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Associations between herbivorous zooplankton, phytoplankton and hydrography in Porsangerfjord, northern Norway

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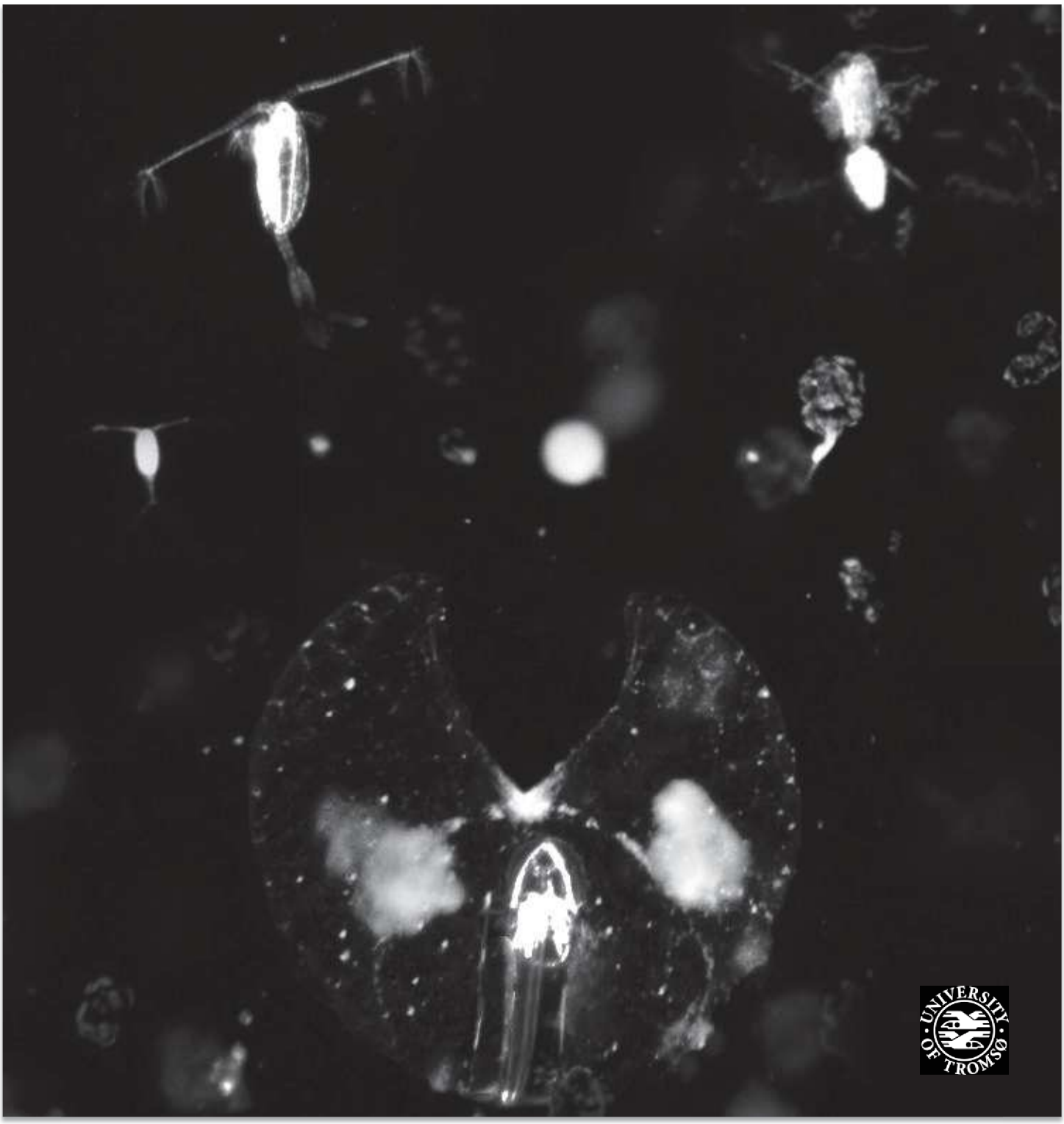

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Contents

Abstract

During three cruises in April, May and November 2014 in Porsangerfjord, northern Norway, the role of hydrography and phytoplankton composition in shaping zooplankton vertical distribution was studied. Simultaneous collection of biological (phytoplankton and zooplankton distribution/abundance) and environmental data (temperature, salinity, density, Chlorophyll *a*) was sampled using a high-resolution autonomous VPR. Phytoplankton species composition was also determined using cell counts. Two stations representing two different hydrographic conditions were sampled, one in the inner part and the other in the outer part of the fjord. The phytoplankton bloom started in May. The outer part was dominated by *Phaeocystis pouchetii* and the inner part by diatoms (*Chaetoceros* spp.). The inner part of the fjord was dominated by small copepods species like *Pseudocalanus* spp., *Microsetella norvegica*, and *Oithona* spp. whereas the outer part was dominated by large copepods like *Calanus finmarchicus*. Zooplankton distribution changed over season, in early bloom they were spread over the water column, during the bloom they were linked to phytoplankton vertical distribution and in the winter situation they were at depths. Hydrography was not the only factor responsible for herbivorous zooplankton distribution. Herbivorous zooplankton was affected by phytoplankton species composition. *C. finmarchicus* and *Pseudocalanus* spp. avoided the dense layer of *P. pouchetii* while *M. norvegica* was observed grazing on *P. pouchetii.* Zooplankton vertical distribution was therefore linked to both abiotic (hydrography) and biotic (phytoplankton composition and distribution) factors which varied in importance throughout the season.

1 Introduction

The patchy distribution of phyto- and zooplankton is well documented, though the exact causes of this patchiness remain unclear (Haury et al. 1978, Mackas et al. 1985). Several water column characteristics, such as hydrography (Gallager et al. 1996) and irradiance (Helbling et al. 1996, Wold & Norrbin 2004), may influence plankton spatial distribution, resulting in a patchy vertical distribution with thin layers of plankton, from a few centimeters to a few meters thick, lying at different depths. Research in the 1990s focused on understanding which processes led to the formation of these layers. Hydrographic features such as density gradients and turbulent diffusion could offer a partial explanation of these layers (Dekshenieks et al. 2001, McManus et al. 2005). The behavior of zooplankton is also an important explanatory factor (Gallager et al. 2004). As such, a knowledge of the fine scale distribution of zooplankton is required to understand why these layers are present.

Traditional methods are unsuitable for studying the fine scale vertical distribution of plankton. They provide essential information of species composition and life stages but disregard the vertical structure of plankton. New techniques of high-resolution sampling, such as the Video Plankton Recorder (VPR), were developed to study the fine scale distribution of plankton (Davis et al. 1992a, Davis et al. 1992b, Gallager et al. 2004). With the VPR, it is possible to observe plankton taxa (large phytoplankton and mesozooplankton) and particulate matter (aggregation of marine snow, fecal pellets) *in situ*, and relate their position to precise hydrography measured by precise instruments attached to the VPR. The quantification of copepods and pteropods from VPR surveys, agrees closely with traditional methods (e.g. MOCNESS) and the non-destructive nature of the VPR leads to better quantification of fragile organisms such as appendicularians (Benfield et al. 1996). Despite the fact that rare organisms are usually underestimated with the VPR because of the small sampling volume (Benfield et al. 1996), it still remains as an effective instrument when it comes to study vertical associations of plankton.

The distribution of plankton of different trophic levels (phytoplankton, herbivorous and carnivorous zooplankton) leads to active habitat selection by herbivorous zooplankton. According to habitat choice theory, herbivorous zooplankton will choose their habitat with regard to resource availability and predation risk (Brown 1998). The value of the resource is predation dependent, a high resource habitat being more risky. Therefore, marine zooplankton needs to find the optimal trade-off between food access and predation risk. For example in May in the Southern Barents Sea, marine zooplankton exhibited a bimodal distribution with large copepods and the predators of small copepods aggregating in the resource-rich, near the surface habitat, and small copepods remaining at depths in a poorer habitat (Fossheim & Primicerio 2008). As several different species are distributed according to the same prevailing conditions (Fager & McGowan 1963), this often results in species associations with different species consistently found together at different times of the year and in different areas (Legendre & Legendre 1978)

Despite their high latitudes, the water properties of northern Norwegian fjords are not truly Arctic, due to comparatively warm, saline water transported along the Norwegian coast by the Norwegian Coastal Current (NCC) (Svendsen 1991, Eilertsen & Skarðhamar 2006, Cottier et al. 2010). In the inner part of the fjords, surface layers are characterized by less saline water due to freshwater discharge from rivers and snow melt (Cottier et al. 2010). Therefore within the fjord, plankton communities face a large range of hydrographic conditions.

Above the Arctic Circle (66°33’38”N), the Polar Night prevails during winter and the Midnight Sun during spring-summer. This extreme light regime induces specific life strategies for both phytoplankton (Ljungfeldt 2001, Degerlund & Eilertsen 2009, Eilertsen & Degerlund 2010) and zooplankton (Norrbin 1994, Dale et al. 1999, Bagøien et al. 2001, Zamora-Terol et al. 2013). Phytoplankton in northern Norway remain in a latent state during winter as bottom-dwelling resting spores (Ljungfeldt 2001). Zooplankton taxa experience a quiet period during winter, some species

enter a dormant state (Norrbin 1994, Dale et al. 1999, Bagøien et al. 2001), while other are simply less active than during the rest of the year (Grønvik & Hopkins 1984, Hopkins et al. 1984).

At high latitudes spring blooms are largely reproducible from year to year with similar species associations and timing (Eilertsen & Degerlund 2010). The succession in the phytoplanktonic assemblage proceeds from small species to larger one in accordance with Margalef's (1958) succession scheme (Degerlund & Eilertsen 2009). Three succession stages are described, starting out with small-celled diatoms, shifting to a mixed community of larger diatoms cells, followed by the last stage dominated by dinoflagellates (Margalef 1958). Over the growing season, this succession of phytoplanktonic species is reflected in the abundance of herbivorous zooplankton (Tande 1982, Grønvik & Hopkins 1984, Lischka & Hagen 2005).

The seasonality of herbivorous zooplankton follows the phytoplanktonic succession. When the spring bloom starts small copepod species react most quickly to end their state of dormancy and migrate upward (Norrbin 1994, Lischka & Hagen 2005). The small and large copepods have a different seasonal importance. Despite the small copepods being early, it takes them time to build up their populations as few individuals survive throughout the winter (Norrbin 1994, Lischka & Hagen 2005, Koski et al. 2013). They peak in late summer and autumn since they are efficient at utilizing less abundant but varied food source (Davis 1987). Large species such as *C. finmarchicus* and *Metridia longa* respond more slowly and terminate their overwintering situation later than the small copepods (Hopkins et al. 1984, Dale et al. 1999, Bagøien et al. 2001). However, these large species feed more efficiently on the spring bloom than smaller species and then retire into diapause in mid-summer (Tande 1982, Hopkins et al. 1984, Davis 1987, Bagøien et al. 2001).

The aim of this study was to describe how vertical distribution of zooplankton was linked to hydrography and to phytoplankton composition during three different situations (pre-bloom, bloom and winter) in a northern Norwegian fjord. Our main hypothesis was that hydrography is the main

factor influencing zooplankton vertical distribution. Our second hypothesis was that with a change in phytoplankton composition, there will be a change in zooplankton vertical distribution. This was made possible by the use of the VPR in Porsangerfjord, northern Norway, in several different environmental and biological conditions.

2 Materials and methods

2.1 Study area and sampling strategy

The data used in this study were collected in connection with a project within the Fjord and Coast Flagship program organized by Fram Centre, Tromsø. The aim of this project is to study the differences in the zooplankton communities between North-Norwegian fjords and Svalbard fjords. The whole sampling plan was part of HMD (Havmiljødata) survey that monitors hydrography along northern Norwegian coast since 1920.

Three cruises were conducted in Porsangerfjord in northern Norway (Figure 1). Porsangerfjord was sampled in April, May, and November of 2014 using R/V *Johan Ruud*. Data from Porsangerfjord was collected at two stations, Østerbotn in the inner basin and Porsangnes Øst in the outer part of fjord (Figure 1, Table 1). However in April it was not possible to collect data in Porsangnes Øst due to bad weather conditions, therefore this study uses Midtre Øst in April instead.

Table 1. Summary of field program.

No.	Station name	Position °N, °E	Basin	Max depth [m]	Cruise
9009	Østerbotn	70.12, 25.18	Inner	110	April, May, November
9006	Midtre Øst	70.51, 25.58	Middle	220	April
9002	Porsangnes Øst	70.87, 26.28	Outer	200	April, May, November

Porsangerfjord is a broad fjord extending from 70°N to 71°N and 25°E to 26°E in a north south direction. Its length is ca 100 km and its width varies from 20 km in the middle part to 15 km at its head and mouth. Its mouth faces the Barents Sea. The outer sill is quite deep at 200 m depth (Figure 2). Porsangerfjord is composed of 3 mains areas, the outer, middle and inner basins. Since the sill of the outer part is deep, water is regularly exchanged with the Norwegian Coastal Current (NCC) (Eilertsen & Skarðhamar 2006).

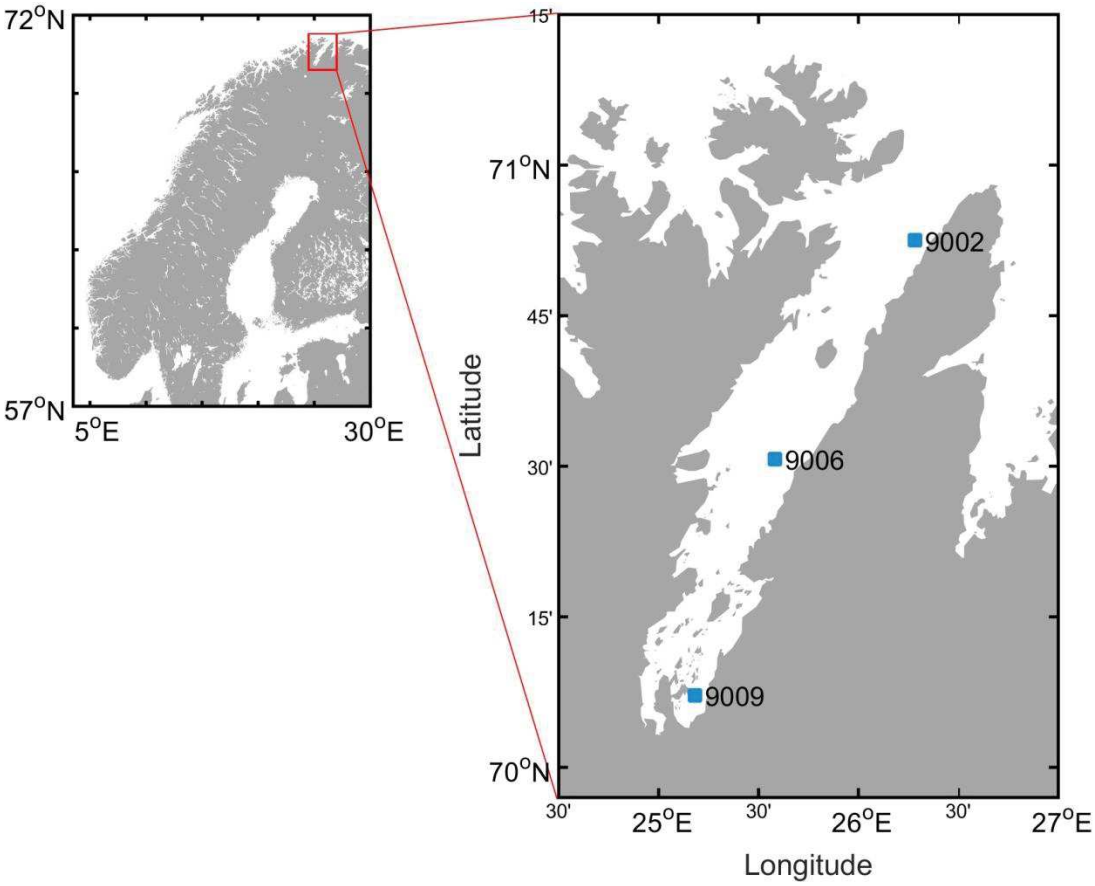


Figure 1. Map of the study area. Blue markers represent stations sampled during HMD surveys.

No sill separates the middle and outer part. The outer and middle basins essentially range from 50 – 180 m depth with a maximal depth of circa 310 m. They are considered a semi-enclosed fjord system (Svendsen 1991). The inner part is isolated from the rest of the fjord by a 60 m deep sill at circa 30 km from the head of the fjord (Mankettikkara 2013). The inner basin is considered as a true arctic environment; this is the only location in Northern Norway where a population of polar cod exists (Fevolden et al. 1999). The discharge from two rivers, Lakselv and Børselv, in the inner part creates a fresher environment in spring. The outer and middle basins are dominated by Atlantic water masses (Mankettikkara 2013).

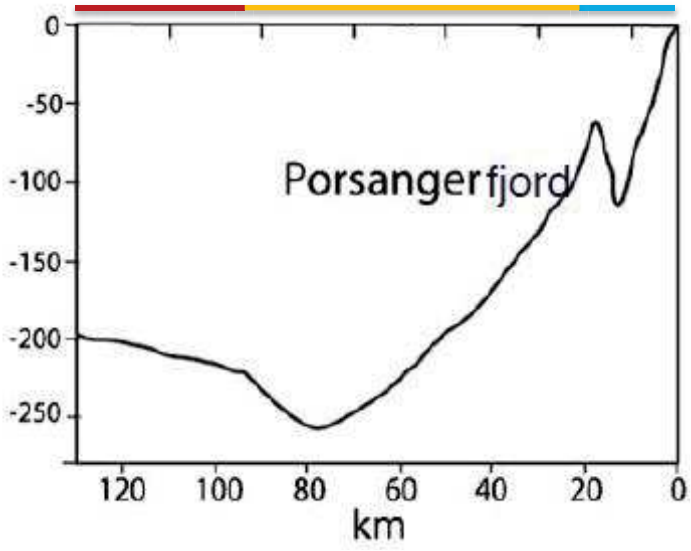


Figure 2. Depth profile of Porsangerfjord (Eilertsen & Skarðhamar 2006). Lines represent the basins: **red**: outer, **orange**: middle and **blue**: inner.

