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THE ARCTIC UNIVERSITY OF NORWAY

Faculty of Biosciences, Fisheries and Economics Department of Arctic Marine Biology

Zooplankton communities on the Northeast coast of Greenland

How can we explain vertical and regional distribution?

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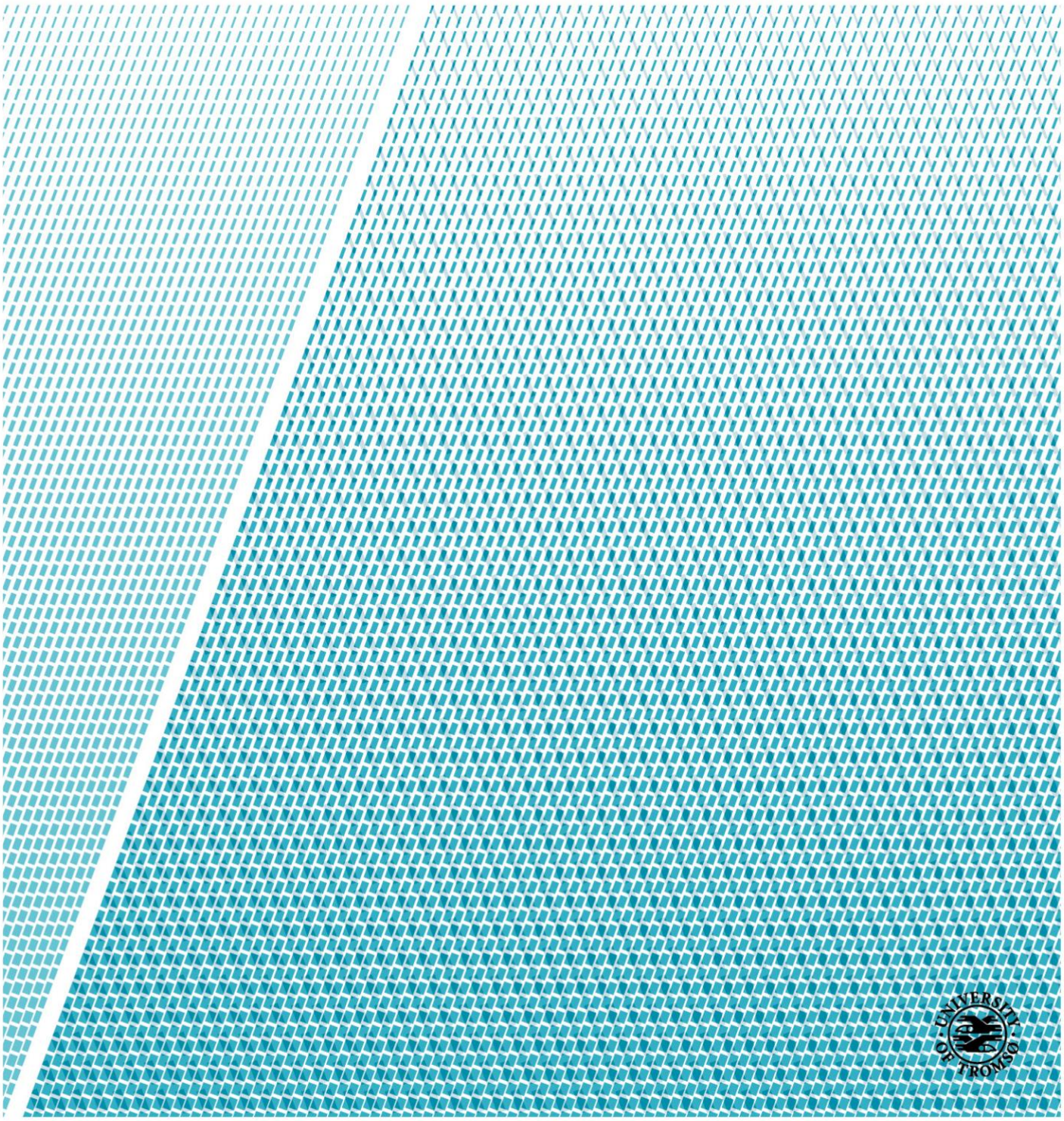
Théo Beroujon

BIO-3950 *Master's thesis in Biology* *May 2019*



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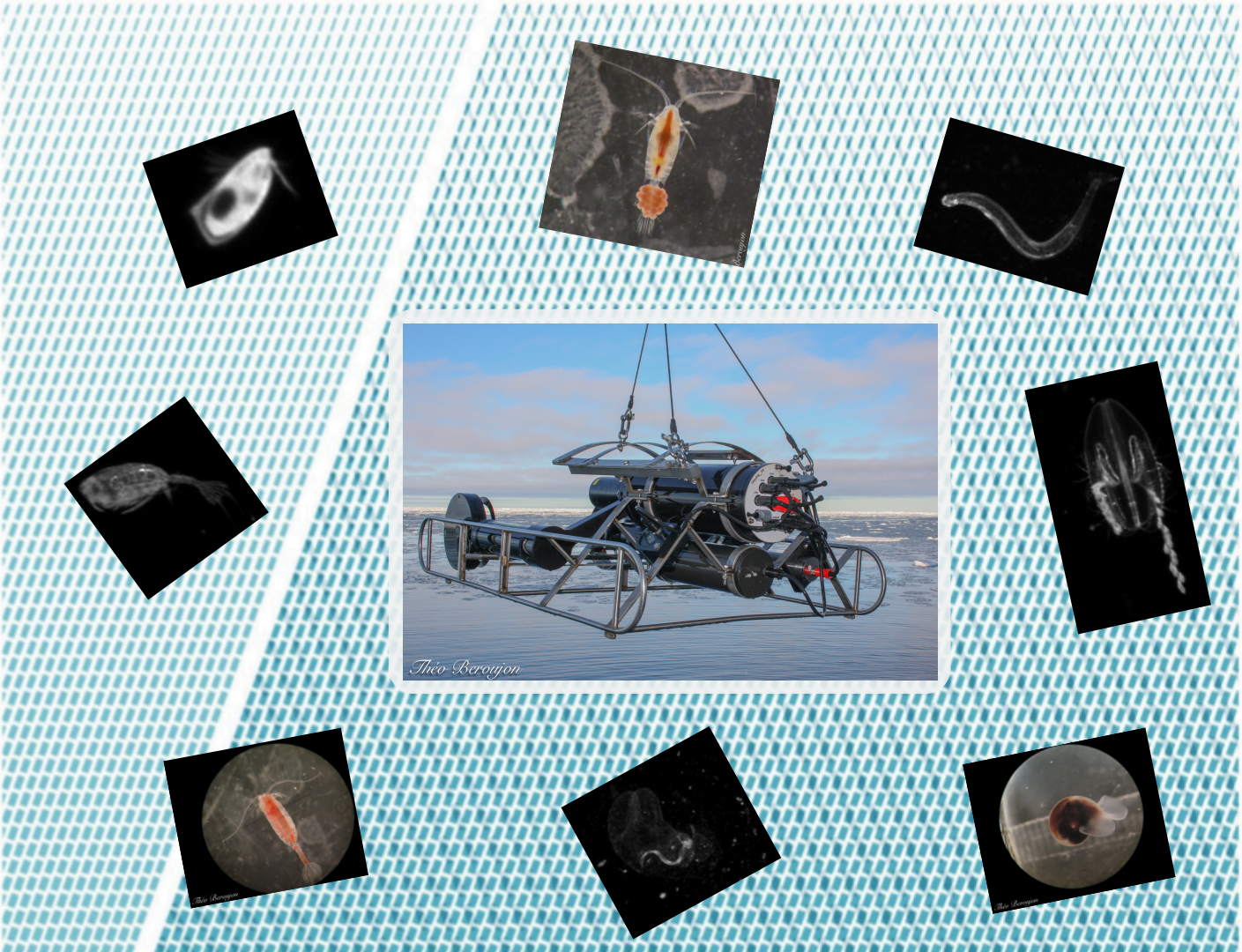

Main supervisor : *Fredrika NORRBIN*
Co-supervisor : *Jørgen Schou CHRISTIANSEN*

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Acknowledgments

After putting a lot of work on this thesis it is time to share it as is the goal of science: sharing the knowledge. In order to get to this thesis a lot of work and people were needed.

First, I want to thank my main supervisor Fredrika Norrbin for giving me this amazing chance to work with zooplankton using this atypical and very interesting device which is the Video Plankton Recorder (VPR). Working on a very remote area such as Northeast Greenland is a rare opportunity which would not have been possible without the TUNU-Program. I am very thankful to Jørgen Schou Christiansen who leads the program and Fredrika Norrbin who gave me the opportunity to go and work on this fantastic region of the globe. A lot of different skills and tools were needed to accomplish all this work and for that I want to thank Svein Kristiansen for providing Chlorophyll *a* data from water samples, Einar Nilsen for is advices in statistical analysis and for sharing his time put into trying different method to display the complex VPR data, Tom Arne Rydningen for creating a topography map of the area with the different location used in this thesis and Pierre Priou for his Matlab scripts helping me making graphs showing VPR results.

This thesis was a very big challenge for me as writing was not easy considering my English grammar at the beginning of it. Thanks to my supervisors Fredrika Norrbin and Jørgen Schou Christiansen as well as Nina Le Trocquer who reviewed this thesis many times we manage to give it a proper thesis-like shape. It takes a lot of perseverance and courage to dive on a long work like it keeping the head up for any comments and critics. Indeed, it is never negative, thanks Coralie Barth Jensen, Daniel Fernández Román and all the people around me for their good ideas, comments and answers to my questions.

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Last but not least, all of this would have never happened without the support from my parents to move far from my hometown and without the brilliant idea to move to Tromsø of my lovely traveller addict Nina Le Trocquer.

Abstract

Most studies on zooplankton investigate the famous, and omnipresent, Calanoid copepods *Calanus* spp., because they are abundant, and constitute the major trophic link in marine ecosystems. Indeed, Northeast Greenland is located on the crossroad of Arctic and Atlantic waters which, potentially, can lead to a high biodiversity originating from different domains of marine life. However, there are very few zooplankton studies from Northeast Greenland and the predicted strong impact of climate change could modify drastically the community composition and interaction in this region. The concern for climate change is growing bigger each day, and in order to estimate its impact, time series are needed. The aim of the present study is to create the first large-scale baseline of zooplankton distribution, taxa composition and abundance in Northeast Greenland. We explored five very different habitats in Northeast Greenland (latitudes 76-79 °N), including an isolated fjord (Bessel Fjord), an open bay (Dove Bugt), as well as banks, troughs and shelf locations offshore. We investigated patterns of biodiversity and abundance across locations. Coastal locations showed a higher zooplankton abundance compared to the offshore shelf locations. On the other hand, biodiversity of zooplankton communities seemed to increase from coastal towards offshore locations.

Besides using a zooplankton net (WP-2) and a Video Plankton Recorder (VPR) to collect data on biodiversity and abundance, we used the CTD data of the VPR to correlate each zooplankton taxon with *in situ* environmental parameters such as temperature, salinity, depth and Chlorophyll *a* (Chl *a*) concentration. In addition, the VPR data provided information about the concentration of marine snow. Some taxa revealed the same environmental preferences such as *Pseudocalanus* sp., *Microcalanus* sp., Cnidaria and Ctenophora which occurred in the upper water column at low salinity and high temperature. Ostracoda and *Metridia* sp., on the other hand, were present mostly in deeper waters with low concentrations of marine snow and Chl. *a*. Radiolaria and *Oithona* sp. occurred mainly in cold waters, whereas Appendicularia and Echinodermata were tightly linked to high concentrations of marine snow and Chl *a* concentration.

Climate change affects zooplankton communities around the world. However, the Arctic seas are particularly susceptible to ocean warming, and therefore, it is crucial to build a baseline and maintain long-term monitoring of the marine biota in Northeast Greenland.

Keywords: Abundance - Arctic - Baseline study - Environmental parameters - Image analysis - Northeast Greenland - Spatial distribution - Video Plankton Recorder - Zooplankton communities - Zooplankton habitat

Abbreviations

- VPR : Digital autonomous Video Plankton Recorder
- WP-2 : Plankton net (in this study modified from UNESCO, 1968)
- CTD : Conductivity Temperature Depth sensors
- NEG : North East Greenland
- EGC : East Greenland Current
- RAC : Return Atlantic Current
- WSC: West Spitzbergen Current
- Chl *a* : Chlorophyll *a* ($mg \cdot m^{-3}$)
- ROIs : Region of Interest from VPR images analysis
- CCA : Canonical Correspondence Analysis
- Anova : Analysis of Variance

Definitions

- Abundance: Number of individuals from a certain species in a certain area ($ind \cdot m^{-2}$).
- Biomass: Total weight of organisms of a certain species in a certain area ($g \cdot m^{-2}$,wet weight).
- Environmental parameter: Physical and biological parameters such as depth, temperature, salinity, Chlorophyll a concentration and Marine snow concentration.
- Holoplankton: Organisms which lives all their life as zooplankton.
- Macrozooplankton: Zooplankton organisms bigger than 20 000 μm.
- Marine snow: Particulate organic matter sinking from the upper water column to the deep.
- Meroplankton: Organisms which lives only a part of their life as zooplankton.
- Mesozooplankton: Zooplankton organisms in the size range of 200 μm to 20 000 μm.
- Spatial distribution: Distribution of organisms with latitude, longitude and along the depth.
- Zooplankton: Heterotrophic plankton drifting in the water column.

Introduction

Zooplankton belong to the first level of the food web after phytoplankton and, therefore, are a key factor to understand how species are distributed in the oceans. Even before being able to study food web interactions it is necessary to understand how and why each species of zooplankton is distributed in the water column both geographically and spatially.

Many Arctic locations are well studied for zooplankton: Svalbard (Daase & Eiane, 2007; Willis *et al*., 2008), the Fram Strait (Svensen *et al*., 2011) and Disko Bay, Western Greenland (Madsen *et al*., 2008). Some recent studies have investigated the remote Northeast Greenland; e.g. investigations on carbon cycle and grazing of zooplankton (Nielsen *et al*., 2007; Middelbo *et al*., 2018) were done in Young Sound (74°N) and some studies were done on *Calanus* in the Northeast Water Polynya (Hirche *et al.*, 1994). Most of the research on zooplankton covers only small well-defined areas such as detailed studies of specific fjords (Tang *et al*., 2011; Middelbo *et al*., 2018). However, considering the long coastline of Northeast Greenland interspersed with isolated fjords and a large offshore shelf, there are big gapes in knowledge. Extrapolation of results from one area to other locations is very unreliable in the Arctic (Wassmann, 2004). Within the TUNU Program (Christiansen, 2012), we investigated the distribution of 29 zooplankton taxa with a plankton net and 14 with a Video Plankton Recorder in Northeast Greenland (NEG) between 76°N, north of Young Sound, and 79°N, south of the northeast water polynya.

Together with currents other abiotic parameters such as temperature, salinity and depth may influence the zooplankton distribution both vertically and horizontally in the water column on a very fine scale (Gallager *et al*., 1996). Zooplankton position themselves in the water column in order to get the best living conditions balancing good food supply and low predation risk (Fossheim & Primicerio 2008; Norrbin *et al*., 2009). For example, some species will tolerate lower temperature than others, do not have the same predators, do not feed on the same organisms, do not tolerate the same particle density or do not react the same way to light conditions.

Northeast Greenland is a remote high Arctic area with no human activities. This makes environmental ecological research less biased by human impact to study zooplankton distribution. Large-scale studies of zooplankton distribution are new to the area. Two currents influence the distribution of zooplankton offshore NEG: The southbound and cold East Greenland Current (EGC) enters the shelf and western part of the Fram Strait from the Arctic Ocean. The second major current, the Return Atlantic Current (RAC), originates from the northbound West Spitzbergen Current (WSC) and brings warmer Atlantic waters from the eastern side of the Fram Strait to the NEG shelf (Straneo *et al*., 2012; Arndt *et al*., 2015). The NEG coastline is influenced by glacial freshwater runoffs creating a low salinity water mass at the surface in fjords (Aagaard & Carmack, 1989). This

phenomenon, common in the Arctic, builds up strong salinity gradients creating water masses with different characteristics – different habitats. The NEG coast and shelf are covered by ice for more than ten months a year, i.e. fast-ice inshore and sea-ice offshore. The minimum sea-ice extent occurs in September. The NEG region is known to have a low productivity on the shelf (Smith, 1995).

As NEG is affected by two different major currents (EGC and RAC), we can expect both Arctic and boreal species. The zooplankton community is likely to be dominated by small species like *Pseudocalanus* sp., *Triconia* sp. and *Oithona* sp. as they represent the highest biomass of in the EGC (Møller *et al*., 2006). Other species like *Calanus* sp., *Metridia* sp., *Acartia* sp., *Microcalanus* sp. and *Microsetella* sp. are likely to be found as they are reported to be present in Young Sound (Nielsen *et al*., 2007), near our study area. Three *Calanus* species can be found in NEG (Hirche & Kwasniewski, 1997), the Arctic species *C. glacialis* and *C. hyperboreus* and the boreal species *C. finmarchicus* (Kwasniewski *et al*., 2003). They are known to have different habitats in the Northeast Water Polynya where *C. hyperboreus* and *C. glacialis* were more abundant in Arctic waters whereas *C. finmarchicus* was more abundant in the Atlantic influenced waters of the Fram Strait (Hirche *et al*., 1994). The boreal *C. finmarchicus* is the smallest of the three species, *C. glacialis* an Arctic coastal cold-water species and *C. hyperboreus* is the biggest one of the three and more oceanic Arctic species. According to Daase & Eiane (2007), the three species can be identified from their body size of their developmental stages.

In the last decades, most of the zooplankton research, not only in the Arctic, has focussed on *Calanus* species, but this is never the only genus present. It is often reported to represent 90% of the zooplankton abundance, like in the Northeast Water Polynya (Hirche & Kwasniewski, 1997). However, this depends on the sampling gear used (Hopcroft *et al*., 2005; Skjoldal *et al*., 2013). On the Greenland East coast, the *Calanus* proportion among zooplankton is less than 50% (Møller *et al*., 2006) which makes it important to study the other taxa with the same dedication as *Calanus*. For this purpose, nets with smaller mesh size than the 180 µm of the ordinary WP-2 and Multinets should be used (Skjoldal *et al*., 2013). Other sampling gear, such as optical instruments, towed or autonomous may also be used.

The overall goal of the present study is to provide the first large-scale baseline for zooplankton in Northeast Greenland. We put forward the following hypotheses:

1) The zooplankton communities differ between inshore and offshore locations.
2) Zooplankton communities on the shelf differs between banks and troughs.
3) Coastal open water locations are more diverse than either enclosed fjord or shelf locations.

To address these hypotheses, the following questions were asked:

1) What is the overall diversity of zooplankton in Northeast Greenland?
2) What is the spatial distribution and abundance of zooplankton taxa (with emphasis on *Calanus*) across inshore and offshore locations?
3) What are the main environmental drivers resulting in the specific zooplankton communities?

We collected zooplankton during the TUNU-VII Expedition in September 2017 in Northeast Greenland between 76°N and 79°N. In order to study zooplankton distribution and abundance on a larger scale, we sampled different habitats, inshore and offshore. The main inshore habitats comprised the isolated Bessel Fjord and the open bay Dove Bugt confined by the long and narrow island Store Koldewey. Offshore, east of Store Koldewey, the main habitats were located on the continental shelf with its pronounced banks and troughs.

Knowing that a wide size range of species can be found in NEG, two types of gear were used to better estimate the abundance and distribution of each species. A modified 85 µm WP-2 net (Norrbin, 1996) was used, as it is known to sample part of the zooplankton well (Skjoldal *et al.*, 2013). As a complement, a Video Plankton Recorder, VPR, was used in addition to the classical net sampling. The VPR gives a fine-scale depth distribution of the zooplankton, the third dimension of the sampling. It has been shown that VPR can better sample large zooplankton and also fragile species, like appendicularians and hydromedusae (Benfield *et al*., 1996; Jacobsen & Norrbin, 2009).

Material and Methods

Study area

This study was performed during the TUNU-VII Expedition (Christiansen, 2012), to Northeast Greenland on R/V Helmer Hanssen (UIT The Arctic University of Norway) on 14-26 September 2017. During these 12 days, we sampled zooplankton at nine different locations (Figure 1), with two sampled twice (day- and night-time; Table 1). Three different sub-areas were visited (Figure 1): Bessel Fjord (F1 and F2), a narrow and deep sill fjord (ca 76°N, 20-22°W), the wide bay of Dove Bugt (D1 and D2) and the shelf (B1, B2, T1, T2 and S) (ca 76-79°N). Location B2 correspond to Belgica Bank, T1 to the Store Koldewey Trough and T2 to the Norske Trough (Arndt *et al*., 2015).
The shelf locations were chosen in order to form a transect along latitude 76°N outside the Bessel Fjord. Shelf locations further north, up to 79°N, gave an indication of which zooplankton species that were advected from the high Arctic via the East Greenland Current (EGC), and thus might affect biota further south.

