1   **Seasonal dynamics of meroplankton in a high-latitude fjord**

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3   Helena Kling Michelsen*[1], Camilla Svensen[1], Marit Reigstad[1], Einar Magnus Nilssen[1],

4   Torstein Pedersen[1]

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6   [1]Department of Arctic and Marine Biology, UiT the Arctic University of Norway, Tromsø,

7   Norway

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9   ***** Corresponding author: Helena.k.michelsen@uit.no

10   Faculty of Biosciences, Fisheries and Economics,

11   Department of Arctic and Marine Biology,

12   UiT the Arctic University of Norway, 9037 Tromsø, Norway.

Abstract

Knowledge on the seasonal timing and composition of pelagic larvae of many benthic invertebrates, referred to as meroplankton, is limited for high-latitude fjords and coastal areas. We investigated the seasonal dynamics of meroplankton in the sub-Arctic Porsangerfjord (70˚N), Norway, by examining their seasonal changes in relation to temperature, chlorophyll *a* and salinity. Samples were collected at two stations between February 2013 and August 2014. We identified 41 meroplanktonic taxa from eight phyla. Multivariate analysis indicated different meroplankton compositions in winter, spring, early summer and late summer. More larvae appeared during spring and summer, forming two peaks in meroplankton abundance. The spring peak was dominated by cirripede nauplii, and late summer peak was dominated by bivalve veligers. Moreover, spring meroplankton were the dominant component in the zooplankton community this season. In winter, low abundances and few meroplanktonic taxa were observed. Timing for a majority of meroplankton correlated with primary production and temperature. The presence of meroplankton in the water column through the whole year and at times dominant in the zooplankton community, suggests that they, in addition to being important for benthic recruitment, may play a role in the pelagic ecosystem as grazers on phytoplankton and as prey for other organisms.

Keywords: Benthic invertebrate larvae; recruitment; temporal change; zooplankton; Porsangerfjord; Norway

1. Introduction

Many benthic organisms have an indirect development, producing pelagic larvae, termed meroplankton, which go through several distinct phases before settling on the sea floor. Meroplanktonic larvae are important for benthic organisms, as their survival and ability to locate a suitable habitat for settlement determines the success of recruitment to the adult population. The balance between mortality and settlement is complex and may be influenced by temperature and salinity, transportation to unfavorable habitats, food availability and predation (Todd, 1998).

In tropical waters, meroplankton are present throughout the year, whereas a more pronounced seasonality is common at higher-latitudes (Giese and Pearse, 1977). Strong seasonal variability in environmental variables such as temperature, salinity, light availability and primary production characterize high-latitude coastal waters. These factors in turn influence reproduction, abundance and distribution of both permanent pelagic residents, holoplankton (Fossheim and Primicierio, 2008; Tande, 1989), and meroplankton (Morgan, 1995). For benthic invertebrates, changes in photoperiod and primary production are thought to be the strongest spawning cues, with temperature and salinity acting as additional triggers (Olive, 1995). Thus, the spawning times of benthic organisms and the resulting composition of meroplanktonic communities vary through the year.

Meroplanktonic larvae can spend intervals from hours to years in the upper water column, where a wide range of predators may prey upon them (Thorson, 1950). During their time there meroplankton display two nutritional modes: some are planktotrophic, feeding as herbivores, carnivores or detritivores, while others are lecithotrophic, not feeding but surviving on yolk and lipid supplied in the egg (Mileikovsky, 1971). A majority of planktotrophic larvae feed on phytoplankton and are dependent on locating food for survival. Thus, spawning just prior to or during the spring and summer phytoplankton bloom provides the best feeding condition for such larvae. High densities of meroplankton have been found in high-latitude coastal waters at the onset of the phytoplankton spring bloom (Kuklinski et al., 2013; Smidt, 1979; Stübner et al., 2016). In contrast, lecithotrophic larvae are not dependent on being spawned during the food-rich periods of spring and summer.

Since meroplankton are drifters, their horizontal distributions are primarily shaped by local adult populations and advective dispersal (Mileikovsky, 1968). Dispersal to new areas not only allows population expansion to suitable new sites, it ensures that sessile adults have the opportunity of exchanging genetic material with other populations (Scheltema, 1986). The

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68 distance a propagule may disperse depends on current speeds and directions and on the

69 vertical swimming behaviour and developmental time of individuals before settlement

70 (Scheltema, 1986).

71   Strong latitudinal trends in benthic reproductive strategies were observed by early polar

72 researchers (Thomson, 1876; Thorson, 1936, 1946, 1950) and led to the formulation of one of

73 the main paradigms in meroplankton research, Thorsons's rule. It states that the number of

74 benthic adults producing non-pelagic larvae increases with latitude and depth (Mileikovsky,

75 1971). The paradigm has received considerable attention, resulting in a growing number of

76 contradictory observations of high proportions of pelagic development at both poles (e.g.

77 Clarke et al., 1992; Fetzer and Arntz, 2008; Pearse, 1994; Stanwell-Smith et al., 1999). Today

78 the paradigm receives less support and has been modified to include the observation of higher

79 proportions of lecithotrophic pelagic larvae at high-latitudes (Clarke 1992; Marshall et al.,

80 2012). However, since some meroplanktonic larvae are found in high abundances during

81 spring and summer they could, depending on their nutritional mode, be important

82 phytoplankton grazers as well as prey in the water column.

83   Studies of seasonal changes in zooplankton at high-latitudes have mainly focused on

84 holoplankton, while meroplankton are typically registered to the level of phylum (e.g.