2.2 Phytoplankton sampling

Phytoplankton samples were collected with Niskin bottles at 0, 5, 10, 20, 30, 50 and 100 m depth in May, and at 0, 20, 50 and 100 m depth in November. Unfortunately, no phytoplankton sample was collected in April because we participated in a student cruise and the sampling was restricted. Species composition and cell counts were conducted with an inverted ZEISS Primo Vert microscope using the Utermöhl method (Paxinos & Mitchell 2000) in the lab after the cruise. Nunclon four-well 2 ml settlement chambers were used for dense samples (May). Prior to cell count, the chambers were left to sediment for 2 h in the refrigerator. Sparse samples, e.g. November cruise in Porsangerfjord, were left in a sedimentation chamber for 24 h and then counted. A minimum of 100 cells of the most abundant species were counted for constructing the species composition.

2.3 Zooplankton net samples

Zooplankton were sampled with a WP-2 net with a 180 µm mesh size, with the exception of November cruise when a 85 µm mesh size was used. The nets were towed vertically from five meters above the bottom to the surface at circa 0.25 $m.s^{-1}$. Samples were then fixed in 4% formalin and 10% 1,2-propandiol (propylene glycol). Except for November when 70% ethanol was used. Species

composition and abundances were determined in the lab after the cruises. In order to determine abundances, the samples were rinsed in seawater and diluted to a known volume. Then, subsamples of a known volume were taken from the homogenously mixed full sample. Subsamples were counted such that 300 individuals of the most abundant species were identified. Abundances were then calculated with the following formulas (Eq.1, and Eq.2):

$$Abundance\ (ind\ m^{-3}) = [n\ (ind) / subsample\ fraction] / Volume\ of\ water\ filtered\ (m^3)$$ **(Eq.1)**

$$Abundance\ (ind\ m^{-2}) = Abundance\ (ind\ m^{-3})\ x\ depth\ range\ (m)$$ **(Eq.2)**

2.4 Video Plankton Recorder (VPR)

Images of plankton were collected using a Digital-Autonomous Video Plankton Recorder (DAVPR; Seascan Inc., USA). At each station, the VPR was run for circa one hour resulting in 6 to 16 vertical profiles depending on the depth. The VPR was equipped with a Uniq B/W 1.4 MPixel camera, a CTD (SBE49, "Fastcat", Seabird Electronics Inc., USA), and a Chl *a* and turbidity sensor (ECO Puck, WET Labs Inc., USA) mounted on the tow body. The camera had a frequency of 20 Hz, the CTD of 16 Hz and the fluorometer of 8 Hz. VPR and CTD data were then collected in a compressed file on a local hard drive. The VPR was set on the low magnification S2 with a window of 22 x 32.5 mm. It has been shown that this magnification is the most relevant to study mesozooplankton and large phytoplankton colonies like *Phaeocystis pouchetii* (Norrbin et al. 2009). During the data collection for this thesis the sampling volume was calibrated and represented a volume of 35.2 ml. The combined total volume of seawater sampled over all the cruises was 2228.17 l.

For processing, the VPR data was then decompressed using the Autodeck software (Seascan Inc., USA). This program detected and extracted the regions of interest (rois) from raw images. Autodeck used different factors to isolate rois such as brightness, sharpness, texture, and size of the objects. Each roi was time-stamped so it could be linked to environmental data. The extraction settings were identical for every cruise. The environmental VPR data was accessed through the Visual Plankton

Matlab package (C.S. Davis, WHOI, USA). The whole tow was extracted for April and November cruises. One leg (up and down) of the tow was sorted in May due to heavy phytoplankton bloom situations that dramatically increased the number of rois captured.

Rois were sorted into the lowest possible taxonomic level in two distinct steps. First, the rois were automatically sorted using the Visual Plankton package. A training set of rois, with an average of 200 pictures per taxa, was created for each station to build a station-specific automatic classifier. Our data was sorted using the COM-SVM (Co-Occurrence Matrix with Support Vector Machine) classifier type. Second, automatically sorted rois had to be manually checked to remove "false positives", e.g. an appendicularian sorted as a colony of *Phaeocystis pouchetii*. The automatic classification could not sort small copepods into genus.

To get a single value representative of the abundance per cubic meter, the different legs of the tow were averaged per depth intervals. The identified taxa and genus are summed up in Table 2. The VPR gave an accurate depth distribution of phytoplankton species but the abundance was overestimated since many diatom chains and *P. pouchetii* colonies were captured in a single roi (Figure 3).

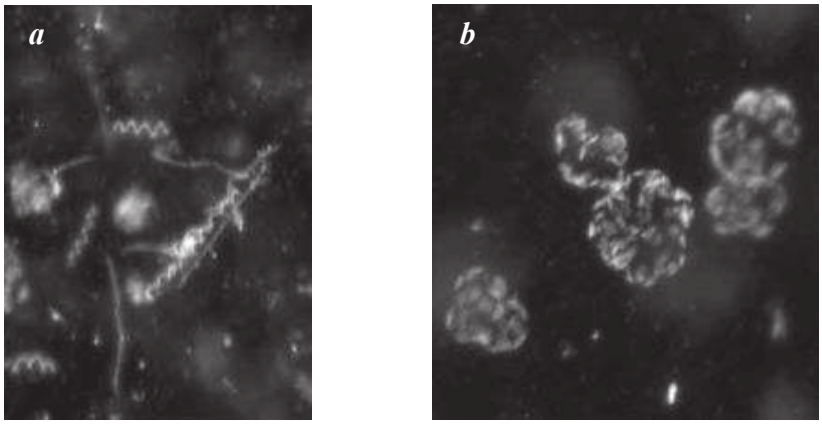


Figure 3. Rois showing diatoms chains (*a*) and *P. pouchetii* colonies (*b*).

Table 2. Groups recorded by the VPR per station and cruise.

Taxon	Station	Cruises
Diatom	Østerbotn, Porsangnes Øst	May
P.pouchetii	Østerbotn, Porsangnes Øst	May
Acartia sp.	Østerbotn, Porsangnes Øst	May, November
C.finmarchicus	Østerbotn, Midtre Øst, Porsangnes Øst	April, May, November
Metridia sp.	Østerbotn, Midtre Øst, Porsangnes Øst	April, May, November
M.norvegica	Østerbotn, Midtre Øst, Porsangnes Øst	April, May, November
Copepod nauplius	Østerbotn, Midtre Øst, Porsangnes Øst	April, May
Oithona sp.	Østerbotn, Midtre Øst, Porsangnes Øst	April, May, November
Pseudocalanus sp.	Østerbotn, Midtre Øst, Porsangnes Øst	April, May, November
Appendicularian	Østerbotn, Midtre Øst, Porsangnes Øst	April, May, November
Fecal Pellets	Østerbotn, Midtre Øst, Porsangnes Øst	April, May, November
Marine snow	Østerbotn, Midtre Øst, Porsangnes Øst	April, May, November

2.5 Hydrographic data

Extra CTD data was collected during the cruises with the onboard CTD (Sea-Bird SBE9, Seabird Electronics Inc., USA). However, the CTD used during May cruise was different (Sea-Bird SBE25, Seabird Electronics Inc., USA) because the previous one was lost at sea.

All hydrographical data used in plots and analyses related to VPR data came from the CTD of the VPR. The physical data used for transects plots came from the vessel CTD.

Pycnoclines were calculated with CTD data from the VPR. The penultimate leg of the tow was used to compute the mixed layer depth and strength. This depth and strength was defined using a finite difference criteria method (Glover & Brewer 1988, Kara et al. 2000).

2.6 Statistics analysis

As many variables and relationships did not meet the assumptions of parametric statistical methods, we had to use non-parametric methods. We refined the dataset by removing species that occurred only once, as such species contributed little information to the analysis. Rare species (i.e. species with less than 5% occurrence) were retained because they describe fine community relationships

(Jackson & Harvey 1989). Two datasets were chosen. The first one was composed of VPR data binned in 1 m bins, e.g. zooplankton, phytoplankton and particulate matter (fecal pellets and marine snow). The second dataset combined zooplankton and particulate matter data from the VPR, and phytoplankton cell counts of the sampled depth (0, 5, 10, 20, 30, 50, 100 m depth). In this dataset, the VPR data was binned in 1 m bins at the Niskin collection depth to detect the associations between phyto-, zooplankton and hydrography.

In order to measure the relationship between our species community and the environmental variables (depth, temperature, salinity, *in vivo* Chl *a*), we used Canonical Correspondence Analysis (CCA) (ter Braak & Verdonschot 1995). This method extracts synthetic environmental gradients, which described the different relations between taxa. To test whether the species and environmental variables were correlated we performed a Monte Carlo permutation test with 9999 iterations. The CCA was performed using PC-ORD (McCune & Mefford, 2011, Version 6, MjM Software, Gleneden Beach, Oregon, USA).

3 Results

3.1 Hydrography and chlorophyll *a*

3.1.1 April

The general pattern of water properties found in April was that the whole water column in the inner part of the fjord was cold (-0.8°C) and quite fresh (33.7‰) while the outer part was warmer (4.0°C) and more saline (34.2‰) in the upper 105 m (Figure 4, Appendix A). From 105 m depth to 190 m depth, the water got colder (2.5°C at the coldest point) and had a similar salinity (34.2‰). From 190 m depth to bottom, water temperature was 4.1°C with a salinity of 35.4‰. The inner part of the fjord had a weak pycnocline at 46 m depth (0.07 kg m^{-3}) while the mouth of the fjord had none (Table 3).

3.1.2 May

The general pattern found in April remained in May with colder and less saline water in the inner part and warmer and more saline water at the outer part of the fjord (Figure 4, Appendix A). However, a general warming of the waters was observed leading to stronger stratification and pycnoclines. Østerbotn surface waters were heating while temperature decreased toward the bottom, 4.0°C and 0.1°C, respectively. A pycnocline was present at the inner station of the fjord at 9 m depth with a strength of 0.49 kg m^{-3} (Table 3). Under this cline, salinity and density had a trough at 11 m depth, with values of 33.6‰ and 26.69 kg m^{-3}. Salinity remained stable toward bottom with a value of 33.8‰. Density steadily increased to reach 27.12 kg m^{-3} at the bottom. The highest temperature was reached in the middle part of the fjord (5.0°C). The mixed layer depth was 19 m in the outer part of the fjord and was stable (0.56 kg m^{-3}) (Table 3). The mixed layer had temperature and salinity of 4.8°C and 34.1‰. Beneath the thermocline, temperature decreased steadily down to 145 m depth (3.3°C) and strongly increased to 4.7°C at the bottom. Salinity remained stable from 15 m depth to 145 m depth (34.2‰) and increased with depth to reach 34.7‰ at bottom. Density gradually rose from 26.97 kg m^{-3} at the surface to 27.50 kg m^{-3} at the bottom.

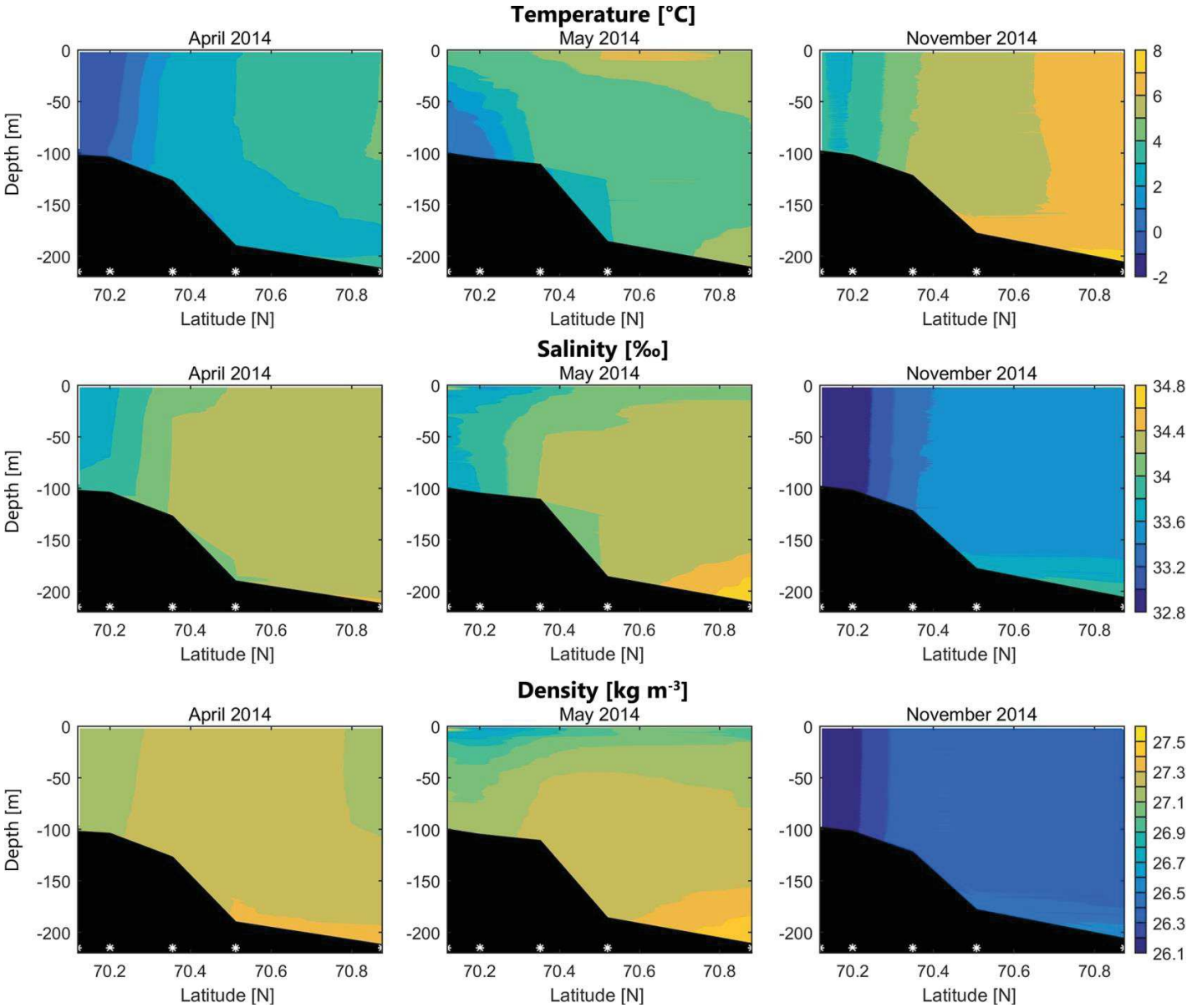


Figure 4. Temperature (*top*), salinity (*middle*) and density (*bottom*) based on 3 to 5 CTD stations of the Eastern part of Porsangerfjord. April, May, and November data came from the CTD of HMD survey. CTD positions are marked by white asteriks at the bottom.

3.1.3 November

November 2014 was characterized by a homogenous water column in most of the fjord except the outer part (Figure 4, Appendix A). In Østerbotn, the temperature was 3.0°C, salinity 32.8‰ and density 26.17 kg m^{-3}. No pycnocline was observed at that time of year in Østerbotn (Table 3). Toward the mouth of the fjord, the temperature rose to 6.7°C, salinity to 33.5‰, and density to 26.35 kg m^{-3} from surface to 150 m depth. The mixed layer reached 139 m depth, but the pycnocline was weak (0.39 kg m^{-3}) (Table 3). Below 150 m depth, temperature, salinity and density were higher, 7.1°C, 33.9‰ and 26.56 kg m^{-3}, respectively in Porsangnes Øst. The influence of this warm and more saline water spread inwards into the middle basin of the fjord. Although previously sampled month (April and May) showed a similar range of variation of temperature, density and salinity, November presented overall lower salinities and densities.

3.1.4 Chlorophyll *a*

Chlorophyll *a* (Chl *a*) concentrations were low in April, both in Østerbotn and Midtre Øst, 0.18 and 0.22 µg l^{-1} averaged over the whole water column, respectively (Table 3). Maximum values were found at 2.1 m depth (0.58 µg l^{-1}) at the inner part and 23.6 m depth (0.41 µg l^{-1}) at Midtre Øst. In Østerbotn, the average concentration was 1.29 µg l^{-1} and the maximum was 6.98 µg l^{-1} at 23.6 m depth. Porsangnes Øst had a similar average concentration (1.28 µg l^{-1}) but lower maximum (5.81 µg l^{-1}) at a comparable depth (21.9 m depth). Chl *a* concentration in November were globally low in the inner part and outer part with 0.16 and 0.11 µg l^{-1}, respectively, over the whole water column.

Table 3. Mixed layer depth, pycnocline strength, Chl a mean, maximum and depth of maximum Chl *a*, at Østerbotn and Porsangnes Øst for each cruise (April, May and November 2014). n.a.: not analyzed.