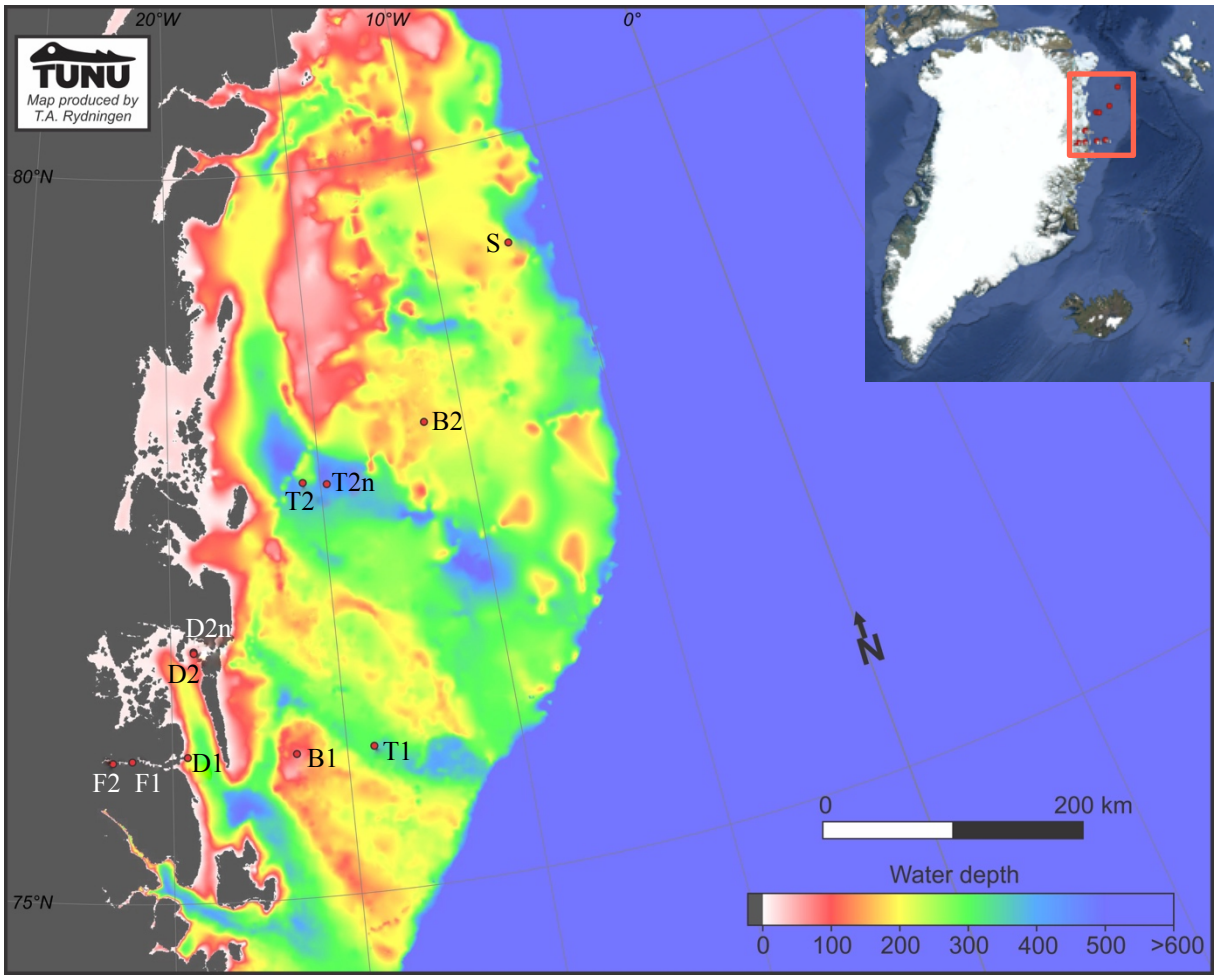

Figure 1: Map of the study area with each location produced by T.A. Rydningen. F1: Middle Bessel Fjord, F2: Inner Bessel Fjord, D1: Mouth Dove Bugt, D2: End Dove Bugt, B1: 76N-Bank, T1: Store Koldewey Trough, B2: Belgica Bank, T2: Norske Trough, S: Northern shelf

Table 1: Locations visited for this project. At each location a CTD equipped with water bottles, a VPR and a modified WP-2 net were deployed. No WP-2 nets were taken at night locations. Sampling was done at local time.

Location name	Location	Date	Sampling time (start VPR)	Latitude	Longitude	Max depth (m)
Middle Bessel Fjord	F1	17/09	10:24	75°59'22.40" N	21° 8'58.85"W	364
Inner Bessel Fjord	F2	17/09	19:17	75°58'23.73"N	21°42'10.15" W	230
Mouth Dove Bugt	D1	18/09	15:57	76° 0'8.73"N	19°33'5.15"W	495
End Dove Bugt day	D2	19/09	14:52	76°44'0.73"N	19°18'0.15"W	214
End Dove Bugt night	D2n	19/09	21:20	76°43'50.73"N	19°19'36.15" W	210
Store Koldewey Trough	T1	21/09	08:20	76° 0'59.98"N	14°13'60.15" W	323
76N-Bank	B1	21/09	18:11	76° 0'59.73"N	16°27'36.15" W	68
Norske Trough day	T2	22/09	11:27	77°51'54.00"N	15°34'60.00" W	404
Norske Trough night	T2n	22/09	18:17	77°49'8.50"N	14°45'0.00"W	435
Belgica Bank	B2	23/09	09:01	78° 9'8.50"N	11°18'7.50"W	170
shelf	S	24/09	08:47	79°16'1.00"N	7° 7'9.00"W	252

Sampling and processing

Hydrography:

At all locations, the ship CTD (Seabird 911 CTD, Seabird Electronics Inc., USA) was deployed from the surface to about 5 m above the bottom. The CTD data allowed us to define the different water masses at each specific location by measuring temperature, salinity and fluorescence (proxy for Chlorophyll *a)*. The data of the ship CTD were compared with those of a smaller CTD attached to the VPR in order to verify the calibration of this last one because the ship CTD works on a finer scale than the VPR CTD and the calibrations are done more often.

The second task of the ship CTD, the Seabird 911, is to link the physical parameters to the chlorophyll *a* data. As we had double data from the physical parameters available for this study we chose to use the VPR CTD. The output from this CTD was directly linked to and measured at the same time as the VPR data (ca. 1 datapoint per frame).

Phytoplankton collection:

The fluorescence registered by the ship CTD was converted to Chlorophyll *a* (Chl *a*, $mg \cdot m^{-3}$) by the CTD directly. At each location, water samples were collected from the 5 L Niskin bottles mounted on the CTD rosette. The sampling depths were: surface, 5 m, 10 m, 40 m, 60 m, 100 m, 200 m, 400 m, and near-bottom water. In addition, the depth of the Chl *a* peak was identified during the down cast of the CTD and water was sampled at the peak on the return. Samples for cell counts were collected in 100 ml dark glass bottles, to which were added one ml of Lugol's solution and kept dark and cool. The samples were then counted using the Utermöhl method (Karlson *et al.*, 2010). This method consists of using 25 ml or 50 ml sedimentation chambers, depending on the phytoplankton concentration, to let the phytoplankton cells settle on a counting plate for 24 hours. This plate was then observed under a Zeiss AXIO A1 (Carl Zeiss, Oberkochen, Germany) inverted microscope and the phytoplankton was identified (Tomas, 1997) and counted. Only the abundances are presented here; the counts will be used for other purposes.

For each depth, water for Chl *a* analysis was collected from the 5 L Niskin bottles and filtered onto 0,7 µm GF/F and 1,2 µm GF/C filters (GE Healthcare, Dassel, Germany), frozen at -18 °C and brought back to the lab at UiT. Here they were extracted in ethanol before measurement of fluorescence using a Turner 10-AU Fluorometer (Turner Designs, Cal., USA). The Chl *a* values were calculated as described in Parsons (2013).

Zooplankton from WP-2 net:

To get a quantitative estimate of the different zooplankton taxa present at each location, a modified WP-2 net (Appendix I) of 85 µm mesh size (Norrbin, 1996) was used. The net was lowered to about 10 m above the bottom at a speed of *ca* 0,50 $m \cdot s^{-1}$ and then pulled up vertically at a speed of ca 0.25 ms^{-1}. The volume sampled was calculated from the opening area of the WP-2 net (0,25 m^2) and the wire length used during sampling (maximum depth of the net opening in m). The net was not clogged and was pulled up with the smallest angle possible at all locations. Once the net was retrieved, it was rinsed with seawater to concentrate the organisms in the cod-end. The contents of the cod-end of the net were collected, filtered and concentrated with an 85 µm sieve. For fixation, 300 ml plastic bottle were filled with sample and filtered seawater, to get a volume of 240 ml. Then it was topped up with 60 ml of borax-buffered formaldehyde: propylene glycol to get a final solution with a 4% formaldehyde concentration.

In the lab after the expedition, the fixed zooplankton samples were counted by eye using a Leica M205C stereo microscope (Leica Microsystems GmbH, Wetzlar, Germany). Each sample was rinsed

with filtered seawater and diluted in a 1 L or 2 L beaker, depending on the zooplankton concentration assessed by eye. The macrozooplankton, organisms >20 000 µm, were counted and identified separately from the rest of the counts. Macrozooplankton were picked out during this sample preparation for microscopy observation, identification and counting. The relative abundance of macrozooplankton per m^2 surface area was calculated and compared with those for each zooplankton taxon in a Principal Correspondence Analysis (PCA) to highlight possible predator-prey interactions.

From the diluted 1 or 2 L samples, subsamples were taken using a small beaker mounted on a stick with a calibrated volume of 34 ml. To ensure the homogeneity of our subsampling, the sample was stirred in a figure-8 pattern. The rest of the sample was covered with aluminium foil and kept under the fume hood. The subsamples were counted in a subdivided petri dish. An assessment of the count was done after going through the whole subsample to know if the counts were sufficient to precisely reflect the location. Taxa were ranked according to the total number of individuals. A total of 300 individuals for the major taxon, and a progressive (i.e. the most abundant taxa is not the only taxa in our counts represented by more than 30 individuals) distribution amongst taxa was considered as sufficient (Personal comment F. Norrbin and UNIS course AB-320, 2018). If this requirement was not achieved, another subsample was taken. Subsamples were counted until the threshold abundance was reached. Organisms were identified to the lowest possible taxonomical level resulting in 29 taxa with the WP-2 data. For some crustacean taxa (*Metridia* sp., *Oithona* sp., *Pseudocalanus* sp. and *Microcalanus* sp.) both juveniles and adult females and males could be identified. To discriminate putative *Calanus* species individuals, the prosome length was measured for each *Calanus* (Figure 2), and the copepodite stage was identified. The *Calanus* species were separated according to size classes as described in Daase & Eiane (2007) (Appendix III).

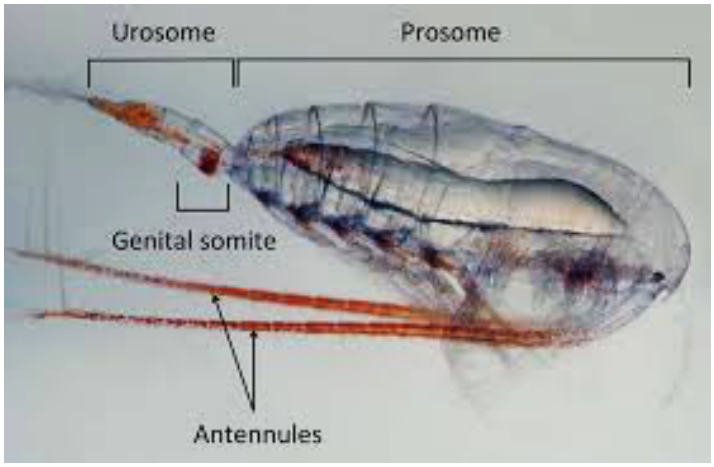

Figure 2: Calanoid copepod morphology (photo from Choquet *et al*., 2018). Number of prosomal an urosomal segments, and number of swimming legs are used for identification of copepodite stages

Zooplankton from Video Plankton Recorder:

To study the distribution of the zooplankton in more detail, we used a digital autonomous Video Plankton Recorder (VPR, Seascan Inc., USA) which can be lowered to a max depth of 1 000 m. The VPR is an ultra-macro camera composed of a computer unit, a camera, a strobe and a hard drive (Figure 3). The VPR is equipped with a SBE49 CTD (« Fastcat », Seabird Electronics Inc., USA), a fluorometer and a turbidometer (ECO Puck, WET Labs Inc., USA). Each image taken by the camera is linked with the corresponding physical parameters, such as the depth and the temperature. It allows us to get the distribution of the zooplankton along the depth axis using images. By pulling the VPR up and down in the water column for one hour, the same water parcels will not be sampled twice, because the ship is slowly drifting due to wind and currents. For this study, the magnification setting S2 was chosen for the VPR camera zoom, which gives the best data for mesozooplankton in an oceanic environment (Norrbin, 2009).

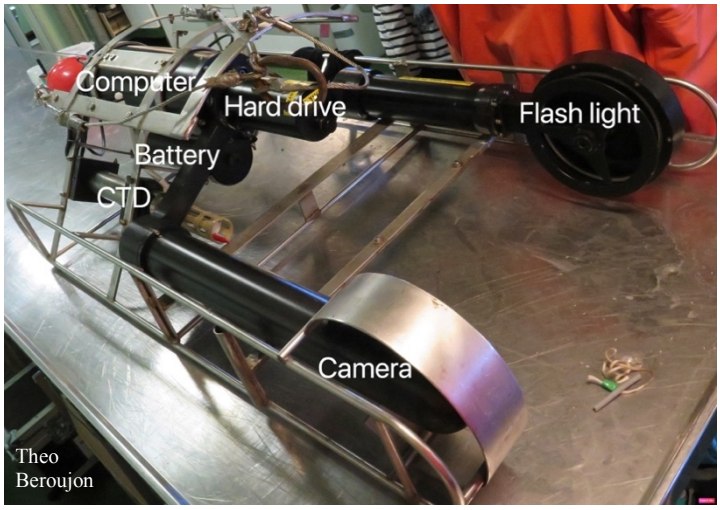

Figure 3: Video Plankton Recorder, VPR, during the BIO-2010 cruise (04/2017).

The VPR was set to take ca 20 pictures (frames) per second. In order to be that fast, the camera had a fixed focus on a small volume of ca 35 ml for the settings we used. Because the observed volume is so small, the VPR was used for about one hour (Appendix II) at a wire speed of 0.8-1 ms^{-1}, resulting in a minimum volume of 2.52 $m^3 \cdot h^{-1}$ calculated from the volume observed (Vo), the volume per frame (Vf = 35 ml), the frame rate (FR = 20 s^{-1}) and time (t =1 h):

$$Vo = Vf \cdot FR \cdot t = 2{,}52\ m^3 \cdot h^{-1}$$

In order to process the data from the VPR, Regions of Interests (ROIs) were extracted. The ROIs consist of a sub-selection of each frame selected to get only parts of the frame where an object/organism is detected using the software Autodeck (Seascan Inc., USA). In Autodeck, the extraction settings can be adjusted to accept a certain blurriness of the image. The program essentially responds to the quality of the water, where turbidity and particle abundance can blur the light traveling from the strobe to the camera. That is why thresholds needs to be adjusted for each expedition. The same settings were used for all locations in order to be able to compare them. These settings (Appendix IV) were adjusted by looking at the first VPR result of the expedition. Autodeck primarily identifies particles by the image processing Sobel function, which finds the edge of the objects from how steep the gradient

is between light and dark parts of the image (Personal comment F. Norrbin, 2018). They are made to obtain the highest proportion of clear sharp pictures taken by the VPR. Once the ROIs have been extracted with Autodeck, all the images that are not relevant need to be removed manually, e.g. bubbles, very cropped objects (except for organism bigger than the view field) and fuzzy images. IrfanView thumbnails (Irfan Skiljan, Austria) was used to view the ROIs which are saved as 10-bit tif-files, which are not easily handled by other image viewers. The ROIs were classified into taxonomic groups. A rough classification could have been done automatically with the VPR software, Visual Plankton. However, the large number of abundant categories with a high degree of morphological similarity between the taxa made this method inefficient. Furthermore, the data sets were not very large. Therefore, ROIs were sorted manually, so that the precision of the classification was increased. Altogether, 14 taxa were identified with VPR data as well as the category "Marine snow" (Table 2).

Table 2: Taxa identified with VPR data *: Meroplankton

Taxon	Size class	Phylum	Subphylum	Subclass	Order
Acartia sp.	Mesozooplankton	Arthropoda	Crustacea	Copepoda	Calanoida
Calanus spp.	Mesozooplankton	Arthropoda	Crustacea	Copepoda	Calanoida
Metridia sp.	Mesozooplankton	Arthropoda	Crustacea	Copepoda	Calanoida
Microcalanus sp.	Mesozooplankton	Arthropoda	Crustacea	Copepoda	Calanoida
Paraeuchaeta sp.	Mesozooplankton	Arthropoda	Crustacea	Copepoda	Calanoida
Pseudocalanus sp.	Mesozooplankton	Arthropoda	Crustacea	Copepoda	Calanoida
Oithona sp.	Mesozooplankton	Arthropoda	Crustacea	Copepoda	Cyclopoida
Triconia sp.	Mesozooplankton	Arthropoda	Crustacea	Copepoda	Cyclopoida
Ostracoda	Mesozooplankton	Arthropoda			
Chaetognatha	Macrozooplankton	Chaetognatha			
Cnidaria * & Ctenophora *	Macrozooplankton	Cnidaria & Ctenophora			
Echinoderm larvae *	Mesozooplankton	Echinodermata			
Appendicularia	Macrozooplankton	Chordata	Tunicata	Appendicularia	

The "Marine snow" is considered an environmental variable to characterise locations. After classifying the ROIs into taxa, the data were pooled into 5 m depth bins to standardize the dataset before data processing for graphs and statistical analyses. The counts were then converted into abundance ($ind \cdot m^{-3}$) for each 5 m bin.

The VPR does not replace the 85 µm WP-2 net but both types of gear have pros and cons which makes them complementary (Table 3). The most obvious difference between the two gears is the built-in CTD on the VPR, which allows us to record the depth distribution of the zooplankton and correlate with environmental variables at a very detailed scale compared to WP2 nets or even Multinet. We might think that the VPR is giving the same data as the 85 µm WP2 net and even more with the 3-dimensional

approach, but it has other limitations. The VPR does not touch or collect the organisms, but simply takes a picture of them. In other words, sampling is inert, the organisms are undisturbed in their environment and even certain types of behaviour may be observed like feeding behaviours for the copepod *Microsetella norvegica*.

Table 3: Advantages and disadvantages of sampling with VPR and WP-2. Importance resolution (from very advantageous: +++ to disadvantageous: -).

Sampling gear	VPR sampling	WP-2 sampling
Small scale depth distribution	+++	-
Mesozooplankton sampling	+	++
Macrozooplankton sampling	+	-
Sampling for lab analysis/manipulation	-	+
Identification of the organisms	+	+++
Observation of the living conditions/behaviour in environment	+	-
Sampling volume/time	-	+
Data conservation time and space	++	-
Difficulty/time to obtain data	-	+

The 85 µm WP-2 net will catch most of the small mesozooplankton, except for the early copepodite stages. Macrozooplankton, on the other hand, may be under-sampled by WP-2 because of the low towing speed allowing the larger zooplankton to escape the net. By contrast, the VPR is set to sample best *Calanus* spp., which is one of the biggest taxa among mesozooplankton. This makes the VPR reliable also for semi-quantitative estimates of macrozooplankton abundances. However, other copepods like *Oithona* sp. are too small to reveal sharp images and so are underestimated.

Data analysis

Biodiversity according to Shannon and Simpson indexes:

For each WP-2 sample, a Shannon index value was calculated to estimate the biodiversity of species. The Shannon index is commonly used in ecology to quantify the biodiversity of a community and combines the number of taxa present at a location and the abundance of each of them.

The formula for the Shannon index is: $\mathbf{SHDI = -\sum_{i=1} N_{pi} \cdot ln_{pi}}$ (Nagendra, 2002), were N is the total number of taxa and pi is the abundance of the taxa «i» at this location. The Shannon index theoretically produces values from 0 to infinity but for biological data the Shannon index usually gives values between 1.5 (low diversity) and 3 (high diversity). During this study, the values obtained with the Shannon index were compared to the values calculated with the Simpson index. The Simpson index

was also used to better examine datasets with many rare species (Nagendra, 2002). The formula for the Simpson index is: $\mathbf{SIDI = 1-\sum_{i=1} N_{pi} \cdot pi}$. The Simpson index values range between 0 and1 where the lower value designates the higher diversity (i.e., opposite of Shannon index).