85 Arashkevich et al., 2002; Hopkins et al., 1989). A modest number of studies have focused on

86 the year around seasonality of meroplankton within Arctic (Smidt, 1979; Falk-Petersen,

87 1982a; Kuklinski et al., 2013; Silberberger et al., 2016; Stübner et al., 2016; Thorson, 1936)

88 and Antarctic waters (Bowden et al., 2009; Freire et al., 2006; Sewell and Jury, 2011;

89 Stanwell-Smith et al., 1999). More short-term surveys looking at the spatial distribution,

90 abundance, biomass and composition in connection to environmental and biological

91 conditions have been conducted in the Arctic (e.g. Andersen, 1984; Clough et al., 1997;

92 Fetzer, 2003; Mileikovsky, 1968, 1970; Schlüter and Rachor, 2001).

93   Here we present a 1.5-year study of the seasonal dynamics of meroplankton in the sub-

94 Arctic Porsangerfjord, Norway. This fjord is located adjacent to the Barents Sea and has a

95 high biomass and active production of benthic invertebrates (Fuhrmann et al., 2015). The

96 main objectives for the study were i) to investigate the seasonal changes in meroplankton

97 abundance, composition and nutritional modes, ii) to identify the environmental drivers

98 responsible for changes in meroplankton composition and iii) to estimate the seasonal

99 proportion of meroplankton in the zooplankton community. Furthermore, the local benthic

100 community and hydrography within the fjord are discussed in relation to meroplankton

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101   dynamics. Two contrasting stations were examined in order to explore the effects of depth and

102   distance from shore on meroplanktonic dynamics.

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104   **2. Materials and methods**

105   *2.1 Study area*

106   Porsangerfjord is a broad fjord that is oriented in a north-south direction between 70-71°N and

107   25-26.5°E, with a length of 100 km and a width of 15 – 20 km (Figure 1) (Myksvoll et al.,

108   2012). There is little freshwater runoff from land and based on bathymetry and water

109   exchange, the fjord is separated into outer, middle and inner basins (Mankettikkara, 2013;

110   Svendsen, 1991). A shallow (60 m) sill approximately 30 km from the head of the fjord

111   delineates the inner basin; a sill at 180 m separates the middle basin from the outer fjord. The

112   outer basin is open to the coast (Myksvoll et al., 2012). The outer and middle basins are

113   classified as semi-enclosed with frequent exchanges of deep water with the Norwegian

114   Coastal Current (NCC) and the Barents Sea (Eilertsen and Skarðhamar, 2006; Svendsen,

115   1995; Wassmann et al., 1996). The water in the inner basin has little contact with the coast

116   and is characterized as Arctic, with temperatures reaching -1.7 ºC (Wassmann et al., 1996).

117   The eastern side of the fjord is characterized by a northward outflow current of water from the

118   fjord, with low temperature and salinity. A southerly inflowing current of warmer, saline

119   coastal water characterizes the western side (Myksvoll et al., 2012).

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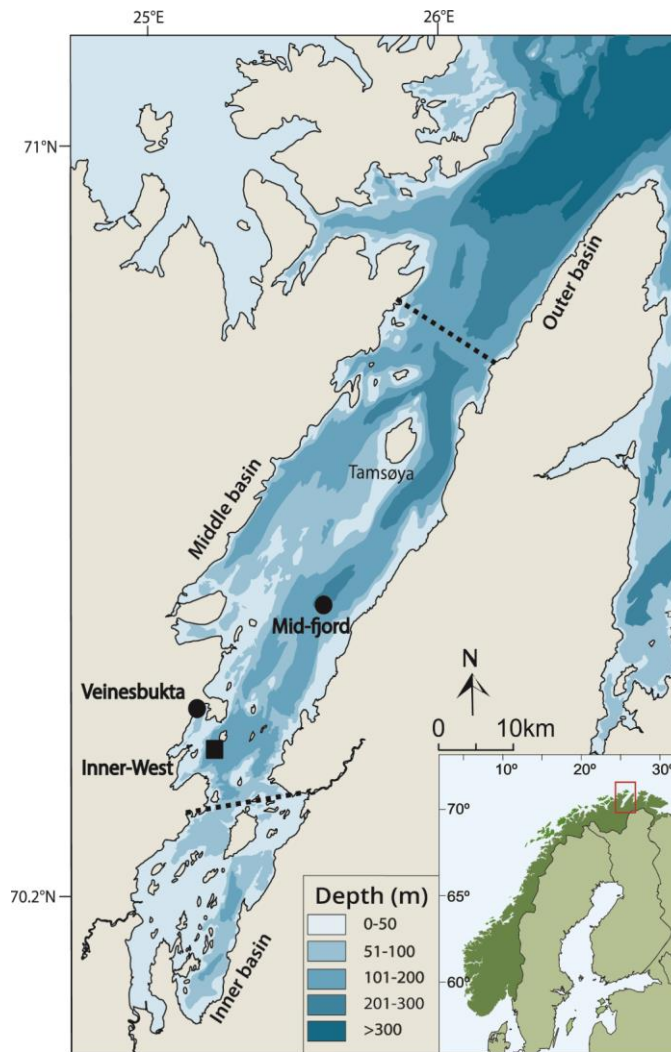
Figure 1. Map of Porsangerfjord, northern Norway. With location of the three sampling
stations Veiensbukta and Mid-fjord (circles), and the CTD station Inner-west (square). Sills
are indicated by dashed lines and sub-basins by names.

