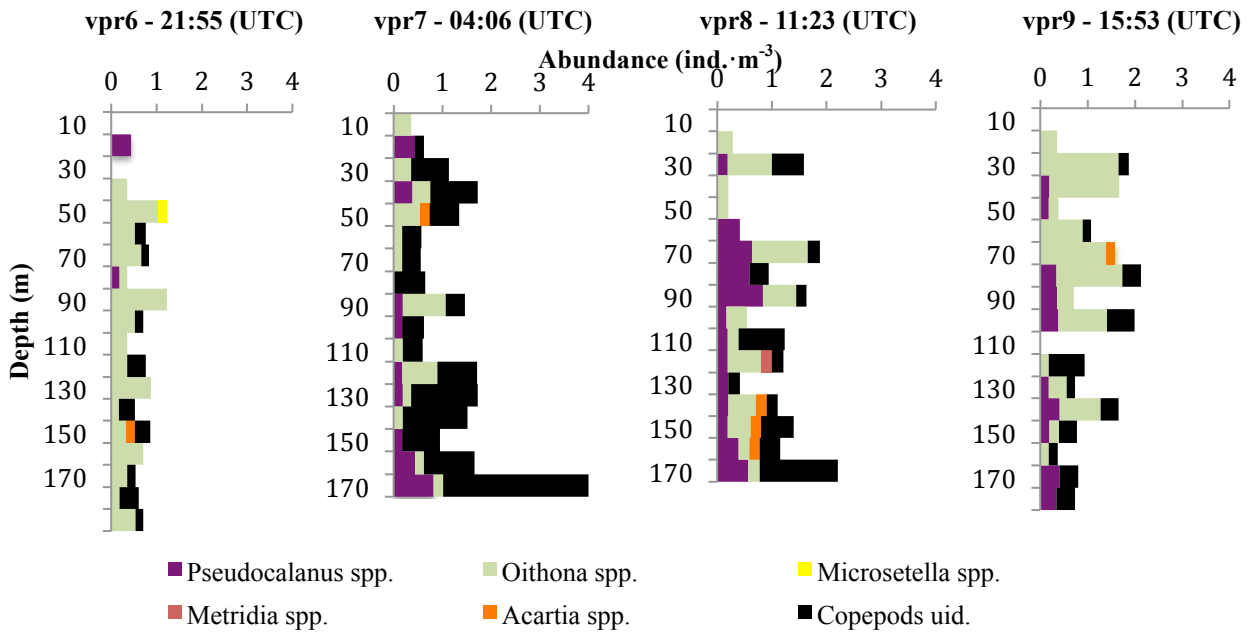
<i>Taxa</i>	vpr6	vpr7	vpr8	vpr9
	Abundance (ind.·m <sup>-2</sup> )			
<i>Calanus spp.</i>	389430	495434	387865	360276
<i>Pseudocalanus spp.</i>	1122	5354	8464	5434
<i>Oithona spp.</i>	15172	8212	10087	19320
<i>Acartia spp.</i>	333	337	1010	348
<i>Metridia spp.</i>			341	
<i>Microsetella spp.</i>	333	333		
Appendicularians	1537	1627	1089	1003
Copepods uid.	4477	24827	9215	7355
Chaetognats	5318	12856	10311	7792
Euphausiids	1670	4724	3536	3843
Pterapods	3093	1684	2975	3906
Pluteus larvae	567	567	771	
Fish uid.	615	958	958	
Fish egg			337	
Gelatinous organisms		982	2128	665
Amphipods			379	
Total abundance	423667	557894	439465	409943

The vertical distribution of *Calanus* spp. showed DVM in the VPR samples (figure 7). For the sampling at 21:55 (UTC), the highest abundance was from 110 m to the bottom, but the highest abundance was located at 150m (34 ind.·m<sup>-3</sup>). Abundance was quite high from the surface to 30m having its maximum in the first 10m (16 ind.·m<sup>-3</sup>). For vpr7 at 04:06 (UTC), the organisms that were at the surface in the previous sampling were distributed from the pycnocline to the deeper layers, and the highest concentration at the bottom (55 ind.·m<sup>-3</sup>). At 11:23 (UTC), almost no abundance of *Calanus* sp. was found between the surface and 60 m in depth, and the population concentrated below with the highest abundance at the bottom (34 ind.·m<sup>-3</sup>). In the last sampling period, at 15:53 (UTC), a weak movement of *Calanus* sp. to surface layers between 20-40 m was observed, but higher abundances remained in the deep layers of the water column with the maximum at the bottom (30 ind.·m<sup>-3</sup>).



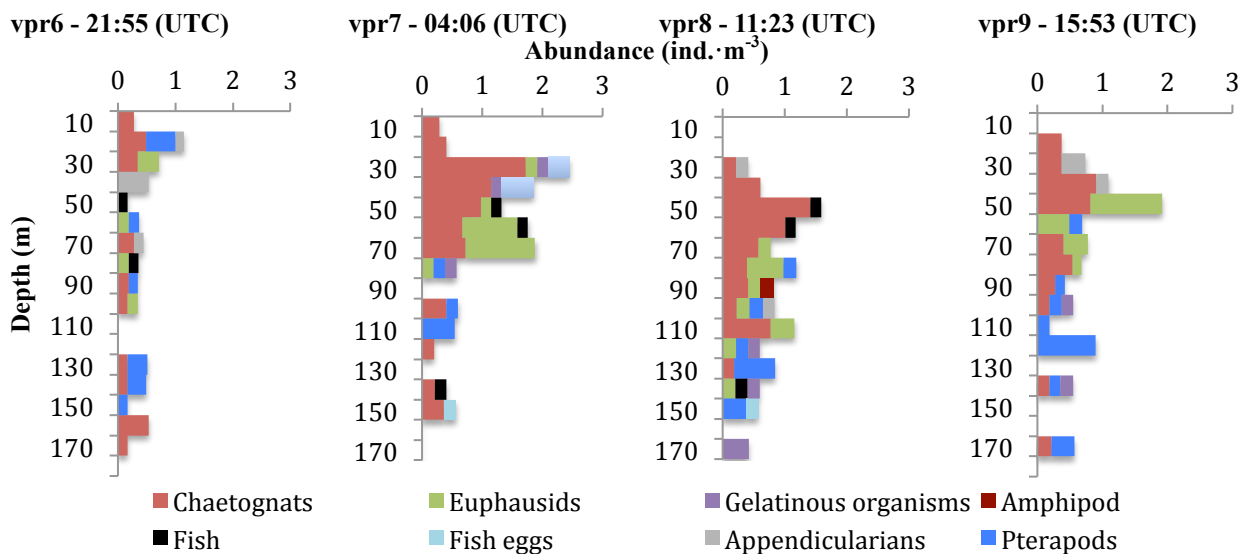
**Figure 7** Billefjorden vertical distribution of *Calanus* spp. for the different sampling times. Note that time is in UTC and local time is UTC+2

The vertical distribution of the other copepods (figure 8) showed low observations compared with other times of the day. For the calanoid copepod *Pseudocalanus* spp. the number of individuals observed was low. They were close to the surface at midnight while for the rest of the times they were distributed throughout the entire water column closer to the surface in the morning, at midday and during the evening in deeper layers; the highest concentrations were observed at midday between 60-90 m. *Oithona* spp. was distributed throughout the entire water column at all sampling times, with the highest abundance between 30-100 m in depth. Low numbers of *Acartia* spp., *Metridia* spp. and *Microsetella* spp. were observed, not enough to consider if those species were doing DVM or not.



**Figure 8** Billefjorden diel vertical distribution of other copepod species. Local time UTC+2.

For the non-copepod species (figure 9), chaetognats represented the main group showing a weak DVM with more abundance close to the surface at night and in deeper layers below the pycnocline during the day. Some chaetognats were observed close to the bottom. But also, DVM was observed for euphausiids, mainly below the pycnocline. Pterapods may have a weak DVM, with some individuals at the surface at night and mainly distributed below 50 m during the day. Few fish were observed below 50 m in depth. Gelatinous organisms were between 30-80 m in the morning sampling and below 90 m during the midday and evening sampling; no individuals were observed at night. Appendicularians were mostly at the pycnocline.



**Figure 9** Billefjorden diel vertical distribution of non-copepod species. Local time UTC+2

## 3.2. Porsangerfjord.

### 3.2.1. Hydrography

At Østerbotn no pycnocline were observed; temperature was the same for the entire water column in March (-1,3 °C), April (-0,75 °C) and November (2,5 °C). Also, salinity presented no different values through the water column. In May, different water masses could be observed with warm and fresh water at the surface (4,4 °C), a pycnocline at 20 m and below, cold and salty water was found, called Winter Cooled Fjord Water (WCFW), at the bottom (0 °C). No Chl *a* was found for the months of March and November, but an increase of Chl *a* could be observed in April (Chl *a* max of 0,57 µg·l<sup>-1</sup>) at the surface, with a huge increase in May (Chl *a* max of 6,9 µg·l<sup>-1</sup>) where the higher concentrations were of pycnocline (21 m).

For the middle and outer parts of Porsangerfjord, different hydrography was observed in the eastern and western parts. An influx of water, from the Norwegian Coastal Current (NCC) with Atlantic water properties, was observed in the western part into the fjord and an out flux of cold water outside the fjord from Østerbotn along the eastern part (appendix I).

At Midtre Øst, the minimum temperature was 2 °C in March and 6 °C in November in the deep layers of the water column, while at Midtre Vest it was 2 and 5 °C. At Midtre Øst and Midtre Vest, no pycnocline were observed in March and April and the entire water column had almost the same temperature and salinity values (appendix I). In May, temperature presented warmer water at the surface, with a huge decrease in the 70 m range at Midtre Øst and 50 m at Midtre Vest; Salinity was less at the surface for both stations; The Chl *a* was different for both stations presenting 3 peaks (ca. 30, 65 and 100 m) at Midtre Øst, with the Chl *a* max of 3,1 µg·l<sup>-1</sup> at 30 m in depth, and at Midtre Vest one clear peak of 4 µg·l<sup>-1</sup> of pycnocline (34 m). In November, both stations showed warmer water at the basin of the fjord from ca. 160 m in depth at Midtre Øst and ca. 85 m at Midtre Vest. Colder water could be found above the pycnocline.

At the outer part of Porsanger (Porsanges and Ytre Øst/Vest), a difference in temperature between East and West could be observed, which varied from month to month, from 2 - 6 °C in the East and 3 - 6 °C from the West. For all the months, a pycnocline was observed, due the influence of the NCC. The water column, for all months, presented warm and fresh water at the surface, with a decrease in temperature from the surface to the pycnocline and with warm and saltier water below. In March, the pycnocline was observed at 180 m, but in May and November at 150 m in depth. No data for the outer part is registered in April. In May, the Chl *a* max was 5,4 µg·l<sup>-1</sup> in the East at 20 m and 4,1 µg·l<sup>-1</sup> in the West at 17 m.

### 3.2.2. Zooplankton composition from the WP-2 nets.

#### 3.2.2.1. General Overview

A total of 34 taxa were observed at Porsangerfjord (appendix III). 23 species were identified, including sex and developmental stages were included for *C. finmarchicus* and *Pseudocalanus* spp. (appendix III).

The regional and seasonal variations in species numbers (S) and diversity (H') are given in figure 10. Along Porsangerfjord, higher numbers of species were found at Østerbotn and lower numbers of species in the outer part of the fjord for all months, except in November, when the highest number of species was found at Midtre Øst and the lowest at Østerbotn. For the middle part of the fjord, higher numbers of species were found for all months in the Eastern part, but also in the outer part of the fjord it was the same situation, except in May, where higher numbers of species were found in the outer Western part.

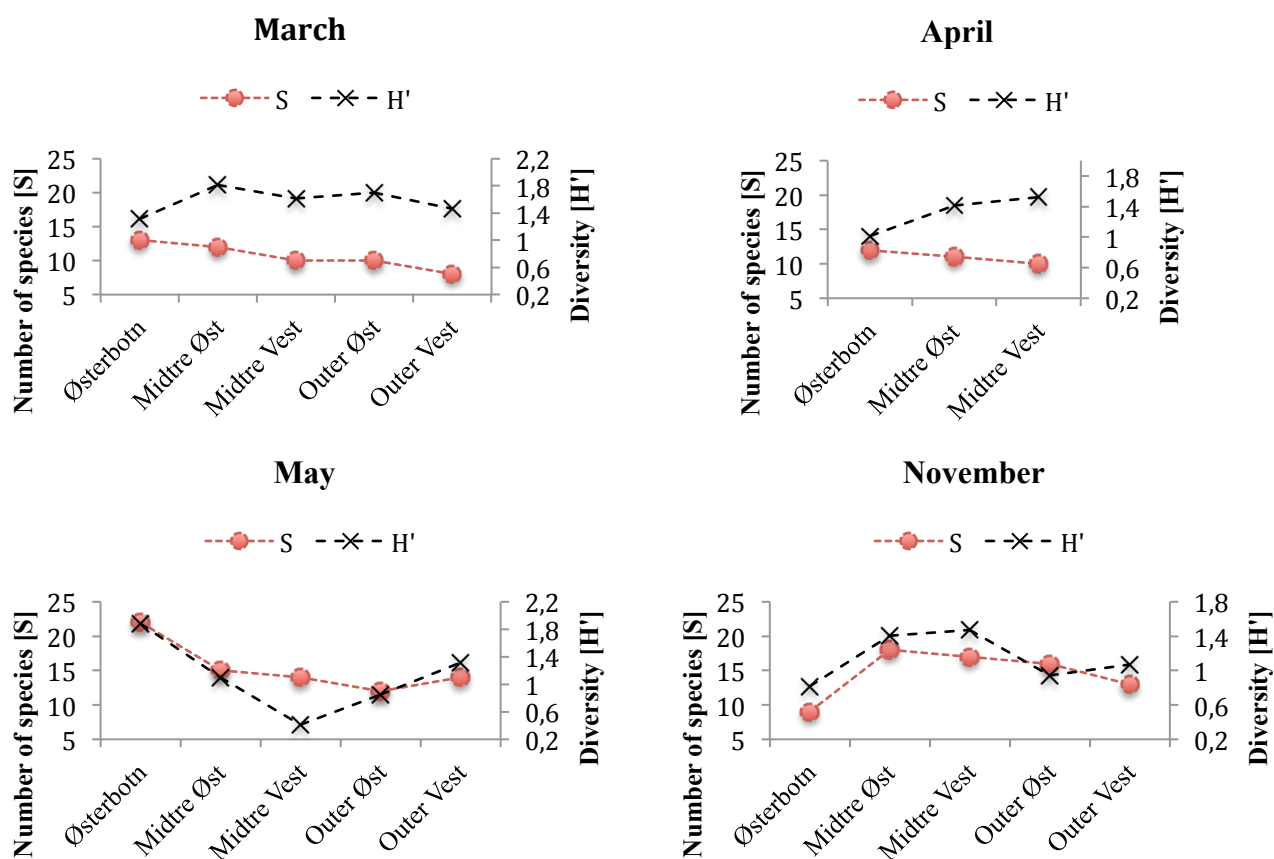


Figure 10 Regional and seasonal distribution of diversity [H'] and species number (S).