The diversity from VPR data was then compared to WP-2 net data. To do so, the WP-2 categories, which are more detailed for mesozooplankton (developmental stages/male/female), were selected and merged to get the same taxonomic categories as the VPR. Then both diversity indices were calculated and compared. Not all the WP-2 data were used here, because some taxa were present only in the WP-2 samples, but they represent very few individuals and very few taxa (the sum of these taxa abundances represent less than 2% of the total zooplankton abundance at each WP-2 station).

For both VPR and WP-2, the indexes were plotted against each other to see if there was a correlation between indexes. This would be the case if the data were normally distributed among taxa. If not, the Simpson index should be trusted more as it means we have a few abundant taxa and many rare taxa (Nagendra, 2002).

Cluster Analysis:

Using Rstudio 3.5.0 (Rstudio Inc., Boston, MA, USA) similarities in the occurrence of taxa were examined for given locations using clustering analysis. For this analysis VPR data were used. The abundances for all depth bins were combined making a 2-dimensional database with observations in individual$\cdot m^{-2}$ for each location. A clustering tree was made using the VEGAN-package (Oksanen *et al.,* 2013). The dissimilarities between taxa and locations were calculated using the Bray-Curtis dissimilarity method (Bray & Curtis, 1957).

Canonical Correspondence Analysis:

For the VPR data we know the depth and also all the environmental parameters like temperature, salinity, fluorescence and marine snow concentration linked to each individual. This last point is important to interpret the geographical and vertical distribution of the plankton. To link this information, multivariate statistical methods may be used, such as Canonical Correspondence Analysis, CCA (Härdle & Simar, 2015). The goal of a CCA analysis is to show the significance of each variable, in our case, environmental parameters, to explain the data, the distribution of taxa. For this method, only the day-stations were used to avoid putting more weight on one location or having an effect of diel vertical migration. Data were standardized by taking the logarithmic value. In order to avoid computing error by log of 0, +1 was added to each original value « x », so log(1)=0. It implies the assumption: log(x) = log (1+x) for $x \neq 0$. The CCA used is included in the VEGAN package, but the function does

not allow us to have rows of biological data with a sum equal to zero, so we had to remove these lines of « no data ».

When running the analysis, two subsets of the data were made for coding purposes; one containing all the biological data, the abundance of each taxa for each depth bin at each location and a second subset with all the environmental parameters (temperature, salinity, density, fluorescence, depth and marine snow concentration) including the location ID. This is to better understand how the abundance of each zooplankton taxon relates to an environmental parameter.

Results

Hydrography

The CTD casts from the ship were conducted just before the VPR sampling (day locations only). The appendix V shows the different graphs produced with temperature, salinity, density and fluorescence profiles used for the comparison with the VPR data. For all locations, temperature ranged between 2 °C and -2 °C and salinity ranged between 28 and 35. The temperature was higher at the surface for Bessel Fjord (F1 and F2) whereas in the Dove Bugt (D1 and D2) and on the shelf locations (T1, T2, B1, B2 and S), the temperature tended to decrease with depth until 100 m and then increased until reaching a higher temperature than at the surface. The salinity tended to increase fast from the surface to 100 m and became stable after 300 m for all locations.

The Bessel Fjord sampling (F1 and F2) depths ranged from 220 to 350 m. The temperature was of 1,5 °C from the surface to 20m and rapidly decreased to -1,4 °C from 50 to 80 m. The salinity was 29 at the surface and increased progressively to 33,4 below 100 m. The open Dove Bugt (D1 and D2) is different from the secluded Bessel Fjord (F1 and F2) with bottom depths ranging between 500 m at the mouth (D1) to 220 m inside the bay (D2). In Dove Bugt (D1 and D2) the temperature was centred around 0 °C at the surface and dropped to -1,5 °C from 50 to 120 m. The temperature increased to 1,2 °C at 220 m and stabilised at 1,6 °C below 300 m at the mouth (D1). The Store Koldewey Trough (T1) was nearly 350 m deep with a temperature just below 0°C at the surface and dropping to -1,6 between 50 to 100 m. It then increased to more than 2 °C at 220 m and decreased to 1,1 °C at 340 m. The salinity in the Store Koldewey Trough (T1) ranged between 28,5 at the surface to more than 34,5 down to 230 m. It was stable below. Further east, the 76N-Bank (location B1), is very shallow with a depth of 65 m. At this location the temperature was negative throughout the water column starting at -0,9 °C in the upper 15 m and reached its warmest at 20 m with -0,6 °C. Below 20 m the temperature decreased to -1,6 °C at 65 m. The salinity was 28,6 from the surface to 15 m and rapidly increased to 31 at 25 m. Below this depth the salinity continued to increase slowly to 32,4 at 65 m. The Norske Trough (T2), was almost

450 m deep. The temperature profile was opposite that of Bessel Fjord (F1 and F2). The lowest temperature was between the surface and 150 m with less than -1,5 °C. Below this depth the temperature increased to 1,7 °C. East of the Norske Trough (T2), lies the shallow Belgica Bank (B2) with a depth of 170 m. The temperature was -1,4 °C at the surface and peaked at 20 m with nearly -0,8 °C. The temperature dropped right below 20 m to reach -1,6 °C from 40 to 80 m, increased slightly to -1,5 °C from 100 to 140 m and, increased rapidly to reach 0 °C at 170 m. The associated salinities increased rapidly from 28 to 31 in the upper 20 m and continued to increase slowly to reach 34,5 at 170 m. The last location visited was the northern shelf (S) were the maximum depth is 250 m. The temperature was -0,7 °C in the upper 20 m, and decreased rapidly to -1,4 °C at 25 m and fluctuated between -1,4 and -1,5 °C until 130 m. The temperature increased to 1,2 °C at 190 m and slowly decreased to reach 1 °C at 250 m. The salinity at this location was very similar to the Belgica Bank (B2), I.e., 29,5 in the upper 20 m followed by a rapid increase to 30,7 at 25 m. The salinity increased until 180 m to reach 34,7 and stayed constant until 250 m.

For all the locations, the density followed the salinity curve (Appendix V).

Phytoplankton

The fluorescence data gathered by the CTD were converted to chlorophyll *a* (Chl *a*) concentration ($mg \cdot m^{-3}$). The Chl *a* values were then compared with those obtained from water sample filtrations and fluorometry (data from S. Kristiansen, 2017, *unpublished*). The values from the fluorometer of the VPR correspond well to the *in vitro* measurements (Figure 4).

The Chl *a* values from the fluorescence data from the VPR matched the total Chl *a* value for all locations except for the 76N-Bank (B1) (Figure 4). This location showed a second peak of chlorophyll *a* at 60 m. The fraction of Chl *a* contained in organisms larger than 10 μm in the area was generally low, i.e. < 25% of the total Chl *a* measured for all locations except for the banks (B1 and B2) and the northern shelf (S). At the 76N-Bank (B1), around half of the Chl *a* present belonged to organisms larger than 10 μm which correspond to the larger part of the nano-phytoplankton and bigger. The values were just above 25% for the Belgica Bank (B2) and shelf (S) (Figure 4). In general, Chl *a* values were low. A peak of Chl *a* was still distinguishable around 30 m for all locations but the concentration did not exceed 0.5 $mg.m^{-3}$ except at the 76N-Bank (B1) where it was just under 1,5 $mg \cdot m^{-3}$ (Figure 4).

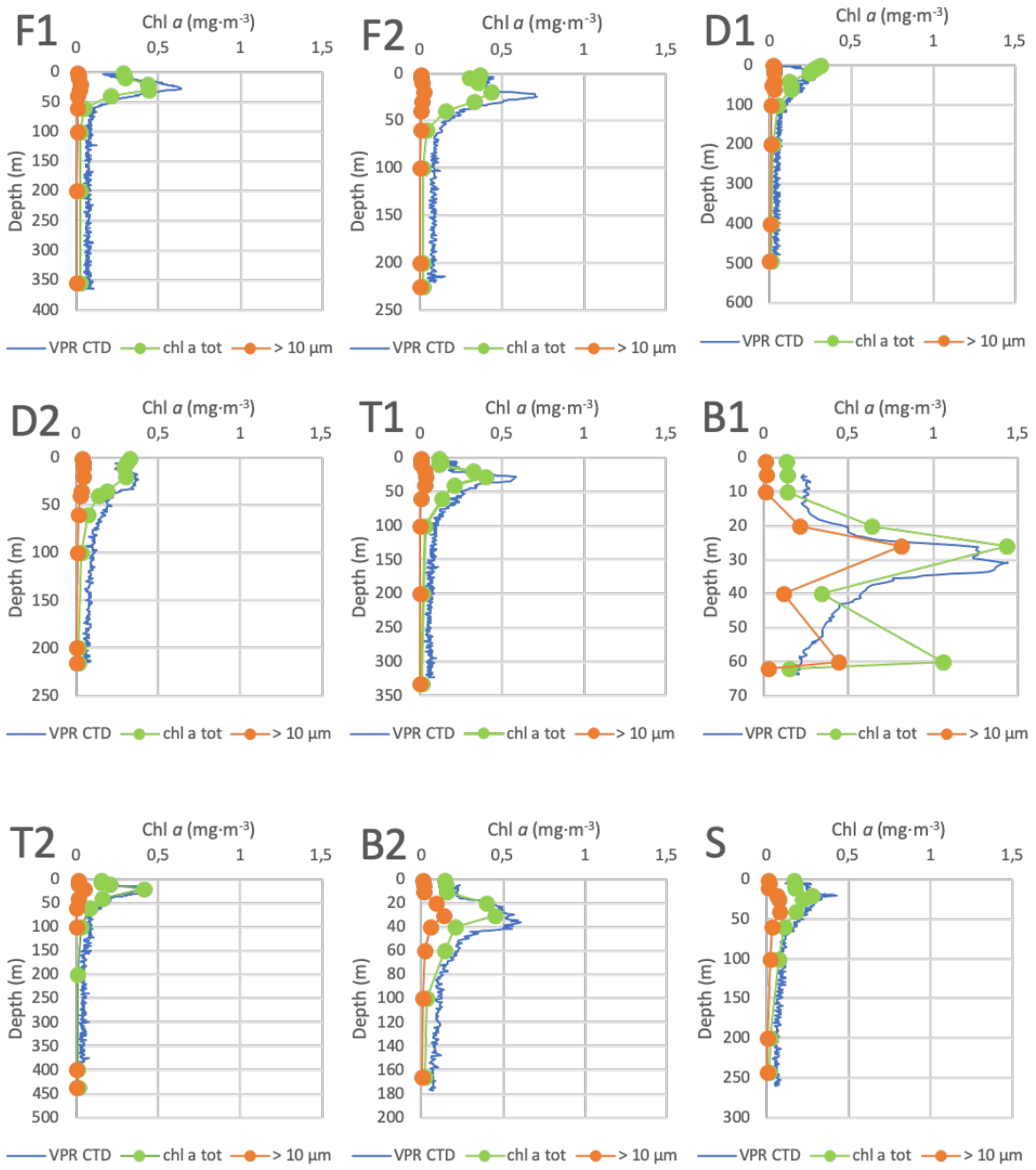

Figure 4: Comparison between chlorophyll *a* measurement from the water samples (Green data are total Chl *a* in the sample and orange data are Chl *a* from organisms bigger than 10 µm) and the converted fluorescence from the VPR fluorometer. F1: Middle Bessel fjord, F2: Inner Bessel fjord, D1: Mouth Dove Bugt, D2: End Dove Bugt, B1: 76N-Bank, T1: Store Koldewey Trough, B2: Belgica Bank, T2: Norske Trough, S: Northern shelf.

WP-2 net

Spatial abundance of zooplankton and biodiversity indexes:

The abundances calculated from the WP-2 counts (Appendix VI) gave very different results depending on the location (Table 4). The Store Koldewey Trough (T1) had the highest zooplankton abundance of all locations with more than 168 000 individuals per m^2 (Figure 5). By contrast, the banks (B1 and B2) and the Norske Trough (T2) had quite low abundances from 40 000 to 60 000 ind·m^{-2} (Figure 5). The Bessel Fjord (F1 and F2) and Dove Bugt locations (D1 and D2) together with the northern shelf location (S) had abundances from 60 000 to 100 000 ind·m^{-2} which is the average abundance for all locations combined.

For macro-zooplankton (Appendix VII), the distribution was very different. At all locations, two species of Chaetognatha dominated the macro-zooplankton. In the Bessel Fjord (F1 and F2), *Parasagitta elegans* was the dominant species as well as on the Store Koldewey Trough (T1) and the northern shelf (S). *Eukrohnia hamata* dominated at the mouth of Dove Bugt (B2), at the Norske Trough (T2) and the Belgica Bank (B2). The two species were equally abundant in the inner part of Dove Bugt (D2) with more than 30 individuals in the whole sample for each species (120 ind·m^{-2}). *Thysanoessa* sp. was also present in low abundance at the mouth of Dove Bugt (D1). The amphipod *Themisto abyssorum* was present but at very low abundance in the inner part of Bessel Fjord (F2), mouth of Dove Bugt (D1), troughs (T1 and T2), the Belgica Bank (B2) and shelf (S).

Even though the overall abundance is quite similar between some of the shelf locations (T2, B1 and B2), the biodiversity varies. The Shannon and Simpson indexes showed a significant and negative correlation (Figure 7). For the Shannon index, values were low, between 1,5 to 1,7 in the inner part of Bessel Fjord (F2), the inner part of Dove Bugt (D2) and the Store Koldewey Trough (T1; Figure 5). Higher values of around 2 were found for the middle Bessel Fjord location (F1) as well as the mouth of Dove Bugt (D1), the 76N-Bank (B1) and Norske Trough (T2). The Belgica Bank (B2) and northern shelf (S) were the most diverse locations with Shannon index values up to 2,5 (Figure 5). The Simpson index showed a similar trend, where low values indicate high diversity.

Table 4: Taxa abundances (ind·m^{-2}) for each WP-2 samples. F1: Middle Bessel Fjord, F2: Inner Bessel Fjord, D1: Mouth Dove Bugt, D2: End Dove Bugt, B1: 76N-Bank, T1: Store Koldewey Trough, B2: Belgica Bank, T2: Norske Trough, S: Northern shelf. *: Meroplankton

Species / Location	F1	F2	D1	D2	T1	B1	T2	B2	S	Total
Acartia sp.	941	0	235	0	235	353	235	0	0	2000
Aglantha digitale	235	0	0	0	0	0	0	0	0	235
bivalve veliger*	1176	941	0	706	0	0	118	0	0	2941
Boroecia sp.	0	0	1059	0	0	0	471	235	0	1765
Calanus spp.	10353	7765	9176	9647	15294	5059	5765	6588	23529	93176
Chiridius obstusifrons	0	0	118	0	0	0	118	0	0	235
Decapoda larvae*	0	0	353	0	0	0	0	0	0	353
Disconchoecia sp.	235	0	471	471	0	0	235	0	0	1412
Echinodermata*	0	471	0	1882	471	1059	353	588	235	5059
Eukrohnia hamata	0	0	0	0	0	0	353	0	235	588
fish egg*	1176	471	0	706	0	1176	235	588	0	4353
Fritilaria sp.	0	0	0	706	235	2824	0	1294	235	5294
Isopoda	0	0	0	0	471	0	118	118	0	706
Metridia sp.	7059	2353	2824	0	3765	235	3059	941	706	20941
Microcalanus sp.	5176	2588	5176	3765	7059	1647	5647	4941	10353	46353
Microsetella sp.	0	0	118	0	0	0	353	0	235	706
Oikopleura sp.	0	0	0	235	0	0	118	3882	941	5176
Oithona sp.	36235	56706	11059	23529	119765	25412	32588	29529	24235	359059
Paraeuchaeta sp.	0	0	235	471	235	0	118	353	0	1412
Parasagitta elegans	235	0	235	0	235	0	118	0	0	824
Polychaeta	0	0	0	0	0	0	0	0	235	235
Pseudocalanus sp.	32471	35294	28706	58824	19529	3412	2353	3294	6353	190235
Pteropoda	0	0	235	0	0	0	0	235	235	706
Radiolaria	235	941	0	235	0	0	0	0	0	1412
Siphonophora	0	0	118	0	0	0	118	0	0	235
Themisto abyssorum	0	235	0	0	0	0	0	0	0	235
Triconia sp.	706	471	3176	4471	941	1765	824	1882	3765	18000
Thysanoessa sp.	0	0	235	0	0	0	0	0	0	235
TOTAL	96235	108235	63529	105647	168235	42941	53294	54471	71294	763882

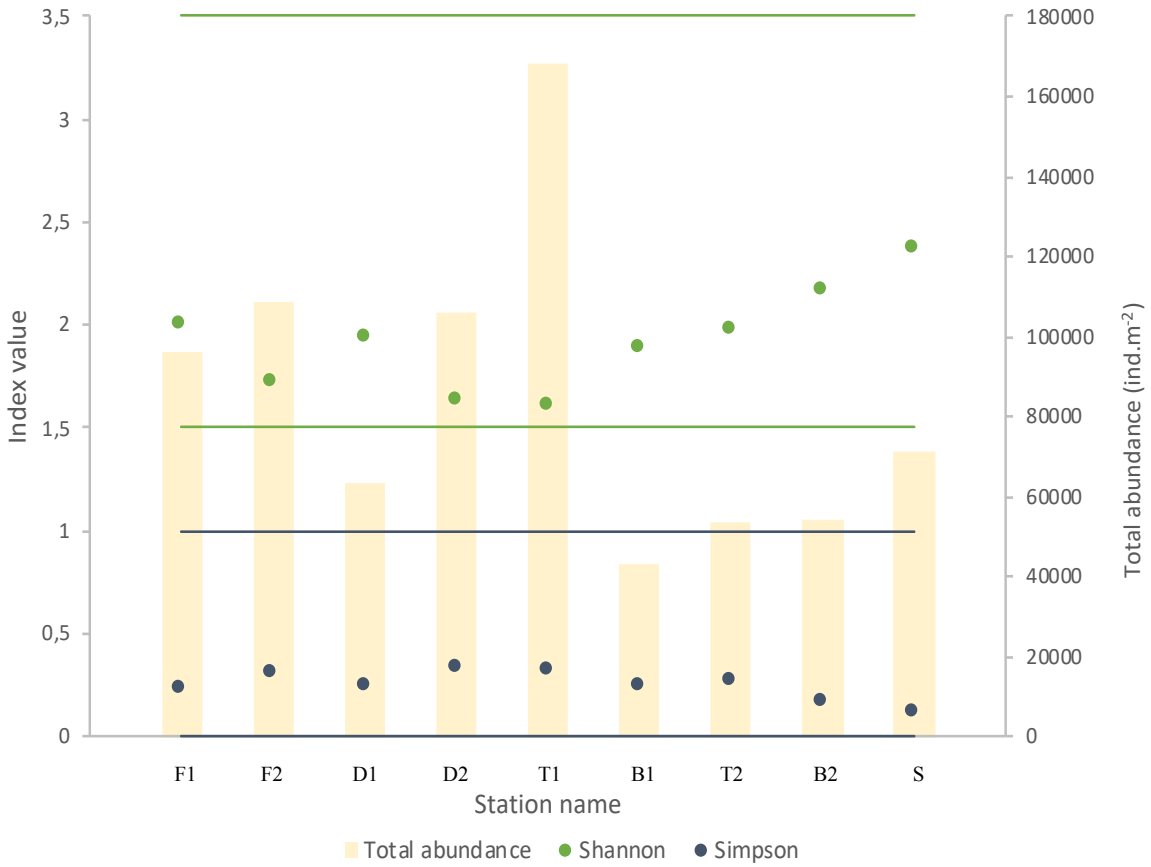

Figure 5: Zooplankton total abundance and diversity indexes. Shannon index and Simpson index calculated with WP2 data. The blue lines are the boundaries of the Simpson index and the green lines are the boundaries for the Shannon index. F1: Middle Bessel fjord, F2: Inner Bessel fjord, D1: Mouth Dove Bugt, D2: End Dove Bugt, B1: 76N-Bank, T1: Store Koldewey Trough, B2: Belgica Bank, T2: Norske Trough, S: Northern shelf.

In order to examine if the two types of sampling gear gave different results, the WP-2 diversity and VPR diversity were compared using the same 14 common taxa. The diversity values (for both the Shannon index and the Simpson index) were similar whether they were taken from the VPR dataset or the WP-2 dataset (Figure 6) even though the abundances of each taxa varies (Table 4 and 5). There are no WP-2 data for the inner part of Dove Bugt at night (D2n) and the Norske Trough at night (T2n). According to both indexes, lower diversities were found during the day compared to the night with VPR data. The decrease was around 25% for both locations (D2 and T2). According to both indexes, the Simpson index showed a higher diversity than the Shannon index for each location.