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2.2 Plankton sampling and hydrography

Mesozooplankton was sampled at two contrasting stations in the middle basin (Figure 1 and
Table 1). One station, Mid-fjord, was deep (190 m) and located on the eastern side of the
fjord. The other, Veinesbukta, was shallow (60 m) and protected, located on the western side
of the fjord. Zooplankton samples were collected bi-monthly or monthly between February
2013 and August 2014 from RV *Johan Ruud* (Table 1). Samples were collected using a WP2
plankton net with a mesh size of 180 µm (Hydrobios, Kiel, 0.57 m^{-2} mouth opening) and a
filtering cod-end. The net was towed vertically from about 10 m above the seafloor to the sea
surface at a speed of 0.5 m s^{-1}, filtering a mean volume of 120 m^3 ($\pm$ 34 m^3) at Mid-fjord and
38 m^3 ($\pm$ 11 m^3) at Veinesbukta. One to three hauls were obtained at each station and

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preserved in 4% buffered formaldehyde in seawater for later analysis. Mid-fjord was not sampled in April 2014 and clogging of the net by the algae *Phaeoystis pouchetii* reduced sampling efficiency at Veinesbukta in April 2014.

CTD-data were provided by the University of Tromsø Sea Monitoring Program, which carries out regular surveying at fixed stations (Mankettikkara, 2013). The Mid-fjord station is located at a fixed site, and a CTD-profile was taken there prior to each WP2 sampling. The closest CTD-station to Veinesbukta was Inner-west, located 2.7 nautical miles southeast of Veinesbukta and was used as a proxy for this station (Figure 1 and Table 1). CTD-profiles were taken at both Veinesbukta and Inner-west in April 2013 and 2014 (Table 1), to test for differences in environmental variables between the two stations using a Signed Rank Test. Temperature and fluorescence did not differ significantly between stations, while salinity differed significantly due to lower concentrations in the surface layers (upper 10 m) at Inner-west. Thus, the strongest drivers of meroplankton seasonality (temperature and fluorescence) did not differ. Because Veinesbukta (60 m) is shallower than Inner-west (160 m), environmental variables from 60 m depth at Inner-west are included in the results to compensate for depth differences. For simplicity, hydrographical data from Inner-west are referred to as Veinesbukta in plots and text. Salinity, temperature and *in situ* fluorescence were measured with a Sea-Bird Electronics SBE9 and a Sea-Bird Electronics SBE25 (Seabird Electronics Inc., USA). Due to loss of instrumentation, there are no CTD-data available for June 2014. *In situ* fluorescence was calibrated to provide an approximate chlorophyll *a* concentration in the water column. In addition to the standard CTD sampling at Mid-fjord and Inner-west, water samples for determination of chlorophyll *a* concentration and CTD-profiles were collected at Veinesbukta in April 2013 and 2014. Water was collected at 0, 10, 20, 30, 40 and 60 m using a 10-liter Niskin bottle. On board the ship, triplicate 100 ml aliquots from each depth were filtered on 25 mm glass fiber filters (Whatman GF/F), wrapped in aluminum foil and frozen at -18˚C. In the laboratory, filters were extracted in 5 ml methanol for 24 hours at 4˚C. Fluorescence was measured before and after addition of 3 drops of 10% HCL, using a Turner 10 AU Fluorometer to measure chlorophyll *a* content. The chlorophyll *a* values were used to calibrate fluorescence values obtained by the CTD-profile.

2.3 Zooplankton enumeration and identification
Zooplankton samples were diluted to a volume of 200 – 2000 mL. Samples with a high concentration of organisms were split to 1/2 – 1/8 subsamples using a Folsom-splitter prior to dilution. Organisms larger than 5 mm (macrozooplankton) were removed, identified and

169   counted before subsampling. Subsample aliquots of 3 – 5 ml from a randomized sample were

170   extracted using a Finnpipette with the tip opening cut at 4 mm diameter. The two main

171   planktonic components, meroplankton and holoplankton, were enumerated and identified.

172   Randomized subsample aliquots were extracted until approximately 300 individuals of each

173   zooplankton component (meroplankton and holoplankton) were counted (600 individuals in

174   total) using a stereomicroscope (Leica MZ16) equipped with a calibrated micrometer. If the

175   sample contained fewer than 600 organisms in total, the sample was counted in its entirety.

176   When possible, meroplankton were identified to species or genus level using available

177   identification keys, while unidentifiable larvae were pooled according to their respective

178   higher taxa or developmental types (e.g. Prosobranchia veliger, Bivalvia veliger,

179   trochophore). After identification, a literature search was done to allocate nutritional mode

180   (planktotrophic or lecithotrophic) to each larval taxon. The dominant nutritional mode within

181   a given larval taxon or morphological larval type was assigned to each. Exceptions to the

182   primary reproductive strategy were also noted (see supplementary data Table 1).

183   Holoplankton were identified to phylum or order (Table 2). Copepods were separated by

184   order into cyclopoid and calanoid copepods and the calanoid copepods were further divided

185   according to size, smaller and larger than 2 mm prosome length. Copepod nauplii were

186   considered as a single group. Due to low representation the remaining holoplanktonic

187   mesozooplankton were identified but designated as "other" in plots (Table 2). The

188   macrozooplankton were also grouped in the "other" category (Table 2).

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190   *2.4 Data analysis*

191   Abundances are presented as number of individuals per cubic meter (ind. m^{-3}), calculated

192   based on the assumption of 100% filtering efficiency. The non-parametric Kruskal-Wallis test

193   (K-W) was used to test whether there was a significant difference between several groups

194   (e.g. seasons), followed by a Dunn test to test for significant differences within each group.