Copepods dominated the zooplankton community for all the months and at all the stations sampled regarding to abundance. The total abundance (table 4) varied a lot during the season and the stations sampled.

**Table 4.** Porsangerfjord seasonal total abundance.

Total Abundance (ind.·m <sup>-2</sup> )	Østerbotn	Midtre Vest	Midtre Øst	Outer Vest	Outer Øst
March	91527	16580	8792	896	9269
April	82377	12884	26864	-	-
May	28115	135783	214927	41953	42801
November	2794035	289660	367496	706738	717556

The thesis focuses on few taxa due to the taxa that could be found with the VPR. The taxa studied at Porsangerfjord are the calanoid copepods (*C. finmarchicus*, *Pseudocalanus* spp., *Acartia longiremis*, *Metridia longa* and *Microcalanus* spp.), harpacticoids (*Microsetella* spp.), cyclopoid copepods (*Oithona similis* and *Oithona atlántica*), euphausiacea (*Thysanoessa* spp., *Meganyctiphanes norvegica*), chaetognata (*Parasagitta* spp. and *Eukrohnia hamata*), ctenophora and medusae.

### 3.2.2.2. March.

Østerbotn was dominated by calanoid copepods *Pseudocalanus* spp. (61%) and *Calanus finmarchicus* (15%). Other copepods were observed in low abundances (<6%). The developmental stages with higher concentrations observed were *Pseudocalanus* spp. with copepodites and adult females; *C. finmarchicus* with stage CV.

Different populations were found between both sides of the fjord in the middle part, with the most abundance of copepod observed being *Oithona similis* (41%) at Midtre Vest and *C. finmarchicus* (21%) at Midtre Øst. The most abundance of copepodite stage for *C. finmarchicus* on both sides was CV. *Parasagittal elegans* were observed at both stations in low abundances.

On the Outer part of the fjord, lower abundances were found and *Microsetella* spp. with the 48% at Porsangnes Vest and 27% at Porsangnes Øst being the most abundant species at both stations. The second most abundant group, at both stations, was *C. finmarchicus* with the copepodite stage CV.

### 3.2.2.3. April.

Østerbotn was dominated by calanoid copepod *Pseudocalanus* spp. (71%) with copepodites stages or adult females as the most dominant. Other copepodites were in low abundances compared to *Pseudocalanus* spp. Of the non-copepod group, the highest abundance were predators *Rathkea* spp. and *Parasagittal elegans*.

In the middle part, the most abundant copepod for both sites was *C. finmarchicus* with 41% in the west and the 50% in the east of the total abundance. The most abundant copepodite stages were nauplii and CVI-Female. Of the non-copepod *Rathkea* spp. (0,5%), *Parasagittal elegans* (0,2%) and fish eggs (0,3%) were observed at both sites of the fjord, but pluteus larvae and *Fritillaria borealis* in the west and *Oikopleura* spp. in the east were observed.

In April, it was not possible to collect samples from the outer part of the fjord.

### 3.2.2.4. May

Østerbotn was dominated by the copepods *Pseudocalanus* spp. (34%) and *Calanus finmarchicus* (17%), with a notable presence of *Oithona similis* (16%). The life stages with higher abundances found for the two main calanoid copepods were: for *Pseudocalanus* spp. Nauplii and copepodite stages and for *C. finmarchicus* nauplii and CI. Of the non-copepod groups, more species than the previous months with *Fritillaria borealis*, *Oikopleura* spp., fish eggs, euphausids nauplii, polychaeta, equinoderm larvae, cirripeda, medusae, megalopa zoea and *Parasagittal elegans* were observed.

The middle part of the fjord was dominated by *Calanus finmarchicus* (93% in the west and 75% in the east) with the most abundant life stages: nauplii and CI. The non-copepods observed were pluteus larvae, *Fritillaria borealis*, polychaeta and euphausids (nauplii and calyptopis stages), but polychaeta in the east were also observed.

The outer part was dominated by *Calanus finmarchicus* (61% west; 78% east). But also, a notable presence of *Oithona similis* (16% West; 10% East) was observed. The most abundant life stages were: *C. finmarchicus* nauplii and CII; *Pseudocalanus* spp. copepodites in the west and adult females in the East. The most abundant non-copepod species were pluteus larvae, euphausids (nauplii and calyptopis) and fish eggs.

### 3.2.2.5. November.

At all stations, extremely high abundances of small harpacticoid *Microsetella* spp. and high abundances of other small copepods were observed.

Østerbotn was dominated by harpacticoid *Microsetella* spp. (76%) followed by calanoid copepods *Microcalanus* spp. (13%) and *Pseudocalanus* spp. (8%). Mostly copepodites stages



of *Pseudocalanus* spp. were observed. Higher abundances were found for chaetognat *Parasagittal elegans* representing more than five times more abundance than for May.

The middle part of the fjord was dominated by *Microsetella* spp. (39% west; 46% east) and *Oithona similis* (33% west; 30% east). Also, *Pseudocalanus* spp. (nauplii and copepodite stages) and *C. finmarchicus* (nauplii and CV stages in the west; CIV and CV in the east) were observed in low abundance compare to the two main species. The most abundant of other non-copepod species were: *Oikopleura* spp. in the west and *Beroe cucumis* in the East. During that month it was not possible to sample both sites of the fjord in the outermost part but Ytre Vest and Øst station could be considered similar. The most abundant species for both sites were *Microsetella* spp. (68% West; 73% East) and *Oithona similis* (16% West; 15% East). The calanoid copepods were mainly represented by *C. finmarchicus* and *Pseudocalanus* spp. and *Microcalanus* spp. in low abundances. Non-copepods, *Oikopleura* spp. was to be found at both stations, while ctenophore *Beroe cucumis* was only observed at Ytre Øst in high abundances.

### 3.2.3. Vertical distribution of the zooplankton using the VPR.

#### 3.2.3.1. Vertical distribution and abundance at Østerbotn.

Copepods dominated in terms of abundance in April (96%), May (98%) and November (81%). In April, some diatoms were found in the water column, being the beginning of the phytoplankton bloom. The most abundant copepod species observed were *Microsetella* spp. (95 ind.·m<sup>-3</sup>), *Pseudocalanus* spp. (67 ind.·m<sup>-3</sup>) and *C. finmarchicus* (59 ind.·m<sup>-3</sup>).

In May, high concentrations of phytoplankton (diatoms 40%; *Phaeocystis* 60%) were observed between the surface and 60 m in depth, with the highest concentration at 20 m in depth. *Microsetella* spp. was the most abundant species of zooplankton with 855 ind.·m<sup>-3</sup> in that period, representing 63% of the total abundance. It is important to mention the notable presence of *Oithona* spp. (17%) and copepod nauplii (4%).

For November, the unidentified copepods (35 ind.·m<sup>-3</sup>) represented 42% of the total abundance, followed by *Pseudocalanus* spp. (12 ind.·m<sup>-3</sup>), *Microsetella* spp. (11 ind.·m<sup>-3</sup>) and *Acartia longiremis* (4 ind.·m<sup>-3</sup>).

For the non-copepod species, chaetognats were the most abundant in April (8 ind.·m<sup>-3</sup>) and November (11 ind.·m<sup>-3</sup>), appendicularians (22 ind.·m<sup>-3</sup>) in May.

The vertical distribution of the zooplankton (figure 11) was different, showing a seasonal vertical distribution for some of the species. Calanoid copepods were distributed throughout the entire water column in April, with the highest abundance for *C. finmarchicus* and *Metridia*

*longa* at 20 m, while *Pseudocalanus* spp. peaked at 50 m in depth. In May, the highest concentrations of *C. finmarchicus* and *Pseudocalanus* spp. were observed over the Chl *a* max (20 m), below *Microcalanus* spp. were observed at 30-40 m and *Metridia longa* at 60 m. In November, the highest concentrations of *C. finmarchicus* and *Pseudocalanus* spp. were observed at the bottom depth, while *Acartia longiremis* was distributed throughout the entire water column.

In April, other copepod species were not found at the surface, but spread from 20 m to the bottom depth, with the highest abundance at 70 m. In May, they were concentrated between 20 and 40 m in depth with the highest concentrations below the Chl *a* max. In November, the whole population was concentrated in deep layers with the maximum concentration at the bottom.

In the month of April, non-copepod species were observed with: chaetognats in the entire water column with the highest concentrations at 50 and 90 m in depth; highest concentrations of euphausiids between 20 - 30 m and 60 - 80 m. In May, appendicularians, pluteus larvae and fish eggs between 0 - 40 m, with the highest concentrations at the Chl *a* max.

### **3.2.3.2. Vertical distribution and abundances in the middle part.**

For the middle part of Porsangerfjord the distribution and species observed were different between the Western (W) and the Eastern (E) part of the fjord. It is important to mention the differences in bathymetry of both stations, with Midtre Øst (190 m) being deeper than Midtre Vest (120 m).

Copepods were the dominant group in March (99% E; 94% W), April (70% E; 37% W) and November (89% E; 82% W). The most abundance of copepods observed for each month was: *C. finmarchicus* (24 ind.·m<sup>-3</sup> E; 9,7 ind.·m<sup>-3</sup> W) in March; *C. finmarchicus* (8 ind.·m<sup>-3</sup> E) and *Oithona* spp. (5 ind.·m<sup>-3</sup> W) in April; *C. finmarchicus* (57 ind.·m<sup>-3</sup> E; 43 ind.·m<sup>-3</sup> W) in November.

Non-copepod group: Euphausiids (0.2 ind.·m<sup>-3</sup> E) and chaetognats (0.3 ind.·m<sup>-3</sup> W) in March; *Balanus nauplii* (4 ind.·m<sup>-3</sup> E) and appendicularians (8 ind.·m<sup>-3</sup> W) in April; Chaetognats (4 ind.·m<sup>-3</sup> E) and appendicularians (9 ind.·m<sup>-3</sup> W) in November.

The vertical distribution (figure 12) was different between the two middle stations. In March, *C. finmarchicus* were distributed in the entire water column at both stations, where the highest abundance was at the bottom at Midtre Øst and at 50 m at Midtre Vest. At Midtre Øst *Pseudocalanus* spp. were observed at a depth and euphausiids at the bottom. At Midtre Vest, chaetognats were observed at 70 m and appendicularians on the surface.

In April, *Calanus* nauplii were observed at Midtre Vest but not at Midtre Øst. Distributions were very different between both stations. At Midtre Øst, *C. finmarchicus* and *Metridia longa* were at a depth, concentrated below 110 m, where a weak pycnocline started to appear, *Microcalanus* spp. and *Microsetella* spp. were at the pycnocline and *Pseudocalanus* spp. and *Oithona* spp. were over the pycnocline between 40 - 70 m in depth. Euphausiids and chaetognats were below the pycnocline, and the highest concentrations of *Calanus* nauplii and appendicularians were on the surface. At Midtre Vest a pycnocline was not observed, and all the copepods and non-copepod species were mostly distributed in the entire water column, but the highest concentrations of *C. finmarchicus* were observed on the surface, *Calanus* nauplii between 30-50 m and appendicularians at 40 and 100 m.

In November, both stations had the highest concentrations of *C. finmarchicus* at the bottom and *Microsetella* spp. in the entire water column. At Midtre Øst, *Pseudocalanus* spp. were observed on the surface. At Midtre Vest, *Oithona* spp. was observed in the entire water column and *Metridia longa* at 50 m. Non-copepod species, Euphausiids and appendicularians were over the pycnocline at both stations. Highest concentrations of chaetognats were observed below the pycnocline (ca.160 m) at Midtre Øst. Low concentrations of gelatinous organisms were observed on the surface and bottom at Midtre Øst and between 70 - 90 m at Midtre Vest.

### **3.2.3.3. Vertical distribution and abundances in the outer part.**

The vertical distribution in the outer part of the fjord (figure 13) was only compared between the East and West in the months of March and November.

The most abundant species was *C. finmarchicus* for both stations, which in March represented 91% in the East and 66% in the West, in May 64% in the East and in November 86% and 90% respectively.

Non-copepods group, low abundances were observed in March, represented by gelatinous organisms and euphausiids with 0.2 ind.·m<sup>-3</sup> each on both sides. At Porsangnes Øst, in May, the abundance of pluteus larvae (31 ind.·m<sup>-3</sup>), euphausiids calyptopis larvae (16 ind.·m<sup>-3</sup>), appendicularians (14 ind.·m<sup>-3</sup>) and fish eggs (4 ind.·m<sup>-3</sup>) was notable. In November, chaetognats (1 ind.·m<sup>-3</sup> on both sides) and euphausiids (<2 ind.·m<sup>-3</sup> in both sides) were the most abundant, with a low concentration of pteropods (0.3 ind.·m<sup>-3</sup>) in the west and gelatinous organisms (0.4 ind.·m<sup>-3</sup>) in the East.

In the month of March, different species of copepods were observed on both sides of the fjord with *C. finmarchicus* in common. The highest concentrations of *C. finmarchicus* were observed in depth on both sides, but also on the surface in the East. Other copepod species observed in

the East were *Oithona* spp. between 40-110 m and *Metridia longa* at 180 m and in the West *Pseudocalanus* spp. between 40-180 m. Jellies were observed at 50 m in the East and at the bottom in the West, while euphausiids were distributed at the bottom on both sides.

In May, the vertical distribution in the Eastern part of the fjord presented almost all the organisms distributed between the surface-water up to 70 m. The highest concentrations of copepods were observed on the surface. Higher concentrations of *C. finmarchicus*, *Pseudocalanus* spp. and *Acartia longiremis* were over the pycnocline from 0-25 m, *Metridia longa* was at 190 m, *Oithona* spp. was mainly at the pycnocline in the 20-30 m layer, while *Microsetella* spp. and calanus nauplii were below the pycnocline from 25 - 80 m. Non-copepod species were all observed in the upper 70 m, in which euphausiids calyptopis larvae and appendicularians were from 0-70 m, pluteus larvae concentrated around the pycnocline between 20-50 m and fish eggs below the pycnocline from 30 - 70 m.

