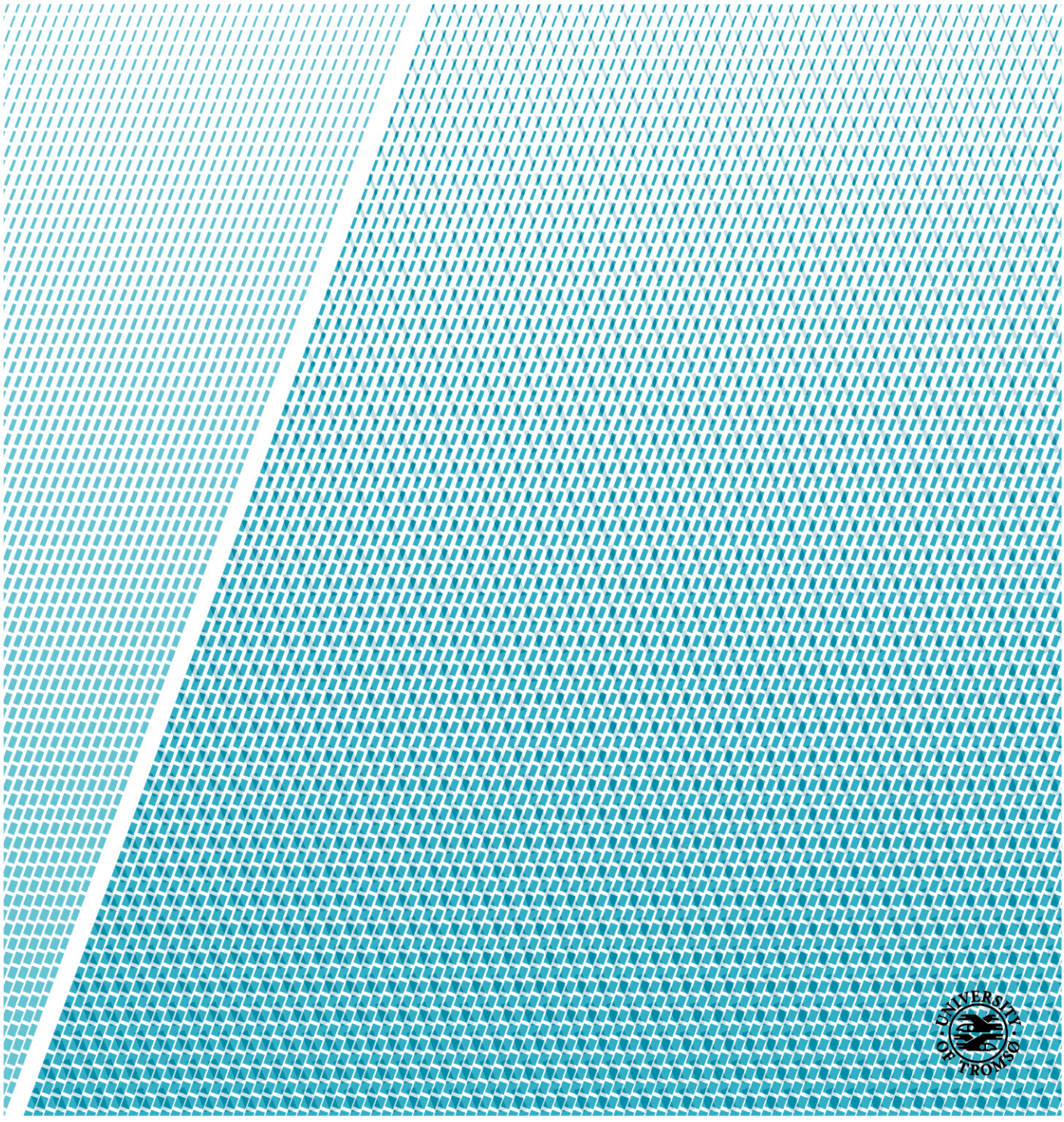
UiT
THE ARCTIC UNIVERSITY OF NORWAY

Faculty of Bioscience, Fisheries and Economics

Department of Arctic and Marine Biology

Seasonal occurrence of *Oithona similis* (cyclopoida), *Microsetella norvegica* (harpacticoida) and *Microcalanus* spp. (calanoida), and productivity of *O. similis*, in three high-latitude Norwegian fjords.

Peter Glad Bio-3950 Master thesis in Biology, May 2018



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

Seasonal occurrence of *Oithona similis* (cyclopoida), *Microsetella norvegica* (harpacticoida) and *Microcalanus* spp. (calanoida), and productivity of *O. similis*, in three high-latitude Norwegian fjords.

Peter Glad BIO – 3950 Master thesis in Biology

May 2018

Supervisors:

Camilla Svensen, UiT The Arctic University of Norway

Coralie Marie Christine Barth-Jensen, UiT The Arctic University of Norway

Acknowledgments

First of all, I would like to thank my two supervisors Camilla Svensen and Coralie Marie Christine Barth-Jensen for their guidance. Thank you, Camilla, for being a splendid supervisor that have given me support and much needed constructive criticism, that have helped me immensely all the way through. Thank you, Coralie, for not only being a fantastic supervisor that have helped me with everything lab-related, but also for allowing me to help you with your work. I will never forget the tiresome days we spent on the cruise north of Svalbard nor the time spent in the cold room doing the egg hatching experiments.

I would like to thank Rahman Mankettikkara for allowing me to join all the five HMD-cruises to collect all samples for my thesis and for sharing CTD-data. To the crew and captain onboard FF Johan Ruud, thank you all for helping me collect all my samples as well as being such lovely and including persons.

Huge thanks to Sigrid Øygarden for showing me how to make important chemical solutions. Great thanks to Einar M. Nilsen for helping me with all statistical work related with SYSTAT with great enthusiasm.

To my friends that I have shared office with these two years, Rosalyn, Rasmuss, Hanna and Julia, and the refrigerator we manage to acquire to have in the office, I thank you. The time we have shared together I will never forget. To all my other friends back home in Vesterålen and that I have met here in Tromsø, I thank you as well.

Lastly, I do not think that I could it this far without the support from my family. I love you more than anything and it means the world for me that you have been there for me during all the ups and downs these past 5 years.

Table of Contents

Abstract....4

1. **Introduction**: 6

1.1 Research aims....10

2. **Material and methods** 11

3.1 Study areas:....11

3.2 Field work....13

3.2.1 Zooplankton sampling 13

3.2.2 Hydrography, chlorophyll a and Particulate organic carbon/nitrogen (POC/PON). 15

3.3 Copepod species identification and enumeration 16

3.4 Statistical work....17

3.5 *Oithona similis* egg hatching experiments 18

3.5.1 Experimental set-up....18

3.5.2 Estimation of Oithona similis production....20

4. **Results** 22

4.1 Environmental parameters....22

4.2 Seasonal distribution of O. similis, M. norvegica and Microcalanus spp. in Balsfjord, Altafjord and Porsangerfjord 27

4.2.1 Comparison between the stations and fjords....27

4.2.2 Seasonal and spatial patterns of developmental stages of *O. similis, M. norvegica* and *Microcalanus* spp. 29

4.3 Oithona similis egg-hatching experiments....30

4.3.1 Egg hatching rate and specific egg production rate....30

4.3.2 Estimated *O. similis* secondary production for 31

5. **Discussion**....34

5.1 Seasonal dynamics of the environmental parameters....34

5.2 Seasonal trends in *Oithona similis*, *Microsetella norvegica* and *Microcalanus* spp. distribution in Balsfjord, Altafjord and Porsangerfjord. 35

5.3 Oithona similis production rates....38

5.3.1 Temperature-dependent egg hatching rates....38

5.3.2 Seasonal *O. similis* specific egg hatching rate (SEPR)....39

5.3.3 *Oithona similis* seasonal and annual secondary production in Balsfjord, Altafjord and Porsangerfjord. 41

6. **Conclusion** 44
7. **References** 45
Appendix A 52
Appendix B 57
Appendix C 58

Abstract

The Seasonal population dynamics of the small copepod species *Oithona similis* (cyclopoida), *Microsotella norvegica* (harpacticoida) and *Microcalanus* spp. were investigated in the northern Norwegian fjords Balsfjord, Altafjord and Porsangerfjord. In this study a WP-2 net with 64 µm mesh size was used to sample all the stages of *O. similis*, *M. norvegica* and *Microcalanus* spp. Copepodite stages CI – CVI were identified for each species to determine seasonal distribution population structure. To assess the relative importance of small copepod species in the marine ecosystem, the seasonal and annual secondary production of *O. similis* in the three study fjords was estimated. Production was estimated with specific egg production rates, that is based on experimentally determined egg hatching rates, and a temperature-dependent method.

The species were present year-round in the fjords but differed from each other in both geographical and seasonal distribution, but all copepodite stages for each specie was present in all sample months. In December, copepod abundance and biomass were low with the exception of inner Porsangerfjord and Balsfjord. In March, peak in total copepod abundance and biomass was observed in inner Porsangerfjord and Balsfjord while in the other areas this remained low. In April, March and October, abundance and biomass were comparatively less than the peak found in March. Population abundance for *O. similis* remained relatively stable during the months and seasons, where all life stages were observed during the study that indicated year-round reproduction. *M. norvegica* accounted for the high abundance found in December and March at inner Porsangerfjord and Balsfjord, that mainly consisted of overwintering stages (females without eggs and CIV – CV copepodites). Egg carrying *M. norvegica* females was first observed in small numbers in April

and in greater numbers in August. All stages of *Microcalanus* spp. was found during this study but was less abundant than the other two species. Reproduction for *Microcalanus* spp. had likely taken place between December and March.

The egg hatching experiments shows there is a strong correlation between *O. similis* egg hatching rate (HR) and egg hatching time (HT), where HR increased with higher temperature and HT decreased. Estimated SEPR showed clear seasonal trend as it remained low during December, March and April (< 0,001 mg C m^{-1} d^{-1}) in all the fjords which increased in August and October when sea surface temperature increased, most notably in Porsangerfjord and Balsfjord. The annual secondary production reveals that *O. similis* were most productive in Balsfjord and the outer area of Porsangerfjord, yielding an annual estimation of > 1 g C m^{-2} y^{-1} in these fjords. This is comparatively less than other copepod species found in sub-Arctic/Arctic waters such as those belonging to the *Calanus* genus, but the fact that productivity remained continuous even during winter is of great importance nevertheless. Temperature is the main regulating factor for *O. similis* productivity as overall low temperatures in the fjords inhibited maximum egg production large portions of the year. A future scenario where sea surface temperature increases in the sub-Arctic/Arctic ecosystem will much likely promote higher seasonal and annual *O. similis* secondary production.

1. Introduction:

Fjords and fjord-like embayment's comprise a substantial part of the coastal environments at high latitudes. The physical and chemical processes that takes place in these fjords as well as the roles they serve, in a climatic, oceanographic and ecological perspective, is crucial to understand. In addition, there are great variations between northern Norwegian fjords in terms of topography, climatology and other dynamic parameters (Mankettikkara 2013). These variations make up for high marine biodiversity found in each fjord as well as great potential for fisheries and harvesting for various marine resources (Nakken, 1998).

Of the pelagic animals that can be found in the coastal zone of northern Norway, copepods are among them. These are planktonic life forms and belong to the sub-group crustacea and are a successful group (Humes, 1985). Unique traits such as a torpedo shaped body, powerful swimming movements and high reproductive rates are features that enables copepods to be numerous in most aquatic systems on earth (Kiørboe, 2011). The potentially high abundance and biomass that copepods can constitute for, makes this group to be an important link between lower and higher trophic levels in the food web (Sakshaug 2004). In high latitude marine systems where the environment undergoes seasonal changes, the population dynamics of copepods varies throughout the year. Because of a strict light regime that restricts primary production during the winter, adaptions in order to survive the winter is crucial (Conover and Huntley, 1991; Hirche and Kosobokova, 2011). The species belonging to the genus *Calanus* is successful in the sub-arctic/marine ecosystem as they adapted to the seasonal changes. These copepods accumulate large amounts of lipids before they migrate to deep water and hibernate for several months (Clarke and Peck, 1991). Their reproduction starts during spring and is timed to when the phytoplankton bloom starts, a major event that many copepod species depend on (Legendre and Rassoulzadegan, 1995). Because of this, it has been believed that there is comparatively less activity in the water column during the winter when the phytoplankton growing season has stopped. However, newer studies have shown that there is relatively high zooplankton activity in the water column during the winter and a majority of these organisms are characterized as having a body length under 1 mm (Turner, 2004; Berge et al., 2015).

There are several definitions on the group “small copepods”, but in this study small copepods are defined as copepod species with a body length less than 1 mm in their adult stage. Examples are the genera *Oithona* sp., *Microsotella norvegica*, and *Microcalanus* spp., that are found the Arctic and sub – Arctic marine ecosystem. It has been argued that the reason for the lack of focus on the smaller size fraction of the zooplankton community is the systematic under sampling of such organisms (Gallienne and Robins, 2001). The usage of 180-200 µm zooplankton nets when sampling for copepods that have been argued to be to coarse to effectively sample small copepod species and their life stages (Harris et al., 2000). With a more unbiased sampling approach (use of nets with mesh under 100 µm), the copepod community structure in the Arctic and sub-Arctic have been investigated that focuses on the smaller copepod species (Turner, 2004; Hopcroft et al., 2005; Svensen et al., 2011). An important is that some of these species such as *Oithona* sp., can remain active year-round in relatively high abundance and are even able to maintain continuous reproduction throughout the year (Auel and Hagen, 2002; Hopcroft et al., 2005; Madsen et al., 2008). But few studies have examined the seasonal abundance, biomass and production of these small copepod species. In the Arctic, this is an especially interesting topic. This is a region with strong seasonal variations in abiotic (temperature, salinity, sea ice cover, light availability, ocean currents and nutrient concentrations) and biotic factors (prey items and predation) which regulates both primary - and secondary production. These seasonal variations has an impact on the plankton community structure leading to variations in abundance, biomass and production (Norrbin, 1994; Eilertsen and Degerlund, 2010; Barthel et al., 1995).

One common method of addressing the role of a copepod species in the marine food web is to estimate secondary production (Huntley, 1992). Since plankton are food for both fish larvae and adult fishes at high latitudes, it has been important to uncover and estimate a species contribution, in terms of their productivity, to the system in terms of carbon (McAllister, 1969; Sommer et al., 2002). This information is important both to fisheries, resource managers and researchers within various fields in marine science. For free-spawning copepod species, that release eggs freely into the water column, egg production has commonly been used to estimate copepod production. The assumption is that adult female copepods do not grow, but allocate ingested carbon into the production of eggs

(Nielsen et al., 2002). For egg-carrying copepods, that produces clutches of eggs at a lower rate and then carry the same clutch up to several days, the method for estimating egg production used for free-spawners does not apply (Nielsen et al., 2002). Both these types of reproductive strategies are represented by small and big sized copepod species (Kiørboe and Sabatini, 1994). The smaller species can potentially contribute significantly to secondary production, as their growth rates are generally higher compared to larger species (Hansen et al., 1997). The fact that small species are capable of maintain high abundance throughout the year, and that some can maintain reproduction year-round in high latitude marine systems, means that species belonging to the smaller size fraction can potentially contribute significantly to the planktonic community and the overall marine food web in terms of secondary production (Madsen et al., 2008; Svensen et al., 2011).

This study will focus on 3 copepod species that can be found in fjords of northern Norway. They all can be defined as smaller copepod species but are of different taxonomic orders. The three species are: *O. similis* (order cyclopoida), *M. norvegica* (order harpacticoida) and *Microcalanus* sp. (order calanoida).

O. similis is a cosmopolitan species that is abundant in coastal and oceanic regions of the tropics, the temperate zone and in polar waters (Wend-Heckmann et al., 2013). Cehpalothorax length for females range from 0.4 – 0.55 mm and 0.7 - 1.0 mm counting both prosome and urosome, while the male is generally smaller than females. Females produces egg clutches, up to 2 at a time, that they carry around for a set time before releasing the clutches into the water column (Castellani et al., 2005). *O. similis* is an ambush feeder (Kjellerup and Kiørboe, 2012) and predates on motile phytoplankton, protists and copepod nauplii (Nakamura and Turner, 1997). It is capable of reproducing year-round (less in winter) and carries its eggs in 1-2 clutches (Drif et al., 2010; Cornwell et al., 2018). It is found be very dominating in terms of abundance in the planktonic community when investigated in arctic ecosystems (Sabatini and Kiørboe, 1994; Nielsen and Sabatini, 1996; Ward and Hirst, 2007; Zamora-Terol et al., 2014). *O. similis* is suggested to be of great significance for the marine food web in high latitudes, serving as an important food source for other copepods, chaetohnaths and fish larvae (Dvoretsky and Dvoretsky, 2009).

M. norvegica can mostly found in the northern hemisphere in marine and brackish water, and is known to be abundant in temperate and sub-arctic marine systems (Dugas and

Koslow, 1984; Krsinic and Grbec, 2012; Uye et al., 2002). It is described as a pelagic copepod, but it can also be found at the sea bottom (Lagadeuc et al., 1997). Size-wise, the females range from 0.35 – 0.53 mm (without setae) and the males from 0.33 – 0.42 mm. They also producing egg clutches, but only producing one clutch at a time which they detach before producing another one. Their reproduction typically starts in late March to April, where they remain in active at the surface during spring and summer. They are omnivorous and feed on motile and sinking particles, but are known to be associated with marine snow aggregates in oligotrophic waters (Koski et al., 2007). The body of *M. norvegica* is fairly laterally flat that is divided into a prosome and an urosome, which can be difficult to differentiate from each other (Huys and Boxshall, 1991). There is limited knowledge on the general biology and ecological importance of *M. norvegica*, but the studies that are available on their life cycle, feeding strategy and reproduction strategy indicates to very numerous and of great importance to the sub-Arctic/Arctic marine ecosystem (Arendt et al., 2013; Koski et al., 2014).

Microcalanus spp. are commonly found in Arctic, sub-Arctic and the Antarctic marine environments. The genus consists of two species, *Microcalanus pusillus* and *Microcalanus pygmaeus*. There is some taxonomic confusion regarding these two species, and it has been argued whether they are two varieties of the same species or two separate species (Wiborg 1954). *Microcalanus* spp. is found in the epi-bathypelagic layer in the water column, but studies shows that the adults have a preference for deeper waters than the younger copepodite stages (Schnackschiel and Mizdalski, 1994; Auel and Hagen, 2002). Female body length ranges from 0.6 – 1.12 mm and males 0.64 – 1.10 mm in total body length. The Body shape resembles that of other calanoid copepods but are characterized as having a much wider body proportion (Sars, 1895). *Microcalanus* sp. is an omnivorous feeding on phytoplankton, microzooplankton and detritus (Norrbin 1994). Unlike most *Calanus* species, *Microcalanus* spp. is not dependent on phytoplankton and the spring bloom and do not undergo a pronounced seasonal vertical migration (Krause and Trahms, 1982). Rather, it has a relatively stable vertical distribution through the seasons and can start reproduction in the middle of the winter (Hopcroft et al., 2005). It has a 1-year lifespan but the possibility of a 2-year lifespan has been discussed (Ashjian et al., 2003). There are relatively few seasonal population dynamics studies that can confirm this.