195   The *p*-values were corrected using the Bonferroni correction. To reduce the influence of

196   highly abundant taxa and to distinguish subtle changes in community composition,

197   meroplankton abundance data were fourth-root transformed prior to data exploration and

198   multivariate statistics. To assess shifts in meroplanktonic composition through the study

199   period, the Jaccard presence/absence dissimilarity coefficients were calculated for the

200   meroplankton community. Further, to assess dissimilarities and changes in both abundance

201   and composition between sampling dates and stations, the Bray-Curtis dissimilarity

202   coefficient was calculated for meroplankton. Hierarchical average linkage dendrograms were

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203 produced for both dissimilarity matrices in order to identify groups (seasons) of stations. To
204 assess whether the clusters in the dendrogram were supported by the dataset, *p*-values for each
205 cluster were calculated by a multiscale bootstrap re-sampling procedure. A multivariate non-
206 parametric permutation ANOVA (PERMANOVA) test was used to evaluate the differences in
207 taxonomic assemblage of meroplankton between different seasons (Anderson 2001).
208 Calculation of the Pseudo-*F* and *p* values was based on 9999 permutations of both the Bray-
209 Curtis and the Jaccard matrices. A canonical correspondence analysis (CCA) plot was
210 produced to assess the effects of environmental factors on the meroplanktonic composition
211 through the study period. All meroplanktonic taxa and six environmental variables (Table 5)
212 were used in the calculation. In the ordination, samples and species were constrained on the
213 environmental variables. Organisms occurring less than twice through the sampling period
214 and/or contributing to less than 0.01% of the total variation were removed from the plot
215 presented. Abbreviations for the taxa presented in the CCA plot are listed in Table 3. The
216 significance of environmental variables and the chosen axes was assessed using an ANOVA-
217 like test with 9999 permutations (Oksanen, 2015). Null hypotheses were rejected at $p < 0.05$.
218 All statistical analysis was performed using R software, version 2.14.2 (R Development Core
219 Team, 2012; http://www.r-project.org), and the *vegan* and *pvclust* packages (Oksanen, 2015;
220 Suzuki and Shimodaira, 2015). Production of graphs was done in SigmaPlot Version 13.0
221 (Systat Software, San Jose, CA).

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223 **3. Results**
224 *3.1 Hydrography*
225 The water column temperature decreased between October and April both years, reaching a
226 minimum of 1.1˚C in April 2013 at Veinesbukta. Surface temperatures increased between
227 May and August at both stations (Figure 2), reaching a maximum in August both years.
228 Maximum surface temperature differed between years and stations, reaching 11˚C in August
229 2013 and 8˚C in August 2014 at Mid-fjord, and 9˚C in August 2013 and 11˚C August 2014 at
230 Veinesbukta. The minimum winter temperature at both stations was lower in 2013, reaching
231 1.1˚C, compared to 2014 when it was 2.7˚C. The sea floor temperature varied less through the
232 year, ranging from 2˚C to 6˚C between April and August at Mid-fjord and between 1.8º and
233 7ºC at 60 m in Veinesbukta (Figure 2).Veinesbukta was in general 0.5 – 1˚C colder than the
234 Mid-fjord station through the whole year. Between January and April, the water column
235 salinity was homogenously 34 g kg^{-1} (Figure 2). During summer, the surface salinity
236 decreased to a minimum of 32 g kg^{-1} in August at both stations. This lower salinity water

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237   penetrated deeper at Veinesbukta compared to Mid-fjord, to 155 m and 95 m, respectively, in

238   2013. In 2014, low salinity water was found in the whole water column at both stations.

239   Chlorophyll *a* concentration was used as a proxy for phytoplankton biomass. In February and

240   January, the concentration was at its lowest (< 0.2 mg m^{-3}). In 2013, the concentration

241   increased in March and April ($0.3 - 0.5$ mg m^{-3}), and the highest concentrations were

242   recorded in June and August (1.9 mg m^{-3}). The following year, the concentration in April was

243   $0.5 - 0.7$ mg m^{-3} with the highest concentrations of $3.5 - 3.8$ mg m^{-3} recorded in May at both

244   stations. In summer 2014, high chlorophyll *a* concentrations penetrated deeper at Mid-fjord.