In November, all *C. finmarchicus* were at a depth on both sides. Other copepods were observed in the entire water column being closer to the surface in the West and deeper in the East. Of the non-copepods, euphausiids were between 40-80 m depth in the East and below 100m in the West, also the highest concentrations of chaetognats were observed in depth.

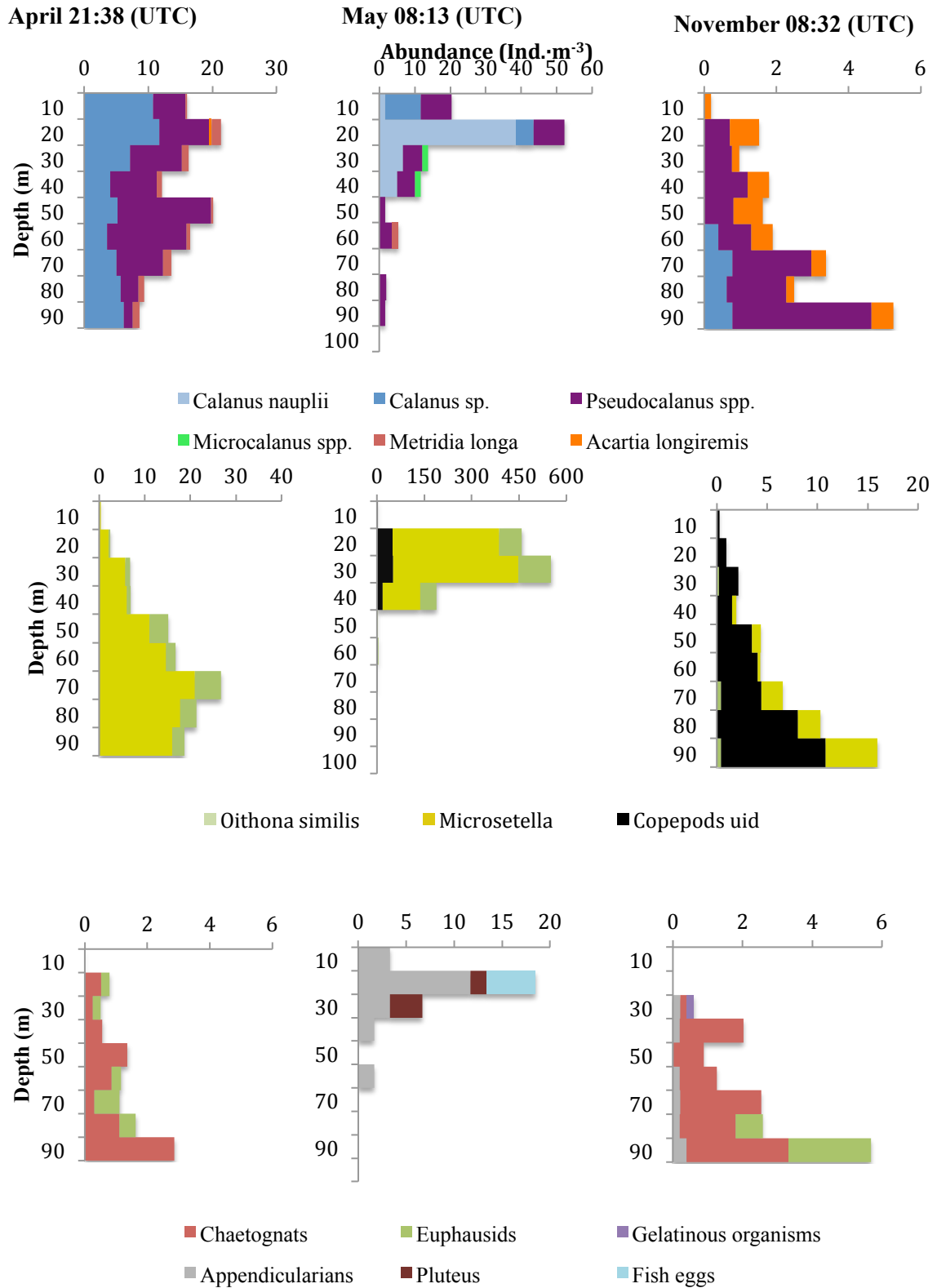
#### **3.2.3.4. Vertical distribution of zooplankton in the inner and outer part of Porsangerfjord in August 2012.**

At Østerbotn (figure 14), *C. finmarchicus* was mainly distributed at depth, the highest abundances of *Pseudocalanus* spp. and *Acartia longiremis* between 40-60 m, *Microsetella* spp. just below the pycnocline and *Oithona* spp. between 20-50 m.

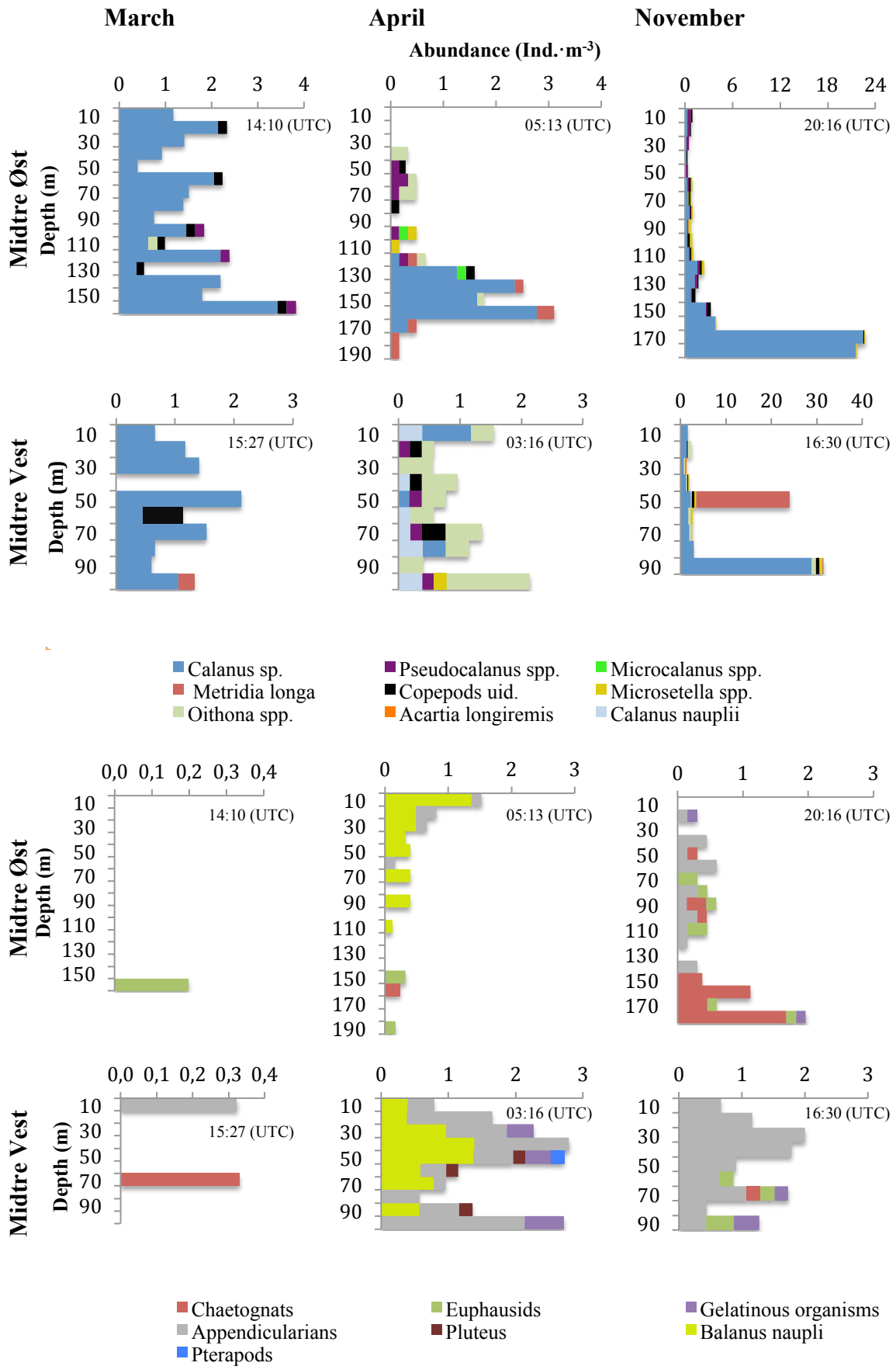
Visual and non-visual predators were at different depths, with gelatinous organisms (*Rathkea* spp. and ctenophores) between 10-30 m and chaetognats were at various depths with the highest concentration between 40 -70 m.

In the outer part (Porsangnes Vest) (figure 14), *C. finmarchicus* were observed in higher concentrations at a depth but also in the upper 50 m. *Microsetella* spp. was distributed in the entire water column. Other copepod species were in the upper 100 m with the highest concentrations between 25 – 75 m. Of the non-copepod species, the most abundant were the gelatinous organisms and the highest abundances were observed in the upper 25 m.

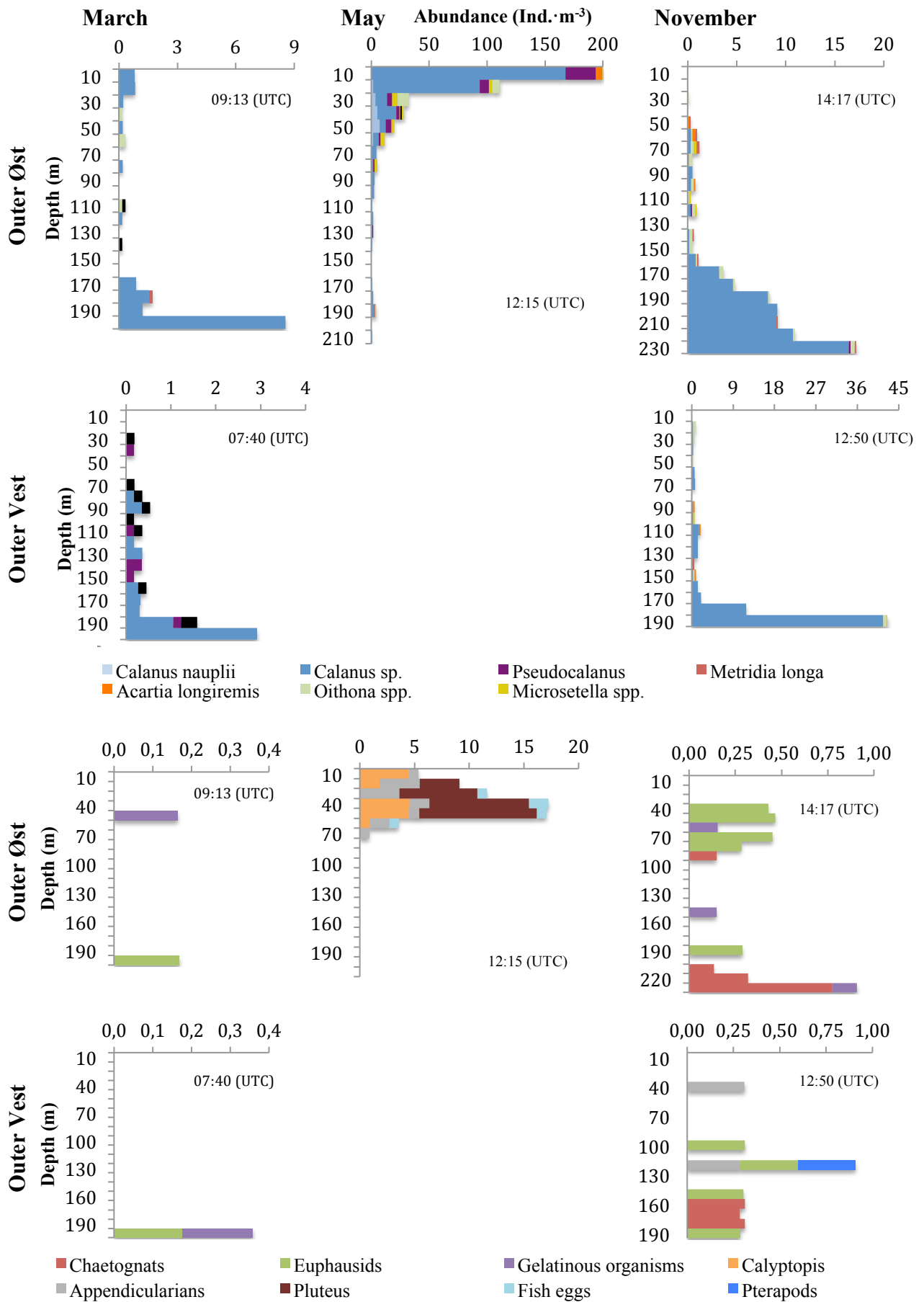
## Østerbotn



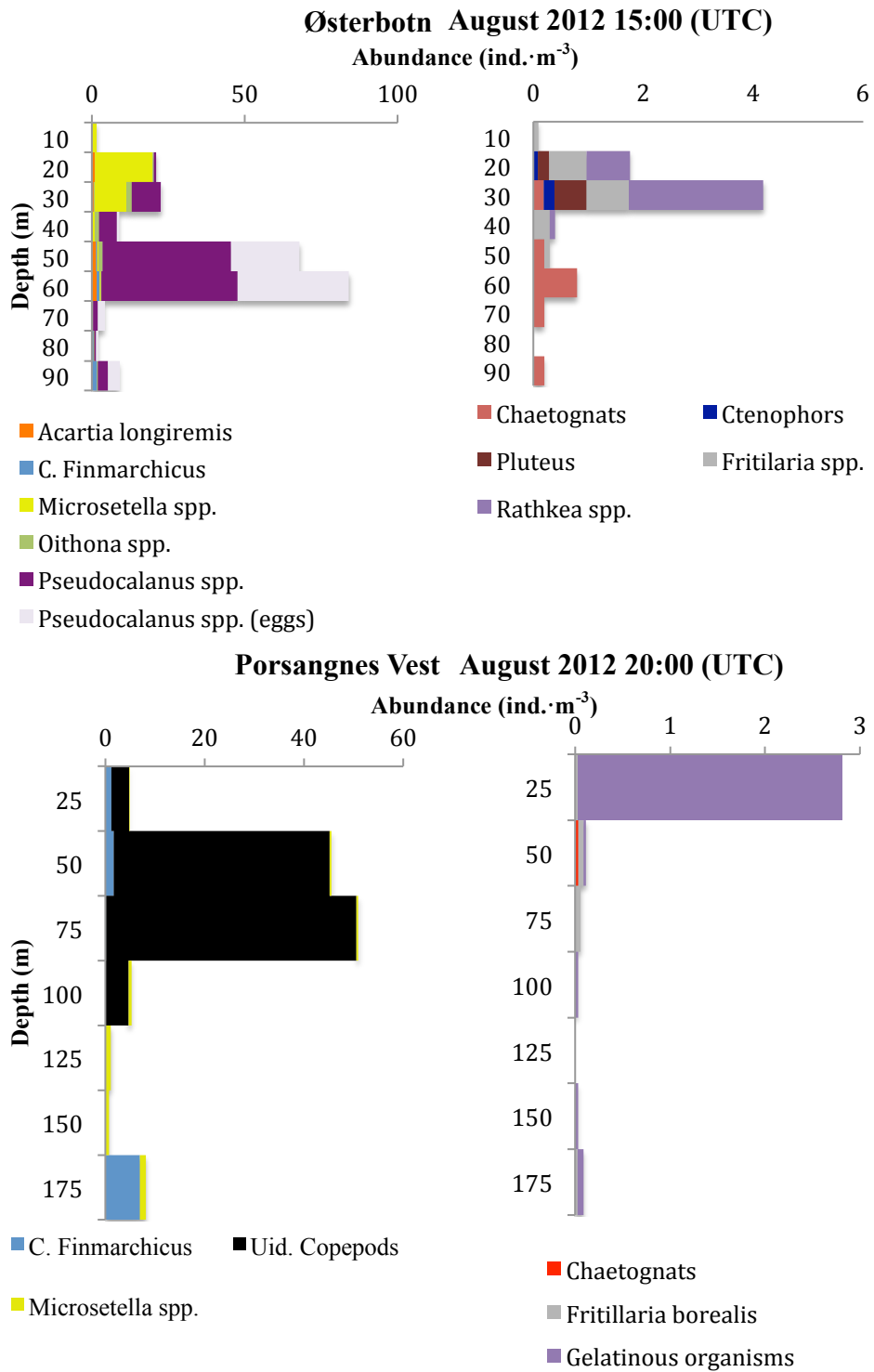
**Figure 11** Porsanger Østerbotn vertical distribution of zooplankton observed with the VPR in April (column 1), May (column 2) and November (column 3) 2014. The first file are calanoid copepods, second file other copepod species and third file non-copepods.