1.1 Research aims

The main aim of this thesis was to investigate seasonal trends in *O. similis*, *M. norvegivca* and *Microcalanus* spp. population abundance, biomass and stage composition in three fjords in northern Norway. These fjords are Balsfjord, Altafjord and Porsangerfjord, the former being the southernmost and the latter the northernmost (fig. 1). Sampling in these fjords took place in December, March, April, August and October starting 2016 and ending in 2017, to cover each season over a period of approximately one year. The seasonal and annual secondary production of *O. similis* was estimated, to investigate the relative importance and contribution to the marine ecosystem of this species in Balsfjord, Altafjord and Porsangerfjord.

Aims:

- To investigate population dynamics of *O. similis, M. norvegica* and *Microcalanus* spp. in three north Norwegian fjords, Balsfjord, Altafjord and Porsangerfjord.
- Investigate temperature-dependent hatching rates of *O. similis* and estimate secondary production of *O. similis* in Balsfjord, Altafjord and Porsangerfjor

2. Material and methods

3.1 Study areas:

Sampling for this study took place in three fjords along the coast of northern Norway, Balsfjord (69°N), Altafjord (70°N) and Porsangerfjord (70°N - 71°N) (fig 1, table 1). These fjords were chosen as they differ in many aspects, such as shape, depth, freshwater influence and connectivity to the open ocean. Different hydrographical properties are also found (such as temperature and salinity), that varies throughout the year.

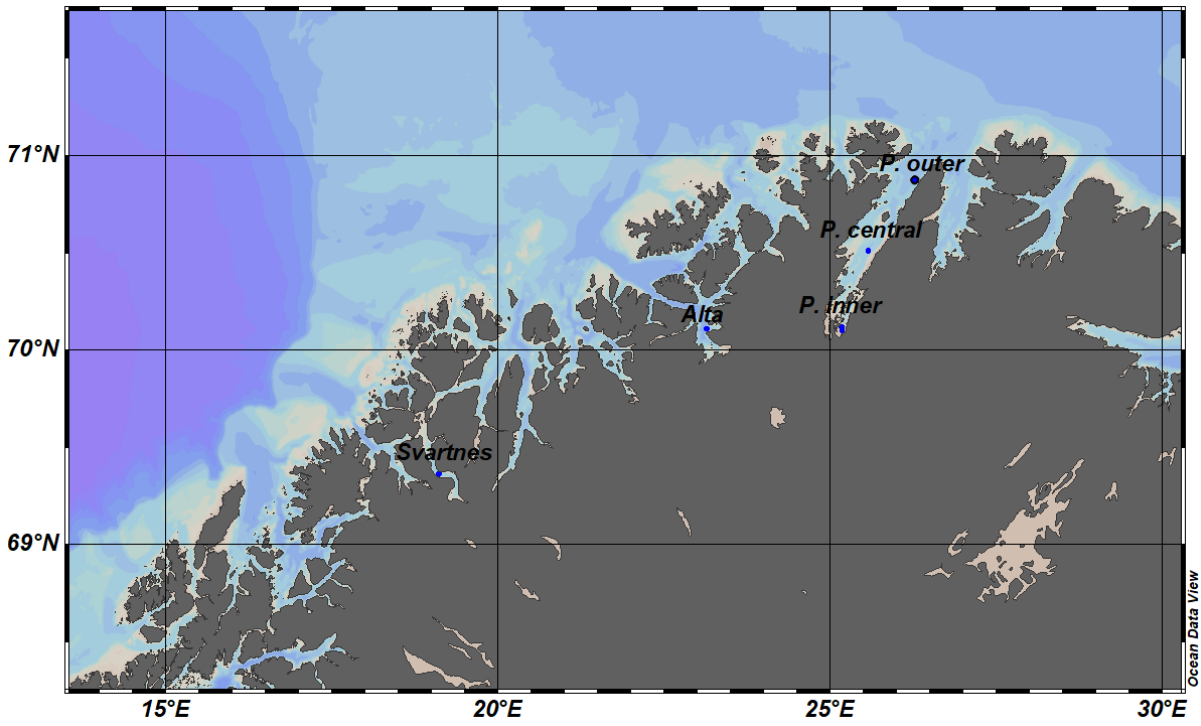


Fig 1: Map of the sampling stations in Balsfjord (Svartnes), Altafjord (Alta) and Porsangerfjord (P. inner, central and inner).

Balsfjord belongs to the county of Troms and is located near Tromsø, between 69˚13'N and 69˚30'N. The fjord is 5 km at its widest and has a south/south-east direction with a total length of 45 km (Mankettikkara, 2013). It is commonly divided into two basins, with an outer basin 130 m deep and an inner basin 190 m deep. It has three relatively narrow sounds with shallow sills (8, 9 and 30 m) which limits the exchange of fjord water with coastal water

(Svendsen, 1995). Of the fjords described in this study, Balsfjord is the only fjord that can be categorized as a true sill fjord. Sampling took place in the middle section of Balsfjord, at station Svartnes (180 m depth), located in the inner basin.

Altafjord: Altafjord is situated between 70˚N and 70˚03'N, located between Balsfjord and Porsangerfjord. The outline of the fjord is non-uniform, as the width varies from 4 km in the middle up to 14 km at the head of the fjord. Three inlets constitute the outer section, Stjernesund, Rognsund and Vargsund with minimum depths at 190, 60 and 50 m respectively. In the intersection part of the fjord, where the open fjord branches out to the three inlets, maximum depth is ca. 450 m and from here inwards the fjord it gets shallower. Altafjord has a sill of 190 m which prevents basin water of the fjord to have free exchange of water with the open sea. The main source of freshwater is the Alta-river located in the innermost part of the fjord. Between the inner and outer section of the fjord, big differences in surface salinity values can be observed with the inner part of Altafjorden, the only area that is icecovered during winter (Mankettikkara, 2013b). Sampling in Altafjord took place beyond the intersection zone, within the sill part of the fjord with a maximum depth of 411 m.

Porsangerfjord: Porsangerfjorden is in the county of Finnmark and is the largest fjord in northern Norway, approximately 100 km long. The fjord is extending from 70˚N to 71˚N and 25˚E to 26˚E in a north-south direction, where the mouth of the fjord is facing the Barents Sea. Porsangerfjord is commonly divided into three sections: outer, middle and inner Porsangerfjorden. The deepest sill in the fjord is found in the outer part at 200 m depth (Mankettikkara, 2013). The outer and middle section has a depth range from 50 – 180 m where there is no sill separating them making these two sections dominated by inflowing Atlantic water masses (Svendsen, 1995). Because of the deep sill, steady exchange of deep water takes place in the system with the Norwegian Coastal Current (NCC) (Eilertsen and Skarðhamar, 2006). A second sill separates the middle and inner parts of Porsangerfjord which is 60 m deep and is located 30 km from the head of the fjord (Mankettikkara, 2013). This isolates the inner parts and water exchange from the middle parts is limiting. Two sources of fresh water are found in the inner parts of the fjord, Lakselv and Børselv, but compared to the size of the fjord the runoff is considered to be low. Ice cover forms in the inner parts of the fjord during winter and is described as a true arctic environment under

these circumstances (Mankettikkara, 2013). Because of the size of the fjord, sampling took place in the outer, middle and inner section of Porsangerfjord.

To cover a full seasonal cycle, samples were collected during five cruises with R/V “Johan Ruud”. Starting in December 2016, the remaining cruises were conducted in 2017 in March, April, August and October (Table 2). The sampling was done in cooperation with the “HMD” -program (Havmiljødata) of UiT, a long-term time series on hydrographical data in Northern Norwegian fjords (Malangen, Balsfjord, Ullsfjord, Altafjord and Porsangerfjord) dating back to 1928.

3.2 Field work

3.2.1 Zooplankton sampling

To be able to get accurate estimates on small copepod species and all the corresponding stages, a WP-2 net (Hydro-Bios) with a 64 µm mesh size (diameter 0, 55 m) was to be used at all stations. The net was lowered down quickly to the preferred depth, but raised up with a slow, even speed of 0.5 m/s to the surface. For each station, the standard sampling depth-interval was from 100 m to the surface. When possible, an additional tow from bottom up to 100 m was done on the deeper stations. Discrete sampling was possible by a closing mechanism that was attached to the net. On deck the cod end was thoroughly and carefully rinsed before transferring the content to a 10 L plastic bucket. Finally, the zooplankton was concentrated using a 64 µm sieve and transferred to a 250 ml PVC plastic bottle. The zooplankton samples were fixed by adding 50 ml Zoofix (buffered formaldehyde, hexamethylenetetramine and propandiol) at a 4 % final concentration. In Balsfjord in April, because of the potential risk of clogging of the net by phytoplankton, a 10 L Nisking-bottle was used to sample zooplankton at 70, 20 and 0 m obtaining 10 L water at each depth. A total of 30 L sea water was pooled in a larger container and the zooplankton was concentrated over 64 µm sieve and transferred to a PVC plastic bottle.

Table 1: Sample stations in the three fjords, in which sampling for zooplankton and environmental parameters took placee. The depths listed are station depths. Sampling started in December 2016, March, April, August and then ending October 2017. Each cruise lasted three days and all the fjords were visited during each cruise except for Altafjord in August.

Fjord	Station name	Station coordinates	Depth (m)
Balsfjord	Svartnes	69°21.9084N, 019°06.1525E	185
Altafjord	Alta	70°06.5701N, 023°08.6440E	410
Porsangerfjord	P. outer	70°52.5N, 26°17.05E	220
	P. central	70°30.7N, 25°35.0E	195
	P. inner	70°07.2N, 25°11.0E	105

Table 2: Overview on sampling date at each station and at what depth interval (m) it was sampled from using a WP-2 net with 64 µm mesh size. Since the boat drifted when it was at station, the noted station depth varies between each month.

Date	Station	Sample depths (m)	Station depth (m)
5/12/16	P. outer	100 – 0	201
5/12/16	P. central	100 – 0	190
5/12/16	P. inner	100 – 0	104
6/12/16	Alta	398 – 100, 100 – 0	408
7/12/16	Svartnes	170 – 100, 100 – 0	185
14/3/17	P. outer	100 – 0	220
14/3/17	P. central	100 – 0	191
14/3/17	P. inner	100 – 0	105
15/3/17	Alta	100 - 0	410
16/3/17	Svartnes	170 – 100, 100 - 0	185
4/4/17	P. outer	100 – 0	219
4/4/17	P. central	100 – 0	194
4/4/17	P. inner	100 – 0	185
5/4/17	Alta	200 – 100, 100 - 0	411
7/4/17	Svartnes	70, 20 and 0*	184
15/8/17	Svartnes	170 – 100, 100 - 0	185
16/8/17	P. outer	100 – 0	206
16/8/17	P. central	100 – 0	190
16/8/17	P. inner	100 – 0	111
17/10/17	P. outer	100 - 0	218
17/10/17	P. central	100 - 0	190
17/10/17	P. inner	100 - 0	110
18/10/17	Alta	398 – 100, 100 - 0	411
19/10/17	Svartnes	170 – 100, 100 - 0	180

*****Sampling was done with a 10 L Niskin – bottle due to risk of clogging the WP-2 net, described in chapter 3.2.1.

3.2.2 Hydrography, chlorophyll a and Particulate organic carbon/nitrogen (POC/PON).

Data on temperature, conductivity and fluorescence was obtained with a CTD (seabird 9-11) as part of the HMD-time series. Water samples were collected at 0, 10, 20, 50 and 100 m with a 10 L Niskin-bottle for Chlorophyll *a* (Chl *a*), Particulate organic carbon and nitrogen (POC/PON). Sub-samples of 300 – 500 ml for each depth was filtered onto designated filter types. For Chl *a*, water was filtered in triplicates onto Whatman GF/F filters for total Chl *a*, and onto 10 µm polycarbonate filters for estimating Chl *a* > 10 µm. For POC/PON analysis, triplicate sub-samples were filtered onto pre-combusted Whatman GF/F filters. All filters were wrapped in aluminum foil and stored at -20°C until further analysis. In the laboratory on land, Chl *a* filters were extracted in 5 ml methanol for 24 h at 4 ˚C and fluorescence was measured, both before and after adding 1 drop of 10 % HCl, using a Turner Designs model 10-AU fluorometer. The following calibration formulas was used to calculate the concentration of both Chl *a* and phaeophytin in cubic meters (mg/m^{-3}), where Fd and Tau are predetermined constants:

$$\text{Chl } a \text{ (mg/m}^{-3}\text{)} = Fd \times Tau \times (\text{Reading before acid} - \text{Reading after acid}) \times \frac{Volume\ methanol\ (ml)}{Volume\ filtrated\ (ml)}$$

$$\text{Phaeophytin (mg/m}^{-3}\text{)} = Fd \times Tau \times (2{,}839 \times \text{Reading after acid}) - \text{Reading before acid}) \times \frac{Volume\ methanol\ (ml)}{Volume\ filtrated\ (ml)}$$

Before analyzing the POC-samples, the filters were placed in a dry heater (60˚C) for 24 h to remove moist. Afterwards, filters were fumed with concentrated HCl for 24 h to remove inorganic carbon and placed back in the dry oven (60˚C) for 24 h. The finalized samples was analyzed with a CHN analyzer (Lab-Leeman 440 elemental analyzer), where POC and PON content was calculated by using acetanlilide as standard. Data on Chl *a* and POC/PON concentration are presented as mg m^{-2} and g C m^{-2}, respectively, for each fjord and sample month

3.3 Copepod species identification and enumeration

Before determining zooplankton composition and abundance from the fixed samples, the formalin was removed. Doing the preparations under a fume hood while wearing chemical gloves, samples were emptied into a 20 µm sieve to remove the formaldehyde-solution from the sample. Thereafter the zooplankton were diluted in filtered seawater for 24 h. In order to quantify the copepods, each sample was diluted to a volume ranging from 1000 to 4000 ml. After homogenizing the diluted sample with a stirring rod, sub-samples à 5 ml were collected with a pipette and counted under a Leica stereoscope (Leica MZ 16). A minimum of 300 copepods in total were counted for each sample. For *M. norvegica* and *O. similis* at least 100 individuals were counted for each sample, while for *Microcalanus* spp. the minimum number was 50 individuals, as they were less abundant. New sub-samples were counted until at least 300 individuals were obtained. Copepod development stages were quantified for each of the three species from copepodite stages CI up to CV, and adult stages males and females. Stages CI – CIII and stages CIV – CV were pooled into two separate groups. Literature and identification keys was used to distinguish the different developmental stages for each species, by examining the number of free, visible somites on the prosome/urosome, number of swimming legs and length of the prosome (Appendix B). The abundance of the copepod species is presented as number of individuals per cubic meter (ind. m^{-3}), calculated based on the assumption of 100 % filtering efficiency of the WP2 net, and as individuals per square meter (ind. m^{-2}), by a trapezoid integration for each depth.

To determine biomass, individual carbon was needed to be calculated. By using a stereoscope (Leica MZ 16) equipped with a calibrated micrometer, prosome length (µm) of 30 individuals of each copepodite stage for each species was measured to obtain average lengths (Table 3). The carbon content for each stage and species was calculated by using the following equations from literature, where C is carbon content (µg C ind^{-1}) and L is prosome length (µm):

Microsetella Norvegica: $C = 2.65 * 10^{-6} * BL^{1.95}$ (Uye et al., 2002)

Oithona similis and *Microcalanus spp.*: $C = 9.4676 * 10^{-7} * BL^{2.16}$ (Sabatini and Kiorboe, 1994)

The population biomass ($C_{population}$) per cubic meter (mg C m^{-3}) for a given stage and species was calculated by multiplying total abundance of the given stage with the mean biomass for a single specimen ($biomass_{ind-1}$, µg C ind^{-1}):

$\Sigma C_{Population}$ = abundance (ind m^{-3}) × $biomass_{ind-1}$

Table 3: Measured mean prosome length (µm) ± SD for the different life stages for Oithona Similis, M. norvegica and Microcalanus spp. In total 30 individuals for each copepodite stage from different samples were picked at random and measured. Stages CI – CIII and CIV – CV were pooled together.

Stages	***O. simili***	***M. norvegica***	***Microcalanus* spp.**
CI	260 ± 22	280 ± 16	235 ± 16
CII	350 ± 12	340 ± 10	280 ± 17
CIII	365 ± 16	380 ± 11	335 ± 19
CI-CIII	310 ± 56	330 ± 42	286 ± 42
CIV-CV	410 ± 21	440 ± 18	420 ± 23
Female	490 ± 23	510 ± 17	520 ± 20
Female w/eggs	510 ± 25	520 ± 21	-
Male	420 ± 10	483 ± 11	510 ± 14

3.4 Statistical work

Correspondance analysis (CAP) was used to look into seasonal and geographical patterns in *O. similis, M. norvegica* and *Microcalanus* spp. stage distribution. The data to be used for the CAP were ranked with a ranked Spearman correlation and resulted in equal differences from the raw-data matrix. SYSTAT 13 (Cranes Software International Ltd, Chicago, IL, USA) was used to apply conduct the CAP.

Calculations were done in Microsoft Excel 2010 for Windows (Microsoft Corp. Redmond. WA, USA). Graphs were made by using both SYSTAT 13 (Cranes Software International Ltd, Chicago, IL, USA) and Rstudio (Version 1.1.447, RStudio, Inc, Boston, Massachusetts 02210).

3.5 *Oithona similis* egg hatching experiments

Copepod egg hatching rates (HR) are correlated with temperature and can be determined experimentally. A common method of experimentally determine HR is called "the incubation method", where adult females with eggs clutches are incubated in separate containers with either natural sea water or filtered sea water. Regular controls are done several times a day and all hatching events, when nauplii are observed fully hatched (out of the egg), is recorded. The hatching rate can then be calculated from the slope of the linear regression between the incubation time and the cumulative hatching percentage. The cumulative hatching percentage is calculated from the sum of all eggs hatched at a given time, divided by the total number of females incubated. The egg hatching time (HT, hours^{-1}), the time predicted for the hatching of 100 % of the produced eggs, and the hatching success (HS, %), the percentage of eggs hatching from the clutch(es), can also be determined through the regression.

In this study, HR for *O. similis* was experimentally determined through "the incubation method" at 4 different temperatures (5, 8, 11 and 14 °C), which was selected from the *in situ* temperature range at the time of the experiments (Table 4). Since the experiments were conducted at *in situ* temperatures, no acclimation of the animals was needed (Nielsen et al. 2002). The calculated HR from the experiments was used to calculate SEPR and local secondary production in the three fjords in different seasons and temperatures (described in chapter 3.5.2).