245   In general, the chlorophyll *a* concentration was higher at Veinesbukta than at Mid-fjord in

246   May, June and August of both years.

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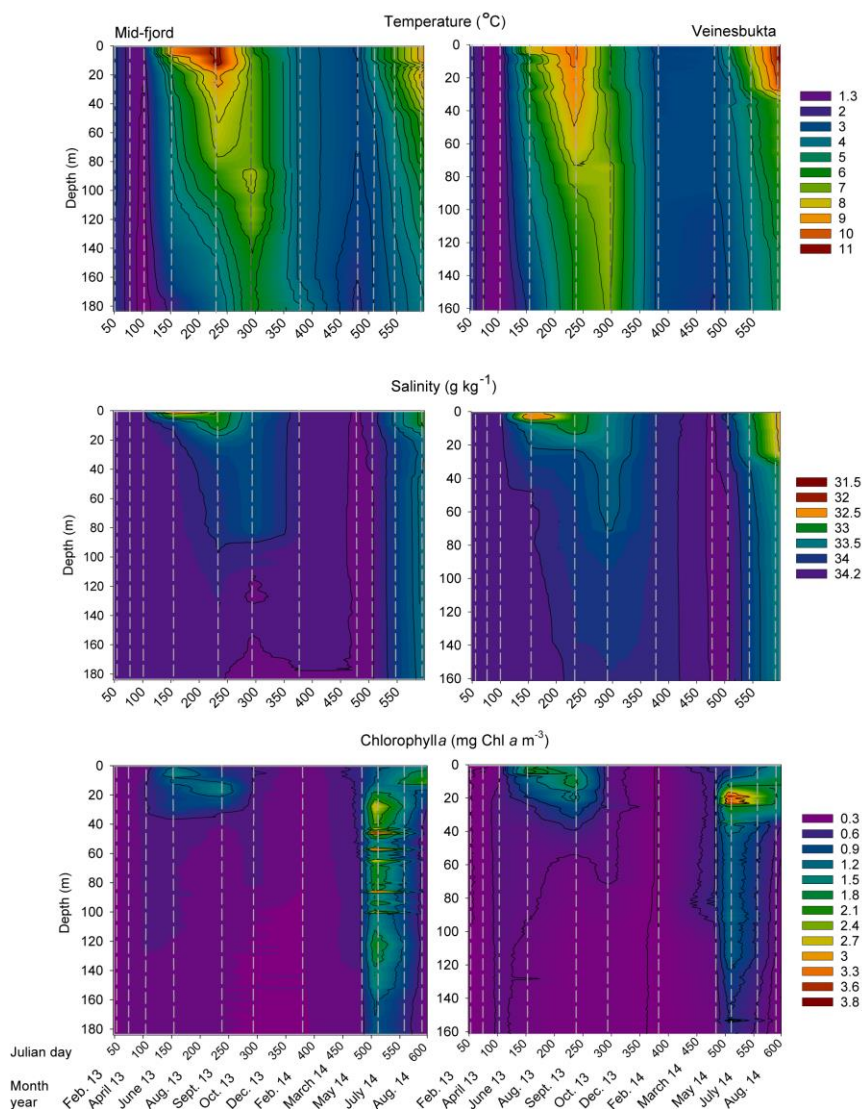
Figure 2. Contour plots of temperature (˚C), salinity (g kg^{-1}) and chlorophyll *a* (mg m^{-3}) at Mid-fjord and Veinesbukta from February 2013 to August 2014. Sampling dates are marked by vertical dashed lines. Julian day was calculated from the first day of 2013 (January 1) to the last sampling date (Table 1).

3.2 Seasonal dynamics of meroplankton

We identified a total of 41 taxa and 56 morphologically distinct larval stages belonging to eight phyla (Table 3). Of these, eleven taxa belonged to Arthropoda, sixteen to Annelida Class Polychaeta, five to Echinodermata, six to Mollusca, and three to Bryozoa, together with single observations of Chordata, Nemertea, Platyhelminthes and Cnidaria (Table 3). The two stations did not differ significantly in terms of community structure and abundance in any month (PERMANOVA, r^2 = 0.03, *p* = 0.9). In order to detect seasonality in meroplankton taxa and abundance, two cluster analyses were performed using dissimilarity indices: Jaccard (Figure 3a) and Bray-Curtis (Figure 3b). In both, two main clusters of samples were observed: a winter group with samples from October to February, and a summer group with samples from March to August. Both groups were further separated into a winter cluster (October 2013, January 2014 and February 2013) a spring cluster (March 2013 and April 2013) and a summer cluster (April 2014, May 2014, June 2013/2014 and August 2013/2014). A stronger seasonality was observed in the Jaccard tree, which separated the summer cluster into early and late summer (Figure 3a). There were some deviations from this main pattern, although the three clusters were significantly supported by the data (bootstrap resampling, *p*-value < 0.05). The summer cluster was not significantly supported in the Bray-Curtis tree (*p* = 0.34) (Figure 3b), nor were the February samples (ME 02.13 and V 02.13) in the Jaccard tree. February samples in the Jaccard tree did not significantly group with either winter (Mid-fjord at p = 0.16) nor spring (Veinesbukta at *p* = 0.14) (Figure 3a).

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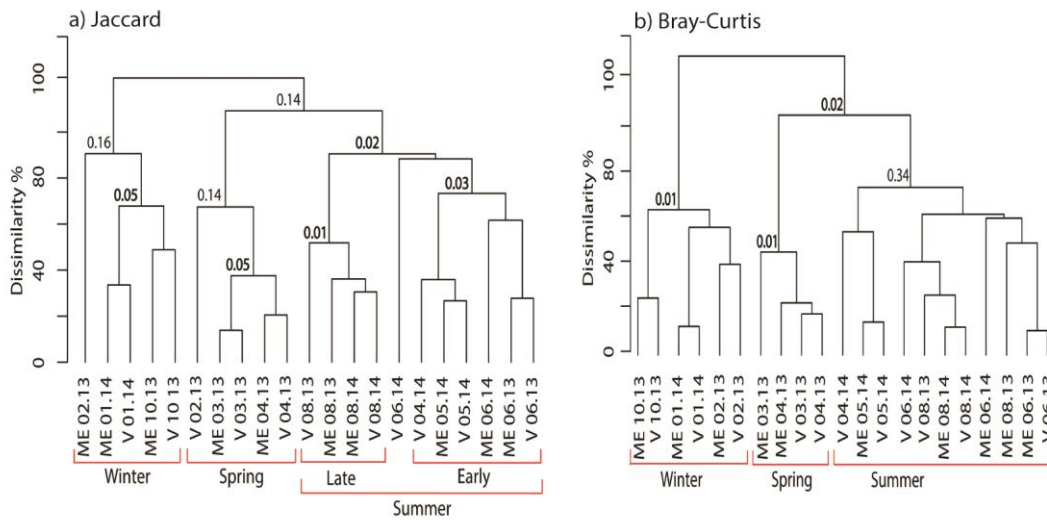
Figure 3. Average hierarchical-cluster plots for a) Jaccard dissimilarity (presence/absence) on community data and b) Bray-Curtis dissimilarity cluster plots on fourth root transformed meroplankton abundance data. The labels (e.g. ME 02.13) stand for station, month and year. Stations are Mid-fjord (ME) and Veinesbukta (V). Red brackets are placed below the three clusters (winter, spring and summer). Above the nodes are the *p*-values calculated by multi-scale bootstrap resampling.