**Figure 12** Porsanger Midtre Øst (file 1 and 3) and Midtre Vest (file 2 and 4) vertical distribution of zooplankton observed with the VPR in March (column 1), April (column 2) and November (column 3) 2014.



**Figure 13** Porsanger Outer Øst (file 1 and 3) and Outer Vest (file 2 and 4) vertical distribution of zooplankton observed with the VPR in March, May and November 2014.



**Figure 14** Porsanger Østerbotn and Porsangnes Vest vertical distribution of zooplankton in August 2012.



### 3.3. Statistical analysis.

#### 3.3.1. Billefjorden

A comparison between Midnight, Dawn, Noon and Dusk was done to see differences in vertical distribution for *Calanus spp.*, *Pseudocalanus spp.*, euphausiids and chaetognats (appendix IV). *Calanus spp.* had significantly different distributions between sampling times with  $p < 0,001$ , except between dawn/noon and dusk/noon where probabilities were higher but significant ( $p < 0,05$ ). For the other species, no significant variations on the distribution were observed at the times of sampling.

A comparison between distributions at the same time of day between species was done (appendix IV). *Calanus spp.* had significantly different distribution compared to the other species, specifically with chaetognats and euphausiids with  $p < 0,001$ . It is important to mention the low numbers registered of other non-*Calanus* species, and important to mention the low number of observations for the midnight sampling.

#### 3.3.2. Porsangerfjord.

The main differences in vertical distribution between species took place mainly in the spring and summer months. The statistical analysis was used at stations where a significant number of individuals of different species were observed. The inner part of Porsangerfjord was analyzed. The month of August is not the same year but it gives an overview on how the situation is during that month.

##### 3.3.2.1. Østerbotn

Different distributions were observed between species for the different months of sampling (table 5).

In April, larger copepods (*C. finmarchicus* and *Metridia longa*) had a significant different distribution compared to small copepods, with no different distribution of chaetognats and euphausiids. Small copepods, specifically *Microsetella spp.* had a significant different distribution than all other species except with *Oithona spp.* which had a significant difference than larger copepods but not with chaetognats and euphausiids.

In May, invertebrate predators were not observed. Calanoid copepods did not present significant different distribution, but *Microsetella spp* and *Oithona spp* had significant different distribution than all other species.

In August, all species presented significant different distributions compared to some other species. The most significant different distribution was for *C. finmarchicus*, *Pseudocalanus spp.*, *Acartia longiremis* and *Microsetella spp.* related to the medusae *Rathkea spp.* The species

*Pseudocalanus* spp. and *Microsetella* spp. had significant different distribution than chaetognats. *Rathkea* spp. and chaetognats that also presented a different distribution.

In November, all species were at a depth not presenting any significant different distribution.

**Table 5** Østerbotn estimated significance levels for the test base on *B* for compare differences in vertical distribution of *Calanus* spp. (cal), *Pseudocalanus* spp. (Pse), chaetognaths (Cha), euphausiids (Kri), *Microrsetella* spp. (Msn), *Oithona* spp. (Oit), *Metridia longa* (Met), appendicularians (App), nauplii (Nau), pluteus larvae (Plu) and *Acartia* spp. (Aca).

<b>April 2014</b>	<i>Cal</i>	<i>Pse</i>	<i>Cha</i>	<i>Kri</i>	<i>Msn</i>	<i>Oit</i>	<i>Met</i>		
<i>Cal</i>	-	<0,001	n.s.	n.s.	<0,001	<0,001	n.s.		
<i>Pse</i>	-	-	<0,001	n.s.	<0,001	<0,001	<0,05		
<i>Cha</i>	-	-	-	n.s.	<0,05	n.s.	n.s.		
<i>Kri</i>	-	-	-	-	<0,05	n.s.	n.s.		
<i>Msn</i>	-	-	-	-	-	n.s.	<0,001		
<i>Oit</i>	-	-	-	-	-	-	n.s.		
<i>Met</i>	-	-	-	-	-	-	-		
<b>May 2014</b>	<i>Cal</i>	<i>Pse</i>	<i>Nau</i>	<i>Mca</i>	<i>Msn</i>	<i>Oit</i>	<i>App</i>		
<i>Cal</i>	-	n.s.	n.s.	n.s.	<0,05	<0,001	n.s.		
<i>Pse</i>	-	-	n.s.	n.s.	<0,05	<0,05	n.s.		
<i>Nau</i>	-	-	-	n.s.	<0,001	<0,05	n.s.		
<i>Mca</i>	-	-	-	-	<0,001	<0,001	n.s.		
<i>Msn</i>	-	-	-	-	-	<0,05	<0,001		
<i>Oit</i>	-	-	-	-	-	-	<0,001		
<i>App</i>	-	-	-	-	-	-	-		
<b>August 2012</b>	<i>Cal</i>	<i>Pse</i>	<i>Msn</i>	<i>Oit</i>	<i>Rat</i>	<i>Plu</i>	<i>App</i>	<i>Aca</i>	<i>Cha</i>
<i>Cal</i>	-	<0,001	<0,001	<0,001	<0,001	n.s.	<0,05	<0,05	n.s.
<i>Pse</i>	-	-	<0,001	<0,001	<0,001	<0,001	<0,001	<0,001	<0,001
<i>Msn</i>	-	-	-	<0,001	<0,001	<0,001	<0,001	<0,001	<0,001
<i>Oit</i>	-	-	-	-	n.s.	n.s.	n.s.	<0,05	n.s.
<i>Rat</i>	-	-	-	-	-	n.s.	n.s.	<0,05	<0,05
<i>Plu</i>	-	-	-	-	-	-	n.s.	n.s.	n.s.
<i>App</i>	-	-	-	-	-	-	-	n.s.	n.s.
<i>Aca</i>	-	-	-	-	-	-	-	-	n.s.
<i>Cha</i>	-	-	-	-	-	-	-	-	-
<b>November 2014</b>	<i>Cal</i>	<i>Pse</i>	<i>Aca</i>	<i>Msn</i>	<i>Cha</i>	<i>Kri</i>	<i>App</i>		
<i>Cal</i>	-	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.		
<i>Pse</i>	-	-	n.s.	n.s.	n.s.	n.s.	n.s.		
<i>Aca</i>	-	-	-	n.s.	n.s.	n.s.	n.s.		
<i>Msn</i>	-	-	-	-	n.s.	n.s.	n.s.		
<i>Cha</i>	-	-	-	-	-	n.s.	n.s.		
<i>Kri</i>	-	-	-	-	-	-	n.s.		
<i>App</i>	-	-	-	-	-	-	-		

## 4. Discussion.

Seasonal and diel vertical migration is important for the survival of zooplankton in high latitudes. The strong seasonality in the arctic produces a lack of food resources important for herbivorous species, which are adapted to overwinter in the absence of food. Also, zooplankton performs diel migrations to survive against predation when accessing to food resources. In this thesis, we will discuss possible differences in vertical distributions and the importance of predators on the diel and seasonal distribution of prey zooplankton species, discussing the results observed using the VPR and nets on vertical distributions and prey and predator distributions.

### 4.1. Vertical distributions.

#### a) Diel vertical distribution in Billefjorden, Svalbard.

Diel Vertical Migration was observed, with some variability between the identified species. This study was carried out during the 4<sup>th</sup> to 5<sup>th</sup> of October, when the dark period increases in time every day, but there is still a long period of light. At the time of our study, Chl *a* started to be low and zooplankton ceased to perform DVM, because of low concentration of food at the surface. The avoidance of surface water by zooplankton was observed, with most of the organisms being below 30 m during the light time. It was observed a wide range of depth distributions for the different species below this upper zone. *Calanus* spp. was the most abundant copepod, which displayed a clear DVM, observed during night at the peak of phytoplankton (4 m). Chaetognaths and euphausiids were observed below 10 m depth. This avoidance of the surface can reduce the risk of visual predation but consequently it aways them from the areas with higher phytoplankton concentrations.

*Calanus* spp. vertical distribution was significantly different throughout all the sampling times. *Calanus* spp. performing DVM was mainly identified in younger stages of development of the two main species (*C. finmarchicus* and *C. glacialis*) but not in adults. The variability between the three *Calanus* species could be explained by other individual states such as gut fullness, energy reserves or other differences in life history strategies (Hays et al. 2001). Large size copepods and other macrozooplankton are more easily detected by visual predators, which being at depth during day offer refuge to *Calanus* species. *C.hiperboreus* and *C. glacialis* generally have a long life span, accumulating reserves of lipids during the phytoplankton bloom to survive the next winter. In addition, they may have sufficient resources, feeding on detritus and marine snow in depth (Hansen et al. 1996). *C. finmarchicus* was the most abundant *Calanus* species in the upper 60 m during light time, that may benefit from risking their life for

feeding, to have high growth. DVM was mainly performed by individuals that still need to build up their reserves of lipids for overwinter.

In the small copepods group a strong DVM was observed for *Pseudocalanus* spp. with the nets. High abundance of Small copepods observed with the nets in contrast to a low abundance with the VPR. The set up of the VPR camera was adjusted to S2, which means that it is useful to capture *Calanus* spp. but not small copepods. Camera should be set up in S1 in order to be able to perform a better investigation of small copepods community. *Pseudocalanus* spp. is an important prey for some predator species. The avoidance of visual predators has been defined as the main cause of DVM in this species (Möller et al. 2013). *Oithona similis* and *Microcalanus* spp. have lower vulnerability to visual predators and are omnivorous species. For this species, food has a more uniform distribution through the water column, which explains the limited DVM (Fortier et al. 2001). In this study, *Oithona similis* showed a uniform vertical distribution with some variability between day and night. DVM was not observed in this species, but *Microcalanus* spp. showed DVM with the nets, avoiding visual predators but also the chaetognaths layers during light period. The VPR underestimated the small copepods abundance and significant different vertical distributions were not observed in Billefjorden during the different sampling times.

Euphausiids were performing DVM and were observed in high abundance and biomass with the nets. Choosing the right depth for the sampling was a problem for this species. Euphausiids are large in size, making them an easy prey for visual predators, but they also have a great swimming capability, allowing them to escape. This makes difficult to study them with nets and VPR. A clear DVM pattern was observed in euphausiids if we compare day and night trawling samples and the different catches seen with the MIK nets. Not significant DVM was observed with the VPR because a low number of individuals were registered, but was possible to see them deeper during day and closer to the surface during night. Smaller individuals were observed in shallow waters and larger individuals in depth, possibly because small individuals have to feed on phytoplankton to grow fast and large individuals survive only with detritus found in depth. Euphausiids are known to perform DVM in other areas (Tarling et al. 1999, Liljebladh & Thomasson 2001).

There was not a significant difference in the vertical distribution of Chaetognaths between day and night, but a weak DVM between surface to 70 m during day and 30 to 110 m during night was observed. Surface water was clearly avoided during light hours. The average size of chaetognaths is between 24 mm and 30 mm. The observed vertical distribution can be

explained comparing the sizes obtained in this study with the October sizes in the table 1 and fig 5 (Grigor et al. 2014). Sizes are similar to the ones found in cohort 1, showing that there were mainly young stages in our study. In other studies younger stages of chaetognaths are always above older stages (Samemoto 1987). The weak DVM can be explained by young stages of chaetognaths that still need to build up reserves for the winter, feeding on small copepods. Older stages can feed on larger copepods found at depth.

#### **b) Seasonal distribution in Porsangerfjord in northern Norway.**

Differences were observed in the plankton community from offshore regions towards the inner part of Porsangerfjord system, being *C. finmarchicus* the dominant specie in the offshore region, whereas small copepods dominated in the inner part. Hydrography in Porsangerfjord is different than in other fjords in Northern Norway. AW affects all outer and coastal stations in the fjords in Northern Norway, but only the inner part of Porsangerfjord and Altafjord are not affected. Temperature in Porsangerfjord is lower than in all other fjords, and it has the narrowest salinity range (Mankettikkara 2013). Bottom water temperatures are ca. 3 °C warmer in the middle part than in the inner part, where temperatures can go below 0 °C in winter. Our study suggests a separation between the inner part and the middle and outer part of the fjord, which affects the species compositions.

In Porsangerfjord the most abundant zooplankton group was composed of copepods. Clear differences in seasonal abundance, vertical distribution and age structure of some of the species were observed. Copepods stayed in depth during winter and in shallow waters during spring and summer. The presence of copepods in March in the entire water column and not at depth in the inner and middle part of the fjord may be because no stratification of the water column. *C. finmarchicus*, *Pseudocalanus* spp., *Microsetella* spp. and *Oithona* spp showed a clear seasonal migration pattern. Other copepods and non-copepods were observed in few stations for some of the months, making difficult to see a clear seasonal vertical distribution.