3.5.1 Experimental set-up

Copepods for the experiments were collected in Balsfjord (station Svartnes, see table 1). All copepods were collected with a WP-2 net with a 64 µm mesh size, 0.57 m diameter, 3 m length with a non-filtering cod-end attached. In order to get active specimens with egg-clutches, several tows were done in the upper 50 – 0 m. On deck the animals in the cod-end was gently transferred to a 30 L plastic container full of sea water. Vertical profile on temperature (T, C˚) was obtained using a CTD and the *in situ* temperature was determined by taking the average of the coldest and warmest temperatures of the water column in the first 50 m: $T\ (C^{\circ})\ in\ situ = \frac{(T\ warm - T\ cold)}{2}$

Table 4: O. similis egg-hatching experiments in June and August, incubation temperature (°C) number of females incubated (N) and duration of the experiments (days).

Month	T (°C)	Exp	Start	N	Duration (days)
	5	E1	June 9.	20 + 40 egg sacs	12
June	8	E2	June 20.	61	6
	11	E3	June 20.	65	6
August	14	E4	August 15.	30	3

Thermaks (KB8400) incubators were used for the incubation. Three of the experiments were conducted in June and one in August. Before collecting and incubating the copepods, each incubation chamber was thoroughly cleaned and preset to 7˚C until the day of collecting the animals. Each incubator was equipped with a temperature logger. A cold room (8 °C) was used to sort the copepods. Two Leica stereoscopes were used when checking the copepods in the cold room, one equipped with a camera. The specimens were incubated in 12-welled culture trays, acid-washed in 10 % HCl and rinsed in MilliQ-water. Before the specimens were place in the trays, 5 of the wells in each tray that were going to be used were filled with 20 ml filtered sea water and placed inside the incubators until they were going to be used.

Using the Leica stereoscopes in the cold room, egg-carrying *O. similis* females were identified and picked out from the copepod-batch and set aside. Each specimen was isolated and photographed using a Leica stereoscope with camera. For each female, prosome length (µm), number of egg-clutches and total number of eggs were noted. The females were placed individually in 12-celled culture trays, 5 in each tray, that were prefilled with 20 ml filtered sea water, and the trays were then placed in the respective temperature incubator.

Three times a day, each well was inspected one at a time. In case of a hatching event, the number of nauplii, hatched and unhatched eggs remaining were recorded. The hatched nauplii were carefully removed from the well with a small glass pipette. After checking each well for all the trays, the remaining unhatched eggs were put back into the incubator chamber. If no new hatching occurred after 72 h in a well after last hatching event, number of eggs remaining was recorded and the well was noted as terminated. If a female died but

the egg clutch(es) looked viable, the female was carefully removed and the clutch(es) left in the well. Every 48 hours the water in each well was exchanged with new filtered sea water by removing almost all the old water was carefully removed under a microscope with a pipette and adding new water. In some cases, more than one female ended up in one well due to a mistake. The extra females were not discarded but placed in a new separate well and was included in the incubation experiment. One issue for the higher temperatures, was the occasional formation of new egg-clutches by some of the females. To prevent confusion and maintain consistency in the experiment(s), these females were removed with the new egg-clutches except for the first produced clutch(es).

We wanted to investigate if the egg hatching time and hatching success of the egg clutches is affected by whether they are attached to the female or not. In experiment E1, egg-clutch(es) from 20 females were carefully detached and placed in individual wells. If a female had two clutches, they were placed in the same well. Both egg hatching time and hatching success for the detached clutches did not differ much compared to clutches attached to the female. It was then decided that in experiments E2-E4 to only use clutches that were attached to the female.

3.5.2 Estimation of Oithona similis production

The hatching rate for each temperature was derived from the slope of the linear curve where the cumulative hatching of clutches (%) and is plotted against time. The specific egg production rate (SEPR) could be calculated by using the HR-equation. This is an estimate on daily copepod fecundity and is the percentage of carbon females spends per day to produce eggs. In order to estimate SEPR for the sampled*O. similis* populations found in the field, knowledge on the ratio of females carrying egg clutches to eggs (attached to females and loose clutches) of the population, the HR (%, day) at *in situ* temperature, and the carbon content of the egg and female (µC ind^{-1}) is required:

SEPR (%, day) = (egg/female) HR (eggC/femaleC) (Nielsen et al. 2002)

The daily *O. similis* secondary production (mg C m^{-2} d^{-1}) for every location in each month was estimated by two approaches. (1) Using a temperature-dependent method described by Huntley and Lopez (1992), where the *in situ* temperature is multiplied with total integrated *O. similis* population biomass:

Daily secondary production (mg C m^{-2} d^{-1}) = Biomass (mg C m^{-2}) x 0,0455 x $e^{0,111Temp}$

(2) using the estimated in field SEPR and multiply it with the total integrated *O. similis* population biomass, assuming specific egg production rates to be equal to juvenile somatic growth rates (Corkett and McLaren 1978; Berggren et al. 1988):

Production (mg C m^{-2} d^{-1}) = SEPR x total integrated biomass (mg C m^{-2})

The annual contribution of *O. similis* in each fjord, in terms of secondary production, was estimated by using the daily production rate based on the temperature dependent method (1) and the SEPR-method (2). This was done by categorizing the five sample points into seasons (Winter = December, Spring = March and April, Summer = August and Autumn = October) and assume that each season represents 91,25 days long (one year = 365 days / 4 seasons). The mean daily production rates at each location in each season are integrated by multiplying these values by 91,25. The seasonal secondary production in each fjord/location are summed up to represent the annual secondary production in the three fjords for *O. similis* (g C m^{-2} y^{-1}).

4. Results

4.1 Environmental parameters

In all the fjords, temperature was generally low in the upper 100-0 m in December, March and April that increased in August and October (fig. 3). Salinity had a narrow range that didn't deviate much through the seasons, except for in August where salinity decreased in the upper 20 – 0 m in all the fjords that gives indication for formation of a halocline at all the stations in August. Temperature at station Svartnes ranged from 3.8 – 9.1 °C and salinity from 32.1 – 33.4 ‰. The formation of a thermocline and halocline at the surface (0 – 20 m) be observed in March and April at Svartnes, where the upper water layer during these months were colder and less saline than deeper water masses. Temperature in Alta ranged from 2.1 – 10.1 °C and salinity from 29.2 – 35 ‰, where temperature varied considerably more in the upper 100 – 0 m that the bottom water strata during the sampling period. Station Alta had a defined thermocline and halocline in March and April that were found much deeper in the water column. The temperature range varied between the locations in Porsangerfjord. In P. outer it ranged from 2.5 – 10.0 °C where the bottom water masses showing higher variation than the upper water masses through the study. At station P. central, temperature ranged from 2.2 – 8.3 °C and from -0.8 – 8.2 °C at station P. inner. Salinity profiles were more or less the same for each of the locations in Porsangerfjord, but P. inner appeared to be generally fresher than the outer stations.

Chlorophyll *a* (Chl *a*) and particulate organic carbon and nitrogen (POC/PON) in the upper 100 m was sampled and measured at all locations to collect information on the potential feeding environment throughout the year for the copepod community. In this study, Chl *a* concentration was used as a proxy for phytoplankton biomass. The concentrations of Chl *a* were size fractionated (< 10 µm and > 10 µm), allowing us to distinguish roughly between different phytoplankton community compositions (i.e. dominance of small versus large cells). The total phytoplankton biomass was lowest in December, < 0.2 mg Chl *a* m^{-2} at all locations. In Balsfjord maximum chl *a* (400 mg m^{-2}) and POC (2 g C m^{-2}) concentration was found in April, as well as POC:Chl *a* ratio of 7. In August and October, the chl *a* concentration decreased in Balsfjord while POC remained above 10 mg C m^{-2}. Peak chl *a* concentration was

also found in April in Altafjord, but lowest measured POC concentration was also found during April for this location. Relatively high Chl *a*:POC ratio (0,2) was found during this month as a result (table 5). The Chl *a* concentration was comparatively lower in Porsangerfjord than the other two fjords in December, March and April, but a notable peak was observed in outer Porsangerfjord in August. This peak was measured to be 500 mg m^{-2} and as high as the peaks observed in March and April in Altafjord and Balsfjord. In October the chl *a* concentration increased as well as the POC:chl *a* ratio in Porsangerfjord. On average for all stations cells > 10 µm accounted for approximately 60 % of the total Chl a biomass throughout this study (fig. 2).

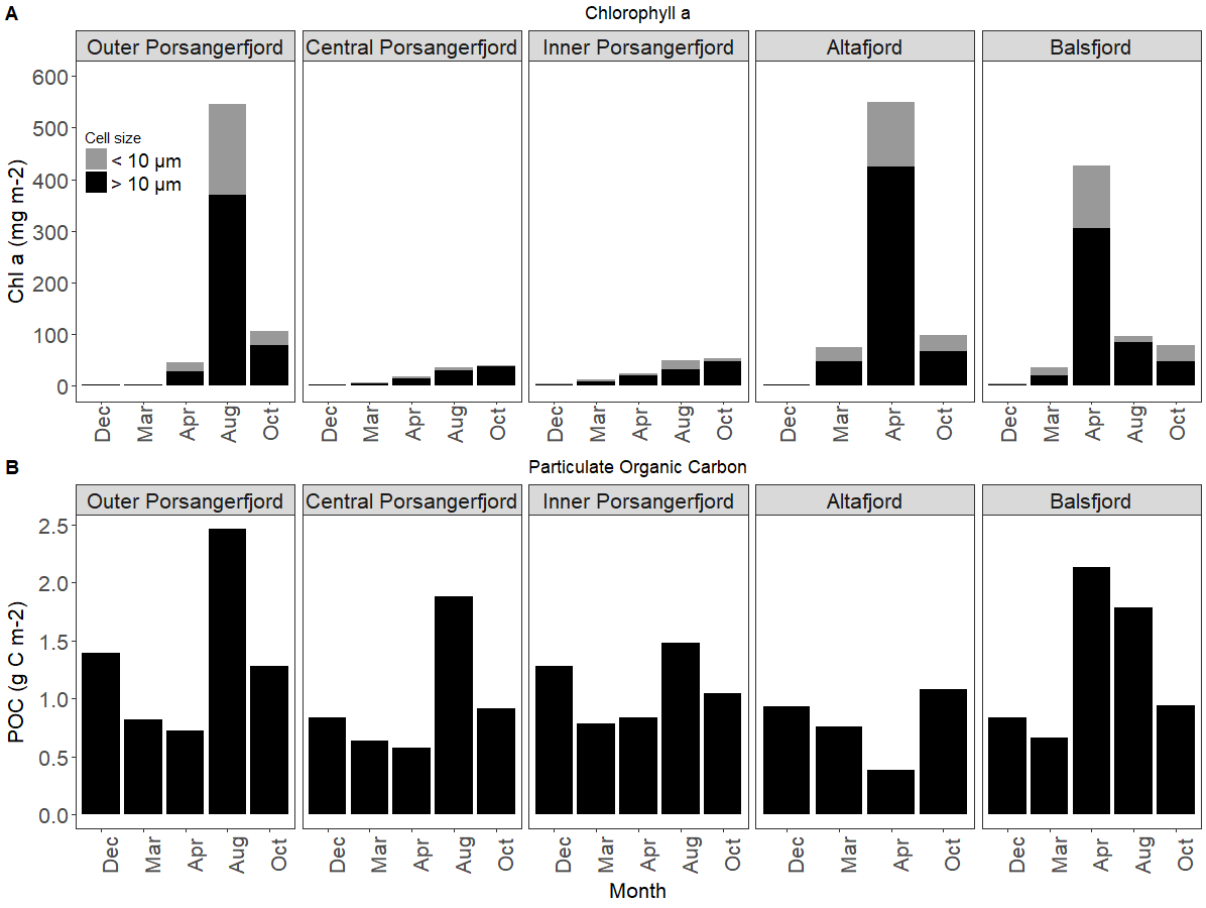


Fig 2: Integrated biomass (mg m^{-2}) in the upper 100 – 0 m of A) Chlorophyll *a* and B) Particulate organic carbon (POC) in the three fjords in December (2016), March, April and October (2017). Note the different scales on y-axes.

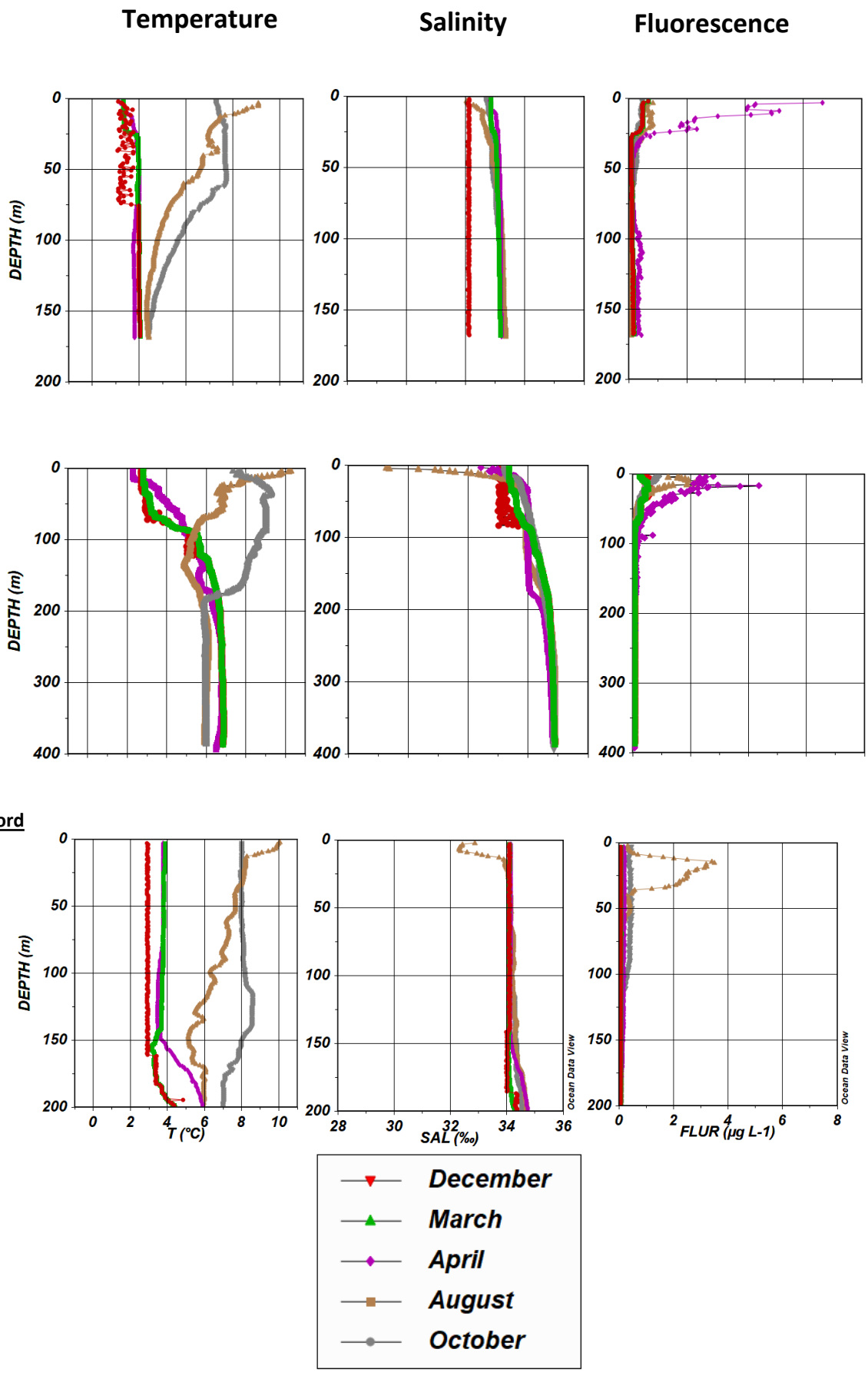
Table 5: Details on average temperature (T, °C) from 100 – 0 m, POC:PON-ratio and Chl *a*:POC ratio from 100 – 0 m during December, March, April, August and October, in Porsangerfjord, Altafjord and Balsfjord.

Month	Location	T (°C)	POC:PON	Chl *a*:POC
December	P. Outer	3,10	12,2	0,002
	P. Central	2,10	9,9	0,003
	P. Inner	-0,93	6,8	0,002
	Alta	4,50	3,8	0,003
	Svartnes	3,83	1,1	0,003
March	P. Outer	3,78	8,2	0,003
	P. Central	2,75	8,9	0,006
	P. Inner	-0,82	5,2	0,012
	Alta	5,83	5,3	0,063
	Svartnes	3,91	5,2	0,031
April	P. Outer	4,10	4,7	0,038
	P. Central	2,38	6,1	0,024
	P. Inner	-0,65	5,9	0,023
	Alta	5,80	38,1	0,253
	Svartnes	3,84	6,4	0,151
August	P. Outer	6,72	5,5	0,150
	P. Central	5,05	6,5	0,016
	P. Inner	3,09	5,7	0,021
	Svartnes	5,60	5,4	0,048
October	P. Outer	7,95	6,6	0,062
	P. Central	6,77	5,8	0,040
	P. Inner	4,26	5,9	0,046
	Alta	7,12	5,6	0,063
	Svartnes	6,27	5,4	0,050

Balsfjord

Altafjord

Outer Porsangerfjord



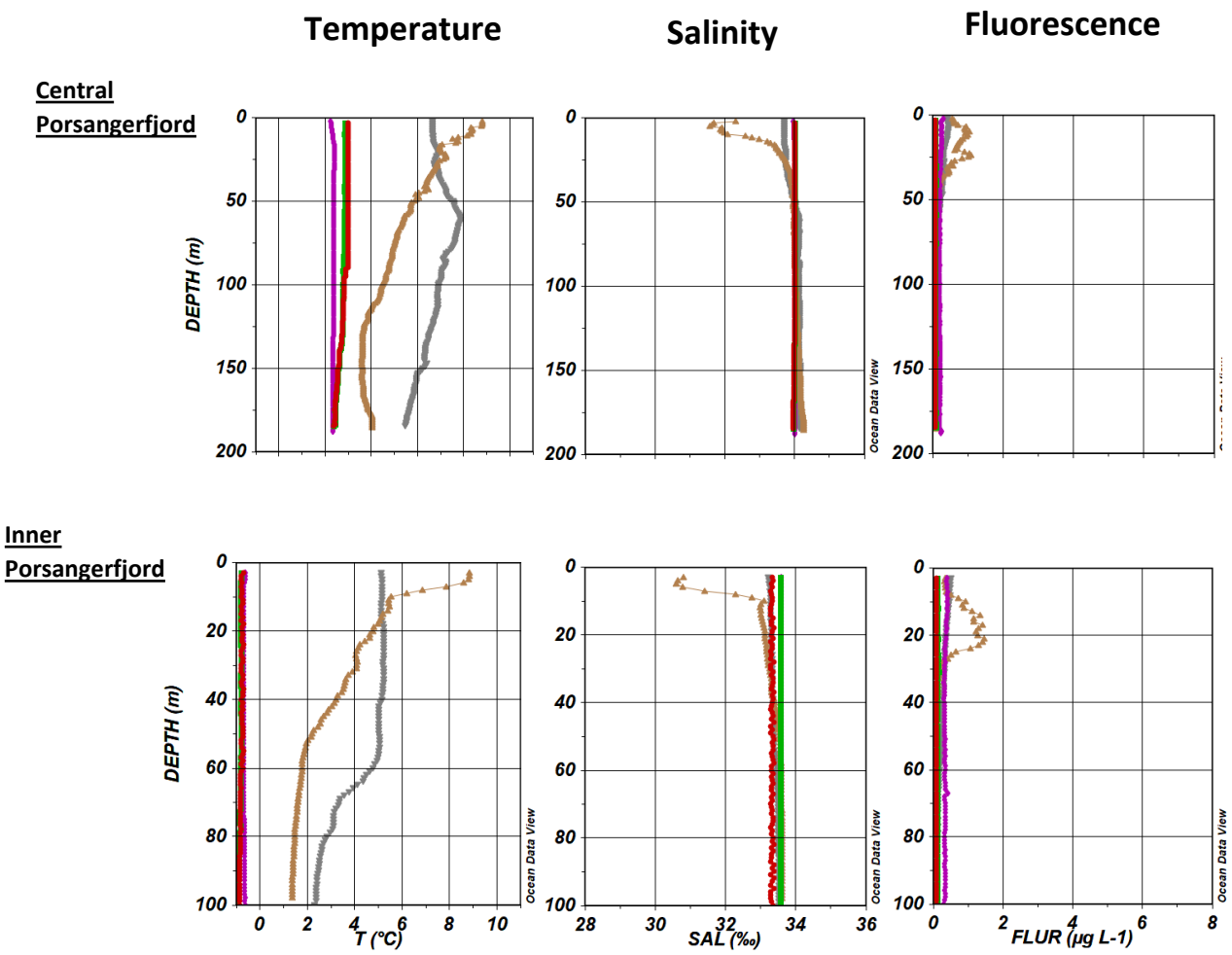


Fig 3: Vertical profiles on temperature (°C), salinity (‰) and fluorescence (µg L^{-1}) at station P. outer, central and inner, Alta and Svartnes in the sample months. The profiles were taken with a seabird-CTD instrument from the bottom and up to the surface at each station.