Cruise	Station	Mixed layer depth [m]	Pycnocline strength [kg m^{-3}]	Mean Chl *a* [µg l^{-1}]	Max Chl *a* [µg l^{-1}]	Depth max Chl *a* [m]
April	Østerbotn	46	0,07	0,18	0,58	-2,1
April	Midtre Øst	n.a.	n.a.	0,22	0,41	-23,6
May	Østerbotn	9	0,49	1,29	6,98	-21,9
May	Porsangnes Øst	19	0,56	1,28	5,81	-20,4
November	Østerbotn	n.a.	n.a.	0,16	0,29	-2,2
November	Porsangnes Øst	139	0,03	0,11	0,17	-53,6

3.2 Phytoplankton

In May 2014, Porsangerfjord had two different bloom situations; one bloom was diatom dominated and the other dominated by *Phaeocystis pouchetii* (Table 4, Appendix B). Both *P. pouchetii* single cells and colonies were observed; however, the phytoplankton counts revealed only single cells and the VPR solely recorded colonies.

Østerbotn was dominated by diatoms, both centric (*Chaetoceros* spp., *Porosira glacialis*, *Skeletonema* sp., *Thalassiosira* sp.) and pennate (*Fragilariopsis* sp., *Thalassionema nitzschoides* and indeterminate pennate diatoms). The abundance of *Chaetoceros* spp. peaked at 30 m depth with an abundance of 1052 ind m^{-3}. Although dominated by diatoms, flagellates were relatively important and were the most abundant group at 50 and 100 m depth. *P. pouchetii* single cells occurred mostly in the upper part of the water column (surface to 30 m depth).

P. pouchetii dominated Porsangnes Øst (68% of all phytoplanktonic abundance), from surface to 50 m depth. *P. pouchetii* cell counts were higher than diatoms counts in Østerbotn. *Phaeocystis* had its highest abundance at 20 m depth (2912 ind m^{-3}), thus slightly shallower than in Østerbotn. Flagellates were the most abundant taxa at 100 m depth and represented 31% of all phytoplanktonic abundance. A scarce amount of diatoms was present, e.g. *Chaetoceros* spp., *P. glacialis* and *T. nitzschoides*.

Overall, abundances were lower in November than in May, both in Østerbotn and Porsangnes Øst. Both of these stations were dominated by flagellates with 85 and 63% of mean relative abundance over the depths sampled respectively. The main difference between these stations occurred with dinoflagellates which was an important phylum in the outer part. They represented 8% of mean relative abundance in the inner part and 30% in the outer part. Diatoms composition was similar between these stations, with mainly pennate diatoms (*Cylindrotheca closterium*, *Pseudo-nitzschia* sp., *T. nitzschoides*).

Table 4. Dominating phytoplankton species at Østerbotn and Porsangnes Øst in May and November 2014. **CSP**: *Chaetoceros* spp., **FLA**: indeterminate flagellate, **PPO**: *P. pouchetii* single cell. *: The mean relative amount of phytoplankton group was computed from cell counts.

Cruise		May		May		November		November	
Station		Østerbotn		Porsangnes Øst		Østerbotn		Porsangnes Øst	
		Species	[ind m^{-3}]	Species	[ind m^{-3}]	Species	[ind m^{-3}]	Species	[ind m^{-3}]
Depths [m]	0	CSP	382	PPO	2230	FLA	19	FLA	9
	5	CSP	404	PPO	2166				
	10	CSP	335	PPO	2804				
	20	CSP	910	PPO	2912	FLA	12	FLA	7
	30	CSP	1052	PPO	817				
	50	FLA	83	PPO	662	FLA	10	FLA	10
	100	FLA	24	FLA	343				
Mean relative amount at all depth [%] *	Diatoms	71		1		6		4	
	P. pouchetii	9		68		0		0	
	Flagellates	19		31		85		63	
	Dinoflagellates	1		0		8		30	

3.3 Abundances of zooplankton taxa

3.3.1 Østerbotn

The stations in the inner and outer part of the fjord had different zooplankton community compositions over time. Østerbotn was characterized by a high abundance of small copepods (*Pseudocalanus* sp., *Microcalanus* sp., *Oithona* spp. and *Microsetella norvegica*) while large copepods (*Calanus finmarchicus*, *Metridia longa)* had an important role in the outer part (Table 5).

In April, the *Calanus* population was pre-reproduction, since it was mainly composed of CV and adult females (6868 ind m^{-2} representing 8% of the total zooplankton community). A month later in May, the nauplius stages of *C. finmarchicus* were the most abundant *Calanus* stages, with an abundance of 3771 ind m^{-2}, and some CI and CII were also found. In November, no *C. finmarchicus* was present. The other large copepod, *M. longa*, was not very abundant in Østerbotn.

Regarding small copepods the pattern is quite different in Østerbotn. All sampled months were dominated by the small copepod community. In April, *Pseudocalanus* sp. represented 72% of the

Table 5. Abundances in ind m^{-2} of identified zooplankton data and percentage (numbers in italic) of species abundance over the whole community. * The net used during November cruise had a 85 µm mesh size, while the net used for other cruises was 180 µm.

Cruise / Station		April Østerbotn		May Østerbotn		November * Østerbotn		April Midtre Øst		May Porsangnes Øst		November * Porsangnes Øst	
		[ind m^{-2}]	%	[ind m^{-2}]	%	[ind m^{-2}]	%	[ind m^{-2}]	%	[ind m^{-2}]	%	[ind m^{-2}]	%
C.finmarchicus	Nauplii	151	*0*	3771	*16*			13156	*50*	7627	*18*		
	CI			591	*2*					4068	*10*		
	CII			250	*1*					7458	*17*		
	CIII			204	*1*			38	*0*	6441	*15*		
	CIV	75	*0*	136	*1*					7797	*18*	71186	*0*
	CV	3245	*4*	45	*0*					3051	*7*	160169	*1*
	Adult female	3623	*4*	91	*0*			226	*1*	339	*1*		
	Adult male	453	*1*					76	*0*				
	Total	7547	*9*	5088	*21*			27	*0*	36781	*86*	231356	*2*
Pseudocalanus sp.	Copepodite	38792	*47*	4588	*19*	205424	*7*	1403	*5*	169	*0*	747458	*5*
	Adult female	19472	*24*	3316	*14*	7119	*0*	303	*1*	339	*1*	195763	*1*
	Adult male	528	*1*			1017	*0*	76	*0*				
	Total	58792	*72*	7905	*33*	213559	*8*	1782	*7*	508	*1*	943220	*6*
Microcalanus sp.		4226	*5*	1976	*8*	365085	*13*	6218	*24*	847	*2*	4840678	*32*
Acartia sp.		226	*0*	23	*0*	9153	*0*	227	*1*	169	*0*	142373	*1*
Oithona sp.		9736	*12*	5043	*21*	93559	*3*	3981	*15*	4237	*10*	1121186	*7*
M.norvegica		1057	*1*	545	*2*	2111186	*76*	341	*1*			7599153	*50*
M.longa		151	*0*	23	*0*			152	*1*			391525	*3*
Appendicularian	*Oikopleura* sp.	75	*0*	659	*3*			76	*0*	169	*0*		
	Fritilaria borealis			2430	*10*								
	Total	75	*0*	3089	*13*			76	*0*	169	*0*		
Total		**81810**		**23691**		**2792543**		**26273**		**42711**		**15269491**	

overall taxa abundance with a high abundance of 58792 ind m^{-2}. The biomass of *Pseudocalanus* decreased to 7905 ind m^{-2} in May, yet it was still the most abundant taxa. The relative importance of *Pseudocalanus* decreased in November (8%). *Microcalanus* sp. abundance remained globally low except for November when it accounted for 13% of the total biomass. *Acartia* sp. was not an abundant taxa over the months sampled. *Oithona* spp. appeared as a numerically important species in Østerbotn. It was present in all months, notably during the bloom situation in May, when its abundance was 5043 ind m^{-2} representing 21% of total abundances. *Microsetella* stocks remained low in April and May then peaked in November when it accounted for 76% of the zooplankton community. Appendicularians were found in May (3089 ind m^{-2}), and *Oikopleura* sp. only in April.

3.3.2 Porsangnes Øst and Midtre Øst

In the outer part of the fjord at Porsangnes Øst, the plankton community was different. *C. finmarchicus* peaked during May with the highest abundance (36781 ind m^{-2}) and represented 86% of total abundances of zooplankton at that time. Nauplius stages of *Calanus* were the most common stage found in April. In May, the *C. finmarchicus* population built up and CII-CIV were the most abundant copepodite stages, respectively 17, 15 and 18%, although nauplii were still abundant (18%). In November, only a few CIV and CV *Calanus* were found. *Metridia* had low abundances in April and November with 152 and 391525 ind m^{-2}, respectively, yet they were more abundant than *Calanus* in November. Regarding smaller copepod species, *Pseudocalanus* had relatively low abundances in April, May and peaked in November (943220 ind m^{-2}). *Acartia* was not an abundant species and was only found in May. *Microcalanus* sp. had the second highest abundance in April, 6218 ind m^{-2}, but decreased in May and November. *Oithona* spp. was an important genus in April, representing 15% of the abundances of all taxa (abundance of 3981 ind m^{-2}). *Oithona* retained a high abundance in May, it was the second most abundant organism. *Microsetella* peaked in late fall and was the most abundant taxa in November (50%). Appendicularians were only found in May.

3.4 Fine scale distribution of zooplankton from the VPR

3.4.1 Østerbotn

The general depth structure of zooplankton evolved during the year (Figure 5). In April, species were distributed throughout the water column, while in May distribution was shallower and in November the organisms were deeper down.

Three main species were found in April, *C. finmarchicus*, *M. norvegica* and *Pseudocalanus* sp. (Figure 5). They had a complementary distribution, meaning that their peaks of abundance were at different depths. *Calanus* had the shallowest abundance peak at 15 m depth (388 ind m^{-3}). From 20 m to 100 m depth, individual observations of *C. finmarchicus* were steady (ca. 110 ind m^{-3}) and then dropped at the bottom. *Pseudocalanus* sp. had its highest abundance between 45 m and 55 m depth (322 ind m^{-3}) and gradually decreased toward bottom. From surface to 40 m depth, *Pseudocalanus* had a stable abundance around 170 ind m^{-3}. The depth of maximum abundance for *Microsetella* was below that of *Pseudocalanus*, at 65 m depth (493 ind m^{-3}). In the upper part of the water column abundance of *M. norvegica* had a rather stable increase from surface to 60 m depth. The other copepod taxa found were *M. longa* which was concentrated in the bottom part, ranging from 75 m and 95 m depth and *Oithona* spp. which were distributed in the middle part of the water column, between 30 m and 85 m depth. Appendicularians were found with a single individual observation at 23 m. The fecal pellets peak was at the same depth as the *Calanus* peak (15 m depth). Marine snow was observed in the deeper part of the water column, mostly between 65 m to 95 m depth.

Highest taxa diversity found was in May, when diatoms, *P. pouchetii* and copepod nauplii were observed, as well as taxa already described in April (Figure 5). Both diatoms and *Phaeocystis* co-occurred from surface to 40 m depth, yet they had different vertical structures. Diatoms were essentially distributed from the surface to 45 m depth, but some observations reached 70 m depth. Diatoms peak was found at 30 m depth.

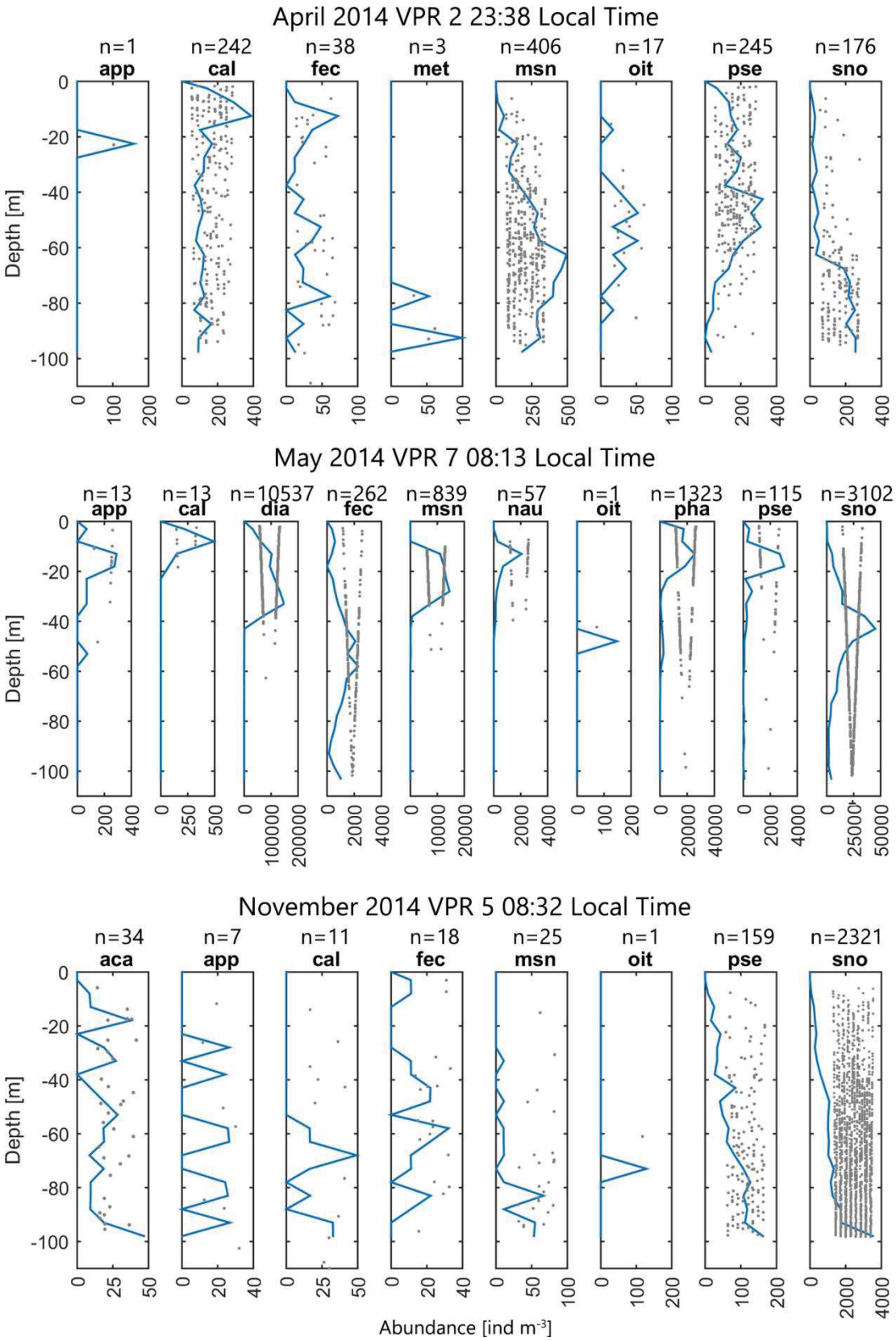


Figure 5. Fine scale position in the water column of groups recorded with the VPR in Østerbotn. *Each dot* represents an individual observation. The blue line represents abundance in 5 m bins. The taxa presented are: **aca**: *Acartia* sp., **app**: appendicularian, **cal**: *C. finmarchicus*, **dia**: diatoms, **fec**: fecal pellets, **msn**: *M. norvegica*, **nau**: copepod nauplii, **oit**: *Oithona* spp., **pha**: *P. pouchetii*, **pse**: *Pseudocalanus* sp., **sno**: marine snow. Please note the different scales of the *x*-axis.

The only visible form with the VPR of *P. pouchetii* was its colonies; it was impossible to see single *Phaeocystis* cells with the VPR (Figure 6). *P. pouchetii* had a shallower peak than diatoms (15 m depth) and ranged from surface to 60 m depth. Another small *P. pouchetii* abundance peak was observed at 55 m depth.

The whole zooplanktonic community had taxa-dependent depth distribution in May. *Calanus* had a shallow and narrow distribution, ranging from the surface to 20 m depth and peaking at 8 m depth (491 ind m^{-3}). *M. norvegica* was the species with the highest abundance (14541 ind m^{-3} at 30 m depth). Its distribution fit that of phytoplankton, ranging from 15 m to 40 m depth. Many rois showed *Microsetella* closely associated with diatoms (Figure 6). Copepod nauplius stages were also present in the upper part of the water column and reached peak abundance at 15 m depth (2059 ind m^{-3}). Nauplii were associated to *Phaeocystis* and diatom blooms. *Pseudocalanus* sp. had few individual observations between surface and 10 m depth, where *Calanus* peaked. From 15 m to 25 m depth, *Pseudocalanus* abundance peaked (3024 ind m^{-3} at 20 m depth). Below 25 m depth, few individuals were observed. *Pseudocalanus* vertical distribution was closely linked to *Phaeocystis* and to a lesser extent diatoms. The last copepod taxa found was *Oithona* which had only one individual observation in the middle of the water column (45 m depth). Appendicularians were present between 5 m and 35 m depth, where the phytoplankton was distributed. Fecal pellets were found all over the water column and had the highest distribution in the middle part of the water column under the phytoplankton bloom (45 m to 55 m depth). The same pattern of vertical distribution was observed in marine snow with highest concentration under the phytoplankton bloom and a sharp peak at 45 m depth.

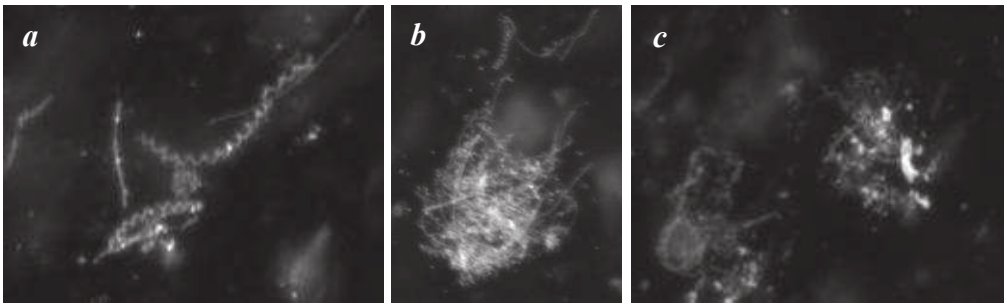


Figure 6. Rois collected in May 2014 in Østerbotn, showing diatom chains (*a*), diatom aggregates (*b*) and *M.norvegica* on a diatom aggregate (*c*). Please note that scales are different between rois.