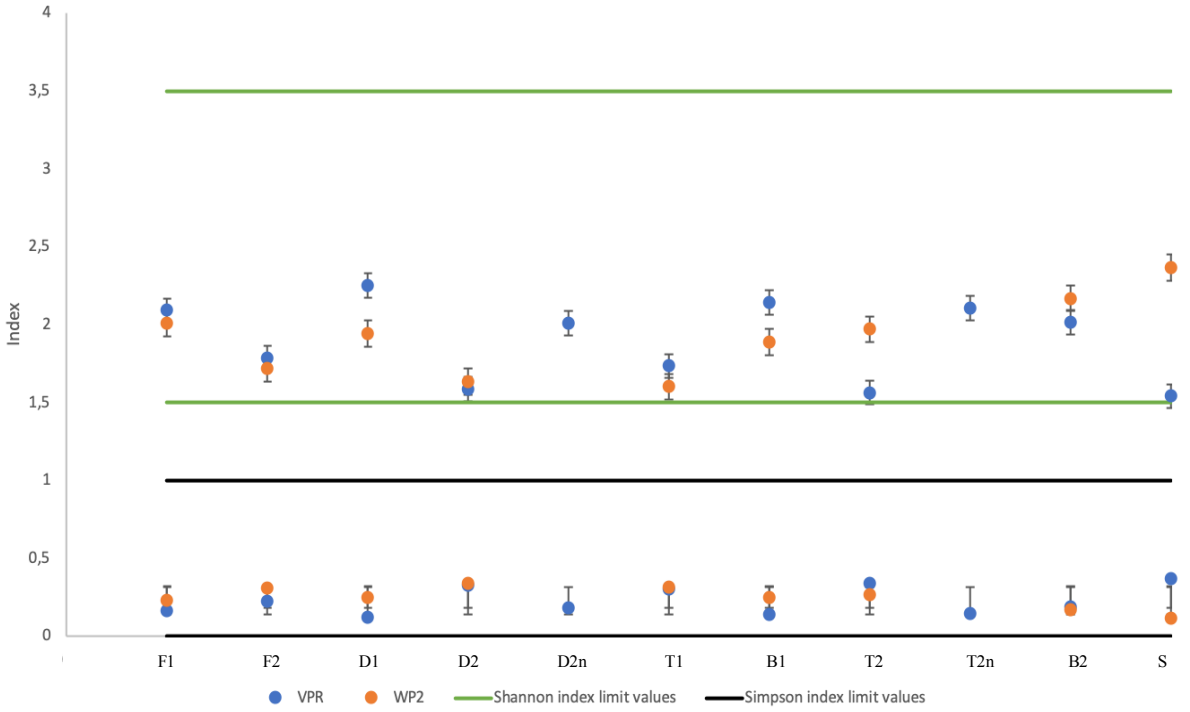

Figure 6: Comparison between VPR and WP-2 data using the same 14 taxa according to the Shannon index and the Simpson index. F1: Middle Bessel fjord, F2: Inner Bessel fjord, D1: Mouth Dove Bugt, D2: End Dove Bugt, B1: 76N-Bank, T1: Store Koldewey Trough, B2: Belgica Bank, T2: Norske Trough, S: Northern shelf.

The variations in the Simpson index seemed to indicate the same trend as the Shannon index values (Figure 7). Figure 7 shows the correlation between each index for both sampling gear. The data fit a linear model with a $R^2 = 0.9512$ for the WP-2 data and 0.9627 for the VPR data.

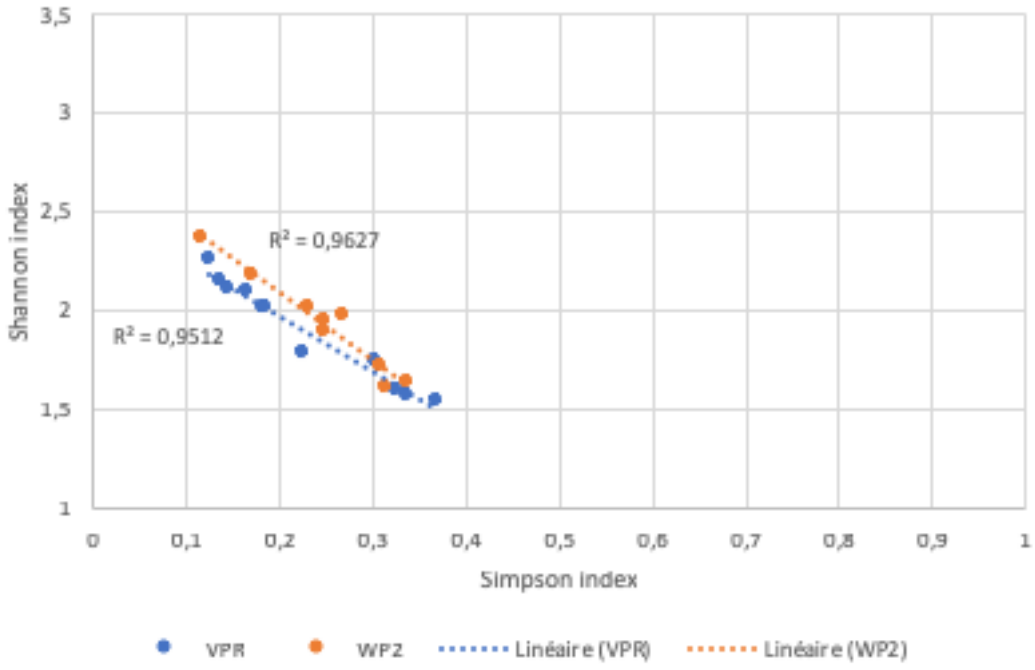

Figure 7: Correlation between Shannon index and Simpson index for VPR and WP-2 data fitting linear models

For the WP-2, the most abundant taxa were *Oithona* sp., *Pseudocalanus* sp., *Calanus* spp. and *Microcalanus* sp., which represented almost 90% of the individuals. The abundance of these four taxa depended on the location. In the middle of Bessel Fjord (F1) *Oithona* sp. and *Microcalanus* sp. were the most abundant species with more than 36 000 and 32 000 ind·m^{-2}, respectively. *Calanus* spp. and *Microcalanus* sp. were less abundant with more than 10 000 and 5 000 ind·m^{-2}, respectively. The total zooplankton abundance at this location was more than 96 000 ind·m^{-2} (Table 4). In the inner part of Bessel Fjord (F2), *Oithona* sp. represented nearly 57 000 ind·m^{-2} for a total zooplankton abundance of 108 000 ind·m^{-2} at this location.

At the mouth of Dove Bugt (D1), the abundance of the two main taxa was opposite that of the inner part of Bessel Fjord (F2). *Pseudocalanus* sp. represented 44% of the total zooplankton individuals at this location with more than 28 000 ind·m^{-2} for around 63 000 ind·m^{-2} in total. *Oithona* sp. was less abundant with slightly more than 11 000 ind·m^{-2}. *Calanus* spp. and *Microcalanus* sp. were almost as abundant as in Bessel Fjord (F1 and F2) with respectively more than 9 000 and 5 000 ind·m^{-2}.

In the inner part of Dove Bugt (D2) *Pseudocalanus* sp. was the most abundant taxa with nearly 59 000 ind·m^{-2} of the 105 000 ind·m^{-2} for all taxa summed up at this location. *Oithona* sp. and *Calanus* spp. were less abundant with respectively more than 23 000 and 9 000 ind·m^{-2} (Table 4). At this location the 4th most abundant taxon was not *Microcalanus* sp. but *Triconia* sp. with a low concentration of less than 4 500 ind·m^{-2}.

The southern tough (T1) was the most zooplankton rich location of this study (Figure 5). It was dominated by *Oithona* sp. representing 70% of the individuals found (Table 4). *Pseudocalanus* sp. and *Calanus* spp. were 2nd and 3rd most abundant taxa, with respectively more than 19 000 and 15 000 ind·m^{-2}. The 4th most abundant taxon was *Microcalanus* sp. with over 7 000 ind·m^{-2} for a total of more than 168 000 ind·m^{-2} all taxa summed up at this location.

The 76N-Bank (B1), the Norske Trough (T2) and Belgica Bank (B2) had similar zooplankton abundances. The total zooplankton abundance for these locations ranged between 42 000 and 55 000 ind·m^{-2}. The most abundant taxon was *Oithona* sp., representing around 60% of the total zooplankton abundance. *Calanus* spp., *Pseudocalanus* sp. and *Microcalanus* sp. were less abundant and each taxon represented 5 to 10% of the total abundance.

The northern shelf (S) was the most zooplankton rich and diverse location according to both diversity indexes (Figure 5), the north of latitude 76°N. *Oithona* sp. and *Calanus* spp. were equally abundant with more than 23 000 ind·m^{-2} for a total zooplankton abundance of nearly 72 000 ind·m^{-2} (Table 4). *Microcalanus* sp. and *Pseudocalanus* sp. were less abundant with about 10 000 and 6 000 ind·m^{-2}, respectively.

Calanus stage distribution:

Three species of *Calanus* were found in Northeast Greenland, i.e., *C. finmarchicus, C. glacialis* and *C. hyperboreus*. The dominant species was *C. glacialis,* with almost 25 000 ind·m^{-2} for all stages summed up. Moreover, *C. glacialis* also appeared to be the *Calanus* species with the largest range of stages present with at least three different stages present at each location (Figure 8).

C. finmarchicus was present mainly as late development stages (C4, C5 and adult females) at all locations except the inner part of Dove Bugt (D2). Some younger stages were found (C3) in the Store Koldewey Trough (T1). The northern shelf (S) presented all stages from C2 to adult female. *C. finmarchicus* was dominating in the Store Koldewey Trough (T1), with stage C5, and very abundant on the northern shelf (S), with stages C3 and C4. For all other locations *C. finmarchicus* was present in very small numbers, bellow 500 ind·m^{-2} for each stage. The C5 stage dominated for *C. finmarchicus* at all locations where *C. finmarchicus* was present except the northern shelf (S), where C3 and C4 dominated.

C. glacialis was present at all locations but especially abundant in the Bessel Fjord (F1 and F2) and the Store Koldewey Trough (T1), with more than 3 500 ind·m^{-2}. The most abundant stage for *C. glacialis* was C4, but in the Bessel Fjord (F1 and F2), stage C5 was also found, with more than 1000 ind·m^{-2}. In the Store Koldewey Trough (T1), *C. glacialis* stage C3 was also very abundant.
The largest of the three species, *C. hyperboreus,* was mainly present at the C5 stage. The C4 was present in the Bessel Fjord (F1 and F2), in Dove Bugt (D1 and D2), and at the northern shelf (S). Stage C3 were found only at the middle Bessel Fjord location (F1). Adult females were present in the inner part of Bessel Fjord (F2), the Belgica Bank (B2) and the Norske Trough (T2). No *C. hyperboreus* were found in the Store Koldewey Trough (T1).

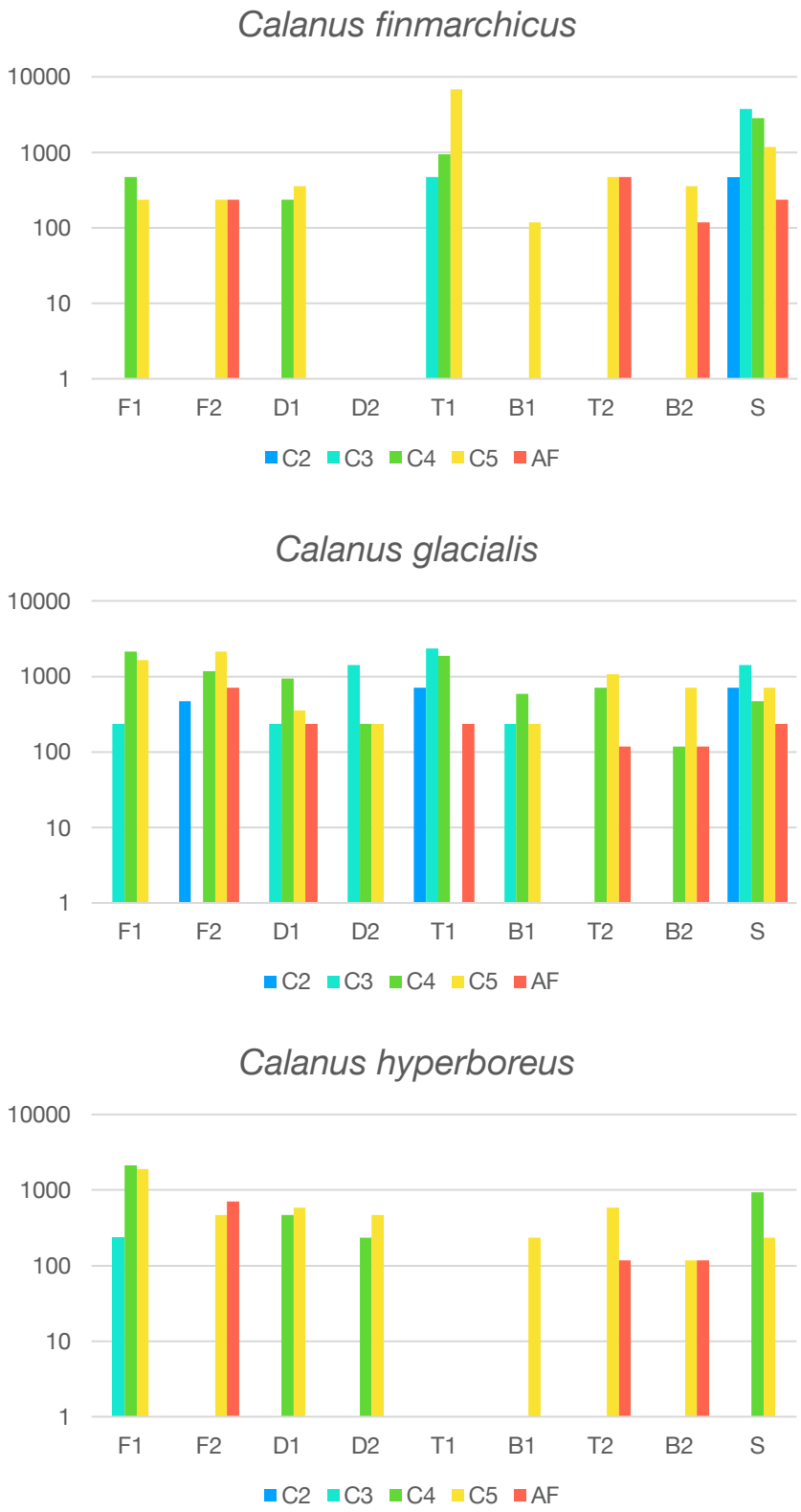

Figure 8: Abundance of each stage of *Calanus* spp. at each station (ind·m^{-2}). F1: Middle Bessel fjord, F2: Inner Bessel fjord, D1: Mouth Dove Bugt, D2: End Dove Bugt, B1: 76N-Bank, T1: Store Koldewey Trough, B2: Belgica Bank, T2: Norske Trough, S: Northern shelf. AF: Adult female, C: Copepodite.

The VPR data gave total abundances of zooplankton from 45 000 to 67 000 ind·m^{-2} in Bessel Fjord (F1 and F2) and in Dove Bugt (D1 and D2) whereas on the northern shelf (S) the abundances were more diverse. The troughs (T1 and T2) had zooplankton abundances between 14 000 to 18 000 ind·m^{-2}. The 76N-Bank (B1) had a very low abundance with just over 3 000 ind·m^{-2} and the Belgica Bank (B2) with more than 18 000 ind·m^{-2}. The northern shelf location (S) was close to the average of the study with 31 000 ind·m^{-2} in total (Table 5). According to the VPR samples, *Calanus* spp. represented 20 to 30% of the total number of individuals found at each location. *Calanus* spp. were present evenly in the whole water column in Bessel Fjord (F1 and F2), as well as in the Norske Trough (T2) and Belgica Bank (B2). At the other locations, *Calanus* spp. were concentrated in the upper part of the water column (Appendix IX). In Bessel Fjord (F1 and F2), the *Pseudocalanus* sp. abundances ranged from 12 000 to 13 000 ind·m^{-2} (Table 5). At the mouth of Dove Bugt (D1), *Pseudocalanus* sp. represented more than half of the total zooplankton abundance, with nearly 35 000 ind·m^{-2}, whereas less than half this number was found in the inner part of Dove Bugt (D2). On the northern shelf (S), *Pseudocalanus* sp. represented less than 10% of the total zooplankton abundance (Table 5). For all locations, *Pseudocalanus* sp. was concentrated around 50 m depth (Appendix IX). *Metridia* sp. was mainly present in Bessel Fjord (F1 and F2), with 4 500 to 6 500 ind·m^{-2} whereas at the rest of the locations, less than 2 300 ind·m^{-2} were found (Table 5). *Oithona* sp. was found in larger abundances in enclosed areas, like Bessel Fjord (F1 and F2) and the inner part of Dove Bugt (D2). The abundance was between 3 300 and 5 000 ind·m^{-2} at these locations, compared to less than 2 500 ind·m^{-2} for the rest of the locations (Table 5). The depth distributions of *Metridia* sp. and *Oithona* sp. did not show any particular patterns (Appendix IX).

In the inner part of Dove Bugt (D2), the distribution was assessed at daytime and night time. For some taxa like *Calanus* spp., *Microcalanus* sp., *Pseudocalanus* sp. and *Metridia* sp., the distribution changed from deeper to shallower depths at night. Sampling at night was done also in the Norske Trough (T2), but there the abundance of each taxon was too low to distinguish a depth distribution pattern.

Appendicularia, Chaetognatha, Ctenophora/Cnidaria, *Microcalanus* sp. and Ostracoda were found in low abundances at all locations. *Acartia* sp. was only present at very low abundances in the middle of Bessel Fjord (F1), and at night in the inner part of Dove Bugt (D2). Echinoderm larvae belong to meroplankton and were found in low abundances of less than 600 ind·m^{-2}, except in the inner part of Dove Bugt (D2) and the Belgica Bank (B2), with abundances between 900 and 1 300 ind·m^{-2}. *Paraeuchaeta* sp. was found in very low abundances (less than 500 ind·m^{-2}), except at the middle part of Bessel Fjord (F1), the Norske Trough (T2), and the northern shelf (S). *Triconia* sp. was mainly present in Bessel Fjord (F1 and F2) with abundances between 2 200 and 3 300 ind·m^{-2} whereas it was rare at all other locations (less than 700 ind·m^{-2}). There were no *Triconia* sp. in the troughs (T1 and T2), and on

the 76N-Bank (B1). Radiolarians were present in low abundances at all locations except at daytime in the Norske Trough (T2). Their abundance was always less than 2 600 ind·m^{-2} (Table 5).

Table 5: Taxa abundances (ind.m^{-2}) for each VPR sample. F1: Middle Bessel Fjord, F2: Inner Bessel Fjord, D1: Mouth Dove Bugt, D2: End Dove Bugt, B1: 76N-Bank, T1: Store Koldewey Trough, B2: Belgica Bank, T2: Norske Trough, S: Northern shelf.

Taxa / Location	F1	F2	D1	D2	D2n	T1	B1	T2	T2n	B2	S	TOTAL
Acartia sp.	852	0	0	0	1353	0	0	0	0	0	0	2205
Appendicularia	2498	402	9136	3227	4920	935	445	226	338	4641	2206	28974
Calanus spp.	16200	16106	10340	13406	10266	8856	731	9482	3831	5697	18255	113172
Chaetognatha	488	788	3019	850	575	467	46	1395	1358	750	557	10292
Cnidaria / Ctenophora	2125	500	3880	1980	1072	795	335	226	345	750	762	12770
Echinodermata	165	0	522	1232	490	0	511	463	0	990	554	4927
Metridia sp.	6452	4892	2279	1781	1470	1130	208	1169	1341	171	1001	21896
Microcalanus sp.	2651	503	6737	3959	6809	798	90	475	2088	412	998	25519
Oithona sp.	4980	3599	2329	3705	3331	952	266	2156	1545	1395	779	25038
Triconia sp.	3306	2225	760	575	409	0	0	0	0	108	553	7936
Ostracoda	2651	3044	3301	97	2361	625	88	1159	1183	730	1009	16248
Paraeuchaeta sp.	324	0	280	463	190	165	0	0	171	85	0	1678
Pseudocalanus sp.	12953	12074	7403	34983	15826	1431	396	459	1737	1310	4444	93016
Radiolaria	986	903	2617	473	505	647	88	0	343	1255	219	8036
TOTAL	56630	45037	52602	66732	49577	16801	3203	17211	14280	18295	31338	371706

Cluster Analysis:

The VPR data comprised 14 taxa (Appendix VIII) and the abundance for each taxon was calculated per m^2 for each location. A cluster analysis was run using the Bray-Curtis method (Figure 9). Four main clusters were revealed with 40 to 90% similarity between the 14 taxa. The main clusters were (1) >50% similarity between *Metridia sp.* (Met), Radiolarians (Rad) and *Microcalanus sp.* (Mic). (2) >40% similarity between *Oithona sp.* (Oit), Jellies (Jel), *Paraeuchaeta sp.* (Euc) and *Calanus spp.* (Cal). (3) >70% similarity between Ostracoda (Ost), Echinodermata (Euc), *Pseudocalanus sp.* (Pse) and *Acartia sp.* (Aca) and (4) >50% similarity between Chaethognatha (Cha), *Triconia sp.* (Onc) and Appendicularia (App) (Figure 10). Two subgroups i.e., *Paraeuchaeta sp.* (Euc) with *Calanus spp.* (Cal) and *Pseudocalanus* sp. (Pse) with *Acartia* sp. (Aca) showed >90% similarity across locations (Figure 9).