4.2 Seasonal distribution of O. similis, M. norvegica and Microcalanus spp. in Balsfjord, Altafjord and Porsangerfjord

4.2.1 Comparison between the stations and fjords

The seasonal abundance, biomass and distribution of the species *Microsetella norvegica, Oithona similis* and *Microcalanus* spp. were investigated in Balsfjord, Altafjord and Balsfjord. The three species were present in all fjords and at all the months investigated, but clear differences were found (fig. 4). At the stations P. inner and Svartnes, the total integrated abundance and biomass of copepods peaked in March, while the peak was found in April in Alta and in October in P. outer and inner. In P. outer, P. central and Alta, distribution in copepod abundance and biomass was more even. There was less variation between the months in P. outer, P. central and Alta compared to inner P. inner and Svartnes. Comparing the abundance found at the sample stations through the study time, *M. norvegica* was the most numerous of the species accounting for on average 56 % of the total number of copepods sampled in total. *O. similis* and *Microcalanus* spp. made up to 35 and 9 % of the copepods, respectively (fig. 4 B). When comparing biomass found in total though this study, *M. norvegica* accounted for 60 % of the computed copepod biomass found in this study, while *O. similis* and *Microcalanus* spp. contributed to 31 and 9 % respectively (fig. 5 B).

With respect to seasonal patterns, the abundance and biomass of *O. similis* was generally low in December, March and April ($1.4 \times 10^4 – 1.3 \times 10^5$ ind. m^{-2} and 1.2 – 79 mg C m^{-2}) at all stations that increased in August and October at all the stations, especially in Porsangerfjord ($1,0 \times 10^4 – 2,8 \times 10^5$ ind. m^{-2} and 7,6 – 113 mg C m^{-2}) (fig. 4 A - 5 A, Appendix A). At station Alta and Svartnes, where deeper water samples were taken, *O. similis* abundance were generally higher at deeper waters. The abundance and biomass of *M. norvegica* was generally higher than *O. similis* and *Microcalanus* spp. at almost all stations during December, March and April, especially in P. inner and Svartnes ($7,8 \times 10^3 – 1,4 \times 10^6$ ind. m^{-2} and 9,6 – 690 mg C m^{-2}) (fig. 4 A - 5 A, Appendix A). In August and October, *M. norvegica* abundance and biomass decreased at all the stations. *Microcalanus* spp. was the least abundant specie compared to the other two species. Relatively high *Microcalanus* spp. abundance was found in March and later in October.

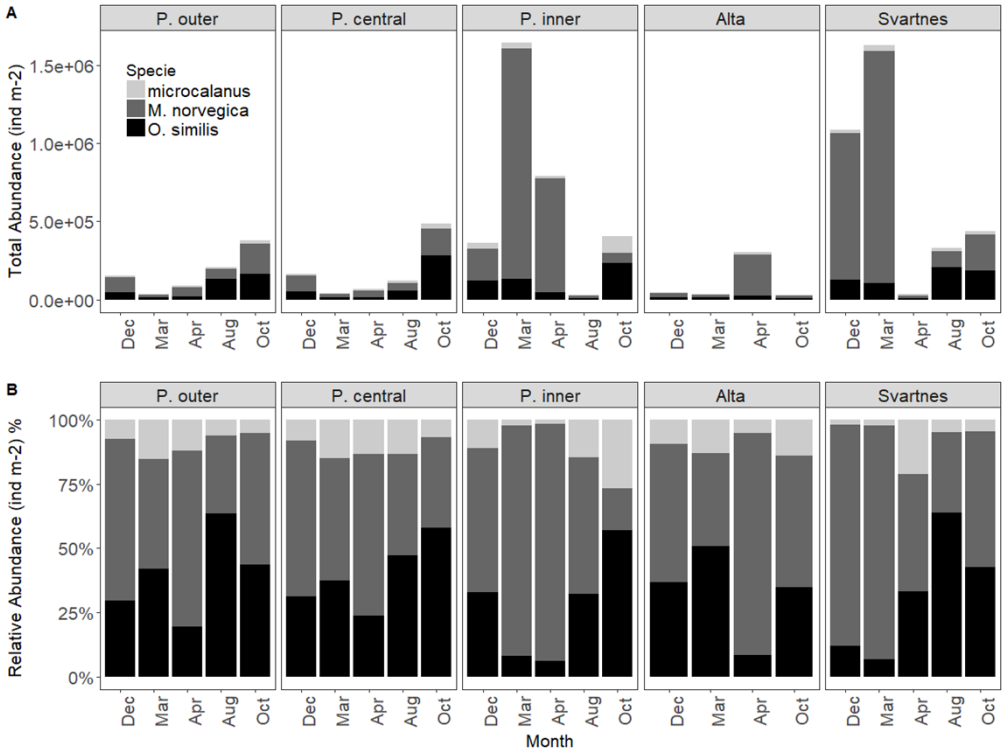


Fig 4: A) Total integrated abundance (ind. m^{-2}) and B) relative abundance (ind. m^{-2} %) of *O.* similis, *M. norvegica* and *Microcalanus* spp. from 100 – 0 m.

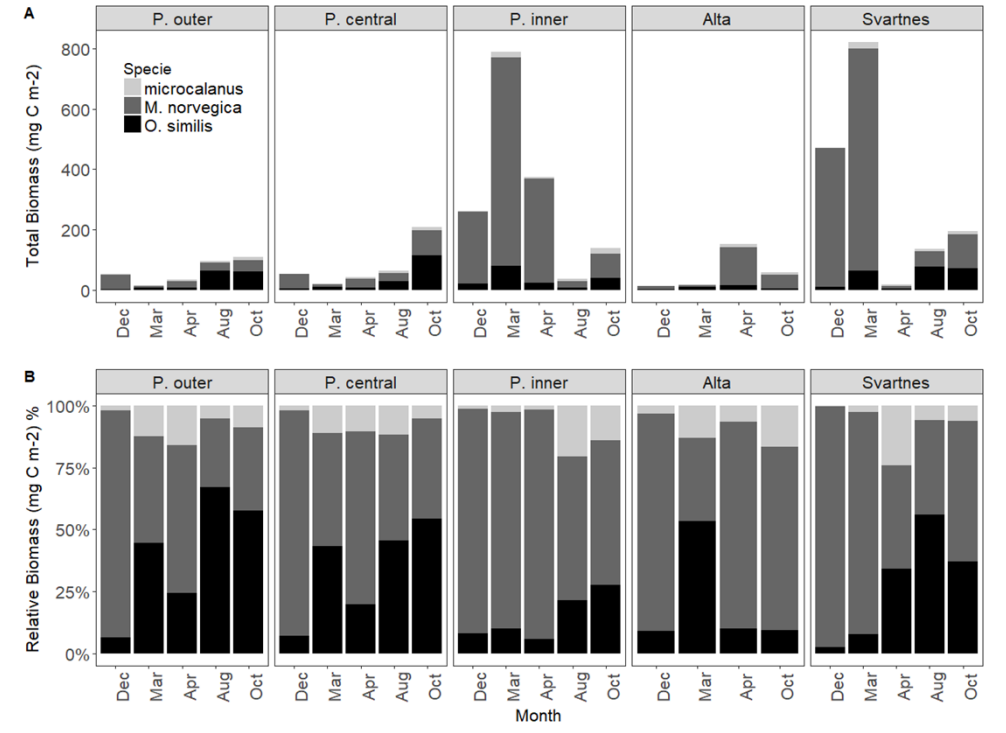


Fig 5: A) Total integrated biomass (mg C m^{-2}) and B) the relative biomass (mg C m^{-2}, %) of *O. similis*, *M. norvegica* and *Microcalanus* spp. from 100 – 0 m.

4.2.2 Seasonal and spatial patterns of developmental stages of *O. similis, M. norvegica* and *Microcalanus* spp.

All *O. similis* developmental stages were found in all the sample months. During December, stages CI – CV amounted for the main proportion of the *O. similis* population at all the stations except for Svartnes (fig. 5). During all the sample months, higher proportion of females than males were found which led to *O. similis* sex ratio being constantly high. Females with egg clutches were found during all the sample months, but in higher numbers in the months April, October and August (Appendix C fig. 2). Copepodite stages CI – CIII were found in all sample months and almost all sample stations, but highest proportion of the young copepodite stages were found in October at all the stations. Based on the high proportion of CI – CV stages in October and December at all the stations, these are the main overwintering stages.

All the developmental stages for *M. norvegica* were present in all the sample months (fig. 6). The adult stages, females without eggs and males, were the main overwintering stages, but CIV – CV copepodites was also found smaller numbers in P. inner, Alta and Svartnes in December (fig. 6). The sex ratio was lower for *M. norvegica* during the sample months than for *O. similis* and *Microcalanus* spp. The sex ratio was at its lowest in March (1,1 in P. inner) and April (1,1 in P. inner and 1,6 in Alta). Females with eggs was first observed in small numbers at station Alta and Svartnes in April and later in August at all the stations and higher abundance. The young copepodite stages CI – CIII was first observed in small numbers in December at station P. inner. Main proportion of young copepodites were found in April, August and October, most notably at station P. outer in August and October (Appendix fig. 1 and 2).

The main overwintering stages for *Microcalanus* spp. were adult females and copepodite stages CIV – CV (fig. 6). The adult stages were dominated by females, and a high sex ratio were recorded throughout the study period. Copepodite stages CI – CIII could be found in small numbers in P. outer and central in December, but a notable increase was observed at all the stations in March for these copepodites. This indicates that reproduction must have taken place between December and March. From April – October, CI – CIII copepodites almost disappeared in all the stations, while abundance of CIV – CV copepodites remained stable.

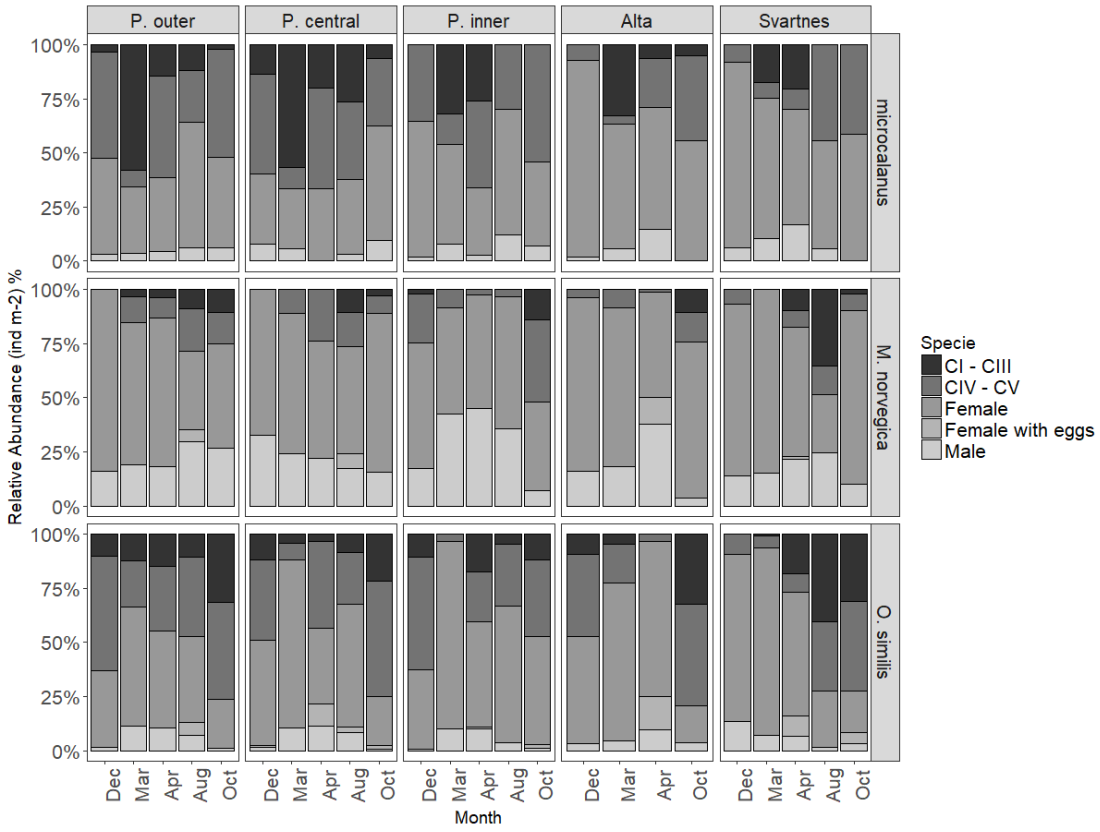


Fig 6: Relative abundance of the developmental stages for O. similis, M. norvegica and Microcalanus spp. from 100 – 0 m during the study period at station P. inner, central and inner, Alta and Svartnes.

4.3 Oithona similis egg-hatching experiments

4.3.1 Egg hatching rate and specific egg production rate

The egg production experiments for *O. similis* was carried out in June and August 2017, and egg-carrying specimens were collected in Balsfjord. The experimentally determined temperature-dependant hatching rate (HR) for *O. similis* is listed in table 6. Lowest hatching rate was found in experiment E1 at 5 °C (9,97 %, day^{-1}) that increased with temperature to the highest hatching rate found in experiment E4 at 14°C (35 %, day^{-1}) (fig. 7). The equation for the temperature - dependent hatching rate for *O. similis* in temperature range 5 – 14 °C is expressed as:

HR (%, day) = 0,28636 T – 6,7661 (fig. 8)

Population specific egg production rate (SEPR, % day^{-1}) was calculated using HR derived from own experiments. Due to low or no abundance of females with eggs and/or loose egg

clutches, SEPR at some locations and sample times was 0. Specific egg production rate was low in December and March in all the fjords where few or no egg-carrying females or loose egg clutches were found. In April, August and October the SEPR increased. Highest production was found at station P. outer in August and Svartnes in October. Here the SEPR was found to be 1,2 %, day^{-1} at both locations. Females with egg sacs and detached egg sacs were found throughout the study period, even in December and March, indicating that reproduction occurred continuously even during winter.

Table 6: O. similis egg hatching experiments at 5, 8, 11 and 14 C° (T C°) where egg-carrying females were incubated (N) to calculate hatching rate (HR) for each temperature. The average clutch hatching success (HS) was calculated by both including unhatched eggs[1] and not including them[2]. Duration is the mean ± SD (standard deviation) time in hours required for all eggs in a clutch to fully hatch.

Experiment	T (C°)	N	HR (%, day)	HS_1 (%)	HS_2 (%)	Duration (hours)
E1	5	60	10	90	93	31 ± 22
E2	8	61	13	76	83	39 ± 36
E3	11	65	24	80	82	36 ± 29
E4	14	30	35	78	81	12 ± 10

4.3.2 Estimated *O. similis* secondary production for

Seasonal secondary production was estimated by two different methods, a temperature dependent method (Huntley 1992) and one using specific egg production rates (SEPR). The SEPR method were based on estimated SEPR using by using the temperature dependent-hatching rate obtained from own experiments (fig. 8). Daily production was lowest in December and highest in October. Out of the five sample stations in October, Svartnes had the highest estimated production of 2,8 mg C m^{-2} d^{-1} (using the SEPR-method) (fig. 9). In addition, total yearly secondary production was also highest in Balsfjord, yielding in total 1,79 g C $m^{-2}y^{-1}$ (fig. 10). Outer Porsangerfjord was the only other location where yearly production was > 1 g C m^{-2} y^{-1}. The estimated production was higher when using the temperature-dependent method than the SEPR-method (fig. 9), and production was never estimated to be zero using this method. Highest yearly secondary production with the temperature-dependent method was at 4 g C m^{-2} y^{-1} (fig. 10).