*Calanus* spp. is the dominant copepod in other fjords of Northern Norway and has one year life cycle (Hopkins 1981, Tande 1982). The low abundances in the inner part of the fjord in winter might be explained by the preference of this species for deeper basins to overwinter. It also accumulates large amount of energy rich compounds during the phytoplankton bloom to survive during winter (between September and April) and mature to adult stages (January to April) (Tande 1982). Mainly copepodites stages CIV, CV and adults were found in March in all the stations, with the exception of Østerbotn, where copepodites stages from CII to adults were observed. Copepodites CII and CIII are not expect to be found overwintering in the fjords,

because they are not able to store lipids. They need to moult to copepodite stages CIV and CV before the winter to be prepared at the end of winter to moult into adults and spawn. This finding can suggest that these copepodites are feeding on other food sources during winter.

A strong seasonal migration of *C. finmarchicus* was also observed in this study. The CTD profiles shown the beginning of the spring bloom in April, which is more intense in May following an increase of the stratification at the surface, due to the rise of temperature of the water at all the stations in Porsangerfjord. The spawning of this species in the Northern Norwegian fjords is in April and it is linked to the phytoplankton bloom (Vinogradov 1997). Nauplii were observed in the entire water column with nets and VPR in early April in the middle part of the fjord and at the surface in May along Porsangerfjord where the highest concentrations of phytoplankton were found. In May, mostly young copepodite stages were observed demonstrating the connection between the phytoplankton bloom and the reproductive period of *C. finmarchicus*. The station sample from August 2012 showed *C. finmarchicus* at different depths. A possible explanation of this may be the presence of gelatinous organisms and possibly fish at the surface. In November, no phytoplankton was observed in the entire water column and *C. finmarchicus* had already descended to depth to overwinter in a state of dormancy (Heath et al. 2004). During this time they survived with the large lipid reserves accumulated during summer (Hagen & H. 2001). *C. finmarchicus* performed the same seasonal vertical distribution observed along other fjords in Northern Norway, but with a special difference in Østerbotn, where almost all *C. finmarchicus* migrated outside to deeper basins in the middle or outer part of the fjord to overwinter.

Small copepods performed seasonal vertical distribution but their overwintering period starts later than *C. finmarchicus*. They are an important part of the Porsangerfjord ecosystem, being more abundant in the inner part of the fjord throughout the year. Small copepods generally have higher growth rates than larger copepods (Banse 1982), and they can play an important role in the food web after *Calanus* spp. leave the upper layers of the water column in summer (Svensen et al. 2011). Small copepods have the same seasonal migration as *C. finmarchicus* and aggregate in higher concentrations than larger copepods at the end of the summer or early autumn. The use of an 180µm mesh size net underestimated the amount of small copepods (Nielsen & Andersen 2002) in April and May 2014 in our study. It is also important to mention that vertical distribution of *Microsetella* spp. was always below the pycnocline. Using the VPR, *Microsetella* spp. often showed a strong co-occurrence with layers of marine snow (obs. Fredrika Norbinn). Small copepods have a limited room for lipids storage, which are used for maturation and not for gonad maturation, but it has been shown that they are not strictly

herbivorous as *C. finmarchicus* and may feed on other sources during winter (Norrbin et al. 1990). Small copepods were observed in higher abundances in fall when higher abundances of *C. finmarchicus* were observed at depth because it has started the overwinter period.

The seasonal migration was possible to be observed in euphausiids, because larval stages were observed at the surface in May and adults at depth in other months. Euphausiids were found in low abundances during the entire study because of their swimming capability that allowed them to escape from the VPR. The reproductive season is between spring and summer for the northern sites (Cuzinroudy et al. 2004), which is in accordance of the observations in this study. High concentrations of nauplii and calyptopis larvae were observed at the surface in Porsangerfjord in May. This period was related to the phytoplankton bloom, which is the same than in other studies in the Barents Sea (Skjoldal & Dalpadado 1991, 1996). In November, euphausiids were at depth in Østerbotn and the West side, but in the East side different distribution was observed with euphausiids between 70 - 110 m in Midtre Øst and 40 – 80 m in Ytre Øst. The difference in depth distribution during November cannot be explain by DVM since time of sampling was relatively close between East and West sides, but possibly by location of food and upwellings in the East side due to wind stress and formation of eddies (Myksvoll et al. 2012). Previous studies showed that euphausiids can feed on detritus in the deeper basins and in copepods in the innermost part of the fjord in winter (Baliño & Aksnes 1993). Euphausiids showed a seasonal migration to the surface during the reproductive season in spring and summer and at depth during winter when phytoplankton is not available and feed in other sources.

The seasonal distribution of chaetognaths was related to the highest concentrations of copepods. Larger chaetognaths were observed in March and April, while smaller chaetognaths in May and November. This finding suggest that chaetognaths reproduce in late spring and summer in Porsangerfjord and new generations grow in size later in the season following the peak of small copepods concentrations. Previous studies in the Arctic showed a life span of over one (Samemoto 1987, Søreide et al. 2010), same findings were observed in Porsangerfjord. *Parasagitta elegans* was the main species observed during all the season, but in November *Eukrohnia hamata* was observed at the outer and middle part of the fjord. *Parasagitta elegans* dominates in shelf seas, whereas *Eukrohnia hamata* may be more common offshore (Kosobokova et al. 2010). Seasonal vertical distribution of chaetognats is dependent on size class age and distribution of their prey.

Gelatinous organisms were observed at the surface in August and in depth in the other months of sampling. It was not possible to identify a seasonal distribution on gelatinous organisms in

Porsangerfjord due to the low abundances observed during 2014. But other studies showed seasonal migrations on Northern Norway fjords. Two species of ctenophores (*Bolinopsis infundibulum* and *Beroe cucumis*) have shown different seasonal migration in Malangenfjord with reproduction in surface layers in summer/fall and overwintering in depth in winter (Falkenhaus 1996). The results of this study also suggested higher abundances at the surface layers during the reproductive season in summer and low abundance overwintering population at depth.

#### **4.2. Prey distributions related to predators.**

Different distributions between predators and prey could only be observed on a few occasions in this data set. In Billefjorden in October and in the inner and outer part of Porsangerfjord, it was possible to have enough observations to allow me to compare predator-prey distributions with statistical methods for all the stations. A clear different vertical distribution was observed between some of the species in October 2014 in Billefjorden and August 2012 in Porsangerfjord, when more predators are present in higher concentrations into the water column.

Significant different *Calanus* spp. distributions were observed in both fjords. In Porsangerfjord, *C. finmarchicus* was avoiding the layer with highest concentrations of gelatinous organisms during day in Østerbotn but not during night in Porsangnes Vest. The different vertical distribution of *C. finmarchicus* might not be because of avoidance to gelatinous organisms and possibly because of the presence of visual predators in the surface layers. Similar results were observed in Billefjorden, where calanoid copepods performed DVM to avoid the surface water possibly because presence of visual predators. VPR is not suitable to study vertical distributions of fish because of their size and swimming capability. The avoidance of the surface layer, where visual predators use to be, is clearly shown in this study for *Calanus* spp.

Euphausiids have an important role in the marine food web, being the link for transfer primary production to higher trophic levels (Falk-Petersen 2000). Euphausiids were only observed at the surface in larval stages in the layer with highest concentration of phytoplankton. During fall and winter were observed below 40 m at the time of sampling possibly avoiding fish or other visual predators. Euphausiids are prey for many commercial fish species such as cod, capelin, and herring, and for many sea birds and whales. The avoidance of layers usually occupied by visual predators may decrease the predation of euphausiids, with only larval stages seen at the surface because need to feed on rich compounds to grow fast.



Gelatinous organisms are known to be one of the main predators of zooplankton. Very little is known about gelatinous organisms compared with chaetognats and euphausiids. Ctenophores and hydromedusae (*Rathkea octopunctata*) were observed in high concentrations in August 2012 in Porsangerfjord, but in low concentrations throughout 2014 at all the stations on the months of sampling. Also, it was not possible to have an overview of the vertical distribution of the gelatinous organisms in Billefjorden with the VPR.

In August 2012, highest concentrations of gelatinous organisms were observed in the surface layers in Porsangerfjord. The distributions of gelatinous zooplankton are related to physical water properties (Siferdl & Conover 1992). But it is also known that *M. ovum* can descend in the winter (Siferdl & Conover 1992), suggesting that they can continue consuming *Calanus* spp. throughout the year (Purcell et al. 2010). The same is observed in Porsangerfjord, where some gelatinous organisms were observed at depths where *C. finmarchicus* were in November. Ctenophores and hydromedusae are abundant in arctic waters (Stepanjants 1989) and feed on a wide variety of prey, mostly mesozooplankton, but also feed in ichthyoplankton, microzooplankton, and other gelatinous species such as appendicularians (Purcell 2003). In this study almost nothing is known on the seasonal distribution of the gelatinous organisms and how it affects the prey populations in Porsangerfjord. *Rathkea octopunctata* was the main hydromedusae observed in August 2012 in Porsangerfjord and was concentrated in a few meters layer close to the surface due to density gradients. In other parts of Northern Norway, this species rapidly produces new generations, and high concentrations can be observed between spring and early fall with a pelagic medusae stage, and not observed the rest of the year because a benthic polyp stage (Jacobsen & Norrbin 2009). Other studies in Northern Norway fjords (Malangen) shown that the predatory impact in summer of two ctenophore species is increased (from 6% to 50%) (Falkenhaug 1996). In August 2012, small copepods and appendicularians seems to be the main source of food for gelatinous organisms in Østerbotn, while in Porsangnes Vest they could have been feeding on *C. finmarchicus* and small copepods.

Chaetognaths, specifically *Parasagitta elegans*, feed almost exclusively on copepods (Welch et al.). Their primary source of food is small copepods like *Pseudocalanus* spp. and *Oithona similis*, but they also consume balanus nauplii, larval stages of euphausiids, occasionally show cannibalistic behaviour upon smaller individuals and will also eat fish larvae (Alvarez-Cadena 1993). Chaetognats can be a prey of gelatinous organisms and a significant different distribution was observed between these two groups of predators in Porsangerfjord in August 2012. Chaetognats might prefer to avoid the layers with high concentrations of gelatinous organisms mainly to avoid predation and competence for food. Also, the highest concentrations

of *Pseudocalanus* spp. were observed where the highest concentrations of chaetognats were found, with similar vertical distribution between those. In August 2012, chaetognats were observed at the same depth of *Pseudocalanus* spp. with eggs, possibly because nauplii of copepods are the most important food source for new generations of chaetognaths (McLaren 1966). It is also possible that the chaetognaths were just at the depth with the richest food source and not because they tried to avoid gelatinous organisms or visual predators at the surface layers. In Billefjorden, there was a clear avoidance of the surface water during day, possibly avoiding predation by fish. High concentrations of *Oithona similis* were also observed in the entire water column, chaetognaths might feed on them. Young stages of chaetognaths *Parasagitta elegans* and *Eukrohnia hamata* mainly feed on cyclopoid copepods and is also the 47% of the diet of older stages that can be predated as well on CV copepods (Sullivan 1980).

Fish might be the most important predator in Porsangerfjord but it was not possible to show the results on time due to the huge amount of acoustic data recorded with the echosounder. Polar cod might be the most important predator in Billefjorden, Svalbard. In Porsangerfjord, Norwegian coastal cod (*Gadus morhua*) lives all year round in the inner part of the fjord (Berg 2003, Jorde et al. 2007), while herring (*Clupea arengus*), capelin (*Mallotus villosus*) and arctic cod appear seasonally in the outer part (Westgaard & Fevolden 2007). All of them feed on zooplankton of different sizes and can be an important predator, affecting the distributions and populations of plankton. The number of fish has declined in Porsangerfjord since the 1970's because of fishing pressure and an increased number of sea urchins. Sea urchins graze heavily upon the kelp forest (Norderhaug & Christie 2009), which is an important feeding and nursery habitat for juvenile fish.. Pluteus larvae were observed with the VPR along Porsangerfjord with higher abundances offshore, which means that sea urchins are present in the benthic environment and may be affecting kelp forest. King crab has been introduced and has succeeded to establish in Porsangerfjord. This decapod has an omnivore diet, mainly feeding on benthic organisms, reducing their populations (Falk-Petersen et al. 2011). Nowadays, a group of scientists are studying the effects of King crab on sea urchins populations and if kelp forest is recovering (SunnSet 2008) . This year, a decrease in the amount of zooplankton was observed compared with other years, which can mean that fish is recovering.

## **5. Conclusions**

Vertical distributions of herbivorous zooplankton were correlated to seasonality of food resources. Seasonal vertical migration was observed for all zooplankton species.

In spring, herbivorous zooplankton are observed at layers with high concentrations of phytoplankton and only in summer and fall, a change on the vertical distribution is related to predators. Summer and fall are the periods when more predators are observed in the water and calanoid copepods were performing DVM. Other small zooplankton with a more omnivorous diet, were not performing any change on the vertical distribution related to predators. Invertebrate predators have the same distribution as copepods in periods of time when resources for herbivorous are scarce.

Vertical distributions of *Calanus* spp. and chaetognats were well represented with the VPR, but small copepods and euphausiids were underestimated. Further research has to be done to study fish and euphausiid populations. The acoustic data recorded will give further details on euphausiid and fish distributions not seen with the VPR, being an important input into this study. Also, further investigations have to be done on marine snow and fecopellets observed with the VPR, which are important sources of food when phytoplankton become limited and can be important for the vertical distribution of omnivorous zooplankton.