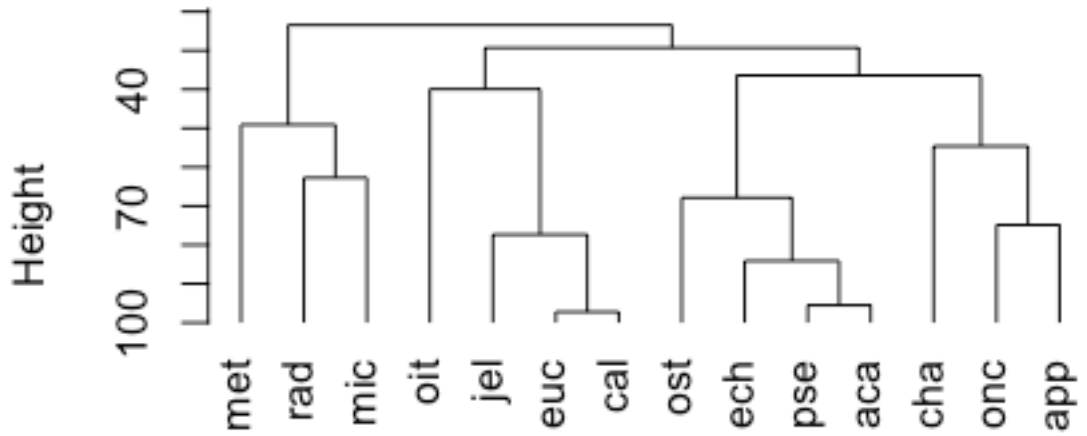

Figure 9: Clustering tree of the VPR data for each taxa depending on their abundance in m³ at each station. Cluster using the Bray-Curtis method. Aca : *Acartia sp.* ; app : Appendicularia ; cal : *Calanus spp.* ; cha : Chaetogntha ; ech : Echinodermata ; euc : *Paraeuchaeta sp.* ; jel : Cnidaria/Ctenophora ; met : *Metridia sp.* ; mic : *Microcalanus sp.* ; oit : *Oithona sp.* ; onc : *Triconia sp.* ; ost : Ostracoda ; pse : *Pseudocalanus sp.* ; rad : Radiolaria

Canonical Correspondence Analysis:

By using Canonical Correspondence Analysis with all data from the daytime VPR stations, some clusters appeared (Figure 10). This test comprises nine locations (Table 1), 14 taxa (Table 5) and five environmental parameters (depth, temperature, salinity, fluorescence and marine snow density). The variance (72,71%) was explained by axis 1 (36,89%) and axis 2 (35,82%), according to the Eigen values for unconstrained axes. In order to verify this model, an Anova was run with 999 permutations:

cca (bio ~ Station + Temperature + Depth-bin + Salinity + Density + Fluorescence, data = phys)
$P < 0{,}001$.

Fluorescence seemed to be higher at shallow depths, and at low salinity. Temperature did not seem to be strongly correlated to any of the other environmental parameters. Marine snow density tended to be negatively correlated to depth. The samples tended to group according to location and depth. The locations Bessel Fjord (F1 and F2), Dove Bugt (D1 and D2) and the Banks (B1 and B2) each formed distinct groups. The troughs (T1 and T2) were similar except along the temperature gradient where the northern through (T2) was colder than the Store Koldewey Trough (T1). The northern shelf (S) was placed in the center of the graph, and thus seemed to be equally affected by the environmental parameters.

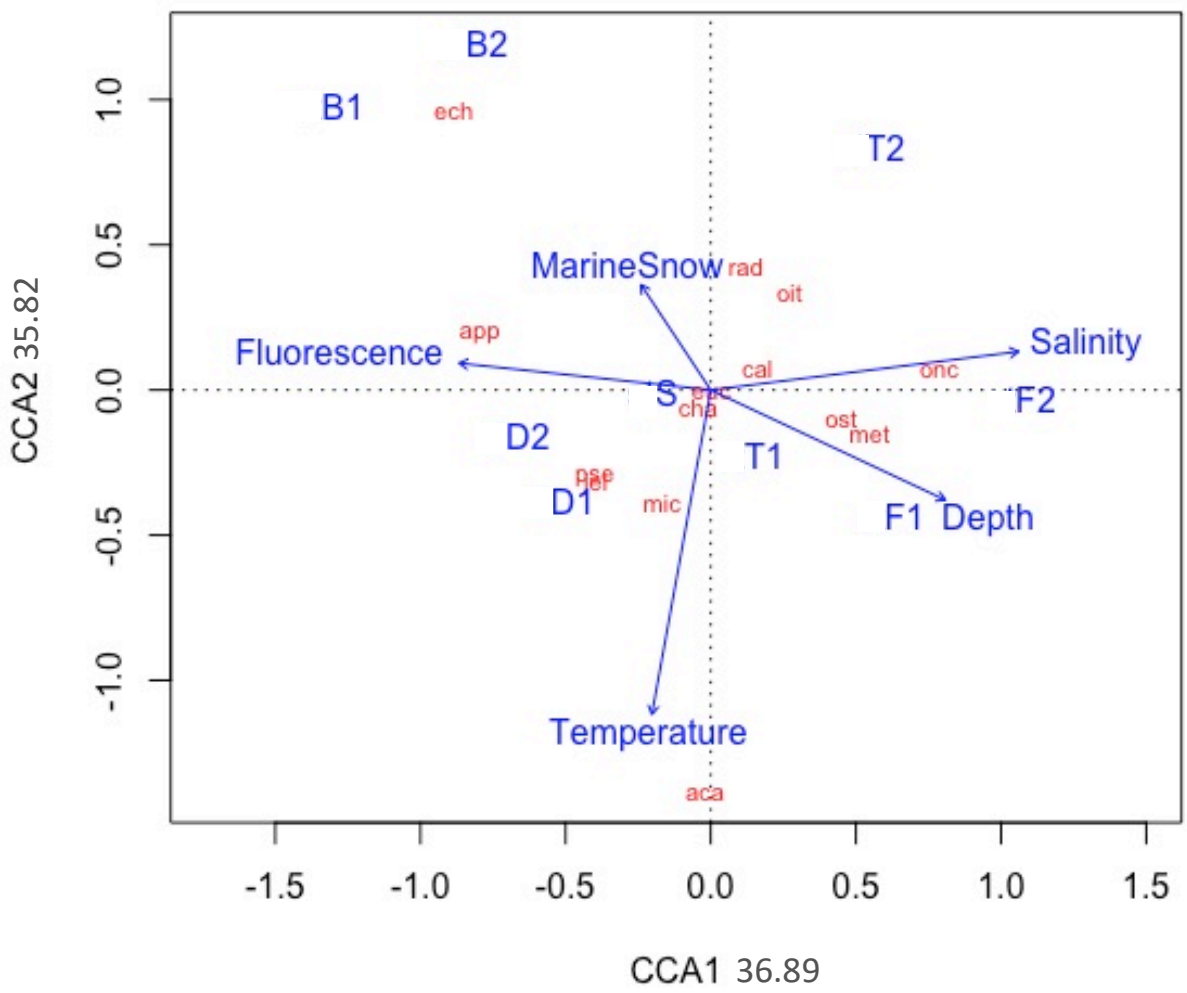

Figure 10: Canonical Correspondence Analysis, CCA, of the VPR data taking into account all taxa (red) against all physical parameters (blue arrows) with the location id (blue « st. ») as a factor.
Aca : *Acartia sp.* ; app : Appendicularia ; cal : *Calanus spp.* ; cha : Chaetogntha ; ech : Echinodermata ; euc : *Paraeuchaeta sp.* ; jel : Cnidaria/Ctenophora ; met : *Metridia sp.* ; mic : *Microcalanus sp.* ; oit : *Oithona sp.* ; onc : *Triconia sp.* ; ost : Ostracoda ; pse : *Pseudocalanus sp.* ; rad : Radiolaria
F1: Middle Bessel Fjord, F2: Inner Bessel Fjord, D1: Mouth Dove Bugt, D2: End Dove Bugt, B1: 76N-Bank, T1: Store Koldewey Trough, B2: Belgica Bank, T2: Norske Trough, S: Northern shelf.

Discussion

The results show that the zooplankton community composition differs between the locations in Northeast Greenland waters. In this section, the horizontal distribution of zooplankton will be discussed via taxa abundances in the context of environmental parameters, such as hydrography and primary production. In a second part we will explain the biodiversity variations between locations. This will be followed by a discussion of the habitat preferences found according to environmental parameters and a comment on abundance variation over time (day and night) for two different locations (D2 and T2). Finally, the benefits of supplementing net samples with VPR profiles is discussed.

Environmental parameters

It was clear that topography had a major influence on the distribution and abundance of zooplankton. The topography map (Figure 1) reveals considerable variations in depth, with fjord basins (F1 and F2), shallow banks (B1 and B2) and deep troughs (T1 and T2). Topography may direct currents on a small geographical scale, and hence affect both the extent of sea-ice cover, freshwater runoff from melting glaciers, and primary production. For example, the glacial Bessel Fjord (F1 and F2) and Dove Bugt (D1 and D2) had very low salinities of less than 29 in the top 20 m of the water column, while the shelf location (S) had a low salinity layer of just 10 m deep. Altogether, this salinity difference can lead to differences in zooplankton diversity by stratification of the water column, which creates a barrier between two water masses.

Photoperiod and light intensity are main limiting factors for primary production in Arctic waters (Rysgaard *et al*., 1999). Compared to similar latitudes on the east side of the Fram Strait, and in the Barents Sea area, Chl *a* was very low in our study area: 0,4- 0,5 $mg \cdot m^{-3}$ at the Chl *a* maximum (all locations except B1) compared to 1- 2 $mg \cdot m^{-3}$ in the Barents Sea in September (Pabi *et al.,* 2008). This can be linked to the sea-ice cover on the cold Northeast Greenland shelf remaining until much later in the season compared to the eastern side of the Fram Strait (Funder *et al.,* 2011) which is heated by warm currents. In fact, the spring bloom can occur only in presence of nutrient and light in the water (Signorini & McClain, 2009). The lenghtly period of sea ice cover in this region delays the input of light which is necessary to trigger the spring bloom in the water column. In consequence, the reproduction and growth of the zooplankton, in turn generally triggered by the spring bloom (Søreide *et al*., 2010; Hirche, 2013), start later in the year in Northeast Greenland. The second Chl *a* peak at 60 m on the 76N-Bank could be due to resuspension of the sunken phytoplankton.

Zooplankton abundance and taxa distribution

Zooplankton community composition changes as you move from the inner fjord basins of Bessel Fjord, with more stationary populations, to the outer coastal areas and shelf locations, where populations are advected from Arctic and Atlantic sources, and mixed. Indeed, most of the small species (*Acartia* sp., *Microcalanus* sp., *Oithona* sp., *Triconia* sp. and *Pseudocalanus* sp.) tend to be less present towards the open ocean compared to coastal areas. This is also the case for the bigger zooplankton species *Metridia* sp. but the other large zooplankton (not only copepods) did not show any distribution pattern between coastal area and more open ocean locations.

The high abundances of zooplankton in Bessel Fjord (F1 and F2), the inner part of Dove Bugt (D2) and the Store Koldewey Trough (T1) might be due to the effect of currents guided by the local land and sea-floor topography. The Store Koldewey Trough (T1) is oriented south-east, east of the shallow 76N-bank (B1) and west of the Store Koldewey island partially closing Dove Bugt (Figure 1). The southbound East Greenland Current (EGC) flows along the coast and could explain the high abundance of zooplankton in the Store Koldewey Trough (T1) as the flow tends to bypass the very shallow 76N-Bank (B1) by flowing on the trough side. This flow can lead to a transport of zooplankton in the Store Koldewey Trough (T1). This may also explain why we have this very low abundance (less than 43 000 ind·m^{-2}) on the 76N-Bank (B1) as the zooplankton would not be guided towards it but around it. The Store Koldewey Trough (T1) is 323 m deep, five times deeper than the 76N-Bank (B1), which gives more space and a wider range of living conditions throughout the water column for the zooplankton. Most of the water flows through the Store Koldewey Trough (T1). This south-flowing water flow might be nutrient poor, which explains the low Chl *a* value at this location (0,3 mg·m^{-3} at Chl *a* max). Grazing from the large quantity of zooplankton (more than 168 000 ind·m^{-2}) may also have reduced the Chl *a*. The high abundances in the semi-enclosed Dove Bugt (D2), and in Bessel Fjord (F1 and F2), might be due to the confined topography which these coastal location present, keeping calm and stable weather conditions for zooplankton to grow. In addition to this, land can provide nutrients via runoff and wind to both locations. The higher abundances found in the inner part of Dove Bugt (D2) may be due to its shallower depth, enhancing a stronger benthic-pelagic coupling than in Bessel Fjord (F1 and F2).

At the entrance of Dove Bugt (D1), zooplankton abundances were very low, less than 65 000 ind·m^{-2}, whereas in the inner part (D2) and in Bessel Fjord (F1 and F2) abundances were higher than 100 000 ind·m^{-2}. This might be explained by the patchiness of the zooplankton (Folt & Burns, 1999) or because of zooplankton accumulate in the basins of Bessel Fjord and Dove Bugt. The current is probably weaker than on the shelf, so zooplankton have a longer residence time in the bay. Here, zooplankton

might have good nutrient supply which can lead to a high reproduction rate explaining their higher abundance.

The shelf location (S) had a low abundance of zooplankton, as it is further away from the coast and at a higher latitude. Indeed, the more offshore a location is, the less productive it will be, as there are less nutrients coming from land (Polis & Hurd, 1996). This far from the coast, the benthic-pelagic coupling would be weak, and the nutrient regeneration low (Rowe *et al*., 1975). Also, the melting of the sea ice came later in the shelf location (S) compared to more southern locations, like the 76N-Bank or the Store Koldewey Trough. In consequence, the zooplankton reproduction and growth were delayed due to a later start of the spring bloom (Skjoldal *et al.*, 1986; Conover & Huntley, 1991; Signorini & McClain, 2009).

The diversity was low in Bessel Fjord, 1,7 at the inner station (F2) and just above 2 at the middle location (F1). The salinity was very low, less than 29 at in the middle part (F1) due to the nearby melting glacier, adding a great proportion of freshwater to the fjord water. Low salinity is known to makes living conditions for zooplankton harder (Sommaruga, 2015). Indeed, not all zooplankton species tolerate living in a low salinity environment. At the entrance of Dove Bugt (D1), we had a higher diversity, as it is the junction between an enclosed area and the shelf area which are two different habitats for zooplankton. The inner part of Dove Bugt (D2) also presented a low diversity, due to freshwater runoffs producing a salinity of less than 29 in the upper 50 m.

On the shelf, both Shannon and Simpson indexes showed low diversity (less than 2 for the Shannon index) for the near shore locations (B1, T1 and T2), compared to offshore locations (B2 and S), where the diversity almost reached 2,5 (Shannon index). This might be the result of advection from two different areas, as two currents meet at these locations (B2 and S): the cold East Greenland Current and the warm Return Atlantic Current, coming from the eastern side of the Fram strait.

In fact, about 50% of the Atlantic water coming to the Svalbard area is estimated to cross the Fram strait (De Steur *et al*., 2014). This advection process could also explain why a high abundance (more than 14 000 ind·m^{-3}) of the boreal *Calanus finmarchicus* were found on the shelf location (S), representing 64% of the total *Calanus* found at this location (S). However, *C. finmarchicus* is not known to reproduce in this area (Jaschnov, 1970; Conover, 1988).

C. glacialis is known to be the dominant species of the *Calanus* genus in cold and less saline waters (Choquet *et al.,* 2017). We found both young and old stages (C2 to adult female) at several locations (Inner part of Bessel Fjord, Store Koldewey Trough (T1) and Shelf (S)) which suggests that they might be reproductive areas for *C. glacialis*. *C. glacialis* overwinter at least once before it reproduces (Scott *et al.,* 2000). Our samples were taken in late September but *C. glacialis* can overwinter only as stage C5 and adult (Scott *et al.,* 2000). Therefore, it is unlikely that the younger stages would reach these threshold stages to survive the winter. The third *Calanus* species, *C. hyperboreus,* is a more Arctic and off-shelf species (Conover, 1988), which correlates with our observation that it was not very abundant

in coastal locations like the Dove Bugt (D1 and D2) or the Store Koldewey Trough. *C. hyperboreus* was only found from stage C4 to Adult female as well as stage C3 at location F1.

Among the macrozooplankton species, the arrow worms *Parasagitta elegans* and *Eukrohnia hamata* showed a peculiar distribution. *P. elegans* is usually found in cold areas whereas *E. hamata* inhabits warmer waters (Eisner *et al*., 2014). However, we found *P. elegans* to be the major Chaetognatha species at the most off-shore location, i.e. the northern shelf (S), which is the warmer location of the study. In addition to that, *E. hamata* was the dominant species at cold locations, like Dove Bugt (D1 and D2) and the Store Koldewey Trough (T1). The hyperiid amphipod *Themisto abyssorum* did not show any specific distribution pattern, whereas the krill *Thysanoessa* sp. was only present in the mouth of Dove Bugt (D1) which makes it difficult to state any habitat preferences. Moreover, because *T. abyssorum* and *Thysanoessa* sp. belong to the most agile zooplankton taxa, they would easily avoid the WP-2 net and thus their abundances tend to be underestimated.

Vertical differences in species distribution – habitat preferences

Groups of taxa tended to cluster in the Cluster Analysis such as the copepods *Paraeuchaeta* sp. and *Calanus* spp.. Some correlations between taxa grouping and distribution could be explained with the Canonical Correspondence Analysis (CCA).

Pseudocalanus sp.*,* Cnidaria, Ctenophora, Appendicularia and the meroplanktonic echinoderm larvae were present in the upper part of the water column. This seems a typical characteristic for *Pseudocalanus sp.* during the productive season (Norrbin, 1987) as also found by Tang *et al*. (2011) in Western Greenland. These taxa also seemed to be associated with a high Chl *a* fluorescence. As for the distribution of echinoderm larvae, it seems to be mainly correlated to the density of marine snow. Indeed, they were both concentrated at the bank locations (B1 and B2). Some other taxa tended to have less specific habitat choices than the five taxa above. Chaetognatha and *Paraeuchaeta* sp. did not show any significant pattern in habitat preference across the tested environmental parameters. The case of the genus *Calanus* is more difficult to interpret, because the taxon comprises at least three different species in Northeast Greenland: *C. finmarchicus,* which is usually high in the water column and in warmer open areas (Conover, 1988), *C. glacialis,* which is more a stenothermal shelf and cold fjord species (Scott *et al.,* 2000; Scheel, 2019) and *C. hyperboreus* which is present in open areas and at depth in fjords (Conover, 1988; Tang *et al*., 2011; Choquet *et al.,* 2017). The copepod *Oithona* sp. was found at all locations with a presumed preference for cold waters. The temperature was the lowest in the upper 100 m at most locations, except in Bessel Fjord where the temperature was less than -1°C below 50 m depth. This agrees with the low abundances of *Oithona sp.* reported below 100 m for West Greenland locations (Zamora-Terol *et al*. 2014). The Bessel Fjord is an exception, as *Oithona* sp. was found in

even abundances below 50 m in Bessel Fjord, which confirms the preference for cold temperature in this genus. (F1 and F2). Radiolarians were also found at low temperatures and associated with marine snow. Indeed, Radiolaria was the taxon with the clearest presence at locations with high densities of marine snow. Ostracods, *Metridia* sp., and *Triconia* sp. were mainly present in deep and saline waters. These conditions were found in Bessel Fjord (F1 and F2) and in the troughs (T1 and T2). Tang *et al.* (2011) showed that *Metridia longa* is the one of the dominant zooplankton occurring in deep fjords, and that they are present throughout the water column, but with higher abundances in the upper 100 m. However, in Kongsfjorden, Spitsbergen, Hop *et al*. (2002) found higher abundances of *Metridia longa* below 200 m. In Bessel Fjord (F1 and F2), *Metridia* sp. was observed in the deeper part of the water column, which suggests that they prefer more saline waters. Lastly, the copepods *Acartia* sp. and *Microcalanus* sp. showed preferences for warm waters, and temperature seemed to be the most important driver for their distributions. *Acartia* sp. are coastal species, rarely found outside fjords or estuaries (pers. comment F. Norrbin).