In November, most of the zooplankton taxa encountered had a deeper vertical distribution and lower abundances compared to previously studied months (Figure 5). An additional copepod taxon was observed, *Acartia* sp. which was spread all over the water column. *C. finmarchicus* was concentrated between 60 m depth and bottom. *M. norvegica* was also concentrated at the bottom and near bottom (80 m depth to 100 m depth), but some individuals were observed at 33 m depth. *Pseudocalanus* sp. was the most abundant taxa and was distributed throughout the water column. Abundances of *Pseudocalanus* gradually increased from surface to 95 m depth where the highest abundance of 162 ind m^{-3} was reached. As seen in previous months, *Oithona* spp. were few in number and occurred in the middle part of the water column (75 m depth). The appendicularians had no accumulation depth, they were found from 30 m to 95 m depth. Fecal pellets were concentrated in the middle part of the water column (between 35 m and 90 m depth). Marine snow was abundant in November and accumulated in the deeper part of the water column, peaking at 100 m depth.

3.4.2 Porsangnes Øst and Midtre Øst

The outer part of the fjord had different patterns due to the change in vertical distributions of taxa (Figure 7). However the shared trend was a higher diversity in May.

In April, *C. finmarchicus* was the most abundant species with a narrow depth distribution, between 120 m to 160 m depth. The peak of abundance was 59 ind m^{-3} at 155 m depth. The second most abundant species was *M. longa* which had a similar range of distribution as *Calanus* and a sharp abundance peak at 135 m depth (25 ind m^{-3}). Two *M. norvegica* individuals

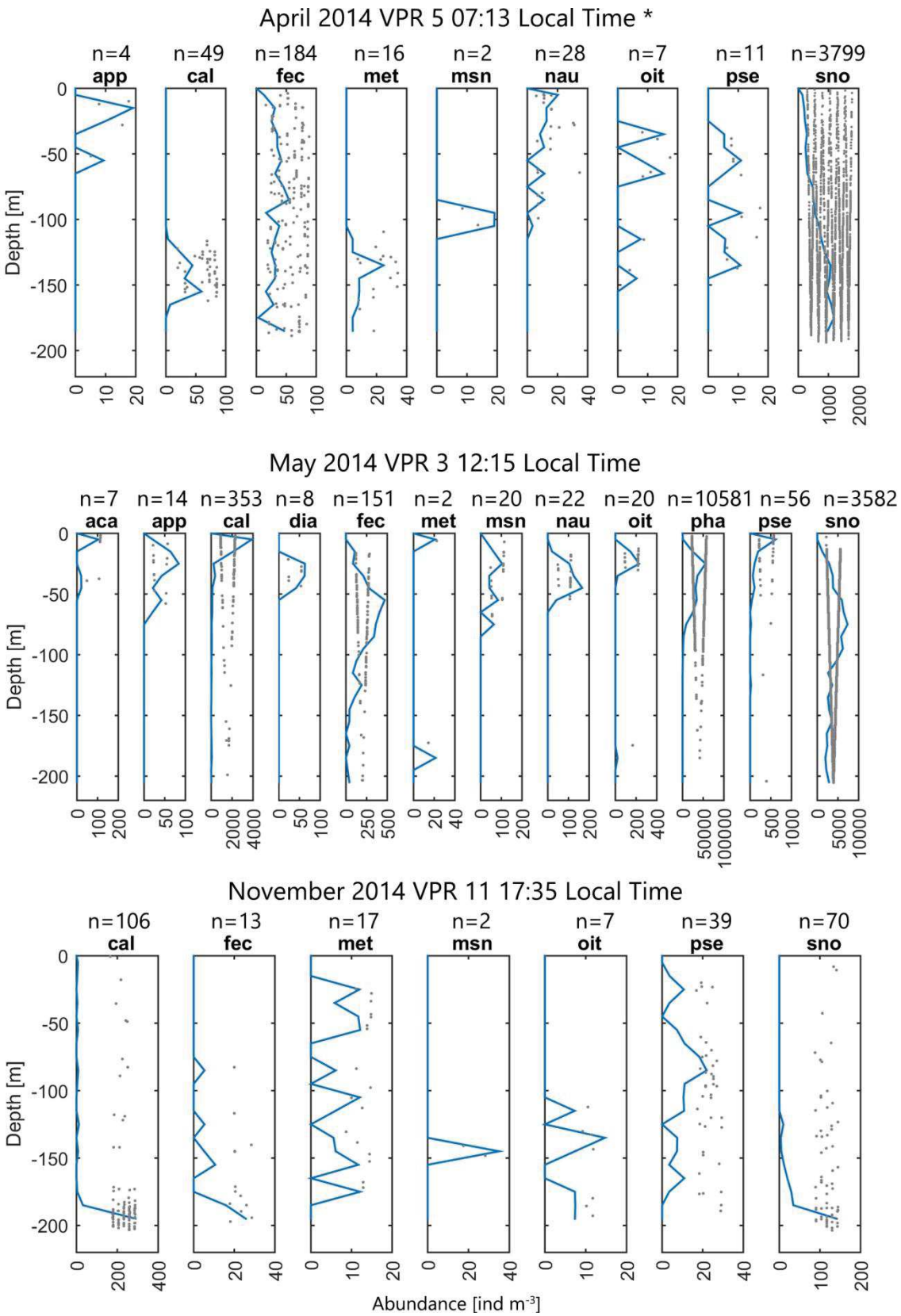


Figure 7. Fine scale position in the water column of groups observed with the VPR in Porsangnes Øst. *April station was collected in Midtre Øst. *Each dot* represents an individual observation. The blue line represents abundance in 10 m bins. The taxa presented are: **aca**: *Acartia* sp., **app**: appendicularian, **cal**: *C. finmarchicus*, **dia**: diatoms, **fec**: fecal pellets, **met**: *M. longa*, **msn**: *M. norvegica*, **nau**: copepod nauplii, **oit**: *Oithona* spp., **pha**: *P. pouchetii*, **pse**: *Pseudocalanus* sp., **sno**: marine snow. Please note the different scales of the *x*-axis.

were observed, both between 90 m and 100 m depth. Copepods nauplii had their highest abundance near the surface, at 5 m depth (20 ind m^{-3}). Below this peak, nauplius stages steadily decreased with depth until 110 m depth, under which no observations were made. Few *Oithona* spp. were present from 35 m to 140 m depth (average ca. 10 ind m^{-3}). A comparable vertical distribution was found in *Pseudocalanus* with similar abundances. Appendicularians were in the upper part of the water column, just below surface with a peak at 15 m depth and another one deeper at 50 m depth. Marine snow was very abundant throughout the entire water column but accumulated at great depth (130 m to 180 m depth).

The May situation was different from that in April. Most of the organisms were higher up in the water column (Figure 7). This is the only cruise where phytoplankton was observed in the VPR images. Diatoms ranged from 20 m to 45 m depth, and were less abundant than *P. pouchetii*. *Phaeocystis* was very abundant with a broader depth distribution than diatoms. As for diatoms in Østerbotn, the abundance of *Phaeocystis* was hard to interpret because many colonies were seen in a single roi (Figure 8). *P. pouchetii* peaked at 25 m depth, and remained at high abundances down to 70 m depth; below that point its abundance decreased until 100 m depth. *Acartia* sp. was mostly found at the surface where it peaked at 5 m depth. A few *Acartia* were also observed at 50 m depth. *C. finmarchicus* were abundant below surface, 3890 ind m^{-3} at 5 m depth. They remained in large numbers until 50 m depth and then decreased, yet some individual observations were made all over the water column and near the bottom. *M. longa* was represented by two individuals, one near surface and the other one close to the bottom. *M. norvegica* distribution was similar to *P. pouchetii* distribution (surface to 160 m depth) with a peak at 30 m depth (103 ind m^{-3}). *Microsetella* was often seen grazing on *Phaeocystis* (Figure 8). Copepod nauplii had a deeper peak compared to *M. norvegica*, its highest abundance was at 45 m depth (166 ind m^{-3}). Analogous with *M. norvegica*, nauplii were often seen *in situ* next to P*haeocystis* colonies (Figure 8). The highest abundance of *Oithona* spp. was at 30 m depth (230 ind m^{-3}), like the peak of *M. norvegica*.

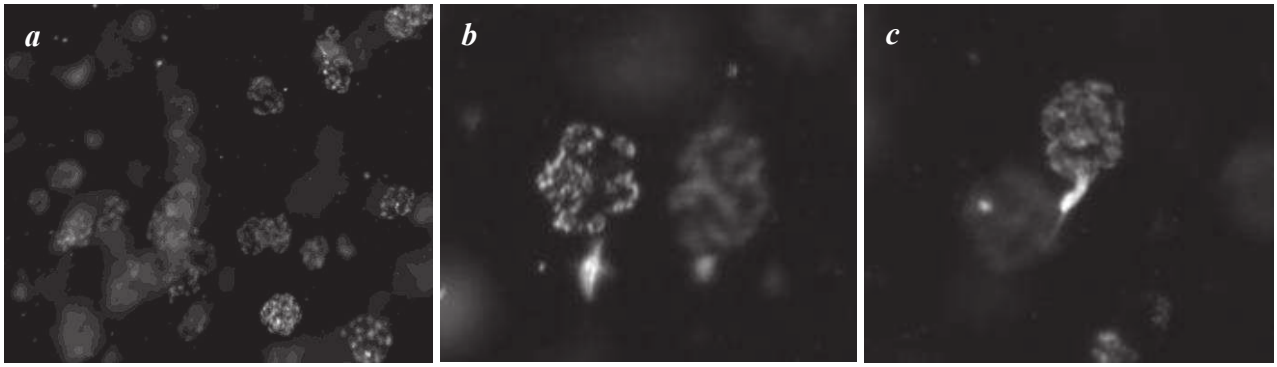


Figure 8. Rois collected in May 2014 in Østerbotn, showing *P. pouchetii* colonies (*a*), nauplius next to *P.pouchetii* colony (*b*) and *M.norvegica* female carrying egg sac on a *P.pouchetii* colony (*d*). Please note that scales are different between rois.

Pseudocalanus sp. had a shallow peak (616 ind m^{-3} at 5 m depth) like *C. finmarchicus* and decreased with increasing depth until 75 m depth. *Pseudocalanus* and *C. finmarchicus* had similar depth distributions. The appendicularian vertical profile was closely linked to that of the phytoplankton. Appendicularians ranged from surface to 70 m depth. Fecal pellets and marine snow had similar abundance profiles. They both peaked below the *P. pouchetii* bloom, yet fecal pellets abundance decreased with increasing depth whereas marine snow remained constant.

The abundances in November were generally lower than May, and similar to April (Figure 7). *C. finmarchicus* was lying at the bottom, between 180 m to 200 m depth. Few individual were recorded in the upper part of the water column but did not show any sign of accumulation. *Metridia* had a different vertical distribution than *Calanus*, most of the observation ranged from surface to 170 m depth just above *C. finmarchicus* accumulation depth. Few *M. norvegica* were recorded. These observations were found at 135 m depth. *Oithona* spp. had a deep distribution between 100 m and the bottom. *Pseudocalanus* occupied the middle part of the water column. It had a surface peak at 25 m depth (10 ind m^{-3}) and a deeper peak at 90 m depth (21 ind m^{-3}). Fecal pellets were encountered in the deep part of the water column. Marine snow accumulated near bottom, at 190 m depth.

3.5 Zooplankton distribution related to water properties

Zooplankton vertical distributions in the inner part of the fjord in April did not show any specific link with environmental variables (Figure 9). The water column was homogenous and zooplankton taxa were distributed over the whole water column.

In May, the surface of the water column heated up, creating a strong stratification and a pycnocline at 19 m depth (Figure 9). *C. finmarchicus* was above the pycnocline and closely linked to high temperature (3 – 4.5°C) and moderate Chl *a* values (1.5 – 3 µg l^{-1}). *M. norvegica* and copepod nauplii had a similar pattern. They were both located right beneath the pycnocline, where the highest Chl *a* concentrations were observed. While few individual observations of *Microsetella* and nauplii were observed at temperatures below 2.5°C, the majority of them were linked to temperature above 2.5°C. *Pseudocalanus* spp. distribution was concentrated below the pycnocline, where the high Chl *a* concentration occurred. However unlike *M. norvegica* and copepod nauplii, temperature did not seem to affect *Pseudocalanus* distribution.

In November, the water column was homogenous; hence, no particular match between zooplankton vertical distribution and environmental variables was observed (Figure 9).

As in the inner part of the fjord, Porsangnes Øst was characterized by a relatively well mixed water column, leading to a broad vertical distribution of zooplankton (Figure 10).

C. finmarchicus distribution was linked to Chl *a* concentrations, ranging from 1.5 µg l^{-1} to 6 µg l^{-1} (Figure 10, Appendix A). *M. norvegica* and copepod nauplii followed the Chl *a* concentration over depth. As in Østerbotn, they were both located below the pycnocline. The depths of the highest Chl *a* concentrations and the distribution of *Oithona* spp. matched well. *Pseudocalanus* spp. was distributed mostly above the pycnocline, its vertical distribution fit Chl *a* concentrations. The vertical distribution of zooplankton in November reflected the homogeneity of the water column. Taxa did not seem to accumulate at certain depth due to environment variables (Figure 10).

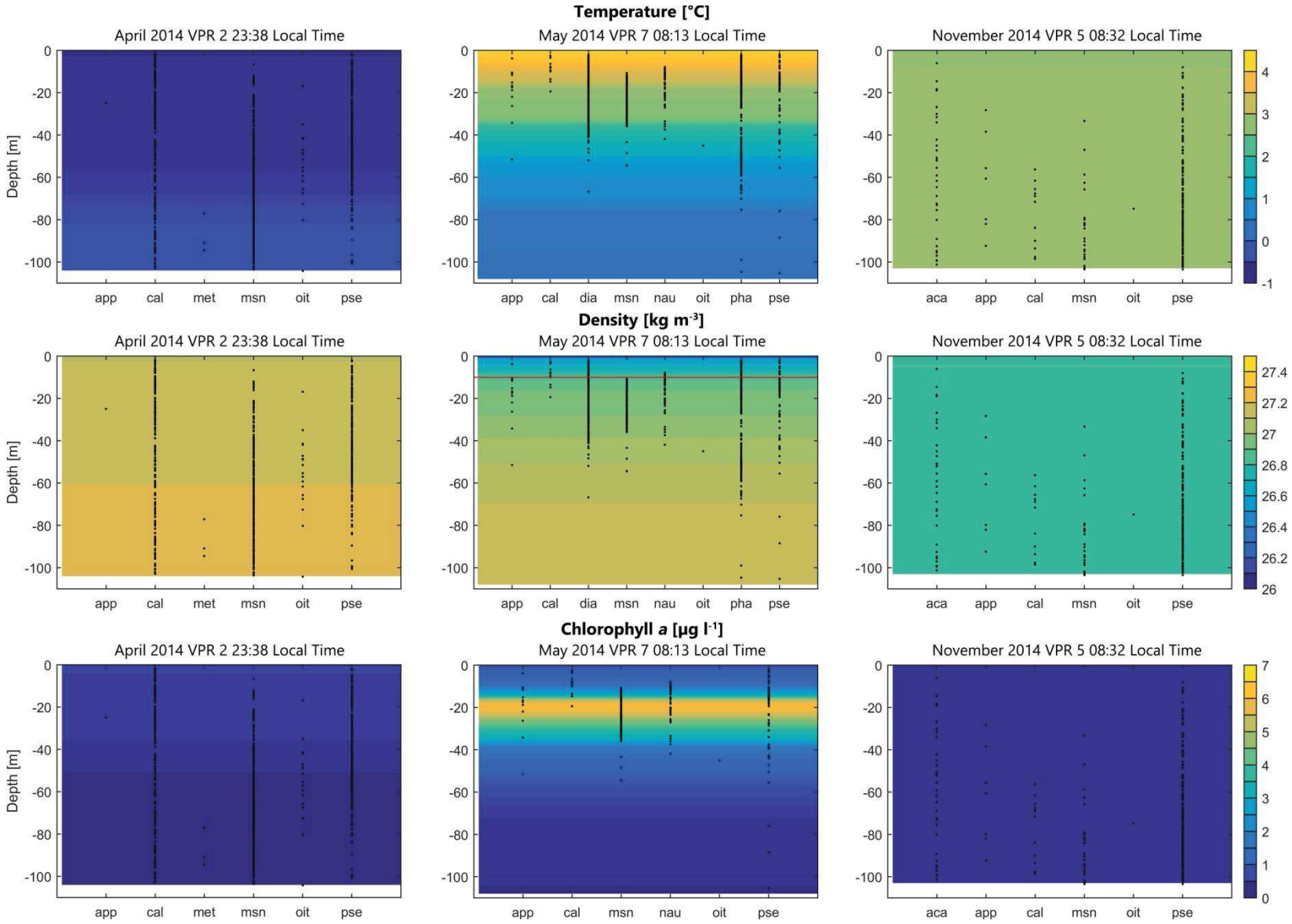


Figure 9. Distribution of zooplankton taxa related to temperature (*top*), density (*middle*) and Chl *a* (*bottom*) at Østerbotn, in April, May and November 2014. *Each dot* represents an individual observation. **aca**: *Acartia* sp., **app**: appendicularian, **cal**: *C. finmarchicus*, **dia**: diatoms, **met**: *M. longa,* **msn**: *M. norvegica*, **nau**: copepod nauplii, **oit**: *Oithona* spp., **pse**: *Pseudocalanus* sp.. The red line symbolizes the pycnocline.