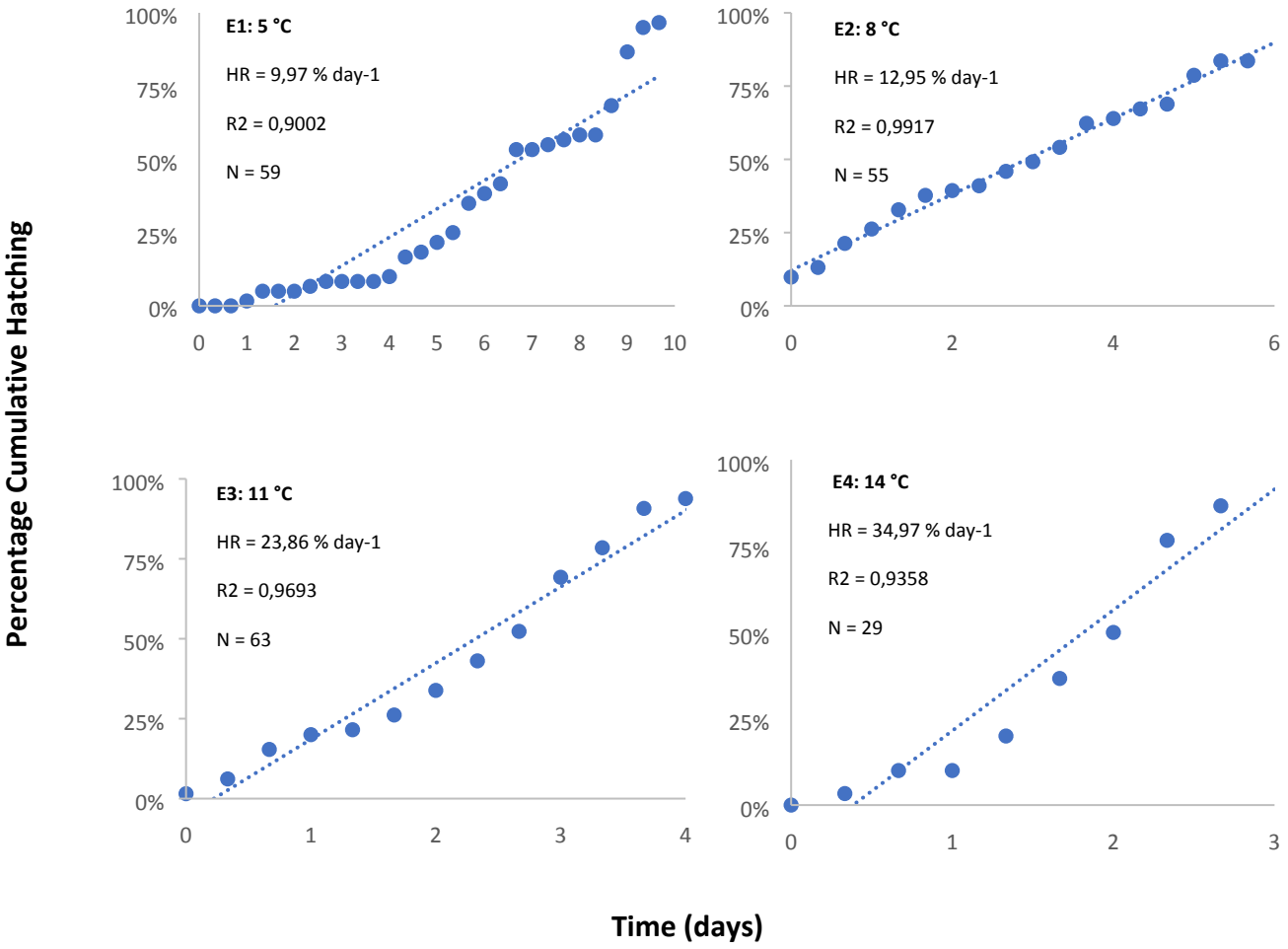


Fig 7: O. similis egg-hatching experiments at 5, 8, 11 and 14 °C. Hatching rate (HR, % day^{-1}), r^2 and n (number of hatches) for the linear regression of cumulative hatching percentage vs. time are shown for each experiment. Note the different scale on the x-axis.

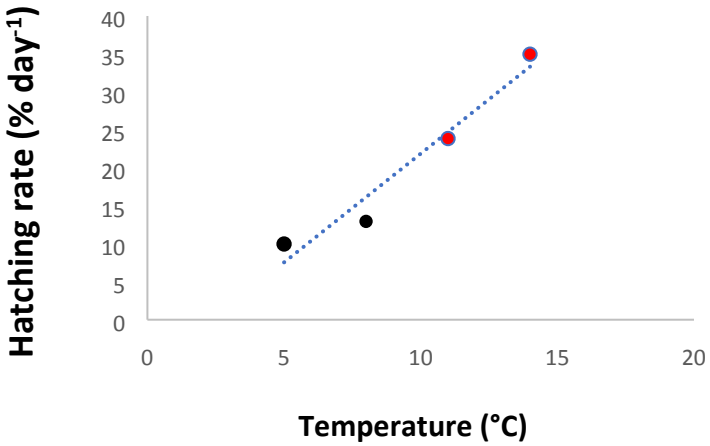


Fig 8: *Oithona similis* egg hatching rate (HR) at 5, 8, 11 and 14 °C. The regression line is described as y =2,8636x - 6,7661, R^2 = 0,9498.

and found in Balsfjord. The station Alta were the only location where estimated yearly secondary production using the SEPR-method were higher than the temperature-method.

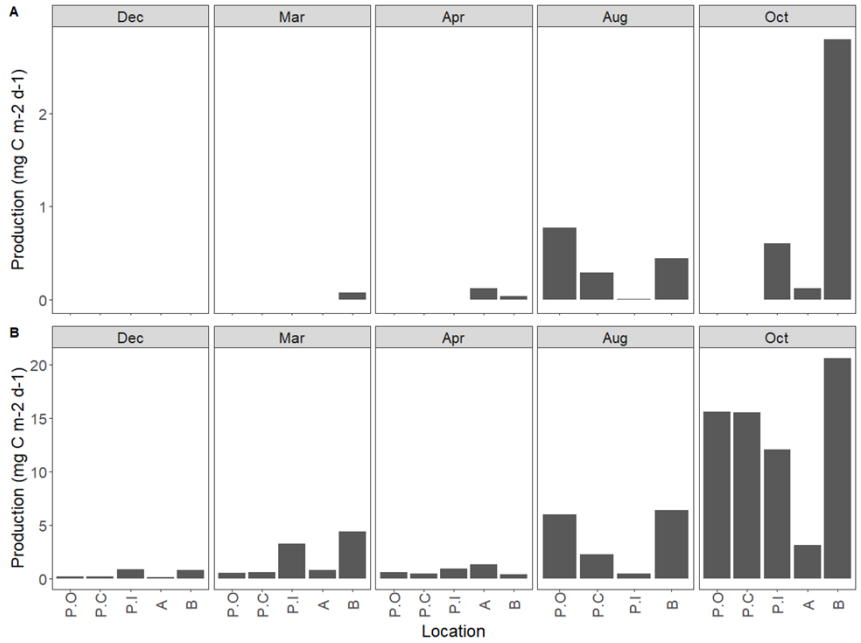


Fig. 9: Seasonal daily secondary production of O. similis in the water column over the sampling period using a A) SEPR and B) a temperature dependent method described by Huntley and Lopez (1992). Note the different scales on y-axis.

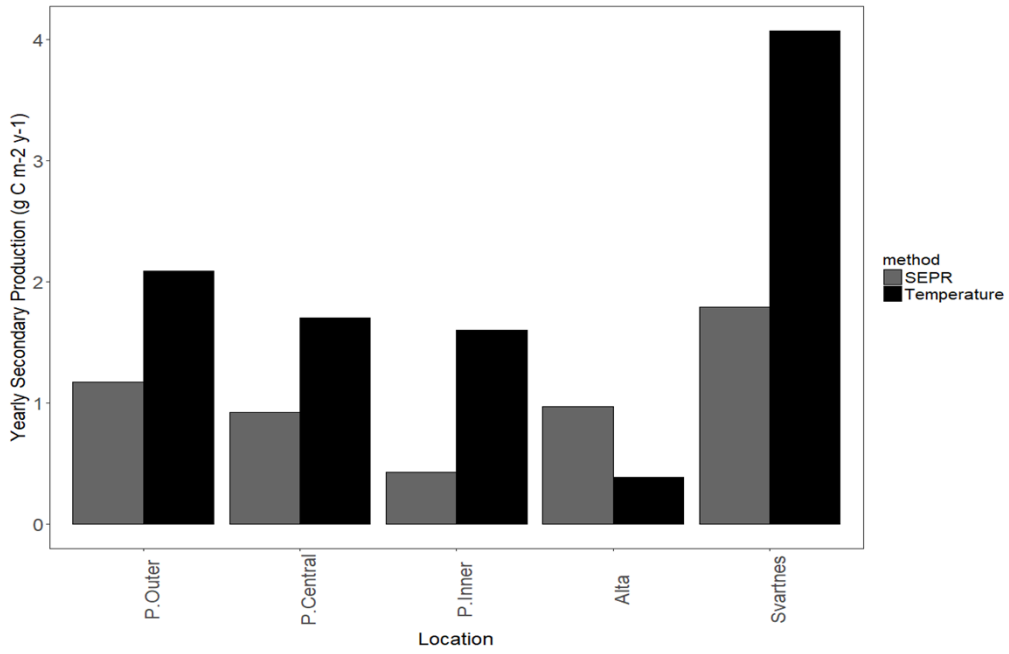


Fig 10: Annual secondary production (g C m^{-2} y^{-1}) at station P. outer, central and inner, Alta and Svartnes based on secondary production via two methods. The SEPR-method that is based on own experimental data and a temperature-dependent method described by Huntley and Lopez (1992).

5. Discussion

5.1 Seasonal dynamics of the environmental parameters

Balsfjord, Altafjord and Porsangerfjord are part of the northern Norwegian coastal system and each fjord have different hydrographical features. Long term hydrographical time series are available for these fjords and the collected data fits well with what has been previously been described for these fjords (Eilertsen and Skarðhamar, 2006; Mankettikkara, 2013; Wassmann et al., 2000). Temperature and salinity changed with season, where December, March and April were the coldest months and August and October the warmest. Balsfjord is a narrow fjord and is enclosed by shallow sills. It is expected that this fjord experiences more cooling (lower winter temperature) and higher summer temperature than other northern Norwegian fjords. Altafjord has free connection to coastal water and is influenced by inflowing Atlantic water, where water masses in the upper 100 – 0 experience more mixing and advection than deeper water masses. Porsangerfjord is the widest of the three fjords and has free connection to the open ocean. The outer areas of the fjord are generally warmer and more saline than the inner areas, where freshwater runoff and the cold "Finnmarksvidda" winter climate leads to a winter situation that resembles the Arctic environment in inner Porsangerfjord.

The observed seasonal variations in chl *a* concentration in the water column in the fjords agrees with the seasonal pattern in phytoplankton dynamics previously described for northern Norway (Norrbin et al., 2009; Eilertsen and Degerlund, 2010; Degerlund and Eilertsen, 2010). During December and March, chl *a* concentration in the water column was at its lowest in all the fjords (< 1 µg L^{-1}). In April the concentration increased substantially to concentrations that would indicate a spring bloom is taking place (> 3 µg L^{-1}). It is however odd that Chl *a*:POC ratio is so low in this study, as it is expected to be much higher during bloom situations. The impact of grazing on the phytoplankton standing stock in the sub-Arctic and Arctic is well documented for bigger copepod species such as those of the *Calanus* genus, but less for smaller species (Rysgaard et al., 1999; Pasternak et al., 2000; Madsen et al., 2001). Though most are omnivores, the grazing impact of small copepod species is speculated to be high because of high abundance small cells in the sub-Arctic/Arctic (Turner, 2004; Archer et al., 2000).

5.2 Seasonal trends in *Oithona similis*, *Microsetella norvegica* and *Microcalanus* spp. distribution in Balsfjord, Altafjord and Porsangerfjord.

This study was meant to investigate and gain knowledge on small copepod species found in fjord systems in northern Norway. In this study small copepod species are defined as species that do not reach a body length over 1 mm and in this study three copepod species belonging to different taxonomic orders was described: *Oithona similis* (cyclopoida), *Microsotella norvegica* (harpacticoida) and *Microcalanus* spp. (calanoida). The seasonal patterns in abundance, biomass and stage composition was investigated over five months (December, March, April, August and October) in three northern Norwegian fjords (Balsfjord, Altafjord and Porsangerfjord). The seasonal and annual secondary production for *O. similis* in the investigated fjords was estimated. This was based on the specific egg production rate for the *in situ* temperature in the study fjords, which was obtained by performing egg hatching experiments on egg carrying *O. similis* females at 4 different temperatures.

O. similis is one of the most common small-sized copepod species in the sub-Arctic and Arctic and is found to be active in the water column year-round (Zamora-Terol et al., 2014). Investigations on the zooplankton community in the sub-Arctic/Arctic have mainly revolved around the large *Calanus* species (Hopcroft et al., 2005). However, because of their overwintering strategies, *Calanus* spp. is only present during spring – early summer and is relatively absent in the water column until the following spring. From September and until March, small copepod species dominate the Arctic/sub-Arctic ecosystem and *O. similis* is perhaps the most prominent of these species (Ward and Hirst, 2007; Dvoretsky and Dvoretsky, 2009; Madsen et al., 2008). It is described to be highly abundant year-round, but maximum abundance, biomass and production of *O. similis* are found during late summer/fall until the end of the primary production season (Zamora-Terol et al., 2013; Cornwell et al., 2018). This fits well with what is observed in the fjords where peak *O. similis* abundance was found in August and October, where CI – CIII copepodites accounted for a high proportion of the abundance. Unlike *Calanus* spp., *O. similis* is unable to store large amounts of lipids due to its small size in order to survive the winter (Narcy et al., 2009). In order to survive the winter, *O. similis* have adapted as omnivores and remain relatively active during the winter, that relies on supplementary food (Castellani et al., 2005). The

benefit of this strategy is that allows *O. similis* to maintain more constant abundance, biomass and reproduction year-round, unlike *Calanus* spp.

The ecological role of *O. similis* have been assessed in previous studies, and it has been pointed out that *O. similis* is strongly linked to the microbial food web (Böttjer et al., 2010; Calbet and Saiz, 2005). Preferred food item for *O. similis* copepodites are motile prey such as heterotrophic protozooplankton that remain relatively abundant almost year-round in sub-Arctic/Arctic waters (Archer et al., 2000; Nakamura and Turner, 1997) (fig. 3). Being able to utilize and potentially have a big grazing impact on protozooplankton and the microbial food web, explains why *O. similis* can survive and reproduce outside the phytoplankton spring bloom (mainly > 10 µm cells) (Svensen et al., 2011). From an ecological perspective this is of great importance, as *O. similis* is then likely to play a key-role in sub-Arctic/Arctic marine food webs. This will be further discussed in chapter 5.3.3.

The harpictocoida *M. norvegica* was also abundant throughout this study especially at station P. inner and Svartnes in December and March. Davis (1976) suggested that *M. norvegica* generally reproduces in April and May in the surface, where they feed and grow until late summer. This fits well with what is observed in this study, as the phytoplankton spring bloom took place, at least in Balsfjord and Altafjord, in April and egg-carrying females was first observed in April at station Alta. Egg-carrying females was found at all stations in August, in addition to a large proportion of the *M. norvegica* population consisted of CI – CIII copepodites, but no egg-carrying females were found in October. Based on the results, main *M. norvegica* reproduction took place between April – August the year for this study. During the reproductive period, *M. norvegica* is capable of producing more than one egg-sac that are released before they have hatched (Koski et al., 2014). It has also been reported that number of egg-sacs during the reproductive period can far exceed the number of females (Antonsen, 2014). This combined strategy, of decrease in egg mortality relative to broadcast spawners, but increasing egg production compared to sac spawners may be the reason why *M. norvegica* reach high abundances (Koski et al., 2014). It has previously been suggested that one trait that allows *M. norvegica* to achieve high reproduction rate and in turn high population abundance, is a relatively even distribution between females and males (Grønvik and Hopkins, 1984; Tande, 1982). *M. norvegica* males were present in all the months and made up a much higher proportion of the population than what was observed for *O. similis*

and *Microcalanus*. The ratio between *M. norvegica* females to males was 1,16 during March and April in inner Porsangerfjord and 1,6 in Altafjord in April. A possible advantage of having an even sex ratio between females and males over a longer period is that it opens up for a longer reproductive period (Antonsen, 2014). *M norvegica* seemed to have a high preference for inner Porsangerfjord and Balsfjord. These locations are enclosed areas in the fjord systems, were advection could be low as well as the temperature that could be preferable for *M. norvegica*. Compared to Balsfjord and inner Porsangerfjord that are more or less sheltered by a shallow sill, the outer and central areas of Porsangerfjord and Altafjord have free connection to open coastal waters. These areas are more influenced by more warm and saline water, and higher advection of water masses in and out of the fjord could potentially affect copepod distribution. This study supports the suggestion that *M. norvegica* is a highly abundant species in coastal sub-arctic fjord ecocystems that can maintain high abundance throughout the seasons even during winter (Dugas and Koslow, 1984). *M. norvegica* has been previously described to graze on particulate related food sources (Kiørboe, 2000; Koski et al., 2005, 2007). Many fjords in Northern Norway is associated with having high chl *a* concentration in the upper water strata from March to August as well as relatively high carbon concentration in the water column during the entire year (Wassmann et al., 1996; Arendt et al., 2013). Areas being enclosed and have a relatively high occurence of aggregates throughout the year could be preferred habitats for *M. norvegica* that allows for high population abundance throughout the year.

Microcalanus spp. was the least abundant of the three species in this study. Furthermore, studies on *Microcalanus* spp. population dynamics in northern Norwegian fjord systems and in the sub-arctic in general are few. Based on present data, *Microcalanus* spp. had taken place in early spring (December – March). This is earlier than reported for other calanoid copepod species such as *Calanus finmarchicus,* that reproduce from April to June in sub-Arctic fjords (Tande, 1982; Norrbin, 1994; Priou, 2015). All developmental stages were also present in August and October, and increased abundance was observed in October, especially at the staions in Porsangerfjord. The seasonal pattern in stage composition observed for *Microcalanus* spp. in this study is comparative to other studies in high latitudes. It is suggested that *Microcalanus* spp. reproduce at the beginning of the year during winter (Digby, 1954; Norrbin, 1991; Atkinson, 1998; Ashjian et al., 2003). These studies report that,

unlike *C. finmarchicus* that will migrate from the upper water strata to enter diapause at deeper depths in June/July, *Microcalanus* spp. continues to be active after summer. Schnack-schiel and Mizdalsk (1994) did a seasonal study in the eastern Weddell Sea in Antarctica on *M. pygmeaus* , and propose that *M. pygmaeus* may have a 2-year life-cycle where breeding occurs in autumn and early to midwinter. Relatively high abundance of CIV – CV and females were recorded in the fjords in December, especially in inner Porsangerfjord and Balsfjord which might be the overwintering stages. It is difficult to evaluate the 2-year life-cycle and multiple spawning in the present study with the data available gathered on *Microcalanus* spp., but it is not unlikely that these species are capable of having a 2-year life-cycle in the sub-Arctic and Arctic marine ecosystem. *Microcalanus* spp. is described as a species that prefers deeper (> 200 m) waters (Kosobokova and Hopcroft, 2010; Kosobokova et al., 2011). It remains active year-round and relies on fat storage and detritivory (Norrbin, 1991). Inconsistent sampling (see material and methods) at deeper depths in the fjords for this study makes it hard to evaluate depth preferences for the *Microcalanus* spp. population. However, maximum abundance for this species in Altafjord in October was found between 411 m and 100 m depth (1,01 x 10^5 ind. m^{-2}) which might be the preferred habitat for *Microcalanus* spp. (Appendix A).