The three seasons were significantly different in terms of both taxon assemblage and total meroplankton abundance (PERMANOVA, $r^2 = 0.4$, $p = 0.0001$ and $r^2 = 0.3$, $p = 0.0001$, respectively). In terms of total meroplankton abundance, winter differed significantly from spring and summer (K-W, $p = 0.05$ and $p = 0.004$, respectively), while spring and summer did not differ significantly (K-W, $p = 1$). Low meroplankton abundance was found during winter; the lowest values were recorded in January 2014 at 1 to 2 ind. m^{-3} (Figure 4). High abundance occurred during summer and spring, with the highest peak in August 2014 at 2122 ind. m^{-3} and 1017 ind. m^{-3} at Mid-fjord and Veinesbukta, respectively. The highest spring values were found in April 2013, with 1530 ind. m^{-3} at Veinesbukta and 216 ind. m^{-3} at Mid-fjord.

We assigned a nutritional mode to a majority of larvae within Arthropoda, Polychaeta, Echinodermata and smaller taxa (e.g. Bryozoa and Acidiacea) (Table 3). However, some propagules identified to morphological type (e.g. trochophores and juveniles), and larvae identified to a high taxonomic level (e.g. veligers of Bivalvia and Gastropoda) were not

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assignable due to the possibility of species belonging to both nutritional modes (13 of 56 larvae) (see supplementary data Table 1). Of the remainder, 39 out of 56 larvae have been described as planktotrophic, (Table 3). There was a simultaneous presence of lecithotrophic and planktotrophic propagules in all three seasons (Table 4). The number of types planktotrophic larvae in the water column increased strongly from winter to spring and summer, with 12 in winter, 23 in spring and 31 in summer (Table 4).
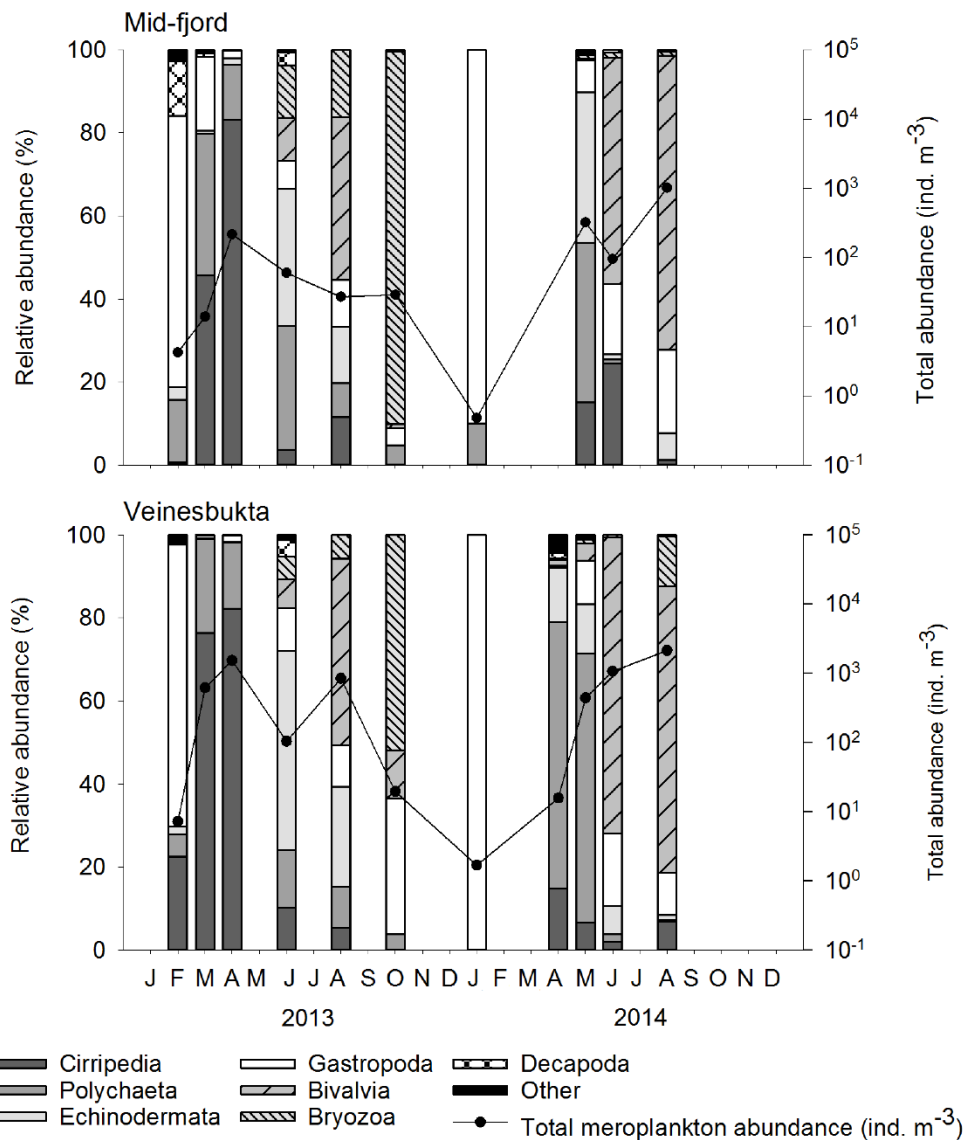
Figure 4. Relative abundance (%) and total abundance (log scale of ind. m^{-3}) of major meroplankton taxa at Mid-fjord and Veinesbukta through a 1.5-year period in Porsangerfjord, Norway.