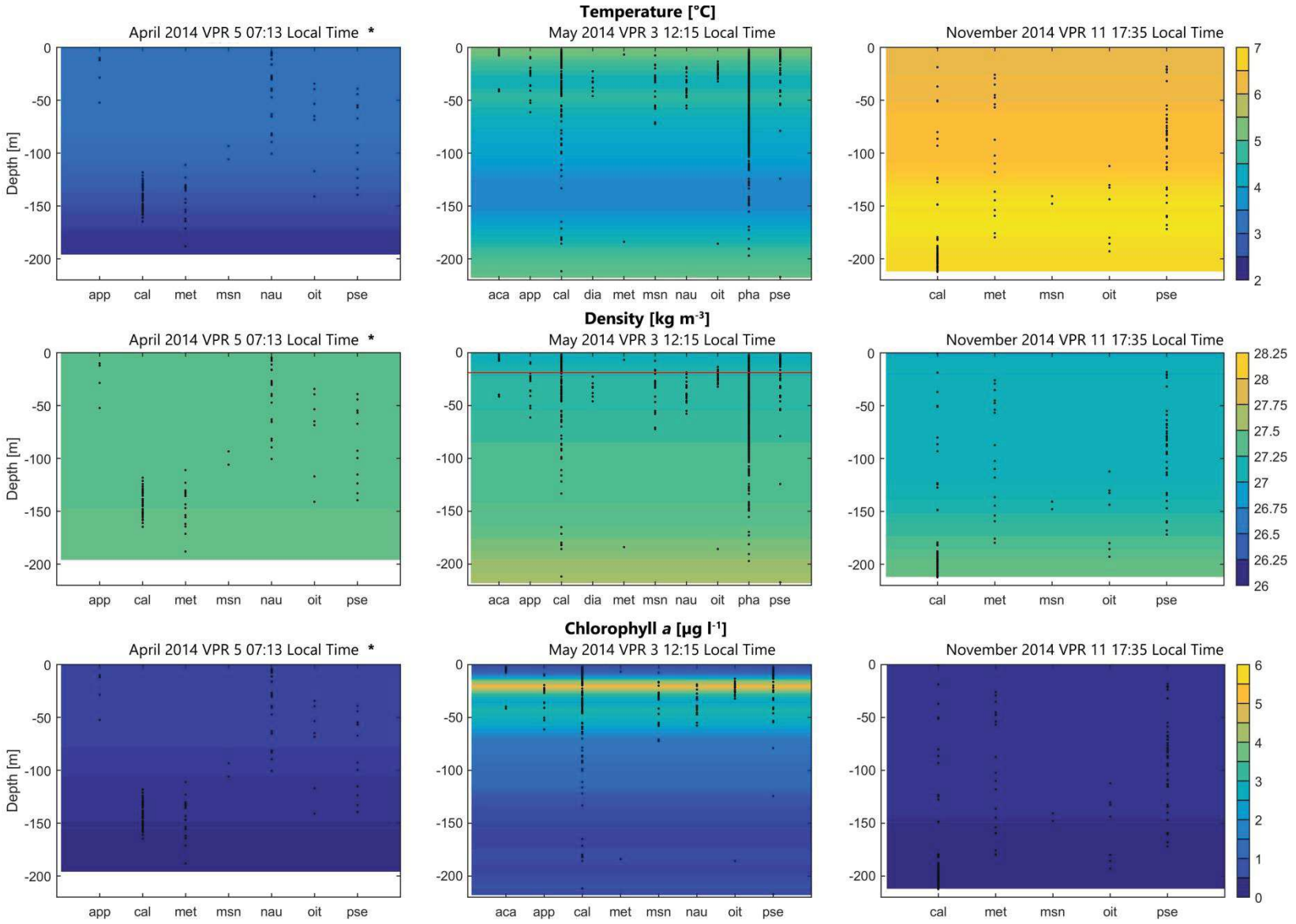


Figure 10. Distribution of zooplankton taxa related to temperature (*top*), density (*middle*) and Chl *a* (*bottom*) at Porsangnes Øst, in April, May and November 2014. *Each dot* represents an individual observation. **aca**: *Acartia* sp. app: appendicularian, **cal**: *C. finmarchicus*, **dia**: diatoms, **met**: *M. longa*, **msn**: *M. norvegica*, **nau**: copepod nauplii, **oit**: *Oithona* spp., **pse**: *Pseudocalanus* sp.. The red line symbolizes the pycnocline. * Midtre Øst instead of Porsangnes Øst.

3.6 Canonical Correspondence Analyses

3.6.1 Zooplankton and hydrography

Results of the CCA using environmental variables, temperature, salinity, Chl *a*, depth, and date, to constrain zooplankton distribution data from the VPR showed that most of the variation (39.3%) explained in the first two axes (Figure 11). A Monte-Carlo permutation test in relation to the CCA analysis showed that environmental variables contributed significantly to species distribution patterns ($p < 0.0001$). Chl *a*, salinity and depth were the driving environmental variables of the first canonical axis, while temperature, salinity, Chl *a* and depth were aligned on the second canonical axis. Seasonality represented by year day (Date in Figure 11), had little influence on the ordination axis. *Microsetella* and diatoms were associated; both occurred in a fresher, colder, and deep environment. On the other hand, *P. pouchetii* was associated with high temperature, salinity, and shallow waters. *Oithona* was the zooplankton taxon most closely related to *Phaeocystis*. Appendicularian and copepod nauplii were linked to medium salinities and temperature and strong Chl *a* concentrations. Larger copepods like *C. finmarchicus* and *M. longa* tended to be linked to low Chl *a* values. Temperature and seasonality had little influence on *M. longa* whereas Chl *a*, salinity, and depth influenced its distribution. *Pseudocalanus* spp. was little influenced by environmental variables. Fecal pellets and marine snow were linked to depth and occurred later in the season.

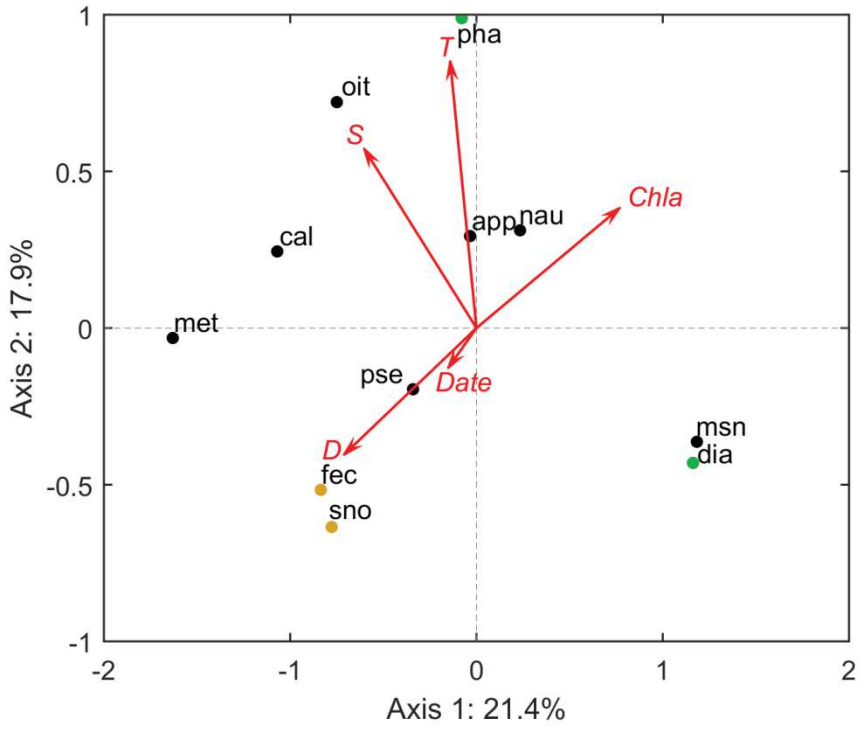


Figure 11. Canonical Correspondence Analysis ordination diagram of taxa WA scores observed with the VPR binned 1 m bins. All cruises were included in the analysis (April, May and November 2014). *Black dots*: zooplankton taxa, *green dots*: phytoplankton taxa, *yellow dots*: particulate matter. Groups shown **are**: app: appendicularian, **cal**: *C. finmarchicus*, **dia**: diatoms, **fec**: fecal pellets, **met**: *M. longa*, **msn**: *M. norvegica*, **nau**: copepod nauplii, **oit**: *Oithona* spp., **pha**: *P. pouchetii*, **pse**: *Pseudocalanus* sp., **sno**: marine snow. Environmental variables are represented as *red arrows*: ***T****:* Sea temperature, ***S***: salinity, ***Chla***: Chlorophyll *a*, ***D***: depth, ***Date***: year day.

3.6.2 Zooplankton, phytoplankton and hydrography

CCA analysis performed using environmental variables (temperature, salinity, Chl *a*, depth and date) with phytoplankton cell counts and zooplankton abundances from VPR in 1 m bins revealed that 45.7% of the variance was explained by the first two axis (Figure 12). The first axis was mostly constrained by temperature, salinity, Chl *a*, and depth. Chl *a*, depth, seasonality (date in Figure 12) and salinity were the most influential environmental variables on axis 2. A permutation test showed that environmental variables and community structure were significantly associated (p = 0.0134). Centric diatoms (*Chaetoceros* spp., *Porosira glacialis*, *Thalassiosira* sp., *Skeletonema* sp.) were separated from *P. pouchetii*, ciliates, flagellates and dinoflagellates by the second axis. Centric diatoms were found early in the season and generally in cold, fresh, and deep environments except

for *Porosira glacialis*, which was linked to mild salinities, temperatures, and shallow depth. Pennate diatoms (*Cylindrotheca closterium*, *Fragilariopsis* sp., *Pseudo-nitzschia* sp., *Thalassionema nitzschoides* and indeterminate pennate diatoms) were distributed over a broad gradient of environmental conditions. For instance, *Fragilariopsis* sp. was linked to cold and fresh environments while *Pseudo-nitzschia* sp. was related to warm and saline environmental conditions. Pennate diatoms tended to appear later in the season. Ciliates were not influenced much by environmental conditions and were associated with deep waters and grew later in the season. Warm and saline waters were related to dinoflagellates (*Ceratium* sp. and indeterminate dinoflagellates) and flagellates (indeterminate flagellate). These groups were present during all sampling times, except *Ceratium* sp. which grew late in the season and occurred most at depths. *P. pouchetii* was linked to warm, saline, and shallow waters.

M. norvegica occurred in the same environmental conditions as most of the centric (*Skeletonema* sp., *Chaetoceros* spp., *Thalassiosira* sp.) and pennate diatoms (*Fragilariopsis* sp.). *Oithona* spp. distribution was not strongly influenced by environmental conditions, although they appeared later in the season. *Oithona* spp. had the same environmental conditions as ciliates, *Thalassionema nitzschoides* and marine snow. *Pseudocalanus* spp. and *P. pouchetii* were closely related, in warm saline waters. *C. finmarchicus* was linked to warm, saline, shallow waters. Hence, *C. finmarchicus* was close to *P. pouchetii*. *M. longa* appeared late in the season in warm and saline waters, same as the dinoflagellate *Ceratium* sp. and the pennate diatom *Pseudo-nitzschia* sp.. Copepod nauplii were related to similar environmental conditions as the centric diatoms (*Chaetoceros* spp., *Thalassiosira* sp. and *Porosira glacialis*) and the indeterminate pennate diatoms. Appendicularians occurred in environmental conditions in between *Pseudocalanus* spp. and copepod nauplii. They were linked to shallow waters and to indeterminate pennate diatoms, flagellates and *P. pouchetii*.

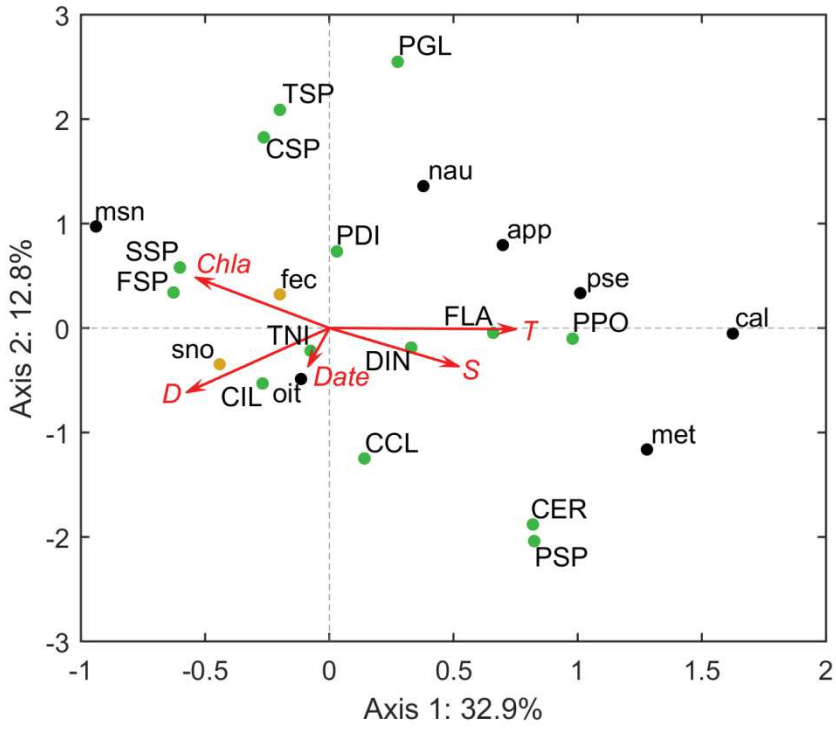


Figure 12. Canonical Correspondence Analysis ordination diagram of taxa WA scores observed with the VPR binned 1 m bins and phytoplankton cell counts. Cruises with phytoplankton cell counts were included in the analysis (May and November 2014). All depths without phytoplankton counts data were removed as well as diatoms and *P. pouchetii* colonies observed with the VPR. *Black dots*: zooplankton taxa, *green dots*: phytoplankton taxa, *yellow dots*: particulate matter. Groups shown are: **app**: appendicularian, **cal**: *C. finmarchicus*, **fec**: fecal pellets, **met**: *M. longa*, **msn**: *M. norvegica*, **nau**: copepod nauplii, **oit**: *Oithona* spp., **pse**: *Pseudocalanus* sp., **sno**: marine snow, **CCL**: *Cylindrotheca closterium,* **CER**: *Ceratium sp.*, **CIL**: Ciliates indeterminate, **CSP**: *Chaetoceros* spp., **DIN**: Dinoflagellates indeterminate, **FLA**: Flagellate indeterminate, **FSP**: *Fragilariopsis* sp., **PDI**: Pennate diatom indeterminate, **PGL**: *Porosira glacialis*, **PPO**: *Phaeocystis pouchetii*, **PSP**: *Pseudo-nitzschia* sp., **SSP**: *Skeletonema* sp., **TNI**: *Thalassionema nitzschoides*, **TSP**: *Thalassiossira* sp.. Environmental variables are represented as *red arrows*: ***Chla***: Chlorophyll *a,* ***D***: depth, ***Date***: year day, ***S***: salinity, ***T***: Sea temperature.

4 Discussion

Our investigation demonstrated that the organisms studied had different vertical profiles at different times of the year. The driving forces constraining vertical distribution of plankton were phytoplankton distribution and composition, temperature, salinity, Chl *a*, depth, and to a lesser extent seasonality. However, these variables representing hydrography cannot fully explain the zooplankton habitat choices. Our main hypothesis is therefore rejected.

Other abiotic factors are involved in vertical distribution of marine zooplankton. A recent study on the effect of light on zooplankton vertical distribution showed that optical properties of the water like PAR (Photosynthetically Active Radiation) light and light attenuation were as important as temperature, salinity, and subsequent density stratification in shaping vertical distributions (Trudnowska et al. 2014). The light spectrum also contains UV radiation and lab experimentation proved that *Calanus finmarchicus* and its nauplii were migrating down when exposed to UV radiation (Wold & Norrbin 2004). Diffuse turbulence also restrains zooplankton vertical distribution. Below a certain threshold the encounter rate between food item and zooplankton increase whereas high turbulence level will disrupt the zooplankton ability to detect their prey (Kiørboe & Saiz 1995).

Although abiotic factors are important, biotic factors like ecological interactions with prey and predator have a dominant role (Basedow et al. 2010). In accordance with the definition of habitat selection, zooplankton will select a depth range where food intake is maximized while predation risk is minimized (Brown 1998). Therefore the prey distribution and composition partly explain the distribution of herbivorous zooplankton. Although predators were not included in our study, they are essential to understand habitat selection (Fossheim & Primicerio 2008). The natural predators of herbivorous zooplankton are carnivorous zooplankton (chaetognaths), hydromedusae, fish larvae, and fish (Dale et al. 1999, Fitzgeorge-Balfour et al. 2013). Therefore, this study cannot elucidate the habitat choice of zooplankton in Porsangerfjord as no natural predators were included.

4.1 Phytoplankton bloom situations

Sverdrup (1953) stated that a necessary condition for triggering a phytoplankton bloom is vertical stratification of the water column. In northern areas and Porsangerfjord, the bloom can start from April until late May in unstratified water columns (Hegseth et al. 1995, Eilertsen & Frantzen 2007). Before the bloom has started the water will remain clear, causing the critical depth to deepen. Thus, the critical depth will be shallower than the mixed layer depth and will initiate the bloom.

The sampling of Porsangerfjord took place the first week of April. Chl *a* concentrations were low and the water column was not stratified. The bloom was still in an early phase at that time period. According to the literature, the phytoplankton community should have been dominated by pennate diatoms like *Fragilariopsis* spp. and flagellates (Degerlund & Eilertsen 2009)

Porsangerfjord was characterized with two different phytoplankton assemblages in May. The inner basin was diatom dominated while the outer basin was *Phaeocystis* dominated. This pattern was identical during spring 1992 (Hegseth et al. 1995).