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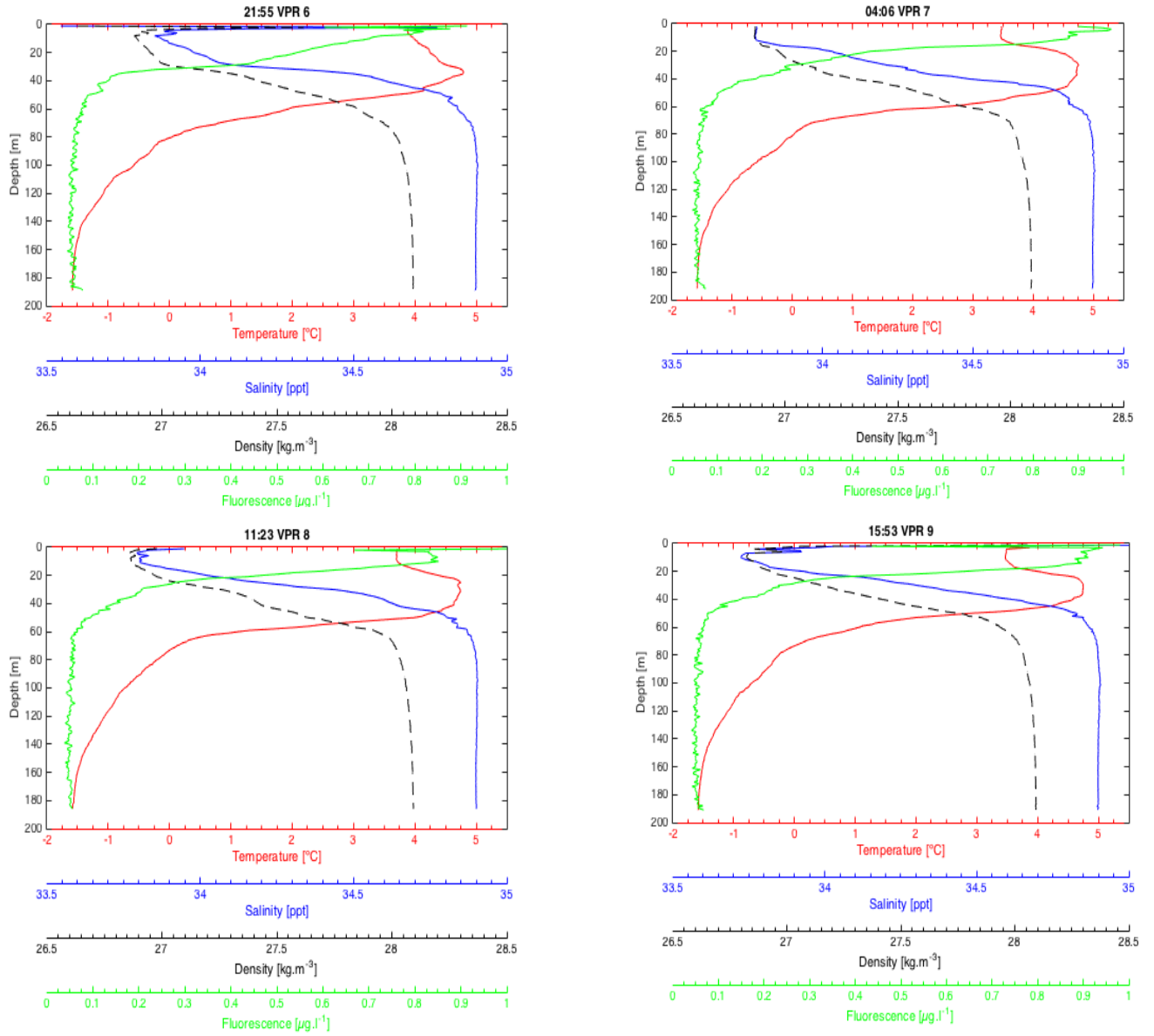
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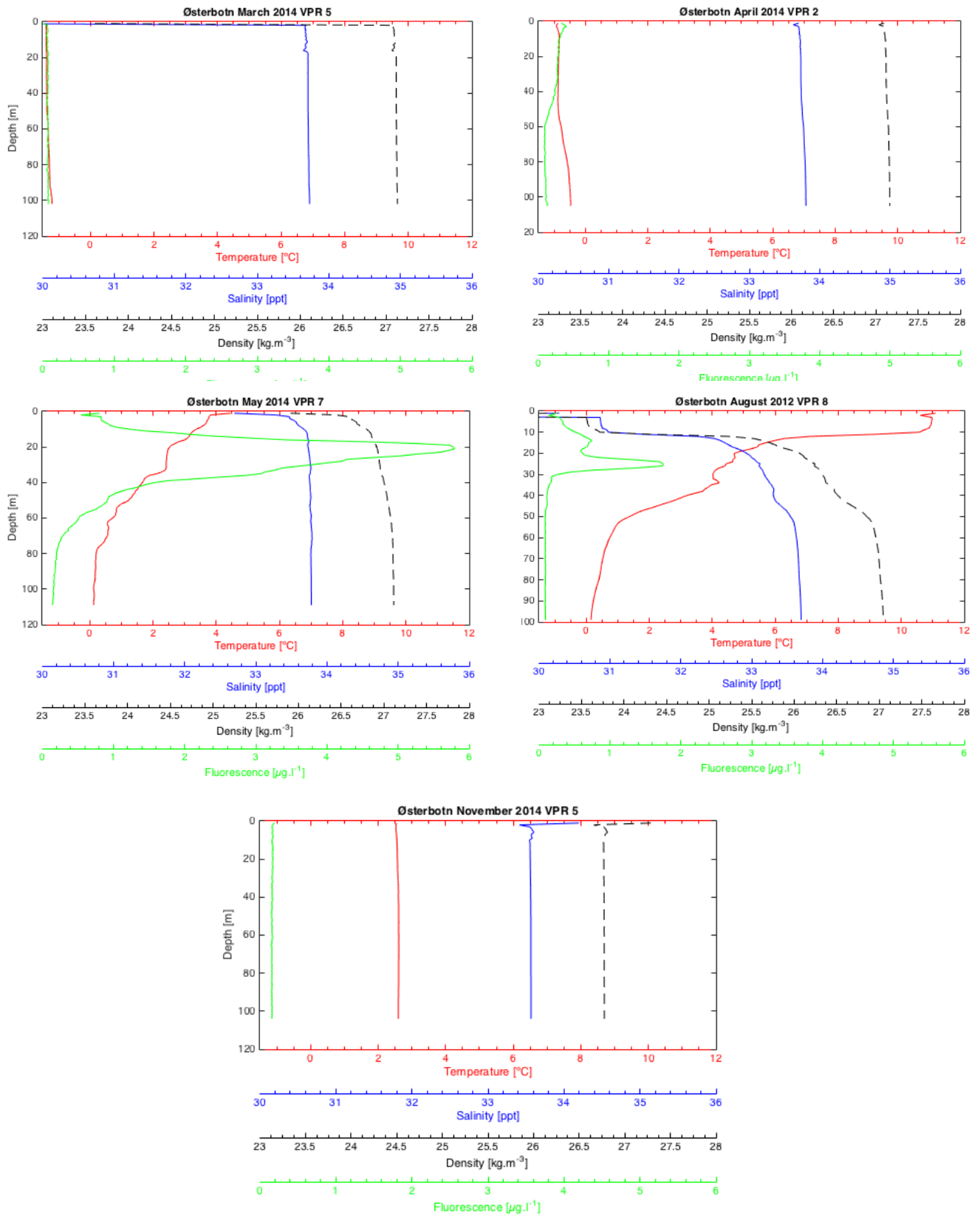
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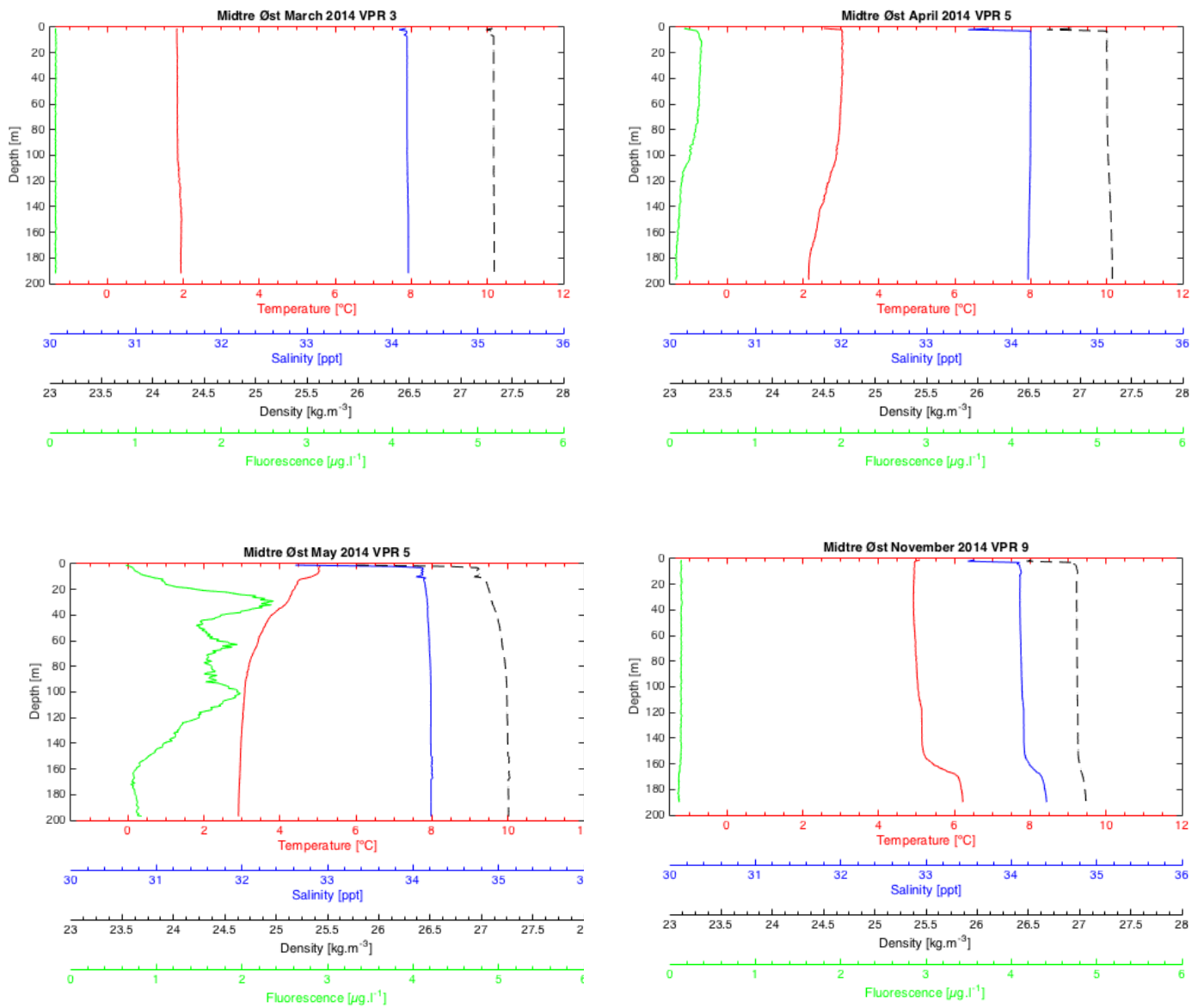
# Appendix I: Hydrography.



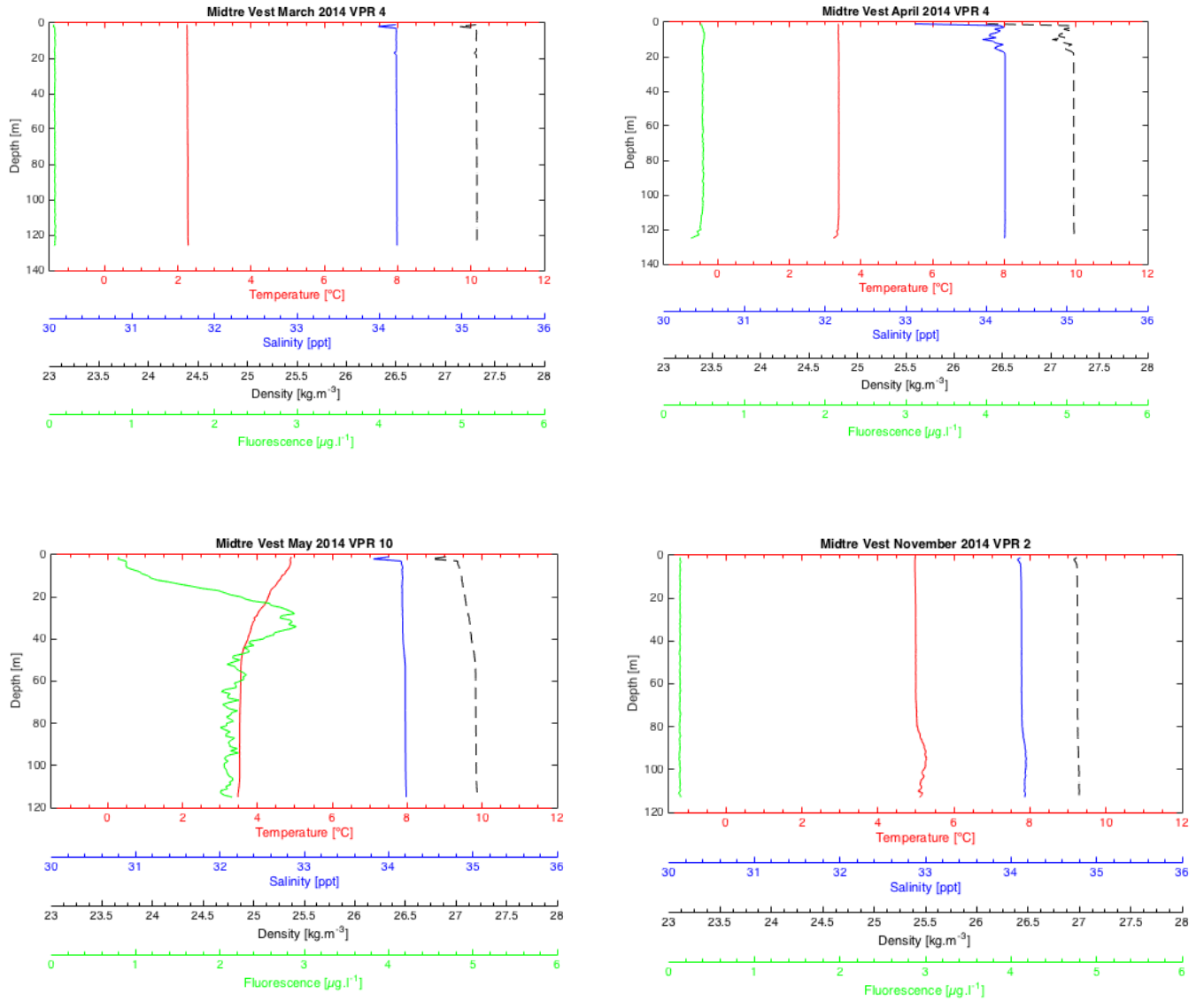
**Figure 1** Billefjorden CTD profiles for vpr6, vpr7, vpr8 and vpr9.