5.3 Oithona similis production rates

5.3.1 Temperature-dependent egg hatching rates

Estimating a copepod species production rates is useful in order to evaluate their contribution to the food web. In this study, egg-hatcing rates and secondary production for *O. similis* was investigated. This was done by egg hatching experiments for egg-carrying females at 4 different temperatures (5, 8, 11 and 14 °C) to obtain the egg hatching rate (HR) for each temperature. The Hatching rates obtained from the experiments were used to calculate seasonal and annual secondary production of O. similis in the three fjords.

The egg hatching experiments demonstrated that there is a strong correlation between *O. similis* HR and temperature, as well as HT (hatching-time), and temperature. At 5 ˚C HR was 9,97 % day^{-1} and it took an average time of 31 hours for a clutch to fully hatch, while at 14 ˚C HR was 35 % day^{-1} and an average hatching time from egg to nauplii of 12 hours. These results show that low temperature have implications for *O. similis* reproduction. If cold

temperature lowers the egg hatching rate and increases the hatching time, maximum egg production cannot be achieved since new egg clutches cannot be produced until the previous ones have hatched or detached from the females. It is however interesting to note that the egg hatching success decreased with increasing temperature in the egg-hatching experiments. This could mean that even if low temperature lowers egg production rate, it would still be advantageous to reproduce during periods with low temperature if egg hatching success is higher.

Based on temperatures in the fjords, reproduction is reduced in the cold months (December, March and April) until the warmer months (August and October). The egg hatching experiments conducted for this study shows that the HR equation is only valid for *in situ* temperatures which is included in the experimental temperature range 5 – 14 °C. When *in situ* temperature is below the range, values for HR and in turn the calculated SEPR becomes negative. Many of the stations in this study, especially in December and March, had *in situ* temperature below 5 ˚C and at P. inner it was below zero. This means our HR equation cannot be used for the winter temperatures that was found in some of the fjords. I will still argue that the experimentally determined temperature dependent hatching rate found in this study is valid. Nielsen et al. (2002) did a similar study on *O. similis* egg-hatching where 20 different experiments was conducted ranging from temperature between -1 – 20.5 °C. When comparing the HR from the present study to Nielsen's HR at 5, 8, 11 and 14 °C the results are comparable, though my HR-equation seems to underestimate HR at lower temperature and overestimate at higher temperature compared to Nielsen et al. (2002).

5.3.2 Seasonal *O. similis* specific egg hatching rate (SEPR)

In December and March, specific egg production rates (SEPR) in all fjords was either very low (< 0,1 % day^{-1}) or zero because few egg-carrying females and detached egg sacs were found in the water column (fig. 9). In August and October egg-carrying females were found in all the fjord, and SEPR was high. Highest SEPR estimates was 1,21 % d^{-1} and this estimation was found in both P. outer in August and in Svartnes in October (fig. 11). The seasonal trend in SEPR could be related to the *in-situ* temperature. Both in field and experimental studies on copepod productivity rates for species found in high latitudes have shown that egg production rate and temperature are highly correlated (Huntley, 1992; Peterson et al., 1991; Madsen et al., 2001; Drif et al., 2010; Pasternak et al., 2013). In general, low sea surface

temperature inhibits high egg production rate, but species react differently to either low or high temperature (Calbet and Agustí, 1999; Holste and Peck, 2006; Peterson et al., 1991).

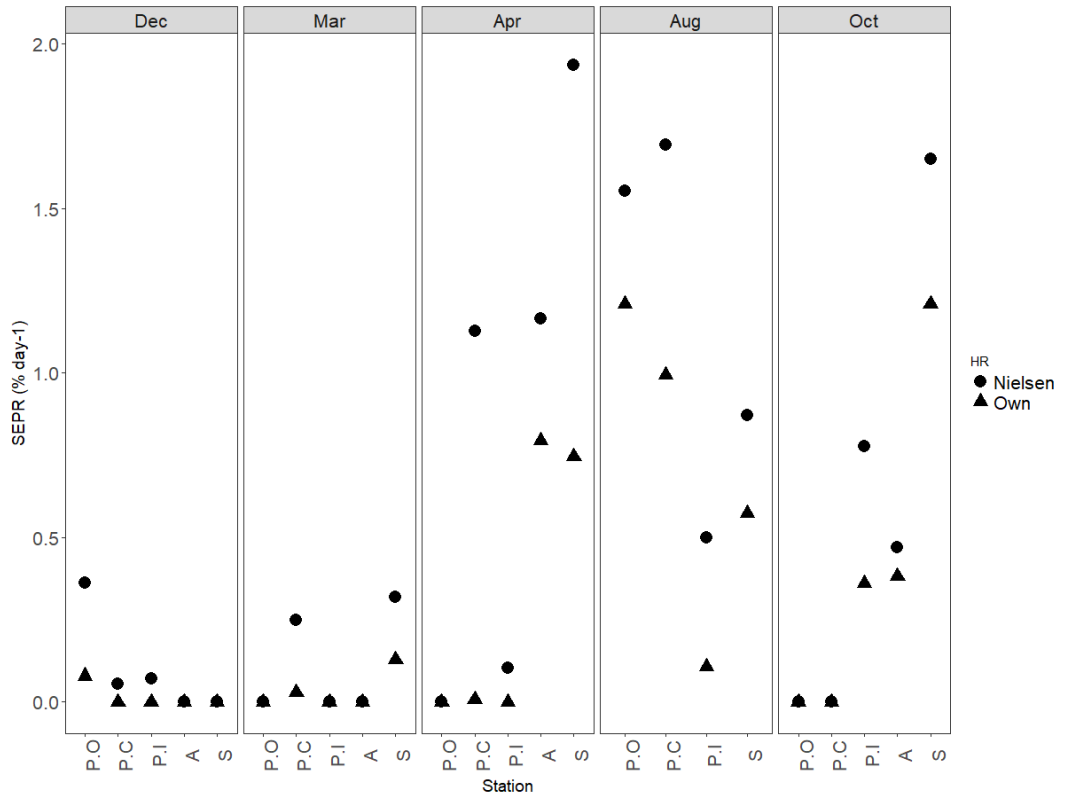


Fig 11: Calculated SEPR (day^{-1}) using HR from own experiments (Own) and from Nielsen et al. (2002). P. O, P. C and P. I = Outer, central and inner Porsangerfjord (respectively), A = Alta, S = Svartnes.

Pasternak et al., (2013) shows that the arctic copepod species *Calanus glacialis* have significantly decrease in its egg production rate at temperatures over 5°C while this seems to increase for the more boreal specie *Calanus finmarchicus*. Based on the egg hatching experiments and the seasonal SEPR found in the field, *O. similis* production rates seem to be much higher at temperatures above 5 °C.

In this study August and October were the warmest month where sea surface temperature almost reached 10 °C in some areas, while in December, March and April the temperature was on average < 5 °C in the water column. *O. similis* is still capable of reproducing at temperatures below 5 °C, but at a decreased rate compared to warmer seasons. Drif et al., (2010) estimated weight specific egg production rates for temperatures -1,6 - 10 °C, which is a realistic temperature range for Arctic waters, to vary from 0,5 - 4 % day^{-1} which is comparable to what was found in the current study. A laboratory study done by Sabatini and

Kiørboe (1994) shows that *O. similis* SEPR to potentially reach 10 % day^{-1} at 15 °C and when temperature is this high, *O. similis* egg production is strongly limited by food concentration. In sub-Arctic fjords, *O. similis* SEPR is more likely governed by temperature than food limitation. It should also be noted that in study conducted by Sabatini and Kiørboe (1994) shows that the specific egg production rate for free spawning calanoids, such as *Calanus* can reach 25 % day^{-1} at 15 °C and suggest that egg production rates, on average, differ by a factor of ~ 2.5 between free-spawning and egg-carrying copepods. In general, free-spawning calanoids have high ingestion and egg production rates as well as higher egg mortality rate in contrast to egg-carrying cyclopoids (Kiørboe and Sabatini, 1994).

5.3.3 *Oithona similis* seasonal and annual secondary production in Balsfjord, Altafjord and Porsangerfjord.

O. similis secondary production was estimated with two methods, one based on *in situ* temperature and biomass (temperature-dependent production), and the other on experimentally obtained hatching rates (HR) that was used to calculate specific egg production rates (SEPR). For both of these methods, the estimated secondary production was lowest in December and highest during October. Both of these methods also show that secondary production in the three fjords was highest in Balsfjord. However, the values estimated for each sampling location and month differed greatly with the method applied. This difference is apparent when comparing peak in secondary production, which was at station Svartnes in October using both methods. With the temperature-dependent method it was found to be 20,6 mg C $m^{-2}d^{-1}$ while with the SEPR-method it was 2,7 mg C $m^{-2}d^{-1}$ at station Svartnes in October. The low estimates with the SEPR-method is due to low occurrence of females with eggs, while the temperature-method don't take this into account. It is however argued that the temperature-dependent method overestimates production. For this method, temperature is the main driver for production. This is not a wrong assumption per se, but it can be argued that this is an over simplification as other factors such as food availability also regulates production (Madsen et al., 2008). In this study it was decided to put more focus on the secondary production estimated on SEPR, as this estimate reflects both the effects on *in situ* temperature and food availability. In December, March and April, secondary production was either low (< 0,1 mg C $m^{-2}d^{-1}$) or zero except for station Alta in April where secondary production was 0,12 mg C $m^{-2}d^{-1}$. In August and October secondary production was substantially higher in comparison to the winter and

spring months, where high proportion of CI – CIII copepodites and egg-carrying females was found (Appendix C fig. 1). It was during these two months that it was clear that station Svartnes had the highest secondary production, as the summed-up estimates found during these two months at this location (3,2 mg C $m^{-2}d^{-1}$) accounted for 60 % of the total secondary production found in this study. Besides Svartnes, relatively high estimates were found in outer Porsangerfjord (0,77 mg C $m^{-2}d^{-1}$), but is still comparatively lesser value than what was found in Balsfjord.

The seasonal pattern of *O. similis* production being highest during summer-autumn and low during winter has also been observed in other studies from high latitude systems (Dvoretsky and Dvoretsky, 2009; Madsen et al., 2008). A study by Nielsen and Andersen (2002), reported *O. similis s*econdary production to range from 2,9 to 3,8 mg C m^{-2} d^{-1} in July. At the same time, secondary production of *Calanus finmarchicus* was between 5,3 and up to 43 mg C m^{-2} d^{-1} in the same study. Madsen et al. (2008) shows in his study on annual population development and production by small copepod species in Disko Bay (Western Greenland), how big difference there is between smaller and larger copepod species in terms of productivity. The integrated annual secondary production between small copepods (*Acartia longiremis, Pseudocalanus* spp*., Oithona* spp., *Oncea* spp., *Microsotella* spp. and *Microcalanus* spp.) and large copepods (*Calanus finmarchicus, C. glacialis* and *C. hyperboreus*) species were compared, and the secondary production was calculated with the same SEPR based method as described in the present study. The total integrated annual secondary production for both of these group was estimated to 5,6 g C m^{-2} y^{-1} and the small copepod species constituted only 4 % of the total copepod community secondary production. It is shown here that the productivity of small copepods is low compared to the large copepods in Disko Bay. Despite this, small copepod species such as *O. similis* is not dependent on high Chla *a* concentration in order to reach high production rates like *Calanus* spp (Bunker and Hirst, 2004). Instead, *O. similis* can maintain reproduction in cold environments where Chl *a* concentration is either very low over a longer period and/or when it is continually low and have continuous reproduction year-round when other species cannot. This trait is not something that should be neglected, as *O. similis* can continuously contribute in terms of secondary production to the ecosystem and food web in high latitudes. There are many factors that regulates secondary production in zooplankton, but

temperature is perhaps the most important factor in the sub-Arctic and Arctic. *O. similis* have high abundance in the arctic throughout the year, but low temperatures reduce productivity during winter. But it has been argued since *O. similis*, and other cyclopoid copepods, are morphologically and anatomically less specialized than calanoids, they are able to adapt to a wider range of habitats and may maintain populations under more disadvantageous conditions (Nakamura and Turner, 1997; Dvoretsky and Dvoretsky, 2009a). *O. similis* can survive and remain active during the winter, feeding on available microzooplankton and microbes allowing it to maintain a stable population abundance and biomass during the winter while overwintering copepods are absent. In Balsfjord, Altafjord and Porsangerfjord, temperature is probably the main factor regulating *O. similis* egg production rate. Comparing the annual secondary production between the fjords, outer Porsangerfjord and Balsfjord are the areas that stands out where the production was estimated to be > 1 g C m^{-2} y^{-1}. Central Porsangerfjord and Altafjord had similar values (0,92 and 0,97 g C m^{-2} y^{-1}, respectively) and were close to 1 g C m^{-2} y^{-1}, but the estimates for inner Porsangerfjord were under half as much as in these two areas (0,43 g C m^{-2} y^{-1}). The outer areas of Porsangerfjord are generally warmer and are more affected by Atlantic water, whilst inner parts of Porsangerfjord is sheltered, generally colder and is described as being a true arctic marine environment. The inner parts of Balsfjord is also sheltered but is characterized as a fjord with a high range in temperature and salinity when comparing hydrography between summer and winter (Mankettikkara, 2013). (Coyle and Pinchuk, 2003) *O. similis* is probably more productive in areas of the coastal zone of northern Norway that have hydrographical characteristics of being generally warmer throughout the year. It has been predicted that a future scenario where the sea surface temperature has increased by 1-2 °C in the sub-Arctic/Arctic marine ecosystem, smaller copepod species such as *O. similis* will play a more important ecological role (Hunsicker et al., 2013). Based on the experimental work on egg-hatching rate and what was observed in the field, *O. similis* will likely benefit if the ocean gets warmer as both seasonal SEPR and in turn secondary production will potentially increase. It has also been predicted in such a scenario, that there will be an gradual shift towards smaller primary producers in the sub-Arctic/Arctic as a result of a warmer ocean (Li et al., 2009; Morán et al., 2010). If this is the case, *O. similis* will play a crucial trophic role in the marine food web by having a significant grazing impact on primary producers and in the structuring of marine food-webs in the sub-Arctic/Arctic.

6. Conclusion

This study reveals that there is great seasonal variation in terms of abundance, biomass and stage composition between the small copepod species *Oithona similis, Microsetella norvegica* and *Microcalanus* spp. in Balsfjord, Altafjord and Porsangerfjord. Despite this, it was discovered these species were active year-round in the fjords, even during winter, and all the copepodite stages for each specie were present in all the sample months. From an ecological perspective this feature is of great importance. If these small copepod species is capable of sustaining high abundance year-round due to their reproductive and feeding strategies, they likely can have significant impacts on the pelagic food chain and ecosystem structure in Balsfjord, Altafjord and Porsangerfjord. Additionally, they may be important to the cycling of organic material during the winter months when the larger copepod species are absent in the water column. Since this study only covered the population dynamics of *O. similis, M. norvegica* and *Microcalanus* spp. over five months, further research is required.

Temperature strongly influences *O. similis* egg hatching rate, hatching time and productivity. This is further reflected in seasonal the specific egg production rate, where this rate was lowest during cold months and highest during warm months in the three sub-Arctic fjords. The overall annual secondary production of *O. similis* is low compared to *Calanus* spp., but the fact that *O. similis* can uphold secondary production year-round is an important ecological trait. This means that this specie can serve as a steady food source throughout the year for predatory zooplankton, fish larvae and other planktivores. It is speculated that in a future scenario where the sea surface temperature increases, and small phytoplankton cells constitutes the main primary producers in the sub-Arctic/Arctic, *O. similis* seasonal and annual secondary production will likely increase. Experimentally determining the temperature-dependent egg hatching rate is a suitable method to determine seasonal SEPR and annual secondary production, that can be used to evaluate the importance of small copepod species. Estimating secondary production to more uknown species is crucial and further work would be to conduct egg experiments for *M. norvegica* and *Microcalanus* spp. Very few experimental production studies have been done on these species and therefore necessary to conduct in order to evaluate their productivity under various abiotic conditions.

7. References

Antonsen, M.T. (2014). Annual population dynamics of the small harpacticoid copepod Microsetella norvegica in a high latitude fjord (Balsfjord, Northern Norway).

Archer, S.D., Verity, P.G., and Stefels, J. (2000). Impact of microzooplankton on the progression and fate of the spring bloom in fjords of northern Norway. Aquat. Microb. Ecol. *22*, 27–41.

Arendt, K.E., Juul-Pedersen, T., Mortensen, J., Blicher, M.E., and Rysgaard, S. (2013). A 5-year study of seasonal patterns in mesozooplankton community structure in a sub-Arctic fjord reveals dominance of Microsetella norvegica (Crustacea, Copepoda). J. Plankton Res. *35*, 105–120.

Ashjian, C.J., Campbell, R.G., Welch, H.E., Butler, M., and Van Keuren, D. (2003a). Annual cycle in abundance, distribution, and size in relation to hydrography of important copepod species in the western Arctic Ocean. Deep-Sea Res. Part -Oceanogr. Res. Pap. *50*, 1235–1261.

Atkinson, A. (1998). Life cycle strategies of epipelagic copepods in the Southern Ocean. J. Mar. Syst. *15*, 289–311.

Auel, H., and Hagen, W. (2002). Mesozooplankton community structure, abundance and biomass in the central Arctic Ocean. Mar. Biol. *140*, 1013–1021.

Barthel, K., Noji, T., and Noji, C. (1995). Zooplankton Dynamics During the Onset of Winter in a Northern Norwegian Fjord - Vertical-Distribution and Metabolic-Activity in Relation to Phytoplankton and Sedimentation. Sarsia *80*, 23–32.

Berge, J., Daase, M., Renaud, P.E., Ambrose, W.G., Darnis, G., Last, K.S., Leu, E., Cohen, J.H., Johnsen, G., Moline, M.A., et al. (2015). Unexpected Levels of Biological Activity during the Polar Night Offer New Perspectives on a Warming Arctic. Curr. Biol. *25*, 2555–2561.

Blaxter, J. H., Douglas, B., Tyler, P. A., & Mauchline, J. (1998). *The biology of calanoid copepods* (Vol. 33). Academic Press.

Böttjer, D., Morales, C.E., and Bathmann, U. (2010). Trophic role of small cyclopoid copepod nauplii in the microbial food web: a case study in the coastal upwelling system off central Chile. Mar. Biol. *157*, 689–705.

Bunker, A.J., and Hirst, A.G. (2004). Fecundity of marine planktonic copepods: global rates and patterns in relation to chlorophyll a, temperature and body weight. Mar. Ecol. Prog. Ser. *279*, 161–181.

Calbet, A., and Agustí, S. (1999). Latitudinal changes of copepod egg production rates in Atlantic waters: temperature and food availability as the main driving factors. Mar. Ecol. Prog. Ser. *181*, 155–162.

Calbet, A., and Saiz, E. (2005). The ciliate-copepod link in marine ecosystems. Aquat. Microb. Ecol. *38*, 157–167.