Day and Night variations

In our study, VPR data for both zooplankton abundance and diversity differed between day and night. Even though different results were obtained between the two sampling times at each station it is not possible to investigate Diel Vertical Migration (Lampert, 1989), as the sampling times were not optimal i.e. not at midday and midnight. Instead, any observed variations might be due to water masses movements. The diversity indexes gave the same trend for both locations (D2 and T2) despite very different environmental conditions (D2 is a shallow 218 m bay location whereas T2 is a deep 449 m trough on the shelf). We found that the zooplankton biodiversity was higher during night time: 21:20 for location D2 and 18:17 for location T2. Indeed, the biodiversity increased ca. 21% (D2) to 26% (T2) at night according to the Shannon index and 43% (D2) to 56% (T2) according to the Simpson index. However, not all taxa varied in abundance between day and night. Also, the variations in taxa abundance were not the same for both locations, the inner Dove Bugt (D2) and the Norske Trough (T2). At both locations, *Microcalanus* sp. was more abundant at night. In the inner part of Dove Bugt (D2), *Acartia* sp. and Ostracoda were more abundant at night, whereas the opposite trend was seen for Ctenophora, Cnidaria and *Pseudocalanus* sp.. At the Norske Trough (T2), *Pseudocalanus* sp., was more abundant at night whereas *Calanus* spp. tended to be more abundant during the day. These variations cannot be due to the environmental parameters investigated in this study as they were very similar between day and night for each location, except for the marine snow concentration. Indeed, the marine snow concentration did change in the inner part of Dove Bugt (D2) but not in the Norske Trough (T2) as it sinks over time or may be advected by currents. As a consequence, marine snow concentrations could not explain abundance variations between day and night for *Microcalanus* sp., *Calanus* spp. and *Pseudocalanus* sp., as they showed different abundances in the Norske Trough (T2) between day and

night. The marine snow concentration was higher during the day in Dove Bugt (D2) which could explain why *Acartia* sp. was not present during the day, but present at night in other water masses. Furthermore, the PCA showed that *Acartia* sp. was negatively correlated with marine snow concentration which suggest that *Acartia* sp. tend to stay in low marine snow concentration water masses even though it is known to prefer high Chlorophyll *a* environment (pers. comment F. Norrbin). Cnidaria, Ctenophora and Ostracoda were not related to marine snow according to the PCA, which might lead to the conclusion that these taxa showed abundance variations between day and night sampling due to patchiness or due to another parameter not investigated here like the light intensity with Diel Vertical Migration (Lampert, 1989).

Comparison between WP-2 and VPR sampling

Despite the differences observed in abundances between WP-2 and VPR for specific taxa, the biodiversity was similar between the two sampling gear according to both the Shannon index and the Simpson index when using the same 14 taxa. In order to study zooplankton communities and abundances, it is useful to use both types of gear, as they are complementary. The VPR samples big mesozooplankton and gelatinous species better, and the modified 85 µm WP-2 captures small mesozooplankton better. Using only one of the two sampling devices would give representative abundances only for a certain part of the mesozooplankton. Moreover, the VPR adds one more parameter: the depth distribution of the zooplankton taxa. This is indispensable, since the zooplankton species are distributed in the water column depending on environmental preferences and in response to other pelagic species. Some zooplankton species are predators, like chaetognaths, which prey on small copepods like *Pseudocalanus* sp. (Tang *et al.*, 2011). In this case, it is interesting to have the depth distribution for each taxon in order to see if there is any avoidance pattern from the prey. In fact, the prey could choose to live in other water masses or just at a different depth than its predator. This would not be possible to observe with a WP-2 net. A Multinet or a MocNess net, on the other hand, may be used to sample discrete depth layers, but would still be less precise than the VPR. Furthermore, the VPR does not only record live zooplankton, but also marine snow and fecal pellets of e.g. krill. Neither plankton nets nor the CTD rosette's water bottles could be used to sample particle depth distributions on this fine scale. As this study shows, marine snow was correlated with the distribution of several taxa, such as echinoderm larvae, Appendicularia and Radiolaria. In addition, it is essential to pelagic carbon export and nutrition for the benthos.

Moreover, incoherencies between the cluster analysis and the CCA analysis might be due to differences in sampling method. The most obvious explanation is that the cluster analysis does not consider the depth distribution but only the distribution integrated for the whole water column, so the result of the cluster analysis uses one less parameter, the depth. Alternatively, the uncertainties for the major environmental parameters correlating with each taxon distribution in the CCA analysis are too large.

Also, in the CCA, if two environmental parameters are important for the distribution of a taxon but are opposite on the graph, the taxon will appear as not having any strong driver.

Conclusion

The aim of this study was to assess and identify distribution patterns of the zooplankton community in Northeast Greenland creating the first large scale baseline study on zooplankton distribution in Northeast Greenland. Even though the late summer period, September, was investigated, the zooplankton abundances were very low even though zooplankton production should have been close to its maximum which occur in mid-August just South, in Young Sound (Digby, 1953). Zooplankton communities in Northeast Greenland varied a lot between sampling areas because of differences in environmental parameters. Here, the occurrence of organisms was correlated with physical parameters, such as temperature, depth, topography and, salinity as well as biological parameters, like fluorescence and marine snow concentration. In future studies, fine scale current data using ADCP for example, should be added in order to provide a better understanding on the possible accumulation of zooplankton at some locations like the inner part of Bessel Fjord (F2) and the inner part of Dove Bugt (D2).

The lack of previous zooplankton studies in this remote area makes it difficult to make conclusions based on a single field campaign. We must only speculate about if these patterns are purely patchiness or if they are reliable to define niches preferences for each taxon.
To continue zooplankton studies in this region, a closer look at the possible differences in the size of *Calanus* spp. oil sacs using the VPR should be measured to investigate the possible link with the primary production and the length of the ice-covered period at each location. A comparison with Northeast Greenland shelf and fjord and bay locations on the Spitsbergen side of the Fram Strait, at the same latitude, would be interesting to do in order to find similarities and differences in zooplankton habitat preferences for given species. Last but not least, a DNA study to differentiate *Calanus* species in this region needs to be held to broaden the study by Choquet *et al.* (2018).

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Appendix

Appendix I: parameters of each WP-2 stations

WP-2 number	Station number	Longitude	Latitude	Max Depth (m)	Location name
1	1286	75°59’2.30"N	21° 8'5.00"W	363	F1
2	1297	75°58'25.00"N	21°42'10.00"W	223	F2
3	1307	76° 0'8.00"N	19°33'5.00"W	470	D1d
4	1317	76°44'0.00"N	19°18'0.00"W	218	D2
5	1339	76° 0'59.98"N	14°13'60.00"W	335	T1
6	1348	76° 0'59.98"N	16°27'40.00"W	58	B1
7	1355	77°51'54.00"N	15°34'60.00"W	449	T2
8	1367	78° 9'8.50"N	11°18'7.50"W	184	B2
9	1373	79°16'1.00"N	7° 7'9.00"W	220	S

Appendix II: parameters of each VPR stations

VPR number	Station number	Longitude	Latitude	Max VPR depth (m)	Start time (UTC)	Stop time (UTC)	Sampling time (min)	Location name
VPR 1	1285	75°59’2.30"N	21° 8'5.00"W	364	10:25	11:23	58	F1
VPR 2	1295	75°58'25.00"N	21°42'10.00"W	230	19:18	20:20	62	F2
VPR 3	1304	76° 0'8.00"N	19°33'5.00"W	495	16:08	17:01	53	D1
VPR 4	1315	76°44'0.00"N	19°18'0.00"W	214	13:53	14:48	55	D2
VPR 5	1321	76°43'50.00"N	19°19'15.00"W	210	20:19	21:16	57	D2n
VPR 6	1337	76° 0'59.98"N	14°13'60.00"W	323	8:20	9:13	53	T1
VPR 7	1347	76° 0'59.98"N	16°27'40.00"W	68	18:10	18:58	48	B1
VPR 8	1353	77°51'54.00"N	15°34'60.00"W	404	11:36	12:36	60	T2
VPR 9	1361	77°49'8.50"N	14°45'0.00"W	435	18:18	19:39	81	T2n
VPR 10	1366	78° 9'8.50"N	11°18'7.50"W	170	9:01	9:56	55	B2
VPR 11	1374	79°16'1.00"N	7° 7'9.00"W	252	8:48	9:48	60	S

Appendix III: Stage description and length classes (Prosome length (µm)) to distinguish *Calanus* species. (Modified from Daase & Eiane, 2007)

Stage	#swimming legs	#urosome segments	#prosome segments	*C. finmarchicus*	*C. glacialis*	*C. hyperboreus*
CI	2	2	3	<810	810-900	>900
CII	3	2	4	<1170	1170-1350	>1350
CIII	4	2	5	<1470	1470-1950	>1950
CIV	5	3	5	<2010	2010-2910	*(>2910)
CV	5	4	5	<2937	>2937	*(>4000)
Adult female	5	4 (5 for males)	5	<3240	>3240	*(>4500)

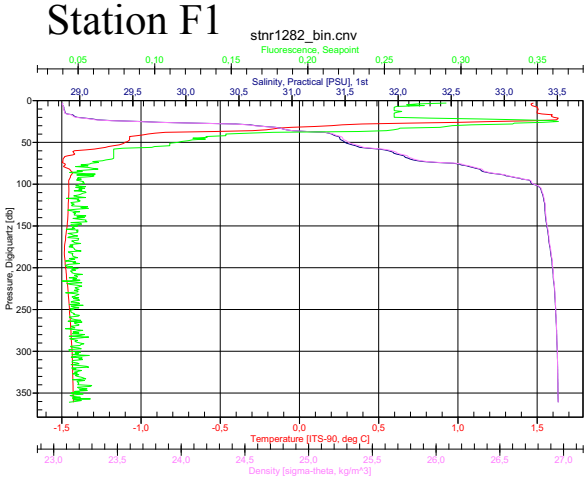
*distinguished by characteristic 5th thoracic segment with acute process

Appendix IV: Settings used for all locations in Autodeck to extract the ROIs

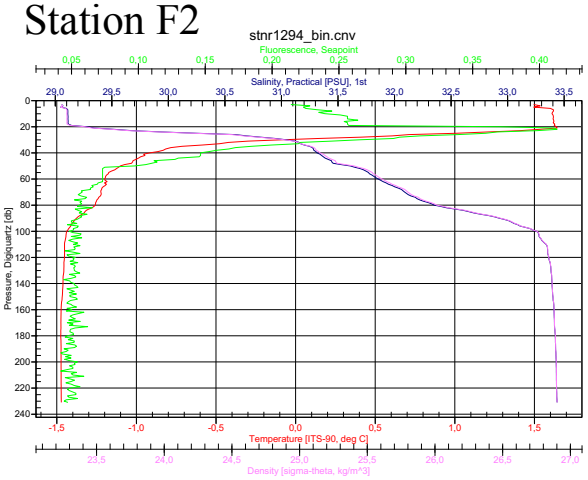
Setting	Value
Segmentation threshold	Low : 0 High : 140
Focus	Sobel : 30 Standard deviation : 10
Growth scale	300%
Blob size	Minimum 50
Join distance	Minimum 25

Appendix V: CTD graphs

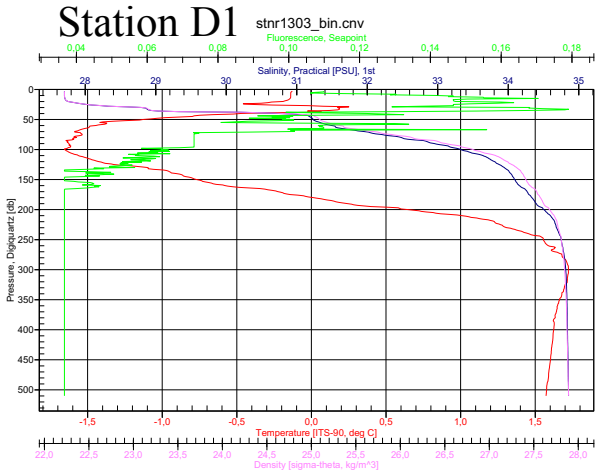
Station F1



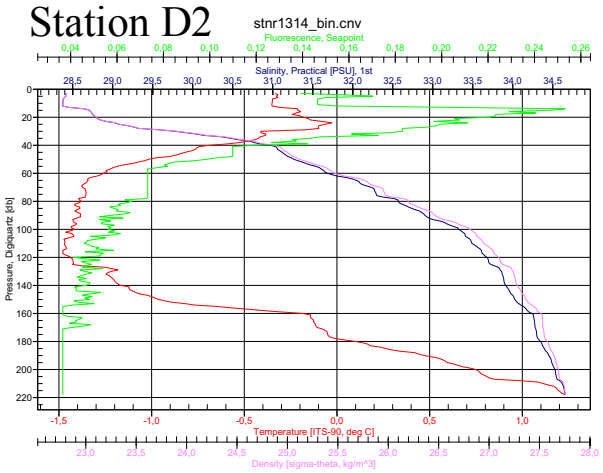
Station F2



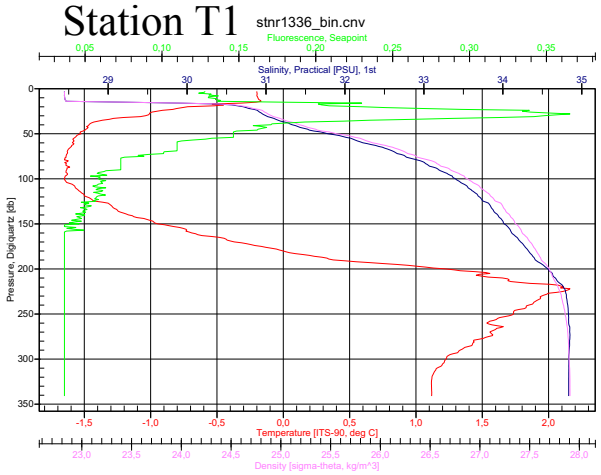
Station D1



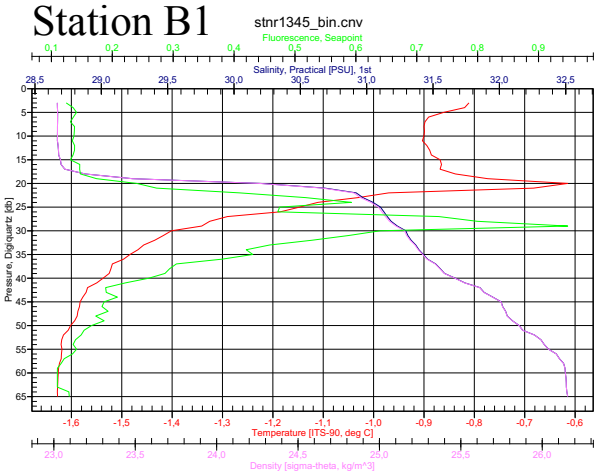
Station D2



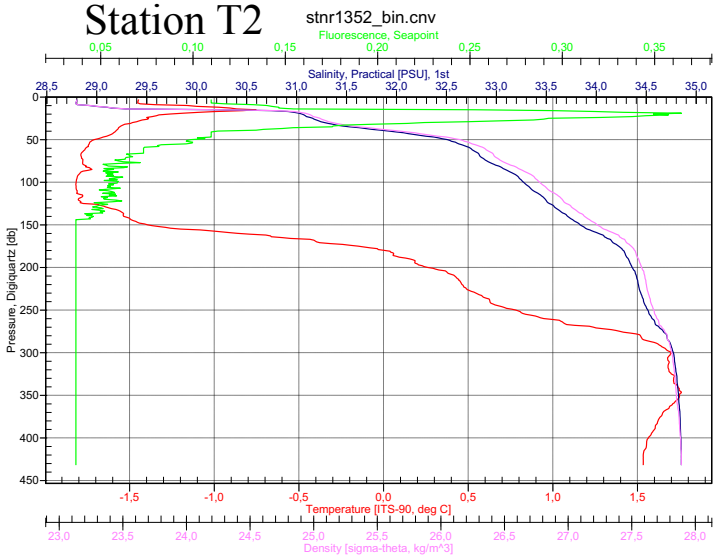
Station T1



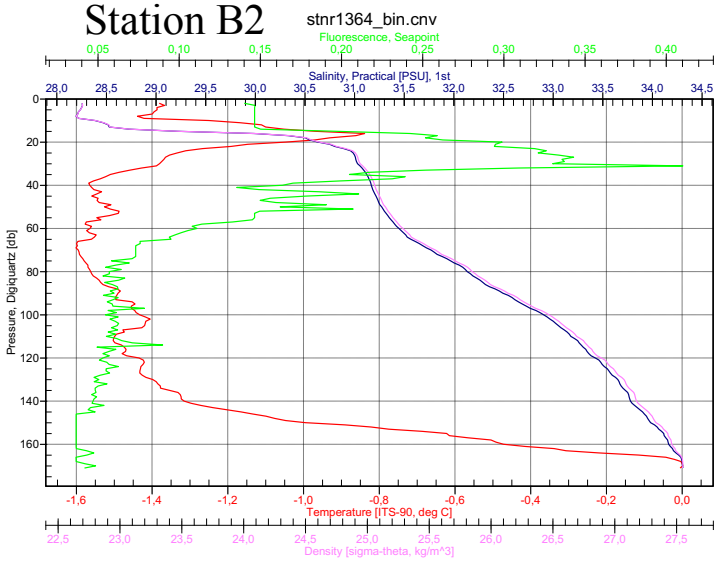
Station B1



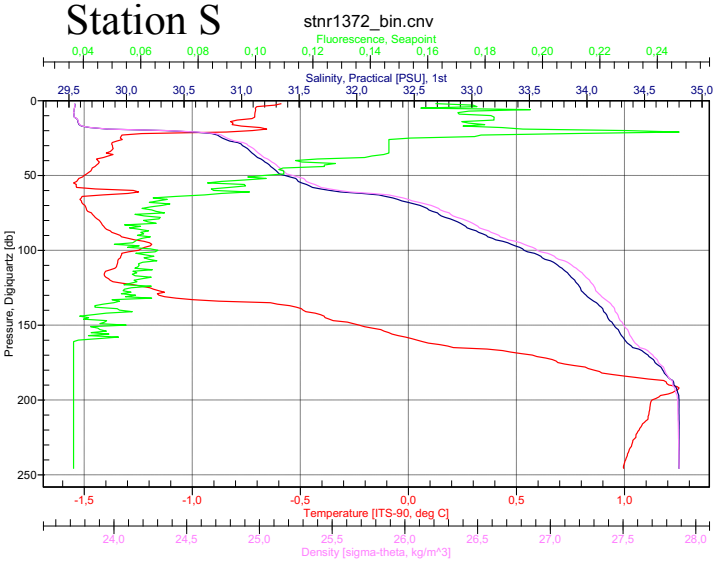
Station T2



Station B2



Station S



Appendix VI: WP-2 counts for each taxon at each location (Cop: copepodite stage, AF: Adult female, AM: Adult male, C#: Copepodite stage C#)