3.3 Seasonally dominant meroplankton

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The six main meroplanktonic taxa (Cirripedia, Polychaeta, Echinodermata, Gastropoda, Bivalvia, Bryozoa and Decapoda) were present in all seasons (Table 4). The abundance of all the main taxa, with the exception of Bryozoa (K-W, $p = 0.13$), differed significantly between winter and summer (K-W, $p < 0.05$). The abundance of Cirripedia and Polychaeta differed significantly between winter and spring (K-W, $p = 0.0007$ and $p = 0.005$, respectively), while Bivalvia (K-W, $p = 0.005$) and Bryozoa (K-W, $p = 0.0008$) differed significantly between spring and summer.

Gastropoda was the dominant taxon in winter, representing an average of 60% of the meroplankton community in the fjord (Table 4). Bryozoa was second most dominant to Gastropoda in October, representing an average 24% of the community (Figure 4 and Table 3 and 4). In February 2013, Polychaeta and Crustacea were found at Mid-fjord (Figure 4), while Cirripedia were the second most prevalent organism at Veinesbukta. Spring samples were dominated by Cirripedia, representing an average of 72% of the meroplankton composition (Table 4). Their highest contribution (83%) was in April 2013 at both stations (Figure 4). This was not observed at Veinesbukta in April 2014, when Polychaeta were dominant. In summer, there was a shift toward a more diverse community (Figure 4 and Table 4). On average Bivalvia was the dominant summer taxon, followed by Echinodermata and Polychaeta (Table 4). The latter two taxa dominated and peaked in abundance in May 2014 at Veinesbukta (Figure 4), while Mid-fjord also had a high occurrence of Echinodermata then. In June 2013, Echinodermata was the dominant taxon at both stations. Bivalvia was the dominant taxon in June 2014 and in August of both 2013 and 2014, representing 39 to 72% of the meroplanktonic community.

3.4 Environmental influence on meroplankton community

A CCA analysis shows the relationships among the relative abundances of meroplankton groups and the environmental variables measured at each station (Figure 5). Together the environmental variables explained 56.1% of the total variance in meroplankton composition and abundance (permutation ANOVA test, $p = 0.0005$). The first two axes account for 32% of the total variation. A permutation test performed for the environmental variables demonstrates that the temperature in the water column, chlorophyll *a* and surface salinity contributed significantly to the ordination ($p < 0.05$ in Table 5). The stations group in a pattern comparable to the Jaccard and Bray-Curtis cluster plots, indicating three seasons (Figures 3 and 5a). The winter stations (circles in Figure 5a), were negatively correlated with chlorophyll *a*, and are situated toward the center of the plot due to a low total abundance of meroplankton

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and the presence of larvae that were common in the other seasons (e.g. Gastropoda veligers). The exceptions were the October 2013 samples that grouped in the upper right corner and were mainly characterized by cyphonautes larvae of the bryozoan *Membranipora membranacea* (Figure 5a and 5b). Polychaete trochophores, nudibranch veligers, asteroid larvae and ascidiacea larvae characterized the winter season (Figure 5b and Table 3). The presence of *Laonice cirrata* larvae (a spionid polychaete) separated the February 2013 Veinesbukta sample from the rest. Spring samples (squares) were positively correlated with surface salinity and negatively correlated with surface temperature (Figure 5a). The taxa characterizing spring were the polychaetes *L. cirrata*, *Dipolydora* sp. and unidentified metatrochophores; the cirripedes *Balanus* spp. and *Balanus crenatus* and zoea of the crab *Paralithodes camtschaticus* (Figure 5b). The April 2014 Veinesbukta sample plotted closer to the summer season (Figure 5b). That station was sampled later in the month and is closer to the summer group in the ordination due to the presence of taxa characterizing that season. The summer stations spread into two groups (diamonds), indicating distinctive early (April 2014, May 2014 and June 2013) and late summer communities (June 2014 and August 2013 and 2014). These two summer groups were correlated with different environmental variables: the early summer samples correlated with chlorophyll *a* and the late summer samples with warmer temperatures (Figure 5a). There was a transition in taxa through the early summer period (Figure 5b). Composition shifted from veligers of the prosobranch *Velutina* sp., larvae of the polychaete *Scolelepis* sp. and unidentified trochophore larvae in April 2014 to the polychaetes *Harmothoe* sp., *Nephtys* sp. and pilidium (Nemertean) larvae in May 2014, and finally to *E. pilosa* bryozoan larvae, *Owenia* sp. polychaete larvae and to holothuroidean pentactula larvae in June 2013 (Figure 5b and Table 3). Late summer stations were characterized by bivalve veligers (some of the *Anomia* sp.), ophiuroid juveniles and unidentified bryozoan cyphonautes larvae.