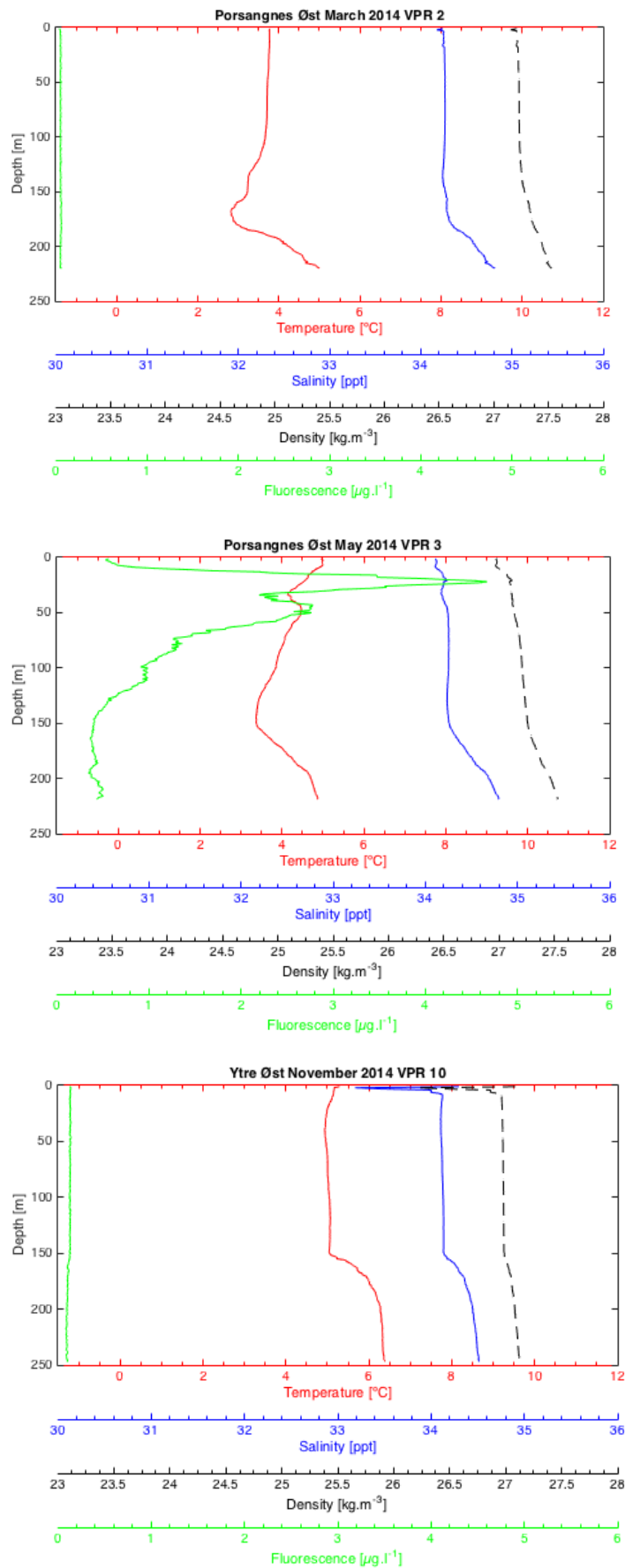
**Figure 2** Porsangerfjord CTD profiles for March, April, May, November 2014 and August 2012 in Østerbotn .



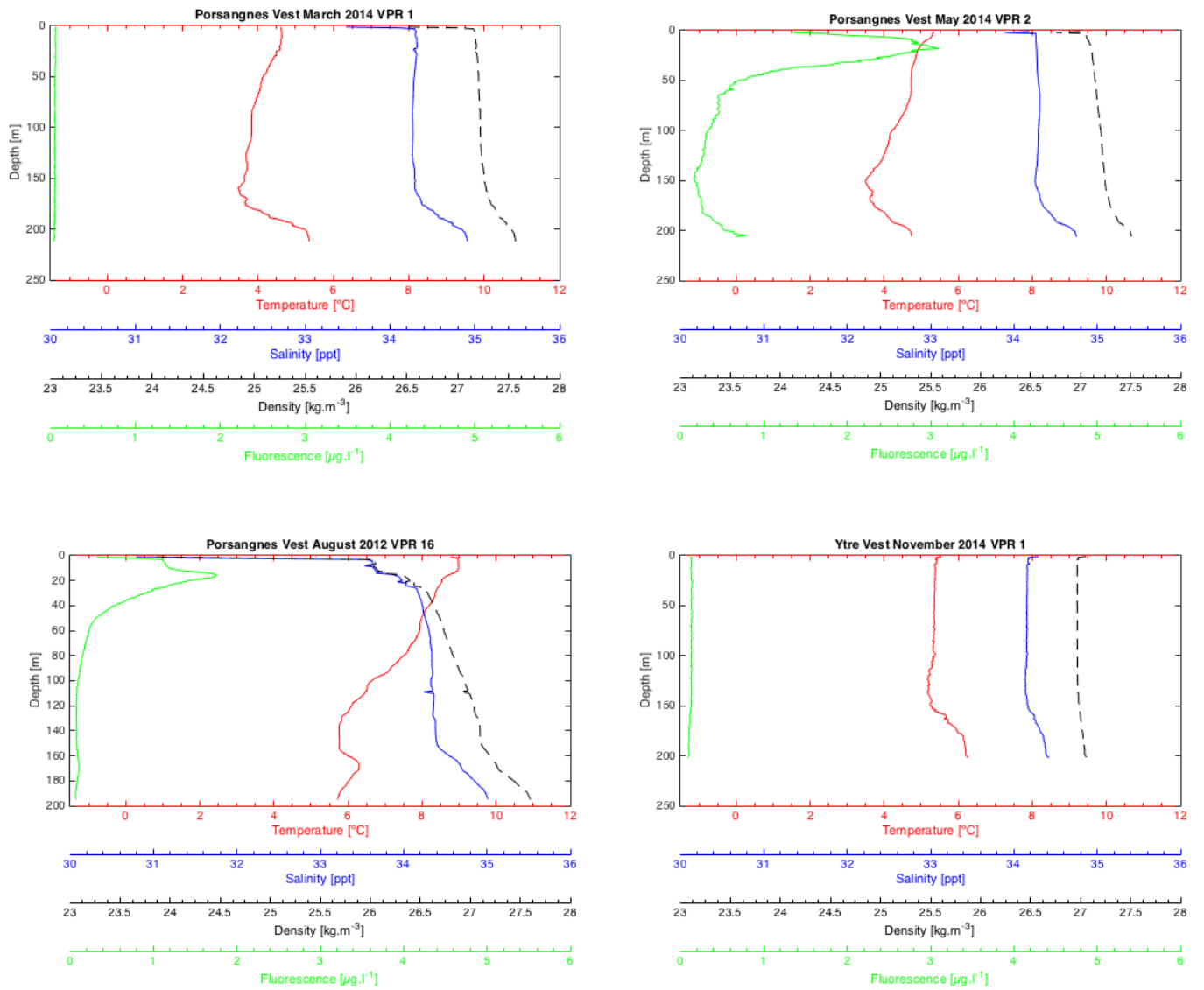
**Figure 3** Porsangerfjord CTD profiles for March, April, May, November 2014 in Midtre Øst .



**Figure 4** Porsangerfjord CTD profiles for March, April, May, November 2014 in Midtre Vest.



**Figure 5** Porsangerfjord CTD profiles for March, May, November 2014 in the outer east.



**Figure 6** Porsangerfjord CTD profiles for March, May, November 2014 and August 2012 in the outer west .



## Appendix II: Zooplankton nets, Billefjorden.

Table 1 Billefjorden diel abundance at different depths of the zooplankton groups observed with the MPS.

Abundance (ind. · m <sup>-3</sup> )	04.10.2014 21:28 (UTC)				05.10.2014 09:18 (UTC)			
	0-30 m	30-60 m	60-100 m	100-182 m	0-30 m	30-60 m	60-100 m	100-182 m
<b>Calanoida</b>								
<i>Calanus finmarchicus</i>	102,2	40,0	96,7	146,3	48,9	44,4	106,3	331,7
<i>Calanus glacialis</i>	71,1	44,4	270,0	686,2	17,8	48,9	337,5	663,4
<i>Calanus hyperboreus</i>			6,7	13,0				19,5
<i>Pseudocalanus spp.</i>	293,3	213,3	176,7	224,4	40,0	288,9	368,8	227,6
<i>Microcalanus spp.</i>	66,7	57,8	106,7	188,6	17,8	57,8	125,0	211,4
<i>Metridia longa</i>	4,4	8,9		16,3		4,4	18,8	16,3
<i>Acartia longiremis</i>			6,7	9,8			6,3	3,3
<b>Cyclopoida</b>								
<i>Oithona similis</i>	5000,0	1128,9	743,3	315,4	3595,6	1502,2	906,3	292,7
<i>Oithona atlantica</i>	151,1		10,0	9,8	102,2	22,2	0,0	3,3
<i>Triconia borealis</i>		13,3	10,0	87,8	8,9	13,3	25,0	74,8
<b>Harpacticoida</b>								
<i>Bradyidius similis</i>		22,2		9,8				3,3
<b>Nauplii</b>								
Copepod						8,9		6,5
Euphausiid				3,3				6,5
Rhizocephala		8,9		0,0		13,3		
Bopyridae larvae				3,3				
<b>Opisthobranchia</b>								
<i>Limacina helicina</i>	22,2		6,7	35,8	4,4	4,4		6,5
<b>Larvacea</b>								
<i>Fritillaria borealis</i>					4,4			
<i>Oikopleura spp.</i>					4,4			
<b>Echinodermata</b>								
Ophiopluteus	8,9				22,2			
Echinopluteus	13,3							
<b>Euphausiacea</b>								
<i>Thysanoessa inermis</i>		0,5	0,6	0,7				0,1
<b>Amphipoda</b>								
<i>Themisto libellula</i>			0,2					
<i>Themisto abyssorum</i>		0,1						
<b>Chaetognata</b>								
<i>Parasagitta elegans</i>	3,6	2,1	1,7	0,7	2,4	3,6	3,5	0,5
<i>Eukrohnia hamata</i>		0,3				0,3		
<b>Medusae</b>								
<i>Aglantha digitale</i>			0,3				0,2	0,1
<b>Bivalvia (veliger)</b>								
		4,4	3,3		8,9	4,4		
<b>Unidentified egg</b>								
	4,4	4,4				4,4		
<b>TOTAL:</b>	5741	1550	1439	1751	3878	2022	1897	1867

**Table 6** Billefjorden diel total abundance at different depths of the zooplankton groups observed with the MIK.

	Depth (m)	total abundance / m <sup>3</sup>	total biomass / m <sup>3</sup>
Midnight	40	16,164	1077,336
	60	14,563	1106,488
	120	19,483	2799,805
Morning	40	7,136	359,489
	60	10,491	891,867
	120	12,490	2453,001
Midday	40	18,387	774,322
	60	7,987	361,258
	120	13,163	1657,042
Evening	40	13,659	513,301
	60	11,971	668,438
	120	5,814	1225,153

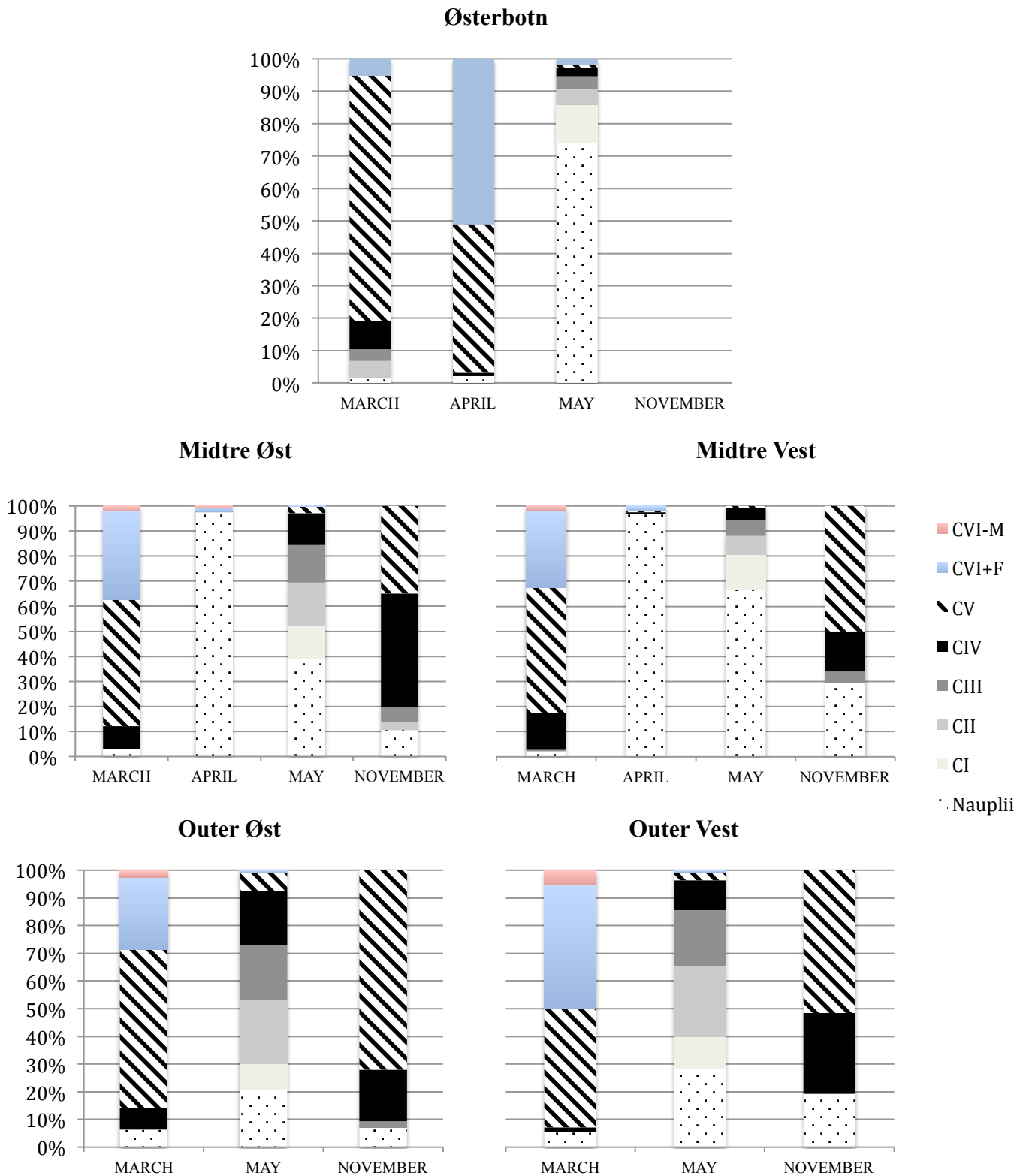
# APPENDIX III. Zooplankton nets, Porsangerfjord.