Castellani, C., Irigoien, X., Harris, R.P., and Lampitt, R.S. (2005). Feeding and egg production of Oithona similis in the North Atlantic. Mar. Ecol. Prog. Ser. *288*, 173–182.

Clarke, A., and Peck, L. (1991). The Physiology of Polar Marine Zooplankton. Polar Res. *10*, 355–369.

Conover, R.J., and Huntley, M. (1991). Copepods in ice-covered seas—Distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. J. Mar. Syst. *2*, 1–41.

Conway, D.V.P. (2012). Identification of the copepodite developmental stages of twenty-six North Atlantic copepods. Occasional Publication of the Marine Biological Association No. 21 (revised edition).

Cornwell, L.E., Findlay, H.S., Fileman, E.S., Smyth, T.J., Hirst, A.G., Bruun, J.T., McEvoy, A.J., Widdicombe, C.E., Castellani, C., Lewis, C., (2018). Seasonality of Oithona similis and Calanus helgolandicus reproduction and abundance: contrasting responses to environmental variation at a shelf site. J. Plankton Res.

Coyle, K.O., and Pinchuk, A.I. (2003). Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000. Fish. Oceanogr. *12*, 327–338.

Davis, C. C. (1976). Overwintering strategies of common planktic copepods in some North Norway fjords and sounds. *Astarte*, *9*(2), 37-42.

Degerlund, M., and Eilertsen, H.C. (2010). Main Species Characteristics of Phytoplankton Spring Blooms in NE Atlantic and Arctic Waters (68–80° N). Estuaries Coasts *33*, 242–269.

Digby, P. (1954). The Biology of the Marine Planktonic Copepods of Scoresby-Sound, East Greenland. J. Anim. Ecol. *23*, 298–338.

Drif, K., Hirst, A.G., and Hay, S. (2010). Seasonal abundance and egg production rates of Oithona similis and Pseudocalanus elongatus in the northern North Sea: a first comparison of egg-ratio and incubation methods. Mar. Ecol. Prog. Ser. *415*, 159–175.

Dugas, J., and Koslow, J. (1984a). Microsetella-Norvegica - a Rare Report of a Potentially Abundant Copepod. Mar. Biol. *84*, 131–134.

Dugas, J.C., and Koslow, J.A. (1984b). Microsetella norvegica: a rare report of a potentially abundant copepod on the Scotian Shelf. Mar. Biol. *84*, 131–134.

Dvoretsky, V.G., and Dvoretsky, A.G. (2009b). Life cycle of Oithona similis (Copepoda: Cyclopoida) in Kola Bay (Barents Sea). Mar. Biol. *156*, 1433–1446.

Eilertsen, H.C., and Degerlund, M. (2010). Phytoplankton and light during the northern high-latitude winter. J. Plankton Res. *32*, 899–912.

Eilertsen, H.C., and Skarðhamar, J. (2006). Temperatures of north Norwegian fjords and coastal waters: Variability, significance of local processes and air–sea heat exchange. Estuar. Coast. Shelf Sci. *67*, 530–538.

Gallienne, C.P., and Robins, D.B. (2001). Is Oithona the most important copepod in the world's oceans? J. Plankton Res. *23*, 1421–1432.

Grønvik, S., and Hopkins, C. (1984). Ecological Investigations of the Zooplankton Community of Balsfjorden, Northern Norway - Generation Cycle, Seasonal Vertical-Distribution, and Seasonal-Variations in Body-Weight and Carbon and Nitrogen-Content of the Copepod Metridia-Longa (lubbock). J. Exp. Mar. Biol. Ecol. *80*, 93–107.

Hansen, P.J., Bjørnsen, P.K., and Hansen, B.W. (1997). Zooplankton grazing and growth: scaling within the 2-2,000- mu m body size range. Limnol. Oceanogr.

Harris, R., Wiebe, P., Lenz, J., Skjoldal, H.-R., and Huntley, M. (2000). ICES Zooplankton Methodology Manual (Elsevier).

Hirche, H.J., and Kosobokova, K.N. (2011). Winter studies on zooplankton in Arctic seas: the Storfjord (Svalbard) and adjacent ice-covered Barents Sea. Mar. Biol. *158*, 2359–2376.

Holste, L., and Peck, M.A. (2006b). The effects of temperature and salinity on egg production and hatching success of Baltic Acartia tonsa (Copepoda : Calanoida): a laboratory investigation. Mar. Biol. *148*, 1061–1070.

Hopcroft, R.R., Clarke, C., Nelson, R.J., and Raskoff, K.A. (2005a). Zooplankton communities of the Arctic's Canada Basin: the contribution by smaller taxa. Polar Biol. *28*, 198–206.

Humes, A.G. (1985). Cnidarians and Copepods: A Success Story. Trans. Am. Microsc. Soc. *104*, 313–320.

Hunsicker, M.E., Ciannelli, L., Bailey, K.M., Zador, S., and Stige, L.C. (2013). Climate and Demography Dictate the Strength of Predator-Prey Overlap in a Subarctic Marine Ecosystem. PLOS ONE *8*, e66025.

Huntley, M.E. (1992). Temperature-Dependent Production of Marine Copepods: A Global Synthesis. Am. Nat. *140*, 201–242.

Huys, R., and Boxshall, G. (1991). Evolutionary Trends within the Copepoda. Copepod Evol. Ray Soc. Ed 169 Lond. 315–370.

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

Kiørboe, T. (2011). What makes pelagic copepods so successful? J. Plankton Res. *33*, 677–685.

Kiørboe, T., and Sabatini, M. (1994). Reproductive and Life-Cycle Strategies in Egg-Carrying Cyclopoid and Free-Spawning Calanoid Copepods. J. Plankton Res. *16*, 1353–1366.

Kjellerup, S., and Kiørboe, T. (2012). Prey detection in a cruising copepod. Biol. Lett. *8*, 438–441.

Koski, M., Kiørboe, T., and Takahashi, K. (2005). Benthic life in the pelagic: Aggregate encounter and degradation rates by pelagic harpacticoid copepods. Limnol. Oceanogr. *50*, 1254–1263.

Koski, M., Møller, E.F., Maar, M., and Visser, A.W. (2007). The fate of discarded appendicularian houses: degradation by the copepod, Microsetella norvegica, and other agents. J. Plankton Res. *29*, 641–654.

Koski, M., Swalethorp, R., Kjellerup, S., and Nielsen, T.G. (2014). The mystery of Microsetella: combination of sac- and broadcast-spawning in an Arctic fjord. J. Plankton Res. *36*, 259–264.

Kosobokova, K.N., and Hopcroft, R.R. (2010). Diversity and vertical distribution of mesozooplankton in the Arctic's Canada Basin. Deep Sea Res. Part II Top. Stud. Oceanogr. *57*, 96–110.

Kosobokova, K.N., Hopcroft, R.R., and Hirche, H.-J. (2011). Patterns of zooplankton diversity through the depths of the Arctic's central basins. Mar. Biodivers. *41*, 29–50.

Krause, M., and Trahms, J. (1982). Vertical distribution of copepods (all developmental stages) and other zooplankton during spring bloom in the fladen ground area of the north sea. Neth. J. Sea Res. *16*, 217–230.

Krsinic, F., and Grbec, B. (2012). Spatial distribution of copepod abundance in the epipelagic layer of the south Adriatic Sea. Acta Adriat. *53*, 57–70.

Lagadeuc, Y., Bouté, M., and Dodson, J.J. (1997). Effect of vertical mixing on the vertical distribution of copepods in coastal waters. J. Plankton Res. *19*, 1183–1204.

Legendre, L., and Rassoulzadegan, F. (1995). Plankton and nutrient dynamics in marine waters. Ophelia *41*, 153–172.

Li, W.K.W., McLaughlin, F.A., Lovejoy, C., and Carmack, E.C. (2009). Smallest Algae Thrive As the Arctic Ocean Freshens. Science *326*, 539–539.

Madsen, S.D., Nielsen, T.G., and Hansen, B.W. (2001). Annual population development and production by Calanus finmarchicus, C-glacialis and C-hyperboreus in Disko Bay, western Greenland. Mar. Biol. *139*, 75–93.

Madsen, S.D., Nielsen, T.G., and Hansen, B.W. (2008a). Annual population development and production by small copepods in Disko Bay, western Greenland. Mar. Biol. *155*, 63–77.

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

McAllister, C.D. (1969). Aspects of Estimating Zooplankton Production from Phytoplankton Production. J. Fish. Res. Board Can. *26*, 199–220.

Morales, C.E., Bedo, A., Harris, R.P., and Tranter, P.R.G. (1991). Grazing of copepod assemblages in the north-east Atlantic: the importance of the small size fraction. J. Plankton Res. *13*, 455–472.

Morán, X.A.G., López-Urrutia, Á., Calvo-Díaz, A., and Li, W.K.W. (2010). Increasing importance of small phytoplankton in a warmer ocean. Glob. Change Biol. *16*, 1137–1144.

Nakamura, Y., and Turner, J.T. (1997). Predation and respiration by the small cyclopoid copepod Oithona similisr: How important is feeding on ciliates and heterotrophic flagellates? J. Plankton Res. *19*, 1275–1288.

Nakken, O. (1998). Past, present and future exploitation and management of marine resources in the Barents Sea and adjacent areas. Fish. Res. *37*, 23–35.

Narcy, F., Gasparini, S., Falk-Petersen, S., and Mayzaud, P. (2009). Seasonal and individual variability of lipid reserves in Oithona similis (Cyclopoida) in an Arctic fjord. Polar Biol. *32*, 233–242.

Nielsen, T.G., and Andersen, C. (2002). Plankton community structure and production along a freshwater-influenced Norwegian fjord system. Mar. Biol. *141*, 707–724.

Nielsen, T.G., and Sabatini, M. (1996). Role of cyclopoid copepods Oithona spp in North Sea plankton communities. Mar. Ecol. Prog. Ser. *139*, 79–93.

Nielsen, T.G., Moller, E.F., Satapoomin, S., Ringuette, M., and Hopcroft, R.R. (2002). Egg hatching rate of the cyclopoid copepod Oithona similis in arctic and temperate waters. Mar. Ecol. Prog. Ser. *236*, 301–306.

Norrbin, M.F., (1991). Gonad Maturation as an Indication of Seasonal Cycles for Several Species. Polar Res. *10*, 421–432.

Norrbin, M.F., (1994). Seasonal Patterns in Gonad Maturation, Sex-Ratio and Size in Some Small, High-Latitude Copepods - Implications for Overwintering Tactics. J. Plankton Res. *16*, 115–131.

Norrbin, M.F., Eilertsen, H.C., and Degerlund, M. (2009). Vertical distribution of primary producers and zooplankton grazers during different phases of the Arctic spring bloom. Deep-Sea Res. Part Ii-Top. Stud. Oceanogr. *56*, 1945–1958.

Pasternak, A., Arashkevich, E., Riser, C.W., Ratkova, T., and Wassmann, P. (2000). Seasonal variation in zooplankton and suspended faecal pellets in the subarctic Norwegian Balsfjorden, in 1996. Sarsia *85*, 439–452.

Pasternak, A.F., Arashkevich, E.G., Grothe, U., Nikishina, A.B., and Solovyev, K.A. (2013). Different effects of increased water temperature on egg production of Calanus finmarchicus and C-glacialis. Oceanology *53*, 547–553.

Peterson, W.T., Tiselius, P., and Kiørboe, T. (1991). Copepod egg production, moulting and growth rates, and secondary production, in the Skagerrak in August 1988. J. Plankton Res. *13*, 131–154.

Priou, P. (2015). Associations between herbivorous zooplankton, phytoplankton and hydrography in Porsangerfjord, northern Norway.

Rysgaard, S., Nielsen, T.G., and Hansen, B.W. (1999). Seasonal variation in nutrients, pelagic primary production and grazing in a high-Arctic coastal marine ecosystem, Young Sound, Northeast Greenland. Mar. Ecol. Prog. Ser. *179*, 13–25.

Sabatini, M., and Kiørboe, T. (1994). Egg production, growth and development of the cyclopoid copepod Oithona similis. J. Plankton Res. *16*, 1329–1351.

Sakshaug, E. (2004). Primary and Secondary Production in the Arctic Seas. In The Organic Carbon Cycle in the Arctic Ocean, (Springer, Berlin, Heidelberg), pp. 57–81.

Sars, G.O. (Georg O. (1895). An account of the Crustacea of Norway, with short descriptions and figures of all the species (Christiania and Copenhagen, A. Cammermeyer).

Schnackschiel, S., and Mizdalski, E. (1994). Seasonal-Variations in Distribution and Population-Structure of Microcalanus-Pygmaeus and Ctenocalanus-Citer (copepoda, Calanoida) in the Eastern Weddell Sea, Antarctica. Mar. Biol. *119*, 357–366.

Sommer, U., Stibor, H., Katechakis, A., Sommer, F., and Hansen, T. (2002). Pelagic food web configurations at different levels of nutrient richness and their implications for the ratio fish production:primary production. In Sustainable Increase of Marine Harvesting: Fundamental Mechanisms and New Concepts, (Springer, Dordrecht), pp. 11–20.

Svendsen, H. (1995). Physical oceanography of coupled fjord-coast systems in northern Norway with special focus on frontal dynamics and tides (Amsterdam: Elsevier Science Publ B V).

Svensen, C., Seuthe, L., Vasilyeva, Y., Pasternak, A., and Hansen, E. (2011). Zooplankton distribution across Fram Strait in autumn: Are small copepods and protozooplankton important? Prog. Oceanogr. *91*, 534–544.

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

Turner, J.T. (2004). The importance of small planktonic copepods and their roles in pelagic marine food webs. Zool. Stud. *43*, 255–266.

Uye, S., Aoto, I., and Onbe, T. (2002). Seasonal population dynamics and production of Microsetella norvegica, a widely distributed but little-studied marine planktonic harpacticoid copepod. J. Plankton Res. *24*, 143–153.

Ward, P., and Hirst, A.G. (2007). Oithona similis in a high latitude ecosystem: abundance, distribution and temperature limitation of fecundity rates in a sac spawning copepod. Mar. Biol. *151*, 1099–1110.

Wassmann, P., Svendsen, H., Keck, A., and Reigstad, M. (1996). Selected aspects of the physical oceanography and particle fluxes in fjords of northern Norway. J. Mar. Syst. *8*, 53–71.

Wassmann, P., Reigstad, M., Øygarden, S., and Rey, F. (2000). Seasonal variation in hydrography, nutrients, and suspended biomass in a subarctic fjord: applying hydrographic features and biological markers to trace water masses and circulation significant for phytoplankton production. Sarsia *85*, 237–249.

Wend-Heckmann, B., Niehoff, B., Niehoff, B., and Boersma, M. (2013). Oithona similis (Copepoda: Cyclopoida) - a cosmopolitan species? Staats- und Universitätsbibliothek Bremen.

Wiborg, K. F. (1954). Investigations on Zooplankton in Coastal and Offshore Waters of Western and Northwestern Norway-With Special Reference to the Copepods.

Zamora-Terol, S., Nielsen, T.G., and Saiz, E. (2013). Plankton community structure and role of Oithona similis on the western coast of Greenland during the winter-spring transition. Mar. Ecol. Prog. Ser. *483*, 85–102.

Zamora-Terol, S., Kjellerup, S., Swalethorp, R., Saiz, E., and Nielsen, T.G. (2014). Population dynamics and production of the small copepod Oithona spp. in a subarctic fjord of West Greenland. Polar Biol. *37*, 953–965.

Appendix A

Collection of tables showing integrated abundance (ind. m^{-2}) and biomass (mg C m^{-2}) for O. similis, M. norvegica and Microcalanus spp. and each of their copepodite stage(s) found in Balsfjord, Altafjord and Porsangerfjord in December. The copepods were sampled with a WP-2 net with 64 µm mesh-size, in the months December (1), March (2), April (3), August (4) and October (5). Standard sample depths were 100 – 0 m, but deeper samples (bottom – 100 m) was also taken where possible.

1) December

Specie	Stage	Outer Porsangerfjord 100 - 0 m	Central Porsangerfjord 100-0 m	Inner Porsangerfjord 100-0 m	Altafjord 350 - 98 m	Altafjord 100-0 m	Balsfjord 170-100 m	Balsfjord 100 -0
Abundance (ind. m^{-2})								
Oithona similis	Female with eggs	784	392	784	0	0	0	0
	Females w/o eggs	18036	25486	43914	48718	8324	54892	99590
	Males	784	784	784	2365	545	2353	17252
	C IV – CV	24309	19212	62734	16791	6379	25878	11763
	C I - C III	4705	6273	12547	2128	1556	784	0
Microsotella	Female with eggs	0	0	0	0	0	0	0
	Females w/o eggs	81554	67439	119194	5990	19800	355117	746531
	Males	15683	32935	35288	1634	3921	44810	128604
	C IV - CV	0	0	46266	233	980	63854	62734
	C I - C III	0	0	3921	0	0	0	0
Microcalanus	Females	5097	4444	25093	17644	3968	11763	16860
	Males	392	1046	784	784	78	523	1176
	C IV - CV	5685	6273	14115	4705	311	1830	1568
	C I - C III	392	1830	0	0	0	523	0
Biomass (mg C m^{-2})								
Oithona similis	Female with eggs	0,5	0,3	1,3	0,0	0,0	0,0	0,0
	Females w/o eggs	11,0	15,6	67,8	49,5	5,1	33,6	61,0
	Males	0,3	0,3	0,9	1,7	0,2	1,0	7,6
	C IV - CV	9,6	7,6	62,5	11,0	2,5	10,2	4,6
	C I - C III	0,9	1,1	5,8	0,6	0,3	0,1	0,0
Microsotella	Female with eggs	0,0	0,0	0,0	0,0	0,0	0,0	0,0
	Females w/o eggs	41,2	34,0	151,6	7,6	10,0	125,5	376,8
	Males	7,0	14,8	39,9	1,8	1,8	14,1	57,7
	C IV - CV	0,0	0,0	44,1	0,2	0,4	16,9	23,7
	C I - C III	0,0	0,0	1,7	0,0	0,0	0,0	0,0
Microcalanus	Females	3,5	3,1	17,5	12,3	2,8	8,2	11,7
	Males	0,3	0,7	0,5	0,5	0,1	0,3	0,8
	C IV - CV	2,5	2,8	6,2	2,1	0,1	0,8	0,7
	C I - C III	0,1	0,3	0,0	0,0	0,0	0,1	0,0