In November, both stations had numerous flagellates and dinoflagellates. These groups are important in early spring, summer, and winter situations (Rat'kova & Wassman 2002, Hodal & Kristiansen 2008). Pennate diatoms also had an important place in the species composition which is usually the case during winter (Degerlund & Eilertsen 2009).

4.1.1 Spring bloom in Østerbotn

Østerbotn is an area which has a physical barrier (sill) limiting connection with the rest of the fjord. Under certain wind conditions, the middle part of the fjord (e.g. Midtre Øst) is a retention area thereby preventing water mass exchange with the inner part (Myksvoll et al. 2012). Hence, the advection into Østerbotn is limited.

It is believed that the inoculum of spring blooms in Northern Norway is contained within the sediment. Bottom-dwelling spores of diatoms are present in large numbers in Porsangerfjord (Hegseth et al. 1995, Ljungfeldt 2001). However, until now, the resting stage of *P. pouchetii* has not been discovered in the sediment or in the water. Hence, that could explain why *P. pouchetii* was not very abundant in Østerbotn in May.

The centric and pennate diatoms present in Østerbotn, *Chaetoceros* spp., *Fragilariopsis* sp., *Thalassiosira* sp., *Porosira glacialis* and *Skeletonema* sp., are the main species described in the *Chaetoceros socialis* association proposed by Degerlund and Eilertsen (2009) for northern Norway. Thus, May sampling in Østerbotn was during the main phase of the bloom.

4.1.2 Spring bloom in Porsangnes Øst

Porsangnes Øst was dominated by *P. pouchetii* in May. This species is known to be predominant in northern fjords like Porsangerfjord (Degerlund & Eilertsen 2009). Phytoplankton counts revealed a dominance of *P. pouchetii* single cells while it was only possible to see colonies with the VPR. Although colonies are big, single cells greatly contribute to *Phaeocystis* biomass (Wassmann et al. 2005).

The dominance of *P. pouchetii* could be explained by its physiological properties. Toxicological studies revealed that *P. pouchetii* produces polyunsaturated aldehyde (2-*trans*-4-*trans*-decadienal) under certain circumstances which restrains growth of cod and sea urchins embryos by reducing mitotic activity (Aanesen et al. 1998, Hansen et al. 2003, Hansen et al. 2004). Hansen and Eilertsen (2006) showed that *P. pouchetii* polyunsaturated aldehyde inhibited the exponential growth of diatoms *in vitro.* No data on polyunsaturated aldehyde concentration *in situ* are available since quantifying methods are not sensitive enough (Casotti et al. 2005). Hence, dominance of *P. pouchetii* may be explained by the production of polyunsaturated aldehydes to inhibits diatoms growth and their ability to grow at low silicate concentrations too low for diatoms (Egge & Aksnes 1992,

Degerlund & Eilertsen 2009). Thus, Porsangnes Øst bloom situation seemed to be in a more advanced stage than inside the fjord.

4.2 Associations of species related to the environment

Zooplankton taxa in Porsangerfjord displayed a distribution in connection with hydrography and with other factors such as phytoplankton assemblages. Traditionally copepods are believed to reside just below the maximum of Chl *a* concentration, which represents the peak of phytoplanktonic biomass (Herman 1983, Longhurst & Harrison 1989). Yet, we observed a change in zooplankton distribution with a change in phytoplankton composition. Hence, the second hypothesis is accepted. This hypothesis was particularly correct during the spring bloom in May, when phytoplankton species were numerous. In November the low diversity and abundance of phytoplankton did not affect zooplankton distributions much.

4.2.1 Large copepods

Calanus finmarchicus

C. finmarchicus was present in all seasons, both in the inner and outer part of the fjord. Yet, the phenology of the species had a slightly different timing between stations. In early April, Østerbotn *C. finmarchicus* had started its ascent to surface layers while they were still at depth in Porsangnes Øst. Moreover, *Calanus* spawned earlier in Porsangnes Øst than in Østerbotn. *C. finmarchicus* females synchronize their spawning with the start of the phytoplankton bloom (Diel & Tande 1992), which agrees with the more advanced bloom state observed in the outer part of the fjord. In May, *C. finmarchicus* population was more advanced in Porsangnes Øst (CII-CIV mostly) compared to Østerbotn (nauplii). Low temperatures slow down *Calanus* metabolism and thereby growth (Clarke & Peck 1991). Therefore, low temperatures in Østerbotn may explain the slower population development of *C. finmarchicus*. In November, the majority of *Calanus* had already migrated down for overwintering in Porsangnes Øst whereas *C. finmarchicus* were more active in Østerbotn. Two

different phenology types are therefore present in *C. finmarchicus* population. The first type is located in the outer part, close to the coast and has a late ascent after dormancy, fast population development, and an early descent to overwinter. The second *C. finmarchicus* group resides in the inner part of Porsangerfjord and has an early ascent after dormancy, delayed spawning, a slower growth rate, and a late descent to overwinter.

The origin of the *C. finmarchicus* population in Porsangnes Øst is uncertain as the lack of a physical barrier (i.e. sill) could advect individuals into the outer part of Porsangerfjord. In comparison with Porsangnes Øst, *C. finmarchicus* had a smaller population in the inner part of the fjord. Østerbotn is a remote area that has limited exchanges with the rest of the fjord (Myksvoll et al. 2012, Mankettikkara 2013). As no sampling took place during summer, part of the *Calanus* population could have been exported to the retention area in the middle basin without our knowledge. The physical properties of the inner part of Porsangerfjord could explain why *C. finmarchicus* CIV and CV were not so abundant in November in Østerbotn.

The habitat of *C. finmarchicus* changed over time but was always driven by temperature and salinity. Although the CCA analysis (Figure 12) revealed *P. pouchetii* and *C. finmarchicus* closely related, the vertical profiles in Porsangnes Øst in May showed that *C. finmarchicus* avoided *P. pouchetii* maximum abundance. The *Phaeocystis* peak of abundance was composed of "healthy" colonies. The avoidance of healthy *P. pouchetii* colonies by large taxa like *Calanus* or *Metridia* has been documented in the Barents Sea at a similar time of year (Estep et al. 1990), while other studies refute it (Norrbin et al. 2009). Mechanisms leading to the production of polyunsaturated aldehydes by *P. pouchetii* remain unknown, but seem to depend on the state of the cell or environmental factors, or both (Hansen et al. 2004). Hence, it is hard to assess if colonies were producing chemical compounds to repulse older *Calanus* copepodite stages, yet, *C. finmarchicus* was found near *Phaeocystis* colonies that were not so highly concentrated. In our study, *C. finmarchicus* had also an association with protozoans. *Calanus* copepodite stages preferentially select for ciliates and dinoflagellates

independently of phytoplankton concentrations (Calbet 2001, Calbet & Saiz 2005). *C. finmarchicus* start by grazing on main phytoplankton species during the phytoplankton bloom (diatoms and *P. pouchetii*) and shift to protozoans later in the season if it has not migrated down for overwintering (Davis 1987, Castellani et al. 2008).

Calanus nauplii occurred together with appendicularians in shallow waters with mild temperature and salinity. They were located below the pycnocline where the phytoplankton bloom was concentrated. Nauplii cannot actively migrate vertically, and do not seem to be able to swim through pycnoclines (Norrbin, personal communication). Nauplii are either ambush predators that jump on motile prey or create a feeding current to catch cells, or a combination of both (Bruno et al. 2012). CCA revealed that nauplii are associated to pennate diatoms, *Porosira glacialis*, and flagellates. Nauplii switched from feeding on ciliates to diatoms when the local concentration of diatoms increased (Irigoien et al. 2003). When the abundance of diatoms decrease during summer, nauplii feed on ciliates at high rates (Irigoien et al. 2003, Castellani et al. 2008). Hence, *C. finmarchicus* nauplii were associated with organisms that have a similar behavior (non-motile, filter feeders) and small phytoplankton and microzooplankton species.

Metridia longa

The other calanoid copepod, *M. longa*, was observed principally in Porsangnes Øst where temperature and salinity were higher than Østerbotn. *M. longa* was negatively correlated to phytoplankton biomass (Chl *a*) and closely related to *C. finmarchicus*, yet their distribution differed. In November, *M. longa* was spread over the whole water column while *C. finmarchicus* remained near the bottom, suggesting an active behavior of *M. longa*. This is supported by investigations conducted in Balsfjorden (Troms), where adults *M. longa* fed sporadically in winter (Grønvik & Hopkins 1984, Hopkins et al. 1984). Our CCA agrees with the previous statement, *M. longa* was associated with the dinoflagellate *Ceratium* sp. and the pennate diatom *Pseudo-nitzschia* sp. which

are species occurring late in the season (Hegseth et al. 1995, Eilertsen & Degerlund 2010). *Metridia* genus is omnivorous (Haq 1967, Båmstedt et al. 1990) and opportunistic, it grazes phytoplankton during the spring bloom and feed on *C. finmarchicus* eggs in early spring when phytoplankton stocks are low (Conover & Huntley 1991). Hence, due to the opportunistic nature of *M. longa*, the associations with other species were hard to assess.

4.2.2 Small copepods

Pseudocalanus spp.

Pseudocalanus spp. was frequently observed in waters with low temperature and salinity. These findings are consistent with data obtained in Balsfjorden (Troms), in the Baltic Sea where *Pseudocalanus* lived in cold, low salinity waters, and in Kongsfjorden (Svalbard) which is influenced by Atlantic waters (Norrbin 1994, Lischka & Hagen 2005, Renz & Hirche 2005). Yet these environmental factors cannot solely explain *Pseudocalanus* spp..

The two different CCA analyses are contradictory regarding *Pseudocalanus* associations and habitat choice, but this can be explained. Environmental variables constraining *Pseudocalanus* habitat differed from one analysis to the other. Phytoplankton was sampled into discrete intervals while VPR data was recorded continuously. Consequently parts of the *Pseudocalanus* population were excluded from the second analysis along with the microalgae species (Figure 12). The same is true for associations between *Pseudocalanus* and phytoplankton species; the VPR only captured *Phaeocystis* colonies whereas phytoplankton cell counts identified mostly *P. pouchetii* single cells, as manipulation of *P. pouchetii* preserved sample disrupt *Phaeocystis* colonies (Wassmann et al. 2005). In Porsangnes Øst, *Pseudocalanus* spp. avoided “healthy” *P. pouchetii* colonies, similar to *C. finmarchicus*, strengthening the idea that these colonies released polyunsaturated aldehydes. Hence, *Pseudocalanus* was associated with *P. pouchetii* single cells, flagellates, marine snow and fecal pellets. These findings agree with the literature as *Pseudocalanus* spp. was recorded feeding on

diatoms, flagellates, ciliates (Peters et al. 2006), and actively feeding on marine snow in the Baltic Sea (Möller et al. 2012).

Oithona spp.

The cyclopoid copepod, *Oithona* spp. was linked to high temperatures and salinities, and occurred both in Østerbotn and Porsangnes Øst. Similar to *Pseudocalanus* spp., both CCA suggest differing species associations for *Oithona.* The differences between the datasets used for the two CCA analyses, a part of the *Oithona* population could have been omitted, in the dataset merging zooplankton and phytoplankton counts, due to discrete sampling of phytoplankton.

In our study, *Oithona* was linked to *P. pouchetii* colonies, ciliates, and *Thalassionema nitzschoides.* We also found a close link to the pennate diatom *Thalassionema nitzschoides* which appears late in the growing season. However, there is a controversy on whether *Oithona* feeds on diatoms; some studies indicate that they do consume diatoms (Pond & Ward 2010) or do not (Nishibe et al. 2010, Zamora-Terol et al. 2013). Yet, *Oithona* preferentially feeds on ciliates (Zamora-Terol et al. 2013).

González and Smetacek (1994) also observed a coprophagous diet of *Oithona* in summer on the eastern shelf of Svalbard but our data does not confirm that statement. We hypothesize that when ciliate concentration is low *Oithona* can sporadically graze on diatoms during spring bloom and can fulfill its carbon requirements by eating fecal pellets when ciliates and diatoms are scarce.

Microsetella norvegica

M. norvegica had a preference for low temperature and salinities and was an abundant species in Porsangerfjord. Investigations in a sub-arctic Greenland fjord revealed that *M. norvegica* was very abundant, representing 87% of the annual copepod assemblage (Arendt et al. 2012). However, to reach such high abundances in a cold environment some adaptations are required. As the metabolic rates are slower in cold environments (Clarke & Peck 1991), *M. norvegica* has an adapted life cycle

rather than an altered physiology (Koski et al. 2013). Indeed, *M. norvegica* has a short reproductive period, high egg production and high mortality thus reducing the impact of cold waters (Koski et al. 2013). These mechanisms could explain high abundances in Østerbotn.

Microsetella occurred right below the pycnocline in Østerbotn and in Porsangnes Øst which is in consonance with the vertical distribution of *M. norvegica* found in the Skagerrak (north of Denmark) (Maar et al. 2006). This tiny harpacticoid copepod may not be able to swim across a thick boundary like the strong pycnoclines found in May.

M. norvegica and diatoms were associated, especially centric diatoms (*Skeletonema* sp., *Chaetoceros* spp. and *Thalassiosira* sp.). Some rois recorded *Microsetella* grazing on *P. pouchetii* colonies and diatoms aggregates (Figure 6, Figure 8). However, *M. norvegica* is too small to graze on *P. pouchetii* colonies. Colonies of *Phaeocystis* also have single flagellates cells that could be eaten by *Microsetella* (Wassmann et al. 2005).

Similar to other small copepods, *M. norvegica* is coprophagous. It feeds on particulate matter like discarded appendicularians houses and marine snow (Koski & Kiørboe 2005, Koski et al. 2007). Its vertical distribution, just below the pycnocline, allows *Microsetella* to feed sinking marine snow (Maar et al. 2006). Our study suggests a shift in food composition for *M. norvegica*. During the bloom, *Microsetella* fed on small diatoms or *P. pouchetii* single cells while during seasons with low phytoplankton availability it grazes on particulate matter.

4.2.3 Other zooplankton taxon

Appendicularians

A lack of previous investigations on appendicularian in northern Norwegian fjords makes the interpretation of patterns complex. Appendicularians were observed in waters with mild temperature ranges and salinities. Distribution of appendicularian is known to be closely related to temperature (López-Urrutia et al. 2005).

Two species were present, *Oikopleura* sp. and *Fritillaria borealis*. In southern Norway, *Fritillaria borealis* dominates in the winter time while *Oikopleura* sp. dominates during the summer (López-Urrutia et al. 2005). Yet these observations were done in Vestlandet (sampling around Bergen), a region located below the polar circle. Hence, this area does not experience polar night and phytoplankton can maintain stable abundances throughout winter, securing a food bank to appendicularians year round. The vertical distributions of appendicularians are therefore probably different for Arctic regions.

Appendicularians and copepod nauplii were found in similar environmental conditions. They both have a limited ability to move vertically, forcing them to stay in the area of their prey items. Appendicularians are filter feeders and are numerous in the Arctic (Bauerfeind et al. 1997). Large *Oikopleura* sp. and *F. borealis* feed efficiently on larger particles than small *Oikopleura* sp. and *F. borealis*, and can filter up to 80% of particles smaller than 15 and 7 µm respectively (Fernández et al. 2002). Appendicularians have also been described to be able to feed on bacteria (Vargas & González 2004). Our investigation showed that appendicularians were associated with flagellates and *P. pouchetii* single cells. Hence, particle size is determinant for appendicularians. Small cells like *Chaetoceros socialis* (early bloom species) and *P. pouchetii* single cells are more easily ingested compared to larger chain-forming taxa (e.g. *Fragilariopsis*, *Thalassiossira*) (Acuña et al. 2002).

4.3 Functioning of plankton community

4.3.1 Østerbotn

Østerbotn is an isolated area in the inner part of Porsangerfjord which has true Arctic hydrography with ice cover in wintertime and no Atlantic water inflow (Aure et al. 1994, Mankettikkara 2013). This particular environment selects for specific phyto-, microzoo- and mesozooplankton communities. The phytoplankton bloom in May was mainly composed by centric diatoms while microzooplankton dominated the winter season. Marine snow was very important in Østerbotn. Appendicularians were abundant in May which explains together with the phytoplankton bloom the high marine snow occurrence. Colonization of marine snow by copepods depends on the size of the aggregates, harpacticoid like *M. norvegica* preferentially settle on small aggregates (~0.1 cm radius) while cyclopoid and calanoid, e.g. *Oithona* sp. and *Pseudocalanus* spp., attach onto large particles (~1 cm radius) (Kiørboe 2000). Hence, the environment is favorable for coprophagous zooplankton like *Oithona* sp., *M. norvegica*, and *Pseudocalanus* sp. (González & Smetacek 1994, Koski & Kiørboe 2005, Möller et al. 2012).

C. finmarchicus had a delayed population development in this area; eggs were hatched later in Østerbotn than in Porsangnes Øst. Female *C. finmarchicus* were found to mature in concordance with the onset of phytoplankton bloom subsequently releasing their eggs (Diel & Tande 1992). In comparison with Porsangnes Øst, phytoplankton abundances peaked later, thus, delaying the population development of *C. finmarchicus*. The cold waters found in Østerbotn probably slowed down the metabolism of *C. finmarchicus* (Clarke & Peck 1991) while some small copepod like *M. norvegica* have an adapted life cycle to deal with low temperatures allowing them to dominate the zooplankton community (Koski et al. 2013).