**Table 1** Porsangerfjord species abundance (ind. · m<sup>-3</sup>) in March and April 2014 using the WP-2 nets.

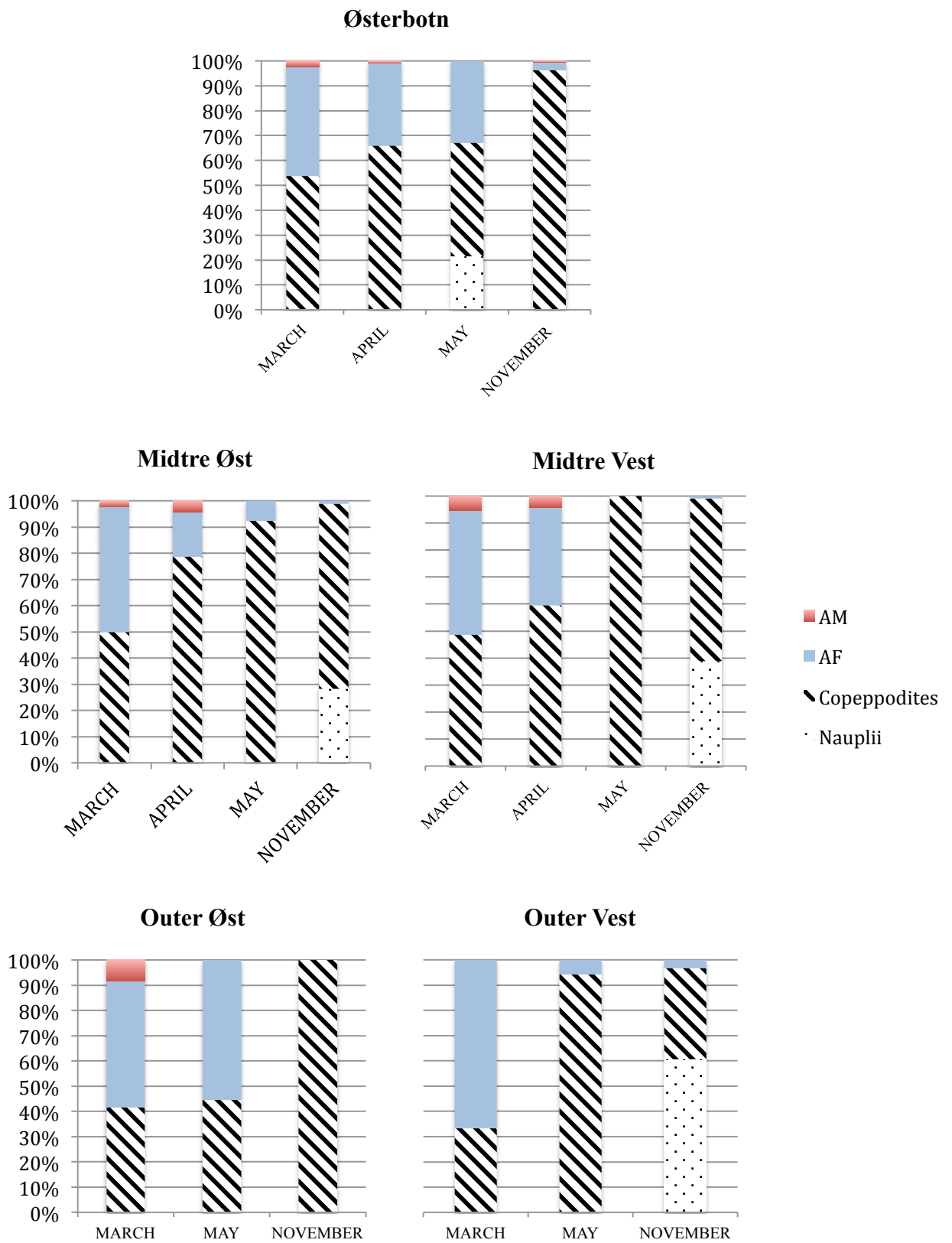
TAXON	MARCH				APRIL			
	Østerbotn	Midtre Vest	Midtre Øst	Outer Vest	Outer Øst	Østerbotn	Midtre Vest	Midtre Øst
<b>Calanoida</b>								
<i>Calanus finmarchicus</i>	128,06	31,35	12,91	1,06	10,69	73,96	1,41	1,76
<i>Calanus hyperboreus</i>								
<i>Pseudocalanus</i> spp.	534,84	6,52	1,78	0,12	0,89	587,92	6,64	9,19
<i>Microcalanus</i> spp.	24,75	21,13	6,90	0,40	6,83	42,26	18,08	32,05
<i>Metridia longa</i>		0,88	1,35	0,06	0,56	1,51		0,78
<i>Acartia longiremis</i>	47,35	1,06	0,47		0,11	2,26		1,17
<i>Euchaeta norvegica</i>		0,35						
<b>Cyclopoida</b>								
<i>Oithona similis</i>	40,89	63,75	9,82	0,38	7,61	92,08	29,10	9,58
<i>Oithona atlantica</i>	4,30	12,68	5,25	0,18	3,97	5,28	3,67	10,94
<i>Triconia borealis</i>								
<b>Harpacticoida</b>								
<i>Uld.</i>	1,08							
<i>Microsetella</i>	72,10	14,27	7,62	2,16	11,51	10,57	2,26	1,76
<b>Uld. Copepods</b>								
<b>Calanus Nauplii</b>	2,15	0,70	0,38	0,06	0,71	1,51	42,80	67,82
<b>Pseudocalanus Nauplii</b>								
<i>Limacina retroversa</i>						0,75		
<i>Limacina helicina</i>			0,08					
<b>Larvacea</b>								
<i>Fritillaria borealis</i>							0,71	0,39
<i>Oikopleura</i> spp.						0,75	1,69	
<b>Echinodermata</b>								
<b>Euphausiacea</b>								
<i>Nauplii</i>								
<i>Calyptopsis</i>								
<i>Thysanoessa inermis</i>								
<i>Thysanoessa longicaudata</i>	0,15							
<i>Thysanoessa raschii</i>	0,04		0,04			0,08		
<i>Meganocyttiphanes norvegica</i>								
<b>Megalopa</b>								
<i>Nauplii</i>								
<i>Zoea</i>								
<i>Swirmp</i>								
<b>Amphipoda</b>								
<i>Uld.</i>	0,08							
<i>Themisto abyssorum</i>								
<b>Chaetognata</b>								
<i>Parasagitta elegans</i>	1,90	0,30	0,06		0,04	1,80	0,17	0,10
<i>Parasagitta setosa</i>								
<i>Eukrohnia hamata</i>								
<b>Medusae</b>								
<i>Rathkea</i>				0,06	0,15	3,02	0,56	0,20
<i>Uld.</i>								
<b>Ctenophora</b>								
<i>Beroe cucumis</i>								
<b>Bivalvia (velliger)</b>								
<i>Polychaeta</i>	2,15	0,35	0,04					
<i>Spionidae</i>								
<i>Trachophorae</i>								
<b>Cirripedia</b>								
<b>Radiolarians</b>								
<b>Tintinids</b>	11,84	0,18			0,04		0,28	2,54
<b>Unidentified egg</b>								

**Table 2** Porsangerfjord species abundance (ind. · m<sup>-3</sup>) in May and November 2014, using the WP-2 nets

TAXON	MAY				NOVEMBER						
	Østerbotn	Midtre Vest	Midtre Øst	Porsanges Vest	Porsanges Øst	Østerbotn	Midtre Vest	Midtre Øst	Ytre Vest	Ytre Øst	
<b>Calanoida</b>											
<i>Calanus finmarchicus</i>	12,55	380,59		515,61	92,37	122,98	0,00	95,53	108,11	84,75	111,60
<i>Calanus hyperboreus</i>	0,22										
<i>Pseudocalanus spp.</i>	75,28	7,70		23,19	14,41	3,55	2135,59	218,80	120,93	81,36	47,43
<i>Microcalanus spp.</i>	18,82	4,62		26,76	8,90	2,76	3650,85	154,08	148,42	162,71	147,87
<i>Metridia longa</i>	0,22			0,85	0,85	0,39		6,16	7,33	10,17	13,95
<i>Acartia longiremis</i>	0,22			0,42	0,42			91,53	9,24	3,66	2,79
<i>Euchaeta norvegica</i>								3,08			
<b>Cyclopoida</b>											
<i>Oithona similis</i>	46,51	24,65		87,42	33,05	19,31	905,08	918,34	604,67	600,00	457,56
<i>Oithona atlantica</i>	1,51	4,62		19,63	6,36	0,79	30,51	30,82	12,83	37,29	11,16
<i>Trichonia borealis</i>	0,22										
<b>Harpacticoida</b>											
<i>Uld.</i>											
<i>Microsetella</i>	5,19						21111,86	1075,50	938,16	2481,36	2142,71
<b>Uld. Copepods</b>											
<i>Calanus Nauplii</i>	35,91	765,79		331,85	36,44	31,93		40,06	12,83	20,34	8,37
<i>Pseudocalanus Nauplii</i>	20,55							138,67	47,64	125,42	
<b>Opisthobranchia</b>											
<i>Limacina retroversa</i>	0,65				0,42			3,08			
<i>Limacina helicina</i>											
<b>Larvacea</b>											
<i>Fritillaria borealis</i>	23,15	9,24		28,55	0,85	0,39		3,08	3,66		
<i>Oikopleura spp.</i>	6,27			21,41		5,52		40,06	5,50	10,17	2,79
<b>Echinodermata</b>	1,95	4,62		5,35	4,66				1,83		
<b>Euphausiacea</b>											
<i>Nauplii</i>	6,27	15,41		21,41	4,66	5,52		0,04	0,02	0,08	0,08
<i>Calyptopis</i>		7,70		26,76		1,97		0,11	0,15	0,08	0,03
<i>Thysanoessa inermis</i>								0,04	0,02		
<i>Thysanoessa longicaudata</i>								0,04	0,15		
<i>Thysanoessa raschii</i>						0,02		0,04	0,23		
<i>Meganctiphanes norvegica</i>								0,04			
<b>Megalopa</b>											
<i>Nauplii</i>				0,02							
<i>Zoea</i>				0,02							
<i>Swrimp</i>				5,35	2,54						
<b>Amphipoda</b>											
<i>Uld.</i>											
<i>Themisto abyssorum</i>								0,28			
<b>Chaetognata</b>											
<i>Parasagitta elegans</i>	0,65	0,18		0,04				0,04	0,02		0,02
<i>Parasagitta setosa</i>											
<i>Eukrohnia hamata</i>											
<b>Medusae</b>											
<i>Rathikea</i>					0,02			0,47	0,91		0,59
<i>Uld.</i>	1,73										
<b>Ctenophora</b>											
<i>Beroe cucumis</i>											
<b>Bivalvia (veliger)</b>											
<b>Polychaeta</b>											
<i>Spionidae</i>	1,73	1,54		5,35	1,69	0,39	10,17		3,66		5,58
<i>Trachophorae</i>	0,22	4,62									
<b>Cirripedia</b>	1,73	1,54		10,70							
<b>Radiolarians</b>											
<b>Tintinids</b>											
<b>Unidentified egg</b>	20,98			1,78	1,69	3,55			1,83	10,17	3,39



**Figure 1** Porsangerfjord seasonal developmental stages of *C. Finmarchicus* for all the stations



**Figure 2** Porsangerfjord seasonal developmental stages of *Pseudocalanus* spp. for all the stations.

## APPENDIX IV. Statistical results

**Table 1** Statistical results comparing diel vertical distributions of *Calanus* spp., *Pseudocalanus* spp., *Chaetognaths* and euphausiids.

Coparison Midnight/Dawn/Noon/Dusk			
<i>Calanus</i> sp.	Time (UTC)	<b>B</b>	<b>p</b>
Midnight-Noon	21:55 - 11:23	72,7215	<0,001
Dawn-Dusk	04:06 - 15:53	23,0883	<0,001
Midnight-Dawn	21:55 - 04:06	72,3334	<0,001
Noon-Dusk	11:23 - 15:53	15,2868	<0,05
Dawn-Noon	04:06 - 11:23	18,6506	<0,05
Midnight-Dusk	21:55 - 15:53	59,7784	<0,001
<i>Pseudocalanus</i> spp.			
Midnight-Noon	21:55 - 11:23	2,6405	n.s.
Dawn-Dusk	04:06 - 15:53	1,3668	n.s.
Midnight-Dawn	21:55 - 04:06	1,6234	n.s.
Noon-Dusk	11:23 - 15:53	1,7578	n.s.
Dawn-Noon	04:06 - 11:23	3,0341	n.s.
Midnight-Dusk	21:55 - 15:53	2,1118	n.s.
<i>Chaetognaths</i>			
Midnight-Noon	21:55 - 11:23	7,5552	n.s.
Dawn-Dusk	04:06 - 15:53	1,5191	n.s.
Midnight-Dawn	21:55 - 04:06	7,8998	n.s.
Noon-Dusk	11:23 - 15:53	2,2624	n.s.
Dawn-Noon	04:06 - 11:23	4,2771	n.s.
Midnight-Dusk	21:55 - 15:53	4,7082	n.s.
<i>Euphausiids</i>			
Midnight-Noon	21:55 - 11:23	1,0014	n.s.
Dawn-Dusk	04:06 - 15:53	1,9641	n.s.
Midnight-Dawn	21:55 - 04:06	4,3722	n.s.
Noon-Dusk	11:23 - 15:53	4,4403	n.s.
Dawn-Noon	04:06 - 11:23	5,6684	n.s.
Midnight-Dusk	21:55 - 15:53	1,9256	n.s.

**Table 2** Statistics results comparing distributions of *Calanus* spp., *Pseudocalanus* spp., chaetognaths and euphausiids.

Comparison species			
<i>Calanus</i> sp. - <i>Chaetoganaths</i>	Time(UTC)	<b>B</b>	<b>p</b>
Midnight	21:55	67,3491	<0,001
Dawn	4:06	152,2188	<0,001
Noon	11:23	113,1481	<0,001
Dusk	11:53	140,8002	<0,001
<i>Calanus</i> sp. - <i>Pseudocalanus</i> spp.			
Midnight	21:55	72,6177	<0,001
Dawn	4:06	44,8760	<0,001
Noon	11:23	57,2571	<0,001
Dusk	11:53	55,9460	<0,001
<i>Pseudocalanus</i> spp. - <i>Chaetognaths</i>			
Midnight	21:55	0,5865	n.s.
Dawn	4:06	10,5151	0,1<p<0,05
Noon	11:23	4,6890	n.s.
Dusk	11:53	4,1296	n.s.
<i>Calanus</i> sp. - <i>Euphausiids</i>			
Midnight	21:55	94,5853	<0,001
Dawn	4:06	110,8435	<0,001
Noon	11:23	113,1481	<0,001
Dusk	11:53	120,5518	<0,001