2) March

Specie	Stage	Outer Porsangerfjord 100 - 0 m	Central Porsangerfjord 100-0 m	Inner Porsangerfjord 100-0 m	Altafjord 100-0 m	Balsfjord 170-100 m	Balsfjord 100 -0
Abundance (ind. m^{-2})							
Oithona similis	Female with eggs	0	0	0	0	2509	0
	Females w/o eggs	8038	12808	117103	12808	60852	93473
	Males	1666	1699	13592	784	6273	7528
	C IV - CV	3137	1307	4182	3137	2509	6273
	C I - C III	1764	653	0	784	0	627
Microsotella	Female with eggs	0	0	0	0	0	0
	Females w/o eggs	9802	13592	721437	9149	632355	1257810
	Males	2843	5097	621063	2265	206394	225841
	C IV - CV	1764	2353	125467	1046	0	0
	C I - C III	490	0	0	0	0	0
Microcalanus	Females	1666	1830	18193	2614	22506	23211
	Males	196	392	3137	261	2196	3764
	C IV - CV	392	653	5646	174	1647	2509
	C I - C III	3137	3790	12547	1481	10978	6273
Biomass (mg C m^{-2})							
Oithona similis	Female with eggs	0,0	0,3	0,0	0,0	1,2	1,3
	Females without eggs	4,9	7,8	71,7	7,8	26,1	57,2
	Males	0,7	0,7	6,0	0,3	1,9	3,3
	C IV - CV	1,2	0,5	1,7	1,2	0,7	2,5
	C I - C III	0,3	0,1	0,0	0,1	0,0	0,1
Microsotella	Female with eggs	0,0	0,0	0,0	0,0	0,0	0,0
	Females w/o eggs	4,9	6,9	364,1	4,6	319,1	634,8
	Males	1,3	2,3	278,5	1,0	92,5	101,3
	C IV - CV	0,7	0,9	47,5	0,4	0,0	0,0
	C I - C III	0,1	0,0	0,0	0,0	0,0	0,0
Microcalanus	Females	1,2	1,3	12,7	1,8	15,7	16,2
	Males	0,1	0,3	2,1	0,2	1,5	2,5
	C IV - CV	0,2	0,3	2,5	0,1	0,7	1,1
	C I - C III	0,5	0,6	2,1	0,3	1,9	1,1

3) April

Specie	Stage	Outer Porsangerfjord 100 - 0 m	Central Porsangerfjord 100-0 m	Inner Porsangerfjord 100-0 m	Altafjord 200 - 100 m	Altafjord 100-0 m	Balsfjord 170-100 m	Balsfjord 100 -0
Abundance (ind. m^{-2})								
Oithona similis	Female with eggs	0	1680	392	7319	4033	1976	1098
	Females w/o eggs	7999	5825	23133	46005	18372	9222	6587
	Males	1882	1904	4705	8364	2465	659	768
	C IV - CV	5332	6721	10978	3137	896	1757	988
	C I - C III	2666	560	8234	1046	0	439	2086
Microsotella	Female with eggs	0	0	0	2875	32935	14272	220
	Females w/o eggs	42737	23917	382675	20911	127036	85083	9551
	Males	11370	9606	329352	15683	98806	37327	3403
	C IV - CV	5881	10390	17252	2353	3137	2196	1208
	C I - C III	2353	0	0	0	0	0	1537
Microcalanus	Females	3764	3137	3764	6796	9149	4391	3980
	Males	471	0	314	1568	2353	1098	1235
	C IV - CV	5176	4391	4862	523	3659	2333	686
	C I - C III	1568	1882	3137	4444	1046	412	1510
Biomass (mg C m^{-2})								
Oithona similis	Female with eggs	0,0	1,1	0,3	4,9	2,7	1,3	0,7
	Females w/o eggs	4,9	3,6	14,2	28,2	11,3	5,6	4,0
	Males	0,8	0,8	2,1	3,7	1,1	0,3	0,3
	C IV - CV	2,1	2,7	4,3	1,2	0,4	0,7	0,4
	C I - C III	0,5	0,1	1,5	0,2	0,0	0,1	0,4
Microsotella	Female with eggs	0,0	0,0	0,0	1,5	16,6	7,2	0,1
	Females w/o eggs	12,1	21,6	193,1	10,6	64,1	42,9	4,8
	Males	4,3	5,1	147,7	7,0	44,3	16,7	1,5
	C IV - CV	3,9	2,2	6,5	0,9	1,2	0,8	0,5
	C I - C III	0,0	0,4	0,0	0,0	0,0	0,0	0,3
Microcalanus	Females	2,6	2,2	2,6	4,7	6,4	3,1	2,8
	Males	0,3	0,0	0,2	1,0	1,6	0,7	0,8
	C IV - CV	2,3	1,9	2,1	0,2	1,6	1,0	0,3
	C I - C III	0,3	0,3	0,5	0,8	0,2	0,1	0,3

4) August

Specie	Stage	Outer Porsangerfjord 100 - 0 m	Central Porsangerfjord 100-0 m	Inner Porsangerfjord 100-0 m	Balsfjord 170-100 m	Balsfjord 100 -0
Abundance (ind. m^{-2})						
Oithona similis	Female with eggs	6273	7842	1568	0	3137
	Females w/o eggs	62734	53324	32412	6496	42345
	Males	13331	9410	4705	366	1568
	C IV - CV	44698	48619	13592	2928	22741
	C I - C III	24309	14115	4705	457	19604
Microsotella	Female with eggs	2353	3659	3137	0	7058
	Females w/o eggs	19212	23002	23525	10292	69791
	Males	14115	18820	8234	6038	23525
	C IV - CV	7450	12547	7450	549	3137
	C I - C III	10194	5751	5097	0	10194
Microcalanus	Females	6587	7580	5489	2676	8103
	Males	627	784	523	549	1046
	C IV - CV	7528	3137	5751	1372	3659
	C I - C III	1255	1568	4182	0	523
Biomass (mg C m^{-2})						
Oithona similis	Female with eggs	5,2	1,0	0,0	1,5	0,0
	Females w/o eggs	32,7	19,9	5,7	18,2	33,6
	Males	4,1	2,1	0,2	0,5	1,4
	C IV - CV	19,2	5,4	1,7	6,3	26,6
	C I - C III	2,6	0,9	0,1	2,5	15,5
Microsotella	Female with eggs	1,6	1,8	1,6	0,0	3,6
	Females w/o eggs	10,3	11,6	11,9	5,2	35,2
	Males	8,4	8,4	3,7	2,7	10,5
	C IV - CV	3,8	4,7	2,8	0,2	1,2
	C I - C III	2,3	1,0	0,9	0,0	1,7
Microcalanus	Females	1,8	5,3	3,8	1,9	5,6
	Males	0,3	0,5	0,3	0,4	0,7
	C IV - CV	1,7	1,4	2,5	0,6	1,6
	C I - C III	1,0	0,3	0,7	0,0	0,1

5) October

Specie	Stage	Outer Porsangerfjord 100 - 0 m	Central Porsangerfjord 100-0 m	Inner Porsangerfjord 100-0 m	Altafjord 390 - 100 m	Altafjord 100-0 m	Balsfjord 170-100 m	Balsfjord 100 -0
Abundance (ind. m^{-2})								
Oithona similis	Female with eggs	0	0	4705	4548	0	0	9410
	Females w/o eggs	54892	37640	64302	115979	25093	1830	36072
	Males	3137	1568	1568	2274	2353	366	6273
	C IV - CV	67439	73712	150561	81867	35288	4940	76849
	C I - C III	84690	51755	61165	27289	18036	3385	58029
Microsotella	Female with eggs	0	0	0	0	0	0	0
	Females w/o eggs	27446	94100	125467	27054	61165	11116	185064
	Males	25093	51755	26662	4548	6273	549	23525
	C IV - CV	13331	28230	14115	25015	20388	2058	17252
	C I - C III	36072	20388	4705	9096	14115	1647	4705
Microcalanus	Females	8155	8234	17775	42450	7842	2333	11763
	Males	941	1176	3137	7580	2509	0	0
	C IV - CV	7214	9802	10456	59126	5646	1647	8234
	C I - C III	0	392	2091	0	627	206	0
Biomass (mg C m^{-2})								
Oithona similis	Female with eggs	0,0	3,1	1,0	0,0	0,0	4,4	6,3
	Females w/o eggs	23,1	39,4	24,5	44,6	1,6	15,5	22,1
	Males	0,7	0,7	0,3	3,0	0,2	1,9	2,8
	C IV - CV	29,1	59,5	11,2	40,4	2,8	21,3	30,4
	C I - C III	9,5	11,2	1,7	9,6	0,9	7,4	10,6
Microsotella	Female with eggs	0,0	0,0	0,0	0,0	0,0	0,0	0,0
	Females w/o eggs	13,9	47,5	63,3	13,7	30,9	5,6	93,4
	Males	11,3	23,2	12,0	2,0	2,8	0,2	10,5
	C IV - CV	5,0	10,7	5,3	9,5	7,7	0,8	6,5
	C I - C III	6,1	3,4	0,8	1,5	2,4	0,3	0,8
Microcalanus	Females	5,7	5,7	12,4	29,6	5,5	1,6	8,2
	Males	0,6	0,8	2,1	5,1	1,7	0,0	0,0
	C IV - CV	3,2	4,3	4,6	26,0	2,5	0,7	3,6
	C I - C III	0,0	0,1	0,4	0,0	0,1	0,0	0,0

Appendix B

*Table showing anatomical differences in prosome, urosome and swimming leg development to M. norvegica, O. similis and Microcalanus spp. The morphology is based on identification keys provided by Blaxter et al. (1998), Conway, (2012)**;** Wend-Heckmann et al., (2013) .*

	Microsotella norvegica				*Oithona similis*				*Microcalanus spp.*			
Stage	Prosome	Urosome	Total somites	No. swimming legs	Prosome	Urosome	Total somites	No. Swimming legs	Prosome*	Urosome	Total somites	No. swimmig legs
CI	3	2	5	2 +1	3	2	5	2	-	2	2	2
CII	4	2	6	3 + 1	4	2	6	3 + 1	-	2	2	2
CIII	5	2	7	4 + 1	5	3	8	4	-	2	2	2
CIV	5	3	8	4 + 1	5	4	9	4	-	3	3	3
CV	5	3	8	5	5	4	9	4	-	4	4	4
Female	5	4	9	5	5	5	10	5	4	4	8	4
Male	5	5	10	5	5	6	11	5	4	5	9	5

**Prosome is described to be fused together in the developmental stages, so identifying Microcalanus spp. copepodite stages were based on length, urosome segments and nr. of swimming legs. Due to this, inaccuracies may have risen when identifying Microcalanus spp. developmental stages.*

Appendix C

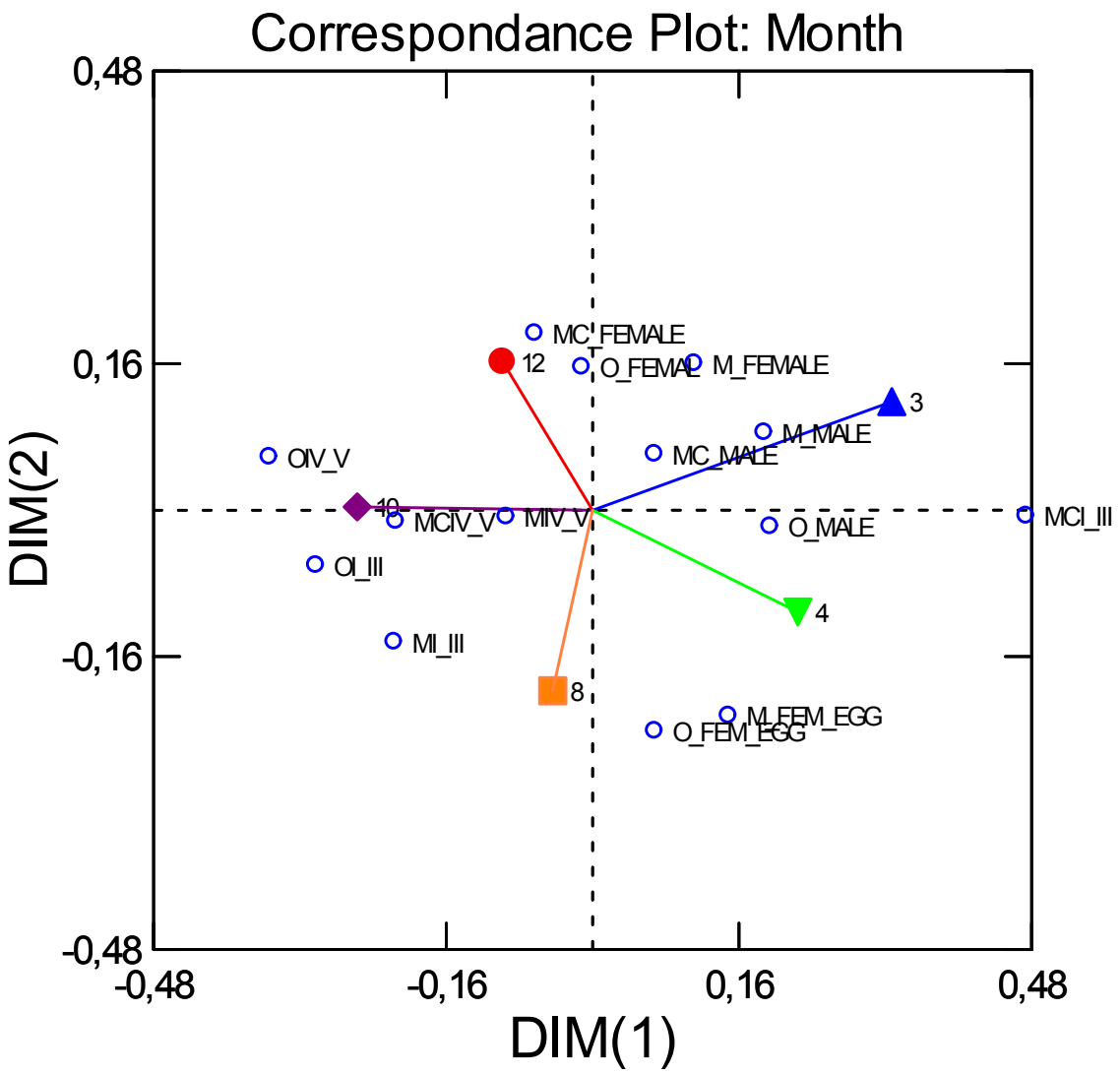


Fig 1: Correspondance analysis plot (CPA) of O. similis, M. norvegica and Microcalanus spp. and their stage distribution relative to the months December (12), March (3), April (4), August (8) and October (10) across Balsfjord, Altafjord and Porsangerfjord. Each copepodite stage for each species is displayed with different codes (blue symbol). The first letter in each code tells what specie it is (O = O. similis, M = M. norvegica and MC = Microcalanus spp.) *while the rest of the letters/symbols is copepodite stage. The plot is based on abundance data for each stage and specie that were ranked with Spearmans-ranked correlation method. DIM (1) explains 63 % of the variance in the data and DIM (2) 86 %.*

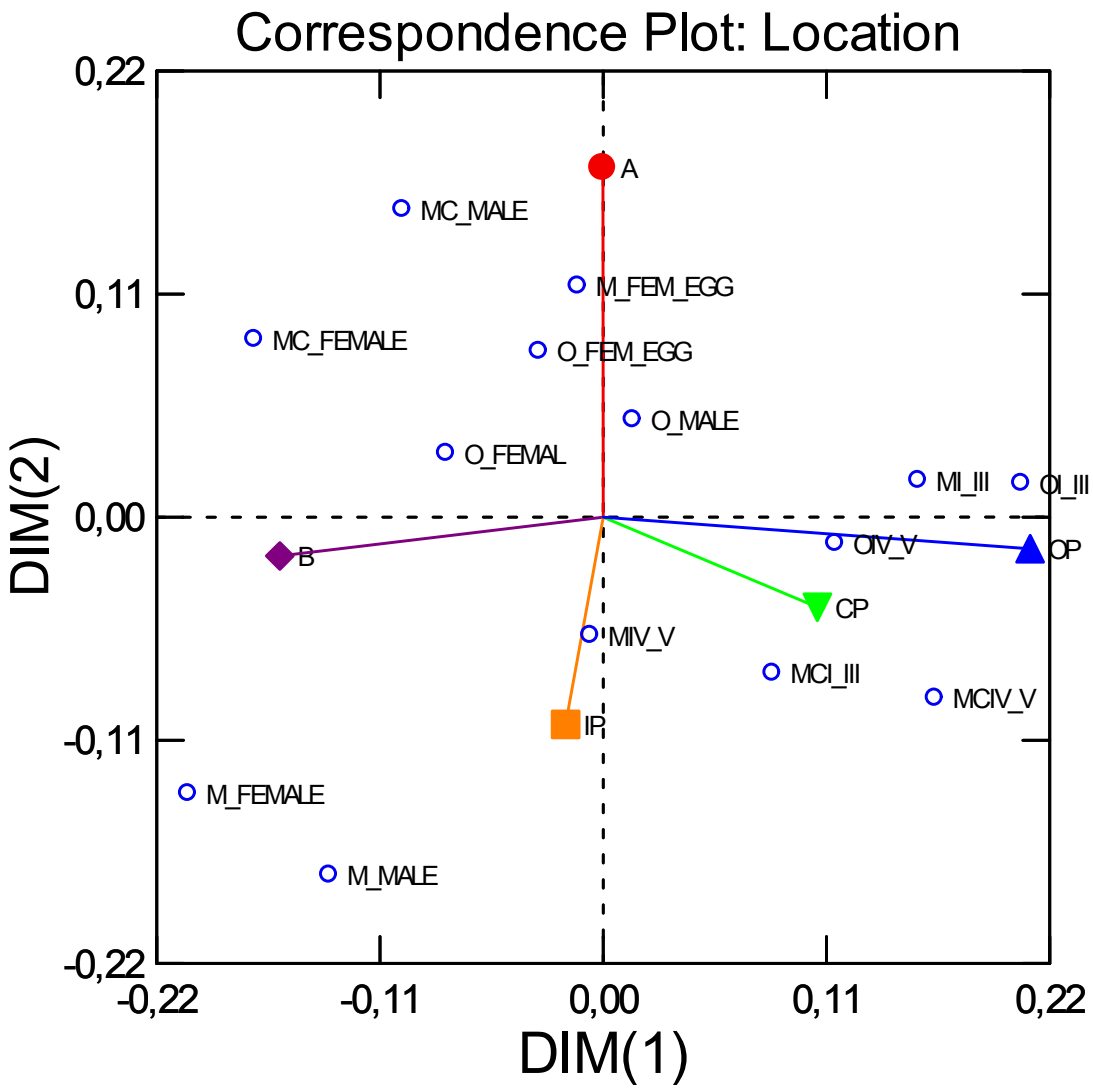


Fig 2: Correspondance analysis plot (CPA) of O. similis, M. norvegica and Microcalanus spp. and their stage distribution relative to sample station OP = P. outer, CP = P. central, IP = P. inner, A = Alta and B = Svartnes. . Each copepodite stage for each species is displayed with different codes (blue symbol). The first letter in each code tells what specie it is (O = O. similis, M = M. norvegica and MC = Microcalanus spp.) *while the rest of the letters/symbols is copepodite stage. The plot is based on abundance data for each stage and specie that were ranked with Spearmans-ranked correlation method. DIM (1) explains 53 % of the variance in the data and DIM (2)*