4.3.2 Porsangnes Øst

Porsangnes Øst is a deep station in the outer part of Porsangerfjord which is influenced by Atlantic waters (Mankettikkara 2013). Over all the sampling points, temperatures and salinities were always higher than in the inner part of the fjord. *P. pouchetii* dominated the phytoplankton bloom in May, while flagellates and dinoflagellates were important in November and at 100 m depth in May. *P. pouchetii* was linked to high water temperatures which is supported by investigations of Degerlund and Eilertsen (2009). The zooplankton community was dominated by large copepods like *C. finmarchicus*. Krill and large copepods species are able to break down the mucus house of *P. pouchetii* colonies therefore dividing the colonies into smaller pieces available for grazing by small taxa (*Oithona* spp., *Pseudocalanus* spp. and *M. norvegica*) (Hansen et al. 1994). *P. pouchetii* single cells were grazed by cyclopoid and harpacticoid copepods, and can also be grazed by microzooplankton (flagellates, dinoflagellates and ciliates) at high rates (Archer et al. 2000). Hence, the whole zooplanktonic community used the *P. pouchetii* bloom.

Zooplankton taxa had a different behavior toward *P. pouchetii*, some avoided it (*C. finmarchicus*, *Pseudocalanus* spp.) while others did not (*M. norvegica*, *Oithona* spp.). *M. norvegica* and *Oithona* spp. may not be affected by toxins produced by *P. pouchetii* colonies. It is possible that they have chemical compounds that allow them to resist the polyunsaturated aldehydes or these colonies did not produce any chemical compounds; therefore, the avoidance of *C. finmarchicus* and *Pseudocalanus* spp. might be due to other factors (predation pressure). Norrbin et al. (2009) suggested that avoidance of *P. pouchetii* could also result from mechanical swimming disturbances due to large, sticky particles of the *Phaeocystis* dense layer. Further studies are needed to improve common knowledge on the biology of *P. pouchetii* and its effect on higher trophic levels to fully understand ecological interactions in a system where *P. pouchetii* occurs.

In comparison with Østerbotn *C. finmarchicus* females spawned earlier and *Calanus* population had numerous copepodite stages (CII-CIV). It suggests that the phytoplankton bloom occurred earlier in

In comparison with Østerbotn, *C. finmarchicus* females spawned earlier and the *Calanus* population had more CII to CIV copepodite stages. It suggests that the phytoplankton bloom occurred earlier in Porsangnes Øst than Østerbotn as *C. finmarchicus* females match the start of the phytoplankton bloom (Diel & Tande 1992). Low abundances in *M. longa* in May could be explained by their delayed spawning compared to *C. finmarchicus* (Grønvik & Hopkins 1984). Yet, in November we observed a partitioning of the water column between these two species. *Metridia* was active and spread over the entire water column whereas *C. finmarchicus* was already overwintering near the bottom.

5 Conclusion

This study aimed to determine the impact of hydrography and phytoplankton assemblage on zooplankton vertical distribution in Porsangerfjord, northern Norway. Factors driving zooplankton distribution in Porsangerfjord is a combination of different abiotic and biotic factors that varies over time.

The hydrography remained an important factor regarding zooplankton composition and distribution. The isolated inner part of Porsangerfjord had environmental conditions that favored small copepods while large copepods were preferentially in the outer part that had strong Atlantic influence. The strong pycnoclines during spring restrained distribution of *Calanus finmarchicus* nauplii and *Microsetella norvegica*. Yet, during bloom situations the vertical distribution of zooplankton seemed to be more related to the phytoplankton distribution.

During the spring bloom two different situations were observed, one bloom was diatom dominated and the other dominated by *Phaeocystis pouchetii*. The zooplankton vertical distribution was strongly influenced by these different phytoplankton compositions. *P. pouchetii*, the microalgae caused the avoidance of *C. finmarchicus* and *Pseudocalanus* spp. in Porsangnes Øst, whereas the diatom bloom was grazed mainly grazed on by small copepods and some *C. finmarchicus*.

Several points remain unclear. Future work should focus on investigating and quantifying the importance of each factor that could influence zooplankton distribution, therefore predation and light should also be integrated in the study design. Furthermore, the importance of the factors regulating the zooplankton vertical distribution varied throughout the year, therefore, a regular sampling would be recommended (winter, pre-bloom, bloom, summer, and fall situations). As some copepods did and did not avoid *P. pouchetii* healthy colonies, some more experimentation on *P. pouchetii* life cycle and biology should be conducted to understand the effect of this important species in northern Norway.

6 References

Aanesen RT, Eilertsen HC, Stabell OB (1998) Light-induced toxic properties of the marine alga *Phaeocystis pouchetii* towards cod larvae. Aquatic Toxicology:109-121

Acuña JL, Deibel D, Saunders PA, Booth B, Hatfield E, Klein B, Mei Z-P, Rivkin R (2002) Phytoplankton ingestion by appendicularians in the North Water. Deep Sea Research Part II: Topical Studies in Oceanography 49:5101-5115

Archer SD, Verity PG, Stefels J (2000) Impact of microzooplankton on the progression and fate of the spring bloom in fjords of northern Norway. Aquatic Microbial Ecology 22:27-42

Arendt KE, Juul-Pedersen T, Mortensen J, Blicher ME, Rysgaard S (2012) A 5-year study of seasonal patterns in mesozooplankton community structure in a sub-Arctic fjord reveals dominance of *Microsetella norvegica* (Crustacea, Copepoda). Journal of Plankton Research 35:105-120

Aure J, Føyn L, Pettersen R (1994) Miljøundersøkelser i norske fjorder 1975 - 1993 2. Finnmark: Tannfjord, Laksefjord, Porsangerfjord og Altafjord. Havforskningsintituttet Rapport: Fisken og Havet 8:68

Bagøien E, Kaartvedt S, Aksnes DL, Eiane K (2001) Vertical distribution and mortality of overwintering *Calanus*. Limnology & Oceanography: Fluids & Environments 46:1494-1510

Båmstedt U, Håkanson JL, Brenner-Larsen J, Björnsen PK, Greetz-Hansen O, Tiselius P (1990) Copepod nutritional condition and pelagic production during autumn in Kosterfjorden, western Sweden. Marine Biology 104:197-208

Basedow SL, Tande KS, Stige LC (2010) Habitat selection by a marine copepod during the productive season in the Subarctic. Marine Ecology Progress Series 416:165-178

Bauerfeind E, Garrity C, Krumbholz M, Ramseier RO, Voß M (1997) Seasonal variability of sediment trap collections in the Northeast Water Polynya. Part 2. Biochemical and microscopic composition of sedimenting matter. Journal of Marine Systems 10:371-389

Benfield MC, Davis CS, Wiebe PH, Gallager SM, Lough RG, Copley NJ (1996) Video Plankton Recorder estimates of copepod, pteropod and larvacean distributions from a stratified region of Georges Bank with comparative measurements from a MOCNESS sampler. Deep Sea Research Part II: Topical Studies in Oceanography 43:1925-1945

Brown JS (1998) Game theory and habitat selection. Game theory and animal behavior:188-220

Bruno E, Andersen Borg CM, Kiørboe T (2012) Prey Detection and Prey Capture in Copepod Nauplii. PLoS ONE 7:e47906

Calbet A (2001) Mesozooplankton grazing effect on primary production: A global comparative analysis in marine ecosystems. Limnol Oceanogr 46:1824-1830

Calbet A, Saiz E (2005) The ciliate-copepod link in marine ecosystems. Aquatic Microbial Ecology 38:157-167

Casotti R, Mazza S, Brunet C, Vantrepotte V, Ianora A, Miralto A (2005) Growth Inhibition and Toxicity of the Diatom Aldehyde 2-Trans, 4-Trans-Decadienal *Onthalassiosira weissflogii* (Bacillariophyceae). Journal of Phycology 41:7-20

Castellani C, Irigoien X, Mayor DJ, Harris RP, Wilson D (2008) Feeding of *Calanus finmarchicus* and *Oithona similis* on the microplankton assemblage in the Irminger Sea, North Atlantic. Journal of Plankton Research 30:1095-1116

Clarke A, Peck LS (1991) The physiology of polar marine zooplankton*. Polar Research 10:355-369

Conover RJ, Huntley M (1991) Copepods in ice-covered seas—Distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. Journal of Marine Systems 2:1-41

Cottier FR, Nilsen F, Skogseth R, Tverberg V, Skarthhamar J, Svendsen H (2010) Arctic fjords: a review of the oceanographic environment and dominant physical processes. Geological Society, London, Special Publications 344:35-50

Dale T, Bagøien E, Melle W, Kaartvedt S (1999) Can predator avoidance explain varying overwintering depth of *Calanus* in different oceanic water masses? Marine Ecology Progress Series 179:113-121

Davis CS (1987) Components of the zooplankton production cycle in the temperate ocean. Journal of Marine Research 45:947-983

Davis CS, Gallager SM, Berman MS, Haury LR, Strickler JR (1992a) The Video Plankton Recorder (VPR): Design and initials results. Arch Hydrobiol Beih Ergebn Limnol 36:67-81

Davis CS, Gallager SM, Solow AR (1992b) Microaggregations of Oceanic Plankton Observed by Towed Video Microscopy. Science 257:230-232

Degerlund M, Eilertsen HC (2009) Main Species Characteristics of Phytoplankton Spring Blooms in NE Atlantic and Arctic Waters (68–80° N). Estuaries and Coasts 33:242-269

Dekshenieks MM, Donaghay PL, Sullivan JM, Rines JEB, Osborn TR, Twardowski MS (2001) Temporal and spatial occurrence of thin phytoplankton layers in relation to physical processes. Marine Ecology Progress Series 223:61-71

Diel S, Tande KS (1992) Does the spawning of *Calanus finmarchicus* in high latitudes follow a reproducible pattern? Marine Biology 113:21-31

Egge JK, Aksnes DL (1992) Silicate as regulating nutrient in phytoplankton competition. Marine Ecology Progress Series 83:281-289

Eilertsen HC, Degerlund M (2010) Phytoplankton and light during the northern high-latitude winter. Journal of Plankton Research 32:899-912

Eilertsen HC, Frantzen S (2007) Phytoplankton from two sub-Arctic fjords in northern Norway 2002–2004: I. Seasonal variations in chlorophyll a and bloom dynamics. Marine Biology Research 3:319-332

Eilertsen HC, Skarðhamar J (2006) Temperatures of north Norwegian fjords and coastal waters: Variability, significance of local processes and air–sea heat exchange. Estuarine, Coastal and Shelf Science 67:530-538

Estep KW, Nejstgaard JC, Skjoldal HR, Rey F (1990) Predation by copepods upon natural populations of *Phaeocystis pouchetii* as a function of the physiological state of the prey. Marine Ecology Progress Series 67:235-249

Fager EW, McGowan JA (1963) Zooplankton Species Groups in the North Pacific: Co-occurrences of species can be used to derive groups whose members react similarly to water-mass types. Science 140:453-460

Fernández D, López-Urrutia Á, Fernández A, Acuña JL, Harris R (2002) Retention efficiency of 0.2 to 6 µm particles by the appendicularians *Oikopleura dioica* and *Fritillaria borealis*. Marine Ecology Progress Series 266:89-101

Fevolden S-E, Martinez I, Christiansen JS (1999) RAPD and scnDNA analyses of polar cod, *Boreogadus saida* (Pisces, Galidae), in the north Atlantic. Sarsia 84:99-103

Fitzgeorge-Balfour T, Hirst AG, Lucas CH, Craggs J (2013) Influence of copepod size and behaviour on vulnerability to predation by the scyphomedusa Aurelia aurita. Journal of Plankton Research 36:77-90

Fossheim M, Primicerio R (2008) Habitat choice by marine zooplankton in a high-latitude ecosystem. Marine Ecology Progress Series 364:47-56

Gallager SM, Davis CS, Epstein AW, Solow A, Beardsley RC (1996) High-resolution observations of plankton spatial distributions correlated with hydrography in the Great South Channel, Georges Bank. Deep Sea Research Part II: Topical Studies in Oceanography 43:1627-1663

Gallager SM, Yamazaki H, Davis CS (2004) Contribution of fine-scale vertical structure and swimming behavior to formation of plankton layers on Georges Bank. Marine Ecology Progress Series 267:27-43

Glover DM, Brewer PG (1988) Estimates of wintertime mixed layer nutrient concentrations in the North Atlantic. Deep Sea Research Part I: Oceanographic Research Papers 35:1525-1546

González HE, Smetacek V (1994) The possible role of the cyclopoid copepod *Oithona* in retarding vertical flux of zooplankton faecal material. Marine Ecology Progress Series 113:233-246

Grønvik S, Hopkins CCE (1984) Ecological investigations of the zooplankton community of Balsfjorden, Northern Norway: Generation cycle, seasonal vertical distribution, and seasonal variations in body weight and carbon and nitrogen content of the copepod *Metridia longa* (Lubbock). Journal of Experimental Marine Biology and Ecology 80:93-107

Hansen B, Verity PG, Falkenhaug T, Tande KS, Norrbin F (1994) On the trophic fate of *Phaeocystis pouchetii* (Haricot). V. Trophic relationships between *Phaeocystis* and zooplankton: an assessment of methods and size dependence. Journal of Plankton Research 16:487-511

Hansen E, Eilertsen HC (2006) Do the polyunsaturated aldehydes produced by *Phaeocystis pouchetii* (Hariot) Lagerheim influence diatom growth during the spring bloom in Northern Norway? Journal of Plankton Research 29:87-96

Hansen E, Eilertsen HC, Ernstsen A, Genevière A-M (2003) Anti-mitotic activity towards sea urchin embryos in extracts from the marine haptophycean *Phaeocystis pouchetii* (Hariot) Lagerheim collected along the coast of northern Norway. Toxicon 41:803-812

Hansen E, Ernstsen A, Eilertsen HC (2004) Isolation and characterisation of a cytotoxic polyunsaturated aldehyde from the marine phytoplankter *Phaeocystis pouchetii* (Hariot) Lagerheim. Toxicology 199:207-217

Haq SM (1967) Nutritional physiology of *Metridia lucens* and *M. longa* from the Gulf of Maine. Limnol Oceanogr 12:40-51

Haury LR, McGowan JA, Wiebe PH (1978) Patterns and Processes in the Time-Space Scales of Plankton Distributions. In: Steele J (ed) Spatial Pattern in Plankton Communities, Book 3. Springer US, New York, 227-377

Hegseth EN, Svendsen H, Hellum von Quillfeldt C (1995) Phytoplankton in fjords and coastal waters of northern Noway: environmental condtions and dynamics of spring bloom. Ecology of Fjords and Coastal Waters:45-72

Helbling EW, Eilertsen HC, Villafañe VE, Holm-Hansen O (1996) Effects of UV radiation on post-bloom phytoplankton populations in Kvalsund, North Norway. Journal of Photochemistry and Pothobiology B: Biology 33:255-259

Herman AW (1983) Vertical distribution patterns of copepods, chlorophyll, and production in the northeastern Baffin Bay. Limnol Oceanogr 28:709-719

Hodal H, Kristiansen S (2008) The importance of small-celled phytoplankton in spring blooms at the marginal ice zone in the northern Barents Sea. Deep Sea Research Part II: Topical Studies in Oceanography 55:2176-2185

Hopkins CCE, Tande KS, Grønvik S (1984) Ecological investigations of the zooplankton community of Balsfjorden, Northern Noway: An analysis of growth and overwntering tactics in relation to niche and environment in *Metridia longa* (Lubbock), *Calanus finmarchicus* (Gunnerus), *Thysanoessa inermis* (Krøyer) and *T. raschi* (M. Sars). Journal of Experimental Marine Biology and Ecology 82:77-99

Irigoien X, Titelman J, Harris RP, Harbour D, Castellani C (2003) Feeding of Calanus finmarchicus nauplii in the Irminger Sea. Marine Ecology Progress Series 262:193-200

Jackson DA, Harvey HH (1989) Biogeographic Associations in Fish Assemblages: Local vs. Regional Processes. Ecology 70:1472-1484

Kara AB, Rochford PA, Hurlburt HE (2000) An optimal definition for ocean mixed layer depth. Journal of Geophysical Research 105:16803

Kiørboe T (2000) Colonization of marine snow aggregates by invertebrate zooplankton: Abundance, scaling, and possible role. Limnol Oceanogr 45:479-484

Kiørboe T, Saiz E (1995) Planktivorous feeding in calm and turbulent environments, with emphasis on copepods. Marine Ecology Progress Series 122:135-145

Koski M, Kiørboe T (2005) Benthic life in the pelagic: Aggregate encounter and degradation rates by pelagic harpaticoid copepods. Limnol Oceanogr 50:1254-1263

Koski M, Moller EF, Maar M, Visser AW (2007) The fate of discarded appendicularian houses: degradation by the copepod, Microsetella norvegica, and other agents. Journal of Plankton Research 29:641-654

Koski M, Swalethorp R, Kjellerup S, Nielsen TG (2013) The mystery of Microsetella: combination of sac- and broadcast-spawning in an Arctic fjord. Journal of Plankton Research 36:259-264

Legendre L, Legendre P (1978) Associations. In: Sournia A (ed) Monogrpahs on oceanographic Methodology Phytoplankton Manual, Book 6. Unesco, Paris, 261-272

Lischka S, Hagen W (2005) Life histories of the copepods Pseudocalanus minutus, P. acuspes (Calanoida) and Oithona similis (Cyclopoida) in the Arctic Kongsfjorden (Svalbard). Polar Biology 28:910-921

Ljungfeldt L (2001) Aspects of the initiation of diatom spring blooms in Northern Norwegian coastal waters—with an emphasis on the role of resting spores. Cand. Scient. thesis, University of Tromsø,

Longhurst AR, Harrison WG (1989) The biological pump: Profiles of plankton production and consumption in the upper ocean. Progress in Oceanography 22:47-123