	F1	F2	D1	D2	T1	B1	T2	B2	S	TOTAL
V sample (ml)	2000	2000	2000	2000	2000	1000	2000	1000	2000	
V subsample (ml)	34	34	68	34	34	34	68	34	34	
Oithona sp. AF	136	232	10	53	361	49	57	119	44	1061
Oithona sp. cop	9	8	84	47	148	167	220	132	59	874
Psedocalanus sp. cop	136	90	244	248	82	29	20	28	27	904
Calanus sp. nauplii	7	8	51	30	20	31	19	42	44	252
Microcalanus sp. cop	5	2	41	16	28	13	39	24	38	206
Psedocalanus sp. AM	0	59								59
Triconia sp.	3	2	27	19	4	15	7	16	16	109
Calanus sp. C4	20	5	13	3	29	5	6	1	18	100
Calanus sp. C5	15	12	10	1	1	5	18	10	9	81
Metridia sp. cop	12	4	23		9	2	23	5	3	81
Microcalanus sp. AF	5	9	3		2	1	9	18	6	53
Calanus sp. C3	2		2	7	12	2			22	47
Fritilaria sp.				3	1	24		11	1	40
Oikopleura sp.				1			1	33	4	39
Echinodermata		2		8	2	9	3	5	1	30
Fish egg	5	2		3		10	2	5		27
Metridia sp. AM	16	4	1							21
Calanus sp. AF		7	2				6	3	2	20
Metridia sp. AF	2	2			7		3	3		17
Boroecia sp.			9				4	2		15
Bivalve veliger	5	4		3			1			13
Acartia sp.	4		2		1	3	2			12
Microcalanus sp. AM	12									12
Oithona sp. AM	9	1								10
Calanus sp. C2		1			3				5	9
Paraeuchaeta sp.			2	2	1		1	3		9
Disconchoecia sp.	1		4	2			2			9
Psedocalanus sp. AF	2	1		2	1					6
Radiolaria	1	4		1						6
Microsetella sp.			1				3		1	5
Parasagitta sp.	1		2		1		1			5
Pteropoda			2					2	1	5
Isopoda					2		1	1		4
Eukrohnia sp.							3		1	4
Dinoflagelate		3								3
Decapoda larvae			3							3
Thysanoessa sp.			2							2
Siphonophora			1				1			2
Chiridius sp.			1				1			2
Aglantha sp.	1									1
Themisto sp.		1								1
Polychaetae									1	1
TOTAL	409	462	540	449	715	365	453	463	303	4158

Appendix VII: Macrozooplankton counts for each location

Location name	F1	F2	D1	D2	T1	B1	T2	B2	S
Aglantha sp.		4		1	3				
Siphonophora			1						
Eukrohnia hamata	8	2	29	32	58		11	12	
Parasagitta elegans	26	23	3	30	3	4	23	1	17
Paraeuchaeta sp.			1				4		1
Thysanoessa sp.	2		19		1				
Meganyctiphanes norvegica			1						
Themisto abyssorum								6	
Themisto libellula		6	2		3		2	1	1
Isopoda								1	

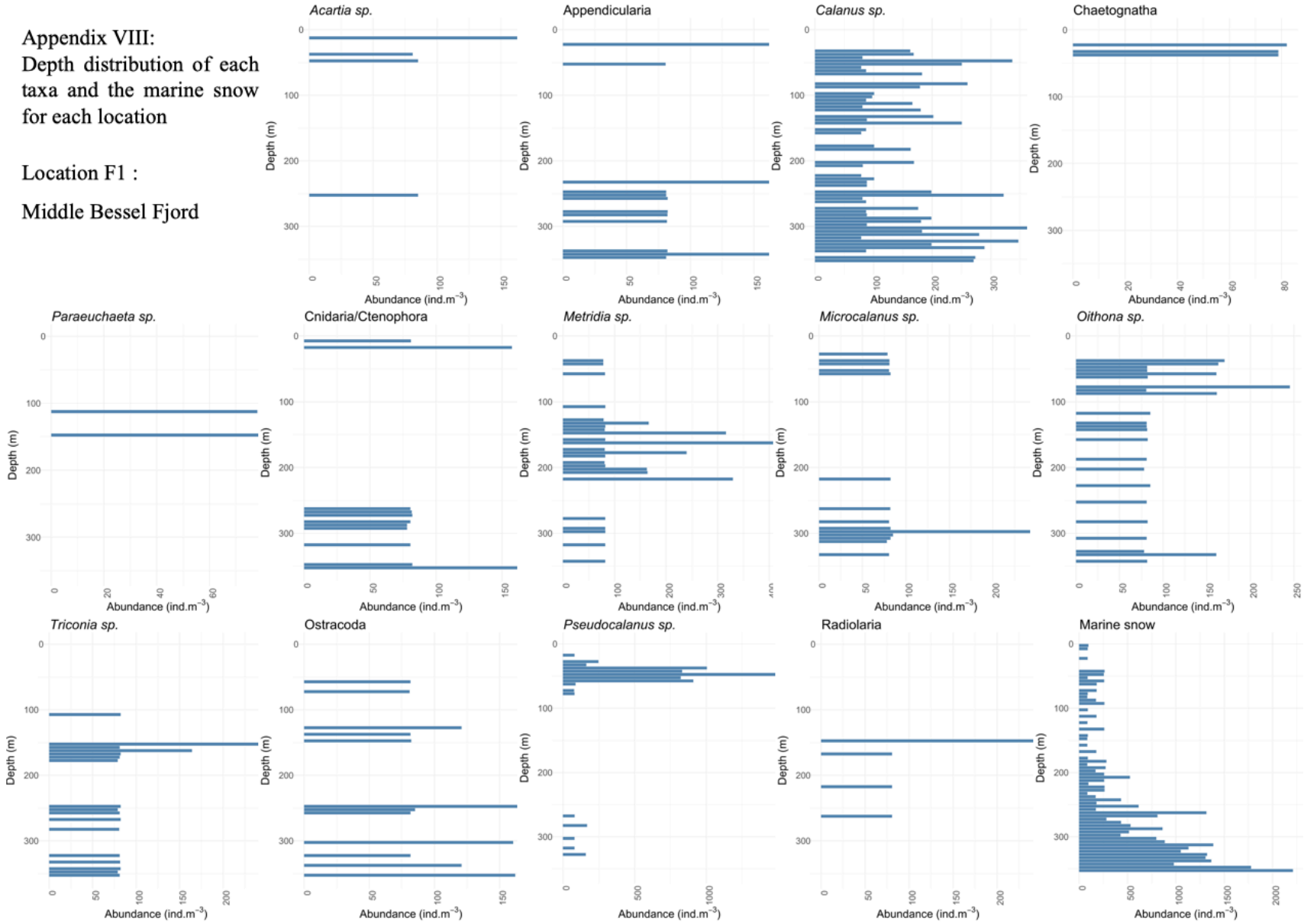
Appendix VIII: VPR counts for each taxon at each location

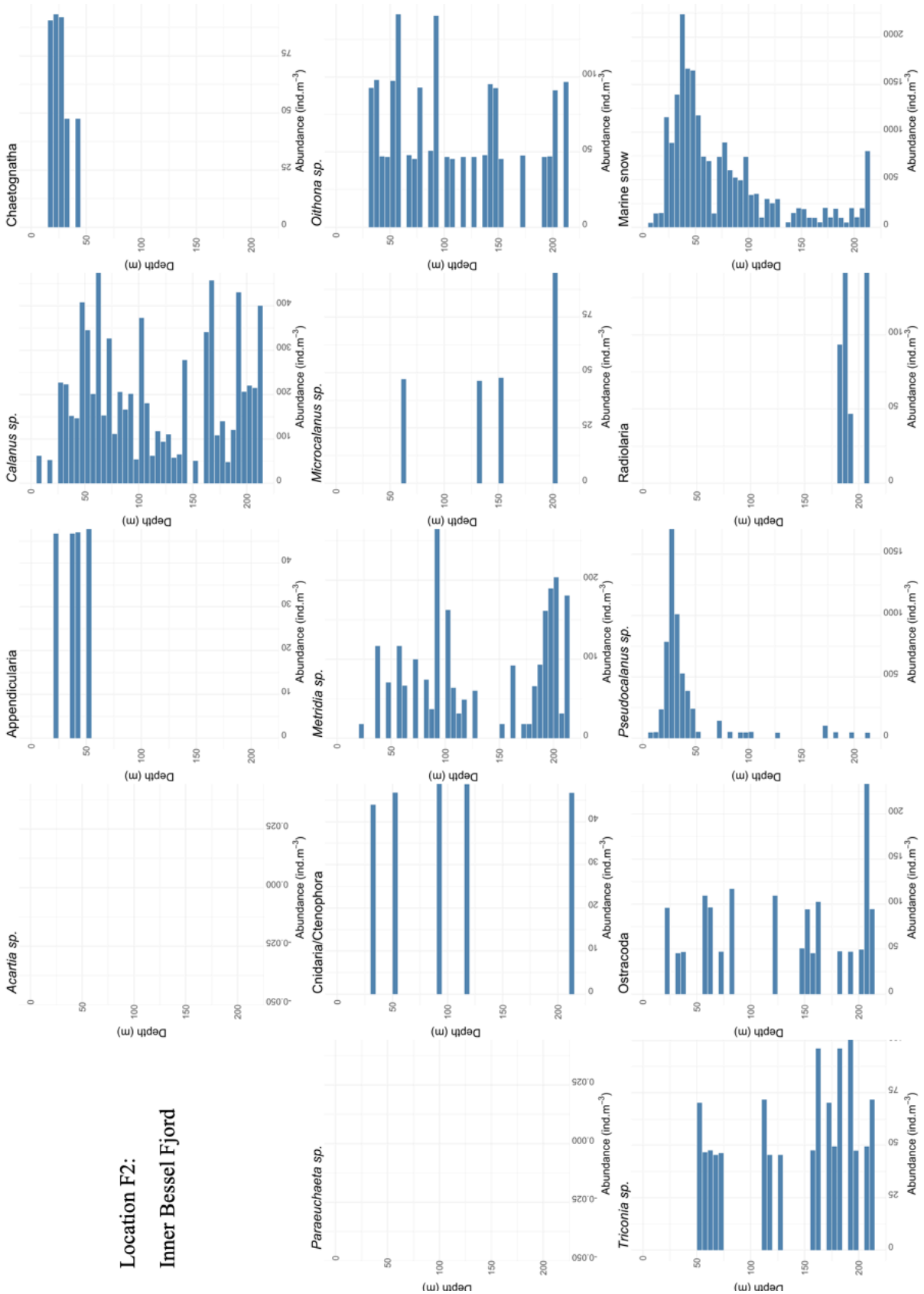
Location name		F1	F2	D1	D2	D2n	T1	B1	T2	T2n	B2	S
VPR number		1	2	3	4	5	6	7	8	9	10	11
Acartia sp.	Aca	6	0	0	0	16	0	0	0	0	0	0
Appendicularia	App	17	4	47	38	59	7	16	1	2	69	22
Calanus spp.	Cal	112	176	53	158	123	69	27	59	22	84	183
Chaetogntha	Cha	3	9	15	10	7	4	2	9	8	11	6
Echinoderm larvae	Ech	1	0	3	15	6	0	19	3	0	15	6
Paraeuchaeta sp.	Euc	2	0	1	5	2	1	0	0	1	1	0
Ctenophora/Cnidaria	Jel	15	5	20	23	13	6	12	1	2	11	8
Metridia sp.	Met	45	54	12	21	18	9	8	7	8	3	10
Microcalanus sp.	Mic	18	6	34	47	82	63	3	3	12	6	10
Oithona sp.	Oit	34	39	12	44	40	7	10	13	9	21	8
Triconia sp.	Onc	23	24	4	7	5	0	0	0	0	2	6
Ostracoda	Ost	18	33	17	1	28	5	3	7	7	11	10
Psedocalanus sp.	Pse	90	132	38	412	190	11	15	3	10	19	44
Radiolaria	Rad	7	10	13	6	6	5	3	0	2	19	2

Appendix VIII:
Depth distribution of each taxa and the marine snow for each location

Location F1 :

Middle Bessel Fjord

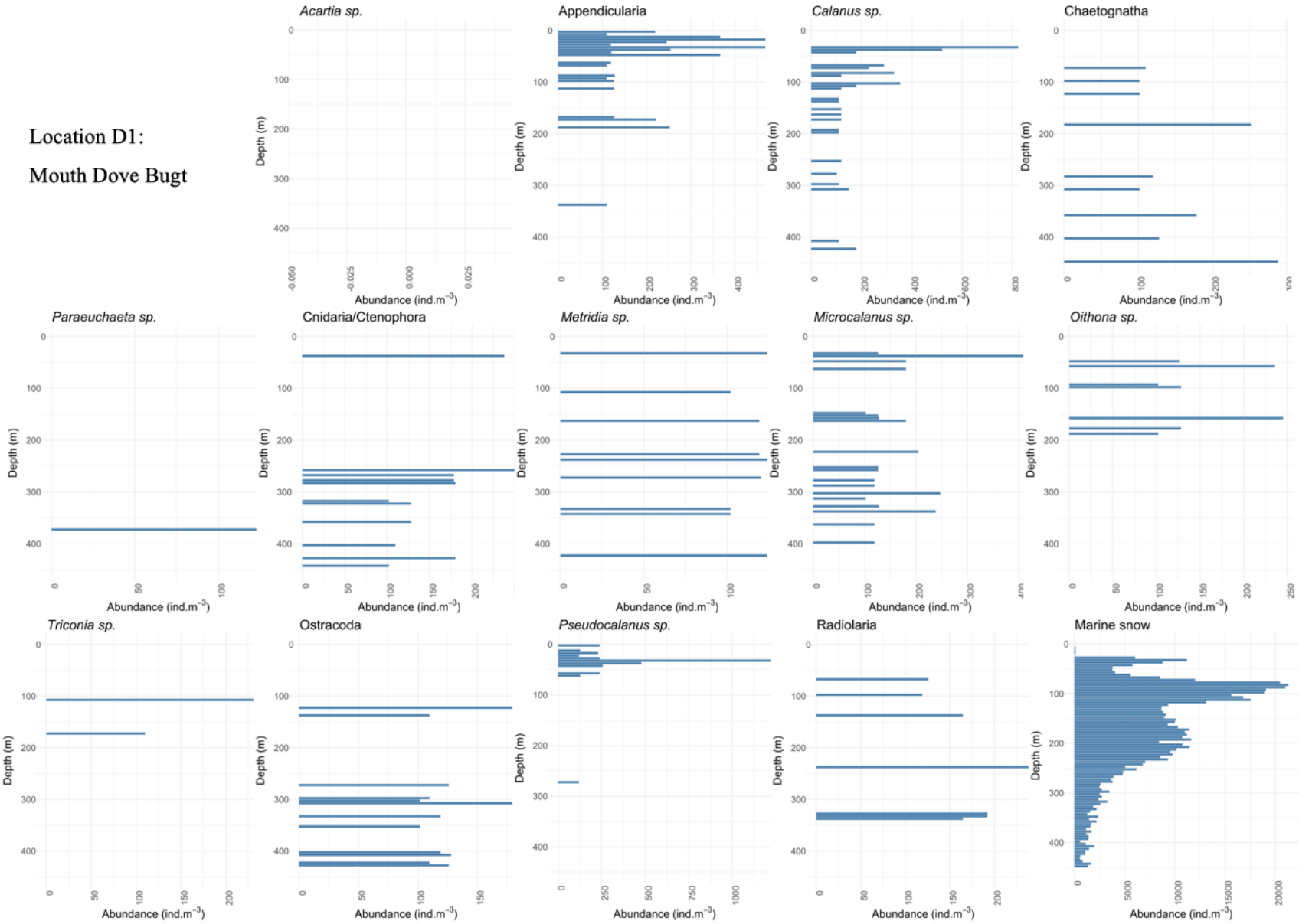




Location F2:
Inner Bessel Fjord

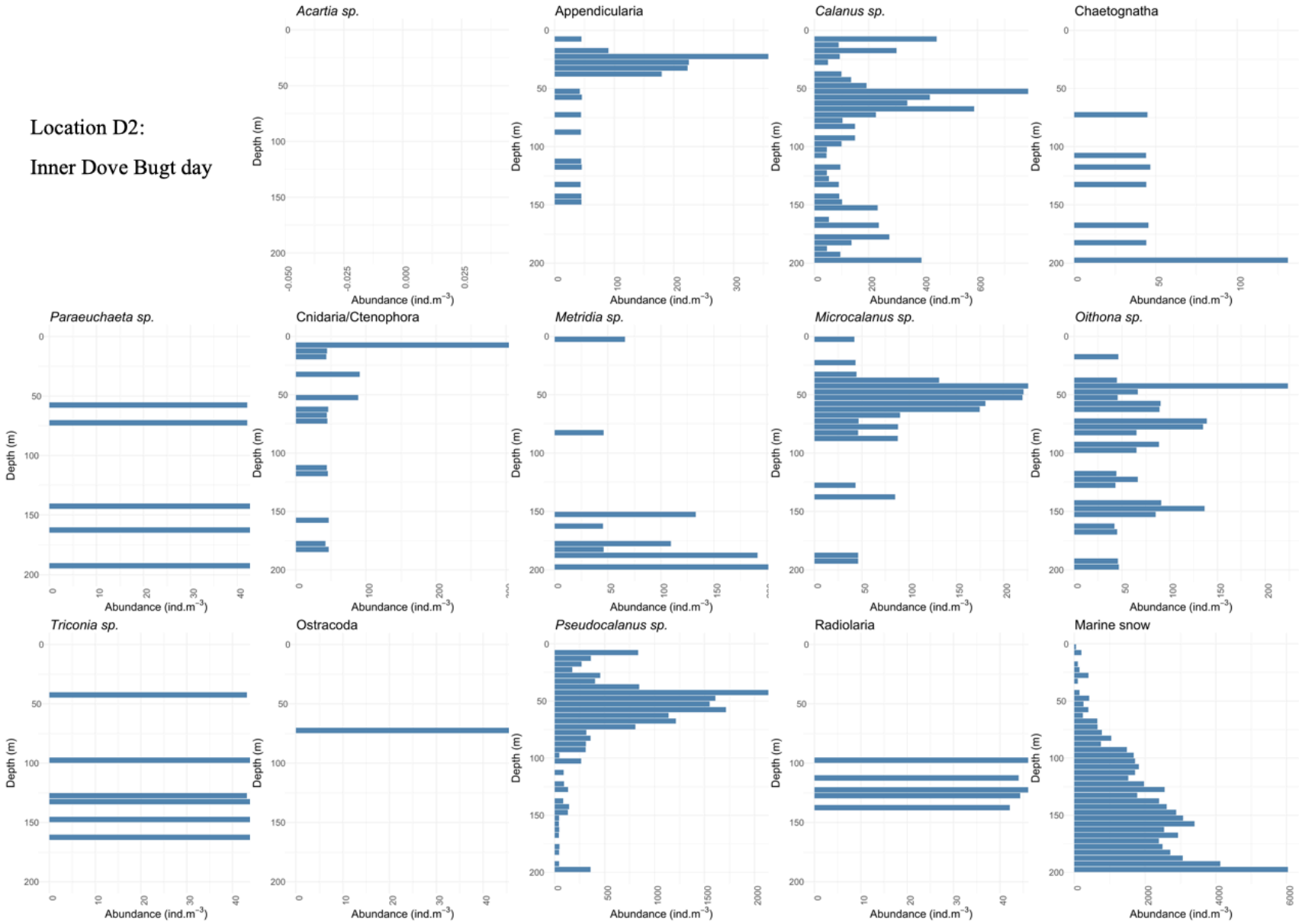
Location D1:

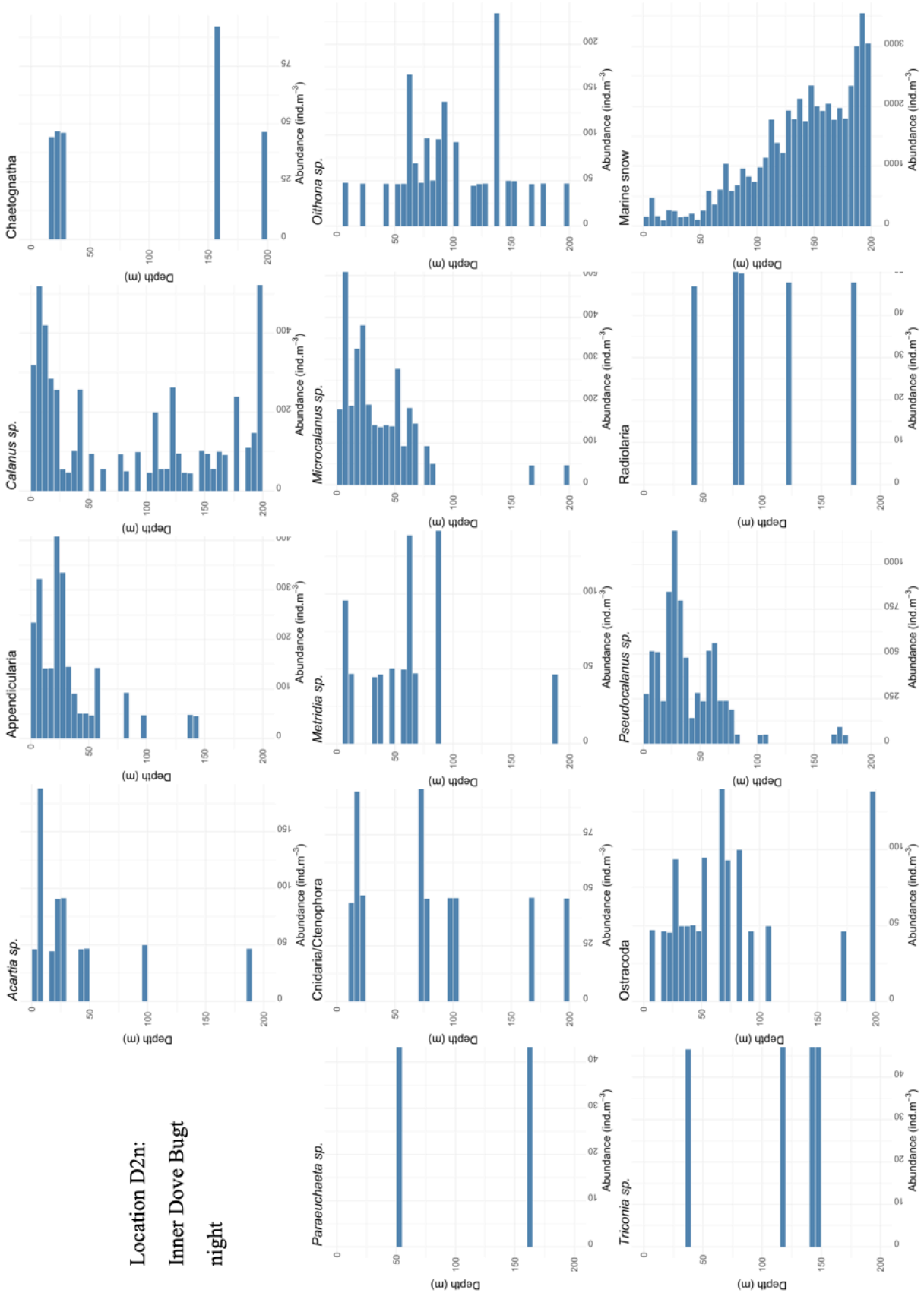
Mouth Dove Bugt



Location D2:

Inner Dove Bugt day



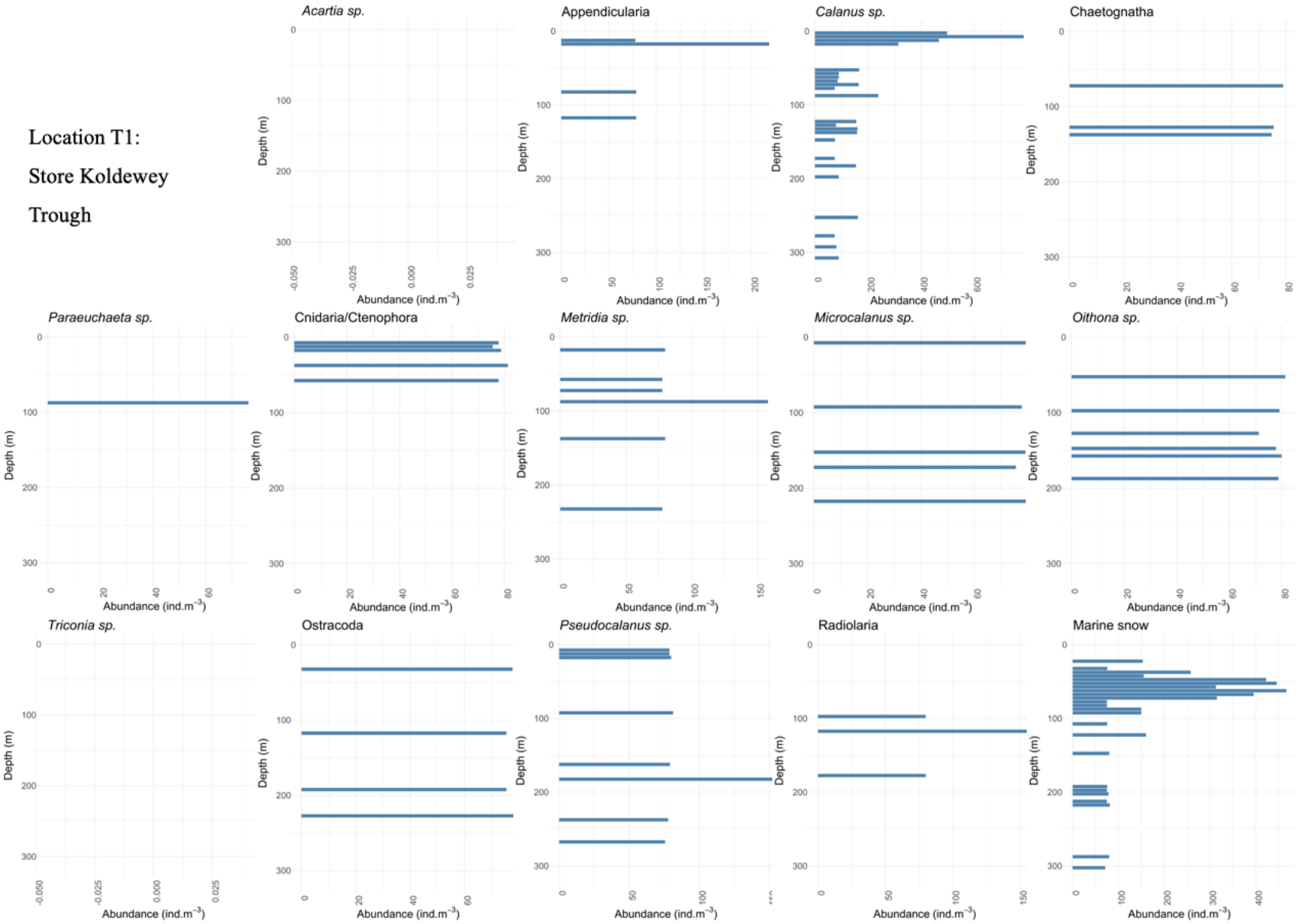


Location D2n:
Inner Dove Bugt
night

Location T1:

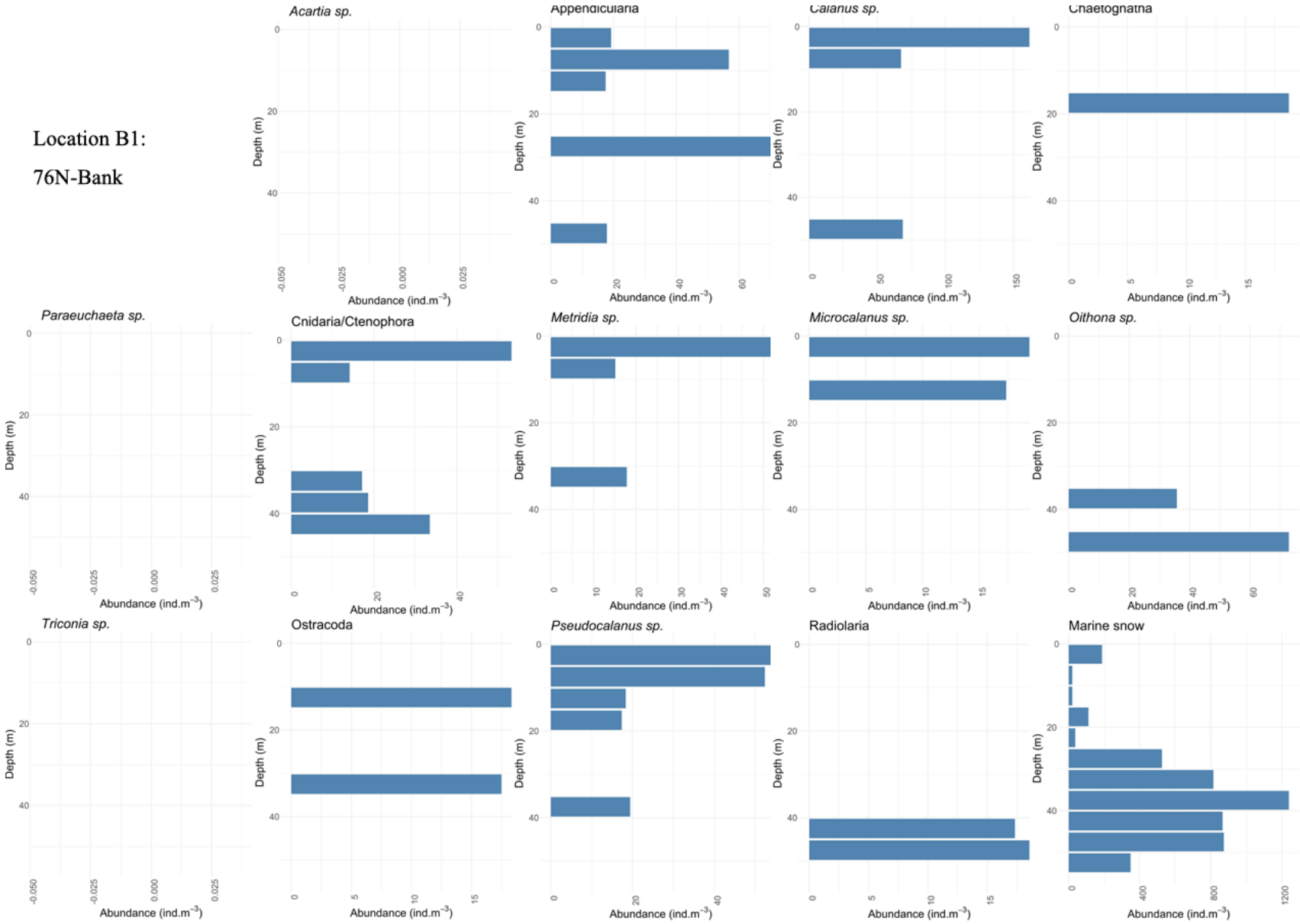
Store Koldewey

Trough



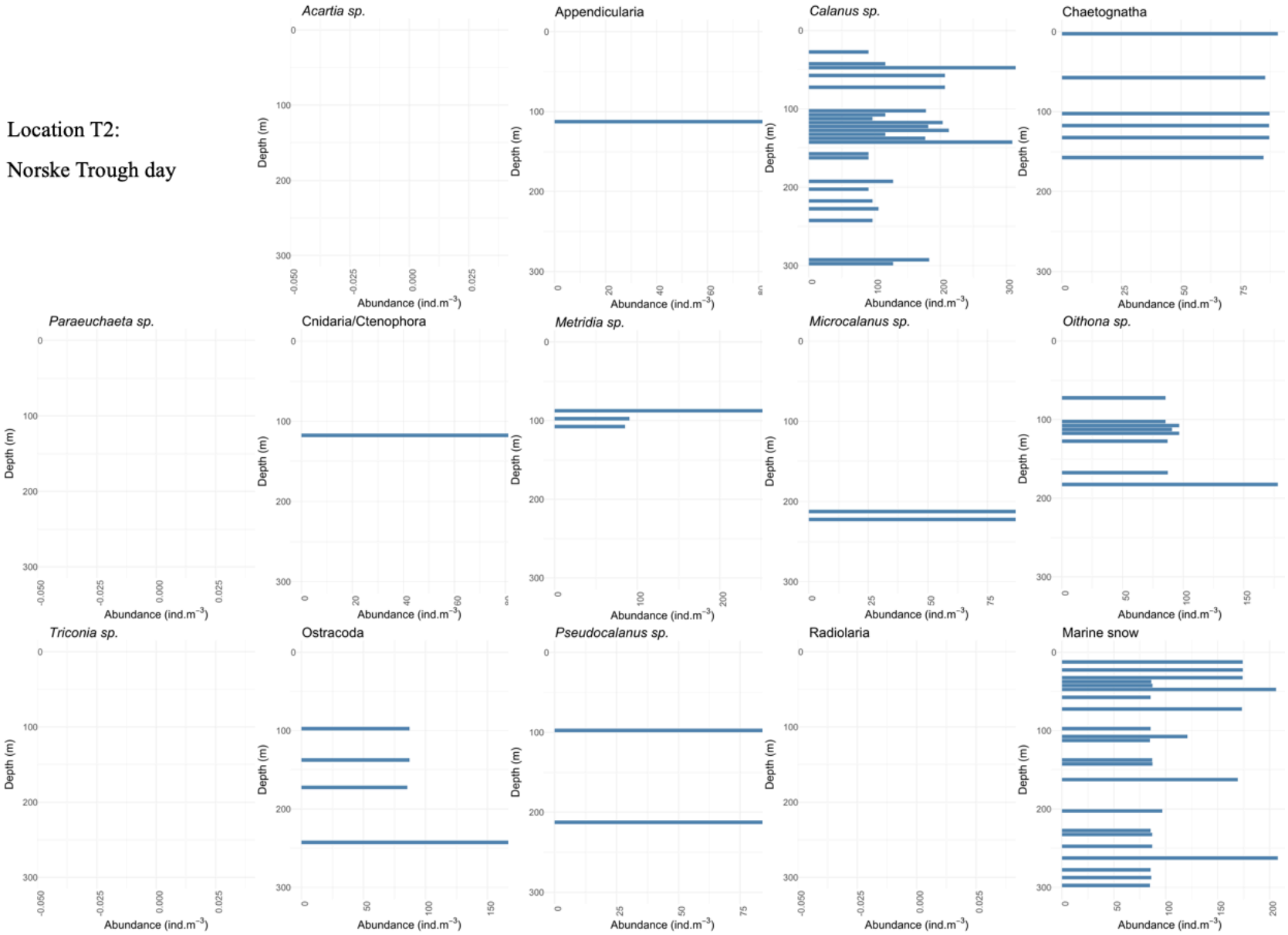
Location B1:

76N-Bank



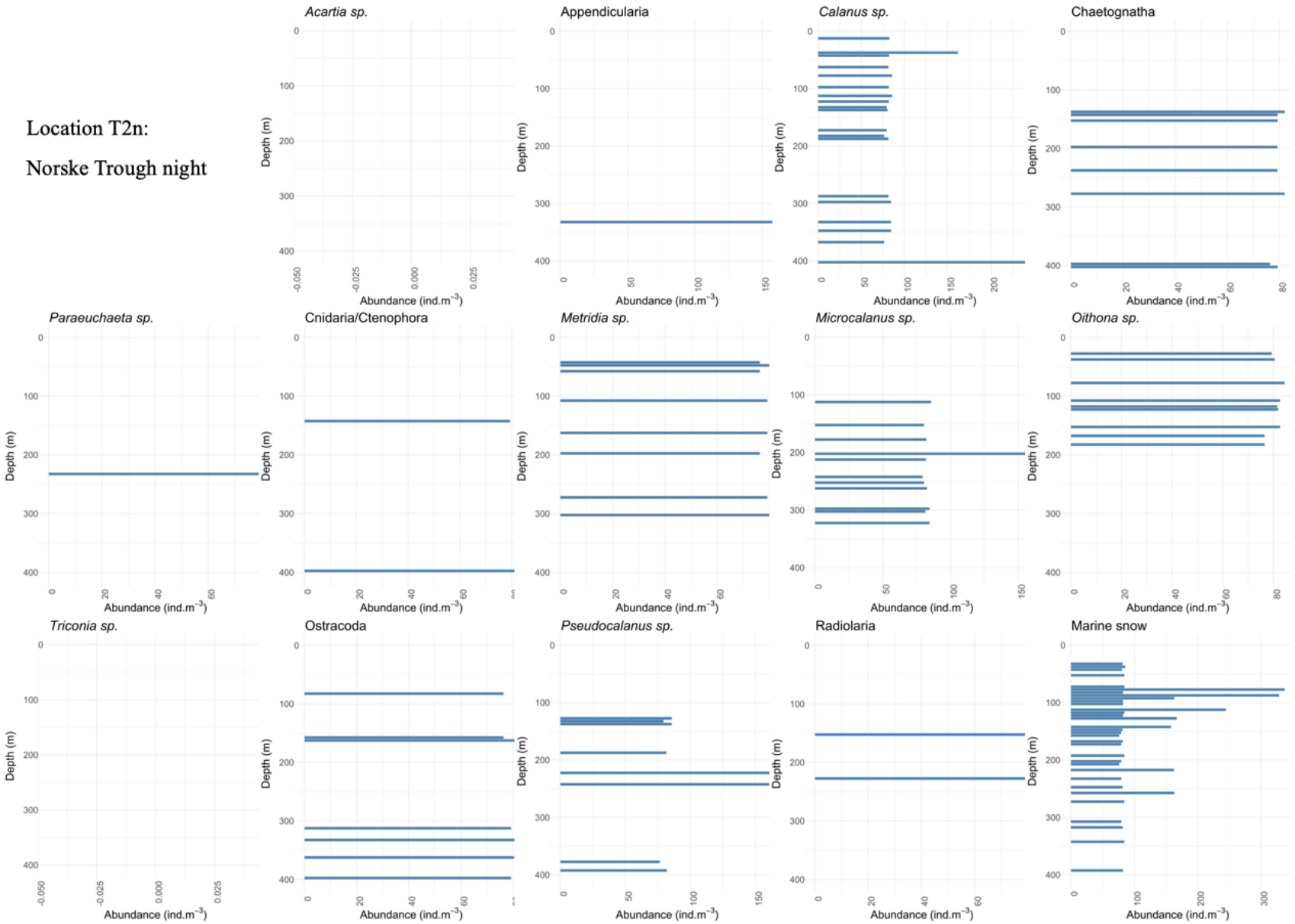
Location T2:

Norske Trough day



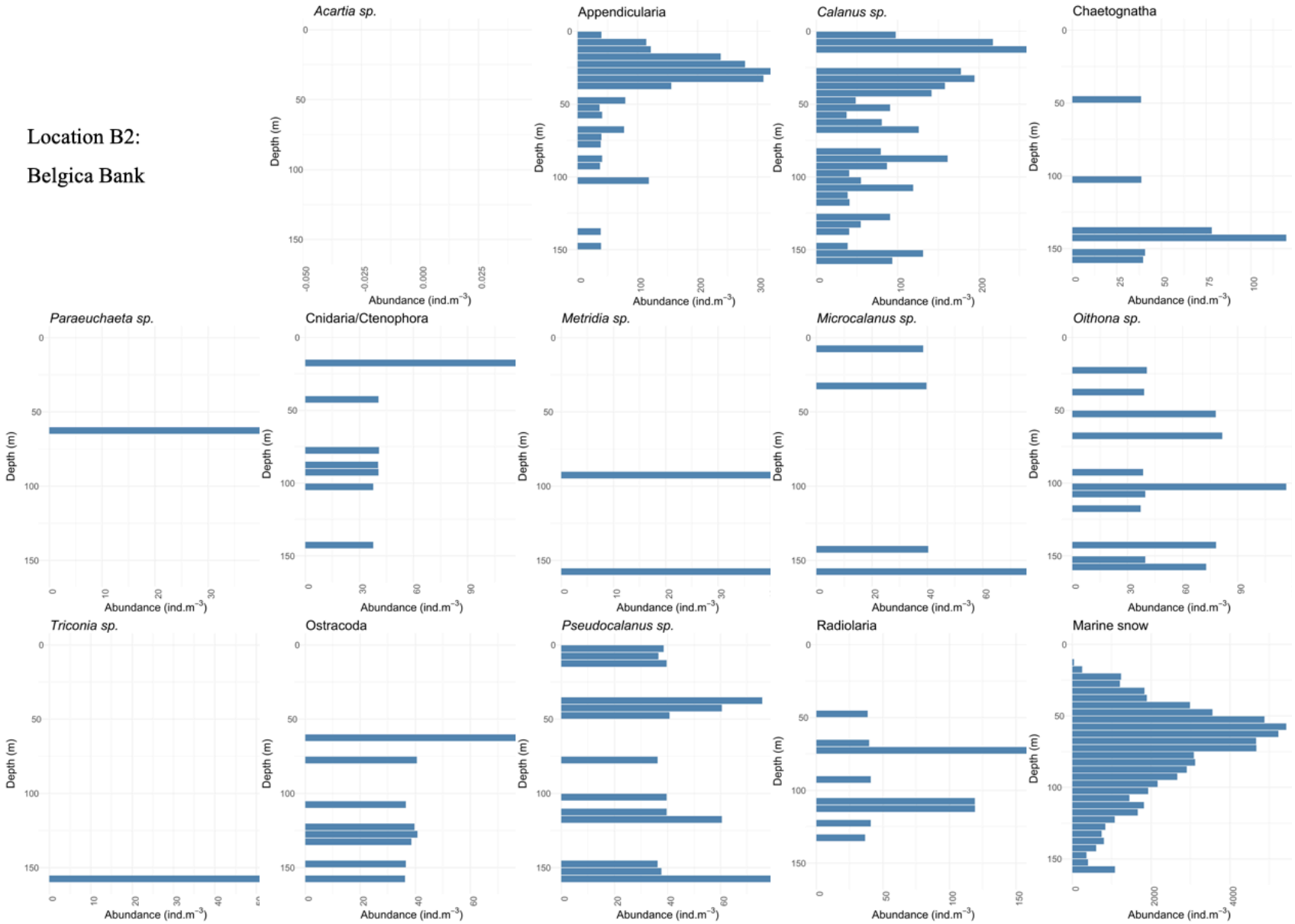
Location T2n:

Norske Trough night



Location B2:

Belgica Bank



Location S:

Northern Shelf