López-Urrutia Á, Harris R, Acuña JL, Båmstedt U, Flood PR, Fyhn HF, Gasser B, Gorsky G, Irigoien X, Martinussen M (2005) A comparison of appendicularians seasonal cycles in four contrasting European coastal environments. In: Gorsky G, Youngbluth MJ, Deibel D (eds) Response of marine ecosystem to global change: Ecological impact of appendicularians. Éditions Scientifiques, Paris

Maar M, Visser AW, Nielsen TG, Stips A, Saito H (2006) Turbulence and feeding behaviour affect the vertical distributions of *Oithona similis* and *Microsetella norvegica*. Marine Ecology Progress Series 313:157-172

Mackas DL, Denman KL, Abbott MR (1985) Plankton patchiness: biology in the physical vernacular. Bulletin of Marine Science 37:652-674

Mankettikkara R (2013) Hydrophysical characteristics of the northern Norwegian coast and fjords. PhD, University of Tromsø, Tromsø

Margalef R (1958) Temporal succession and spatial heterogeneity in phytoplankton. University of California press

McManus MA, Cheriton OM, Drake PJ, Holliday DV, Storlazzi CD, Donaghay PL, Greenlaw CF (2005) Effects of physical processes on structure and transport of thin zooplankton layers in the coastal ocean. Marine Ecology Progress Series 301:199-215

Möller KO, St John M, Temming A, Floeter J, Sell AF, Herrmann JP, Möllmann C (2012) Marine snow, zooplankton and thin layers: indications of a trophic link from small-scale sampling with the Video Plankton Recorder. Marine Ecology Progress Series 468:57-69

Myksvoll MS, Sandvik AD, Skarðhamar J, Sundby S (2012) Importance of high resolution wind forcing on eddy activity and particle dispersion in a Norwegian fjord. Estuarine, Coastal and Shelf Science 113:293-304

Nishibe Y, Kobari T, Ota T (2010) Feeding by the cyclopoid copepod *Oithona similis* on the microzooplankton assemblage in the Oyashio region during spring. Plankton Benthos Res 5:74-78

Norrbin F (1994) Seasonal patterns in gonad maturation, sex ratio and size in some small, high-latitude copepods: implications for overwintering tactics. Journal of Plankton Research 16:115-131

Norrbin F, Eilertsen HC, Degerlund M (2009) Vertical distribution of primary producers and zooplankton grazers during different phases of the Arctic spring bloom. Deep Sea Research Part II: Topical Studies in Oceanography 56:1945-1958

Paxinos R, Mitchell JG (2000) A rapid Utermöhl method for estimating algal numbers. Journal of Plankton Research 22:2255-2262

Peters J, Renz J, van Beusekom J, Boersma M, Hagen W (2006) Trophodynamics and seasonal cycle of the copepod Pseudocalanus acuspes in the Central Baltic Sea (Bornholm Basin): evidence from lipid composition. Marine Biology 149:1417-1429

Pond DW, Ward P (2010) Importance of diatoms for Oithona in Antarctic waters. Journal of Plankton Research 33:105-118

Rat'kova T, Wassman P (2002) Seasonal variation and spatial distribution of phyto- and protozooplankton in the central Barents Sea. Journal of Marine Systems 38:47-75

Renz J, Hirche H-J (2005) Life cycle of Pseudocalanus acuspes Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I. Seasonal and spatial distribution. Marine Biology 148:567-580

Svendsen H (1991) Preliminary results from a hydrophysical investigation of Porsangerfjord, Altafjord and adjacent coastal waters, June-August 1990. In: Bergen Uo (ed). Geophysical Institute, Department of Oceanography

Sverdrup H (1953) On conditions for the vernal blooming of phytoplankton. Journal du Conseil 18:287-295

Tande KS (1982) Ecological investigations on the zooplankton community of Balsfjorden, northern Norway: generations cycles, and variations in body weight and body content of carbon and nitrogen related to overwintering and reproduction in the copepod *Calanus finmarchicus* (Gunnerus). J Exp Mar Biol Ecol 62:129-142

ter Braak CJF, Verdonschot PFM (1995) Canonical correspondance analysis and related multivariate methods in aquatic ecology. Aquatic Sciences 57:255-289

Trudnowska E, Sagan S, Kwasniewski S, Darecki M, Blachowiak-Samolyk K (2014) Fine-scale zooplankton vertical distribution in relation to hydrographic and optical characteristics of the surface waters on the Arctic shelf. Journal of Plankton Research 37:120-133

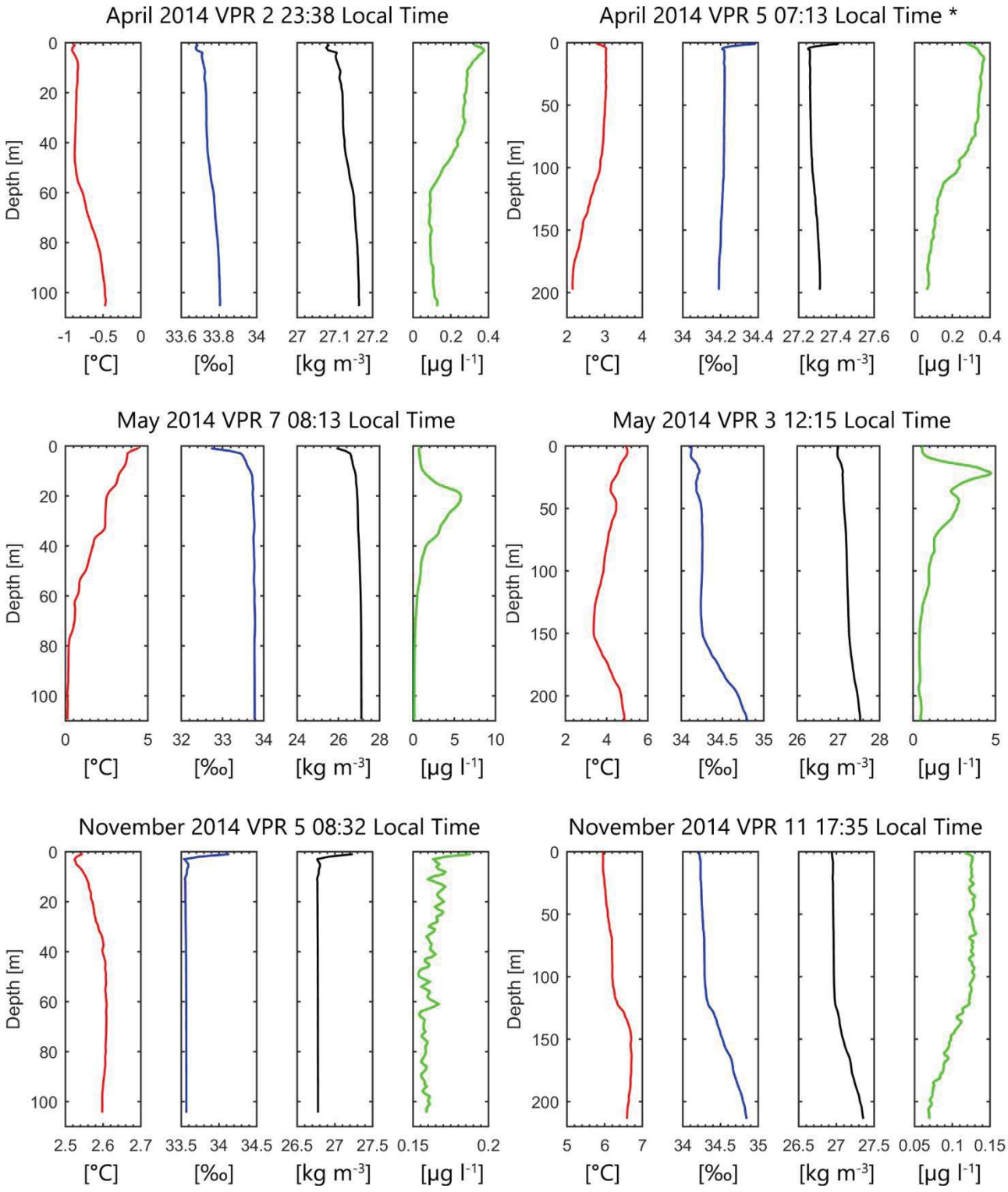
Vargas CA, González HE (2004) Plankton community structure and carbon cycling in a coastal upwelling system. I. Bacteria, microprotozoans and phytoplankton in the diet of copepods and appendicularians. Aquatic Microbial Ecology 34:151-164

Wassmann P, Rat'kova T, Reigstad M (2005) The contribution of single and colonial cells of Phaeocystis pouchetii to spring and summer blooms in the north-eastern North Atlantic. Harmful Algae 4:823-840

Wold A, Norrbin F (2004) Vertical migration as a response to UVR stress in *Calanus finmarchicus* females and nauplii. Polar Research 23:27-34

Zamora-Terol S, Nielsen TG, Saiz E (2013) Plankton community structure and role of Oithona similis on the western coast of Greenland during the winter-spring transition. Marine Ecology Progress Series 483:85-102

Appendix A



Appendix A. CTD profiles from the VPR CTD, at Østerbotn (*left* figures) and Porsangnes Øst (*right* figures), in April (*top*), May (*middle*), and November 2014 (*bottom*). **Red** line represents temperature in °C, **blue** line represents salinity in ‰, **black** line represents density in kg m^{-3}, and **green** line represents Chl *a* in µg l^{-1}. Please note the different scales of the *x*-axis. * Midtre Øst instead of Porsangnes Øst.

Appendix B

Appendix 1B. Phytoplankton counts in cell m^{-3}, at Porsangnes Øst in May 2014.

Cruise	Station name	Depth [m]	Species name	Abundance [cell m^{-3}]
May	Porsangnes Øst	0	*Phaeocystis pouchetii* single cell	2230
May	Porsangnes Øst	0	Flagellate indeterminate	543
May	Porsangnes Øst	5	*Phaeocystis pouchetii* single cell	2166
May	Porsangnes Øst	5	Flagellate indeterminate	878
May	Porsangnes Øst	10	*Phaeocystis pouchetii* single cell	2804
May	Porsangnes Øst	10	Flagellate indeterminate	1206
May	Porsangnes Øst	10	Pennate diatom indeterminate	44
May	Porsangnes Øst	10	Dinoflagellate indeterminate	19
May	Porsangnes Øst	10	*Chaetoceros* sp.	6
May	Porsangnes Øst	20	*Phaeocystis pouchetii* single cell	2912
May	Porsangnes Øst	20	Flagellate indeterminate	1427
May	Porsangnes Øst	20	Pennate diatom indeterminate	25
May	Porsangnes Øst	20	Dinoflagellate indeterminate	13
May	Porsangnes Øst	20	*Chaetoceros* sp.	6
May	Porsangnes Øst	20	Ciliate indeterminate	6
May	Porsangnes Øst	30	*Phaeocystis pouchetii* single cell	817
May	Porsangnes Øst	30	Flagellate indeterminate	402
May	Porsangnes Øst	30	Ciliate indeterminate	19
May	Porsangnes Øst	30	Pennate diatom indeterminate	12
May	Porsangnes Øst	30	*Thalassionema nitzschioides*	12
May	Porsangnes Øst	30	*Porosira glacialis*	6
May	Porsangnes Øst	30	Dinoflagellate indeterminate	2
May	Porsangnes Øst	50	*Phaeocystis pouchetii* single cell	662
May	Porsangnes Øst	50	Flagellate indeterminate	192
May	Porsangnes Øst	50	Ciliate indeterminate	25
May	Porsangnes Øst	50	Pennate diatom indeterminate	12
May	Porsangnes Øst	100	Flagellate indeterminate	343
May	Porsangnes Øst	100	*Phaeocystis pouchetii* single cell	31
May	Porsangnes Øst	100	*Porosira glacialis*	22
May	Porsangnes Øst	100	Ciliate indeterminate	9
May	Porsangnes Øst	100	Pennate diatom indeterminate	6
May	Porsangnes Øst	100	Dinoflagellate indeterminate	3

Appendix 2B. Phytoplankton counts in cell m^{-3}, at Østerbotn in May 2014.

Cruise	Station name	Depth [m]	Species name	Abundance [cell m^{-3}]
May	Østerbotn	0	*Chaetoceros* sp.	382
May	Østerbotn	0	*Phaeocystis pouchetii* single cell	85
May	Østerbotn	0	*Porosira glacialis*	60
May	Østerbotn	0	*Thalassiosira* sp.	19
May	Østerbotn	0	Flagellate indeterminate	47
May	Østerbotn	0	Pennate diatom indeterminate	6
May	Østerbotn	5	*Chaetoceros* sp.	404
May	Østerbotn	5	*Phaeocystis pouchetii* single cell	123
May	Østerbotn	5	*Porosira glacialis*	25
May	Østerbotn	5	Pennate diatom indeterminate	16
May	Østerbotn	5	Flagellate indeterminate	3
May	Østerbotn	10	*Chaetoceros* sp.	335
May	Østerbotn	10	Flagellate indeterminate	155
May	Østerbotn	10	*Phaeocystis pouchetii* single cell	79
May	Østerbotn	10	*Porosira glacialis*	44
May	Østerbotn	10	*Thalassiosira* sp.	35
May	Østerbotn	10	Pennate diatom indeterminate	28
May	Østerbotn	10	Dinoflagellate indeterminate	25
May	Østerbotn	20	*Chaetoceros* sp.	910
May	Østerbotn	20	*Phaeocystis pouchetii* single cell	189
May	Østerbotn	20	Flagellate indeterminate	95
May	Østerbotn	20	Pennate diatom indeterminate	51
May	Østerbotn	20	*Porosira glacialis*	44
May	Østerbotn	20	*Thalassiosira* sp.	44
May	Østerbotn	20	Ciliate indeterminate	13
May	Østerbotn	30	*Chaetoceros* sp.	1052
May	Østerbotn	30	Flagellate indeterminate	483
May	Østerbotn	30	*Fragilariopsis* sp.	112
May	Østerbotn	30	*Thalassiosira* sp.	99
May	Østerbotn	30	Pennate diatom indeterminate	37
May	Østerbotn	30	*Phaeocystis pouchetii* single cell	25
May	Østerbotn	30	*Skeletonema* sp.	19
May	Østerbotn	30	Dinoflagellate indeterminate	12
May	Østerbotn	30	*Thalassionema nitzschioides*	7
May	Østerbotn	50	Flagellate indeterminate	83
May	Østerbotn	50	*Chaetoceros* sp.	52
May	Østerbotn	50	*Fragilariopsis* sp.	36
May	Østerbotn	50	Dinoflagellate indeterminate	6
May	Østerbotn	50	Pennate diatom indeterminate	2
May	Østerbotn	50	*Thalassiosira* sp.	2
May	Østerbotn	100	Flagellate indeterminate	24
May	Østerbotn	100	*Chaetoceros* sp.	5
May	Østerbotn	100	Ciliate indeterminateerminate	2
May	Østerbotn	100	Pennate diatom indeterminate	1

Appendix 3B. Phytoplankton counts in cell m^{-3}, at Porsangnes Øst in November 2014.

Cruise	Station name	Depth [m]	Species name	Abundance [cell m^{-3}]
November	Porsangnes Øst	0	Flagellate indeterminate	9
November	Porsangnes Øst	0	Dinoflagellate indeterminate	5
November	Porsangnes Øst	0	*Skeletonema* sp.	1
November	Porsangnes Øst	0	*Chaetoceros* sp.	0
November	Porsangnes Øst	0	Ciliate indeterminate	0
November	Porsangnes Øst	0	*Cylindrotheca closterium*	0
November	Porsangnes Øst	0	*Pseudo-nitzschia* sp.	0
November	Porsangnes Øst	20	Flagellate indeterminate	7
November	Porsangnes Øst	20	Dinoflagellate indeterminate	4
November	Porsangnes Øst	20	*Ceratium* sp.	0
November	Porsangnes Øst	20	Ciliate indeterminate	0
November	Porsangnes Øst	20	*Cylindrotheca closterium*	0
November	Porsangnes Øst	20	*Pseudo-nitzschia* sp.	0
November	Porsangnes Øst	50	Flagellate indeterminate	10
November	Porsangnes Øst	50	Dinoflagellate indeterminate	3
November	Porsangnes Øst	50	*Ceratium* sp.	0
November	Porsangnes Øst	50	Ciliate indeterminate	0
November	Porsangnes Øst	50	Pennate diatom indeterminate	0
November	Porsangnes Øst	50	*Skeletonema* sp.	0

Appendix 4B. Phytoplankton counts in cell m^{-3}, at Porsangnes Øst in November 2014.

Cruise	Station name	Depth [m]	Species name	Abundance [cell m^{-3}]
November	Østerbotn	0	Flagellate indeterminate	19
November	Østerbotn	0	Dinoflagellate indeterminate	2
November	Østerbotn	0	*Ceratium* sp.	0
November	Østerbotn	0	*Chaetoceros* sp.	0
November	Østerbotn	0	Ciliate indeterminate	0
November	Østerbotn	0	Cylindrotheca closterium	0
November	Østerbotn	0	*Thalassionema nitzschioides*	0
November	Østerbotn	20	Flagellate indeterminate	12
November	Østerbotn	20	*Cylindrotheca closterium*	1
November	Østerbotn	20	Dinoflagellate indeterminate	1
November	Østerbotn	20	*Pseudo-nitzschia* sp.	1
November	Østerbotn	20	Ciliate indeterminate	0
November	Østerbotn	20	*Thalassionema nitzschioides*	0
November	Østerbotn	50	Flagellate indeterminate	10
November	Østerbotn	50	*Chaetoceros* sp.	1
November	Østerbotn	50	Ciliate indeterminate	0
November	Østerbotn	50	*Cylindrotheca closterium*	0
November	Østerbotn	50	Dinoflagellate indeterminate	0