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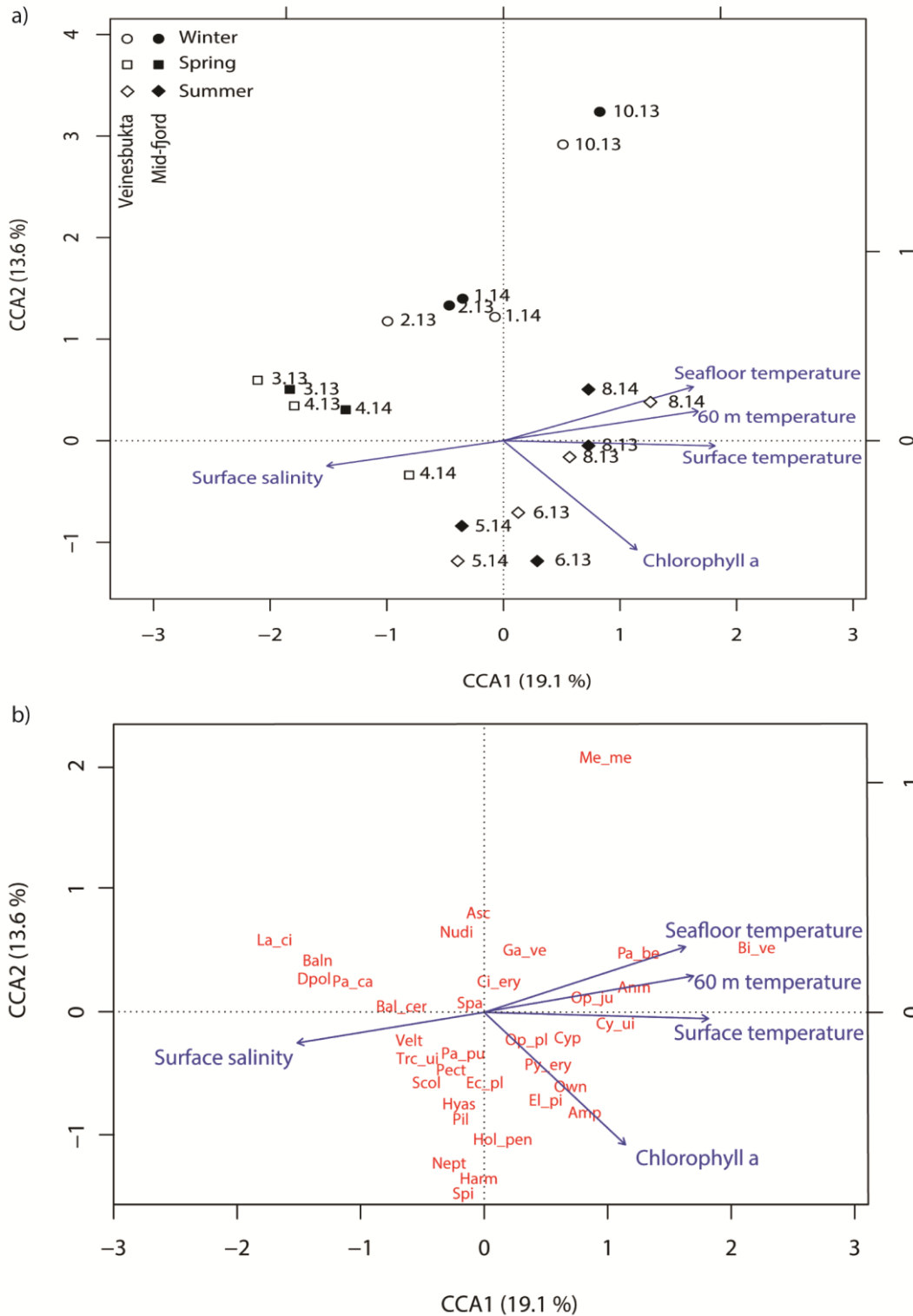
Figure 5. Canonical correspondence analysis (CCA) on fourth root transformed abundance data. Panel a) displays the CCA ordination with station and environmental variables and panel b) displays the CCA ordination with taxa and environmental variables. The eigenvalues as percentages are provided for dimensions I and II with a total of 32% variance explained. Taxa

representing > 0.01% of the variation are presented, their abbreviations are found in Table 3.

Filled symbols are samples from Veinesbukta and unfilled symbols are samples from Mid-fjord; the three symbol shapes represent the three clustering groups in Figure 3.

3.5 Seasonal zooplankton abundance and composition

The lowest total abundance of zooplankton (holoplankton and meroplankton) was found in winter and spring, reaching a minimum of 138 ind. m^{-3} at Mid-fjord in March. Two peaks in zooplankton abundance were observed (Figure 6), the highest in May 2014 with approximately 13 500 ind. m^{-3} at both stations. During winter, cyclopoid copepods were the dominant component in the zooplankton community, representing between 47 and 57% of the zooplankton community at the Mid-fjord station and 31 to 78% of the community in Veinesbukta (Figure 6). Calanoid copepods in the smallest size fraction were the second most numerous in that season. During spring 2013, the zooplankton composition changed to a dominance of meroplankton at Veinesbukta, representing 60% in March and 70% in April. Similar dominance was not observed in April 2014, when they made up a mere 4% of the assemblage. An increased presence of meroplankton in spring was also observed at the Mid-fjord station; however, they did not dominate, contributing 7% in March and 33% in April. During summer, the composition changed to a dominance of calanoid copepods in both size fractions. Copepods in the large size fraction appeared to be more important at the Mid-fjord station, while the small size fraction contributed more at Veinesbukta. Copepod nauplii also increased in relative importance during this season with their peak abundance and relative abundance occurring in May 2014 at Mid-fjord (22%) and in June 2014 at Veinesbukta (11%) (Figure 6 and Table 3). Meroplankton had a small increase in relative abundance in June and August 2014, representing between 5 and 25% of the community.

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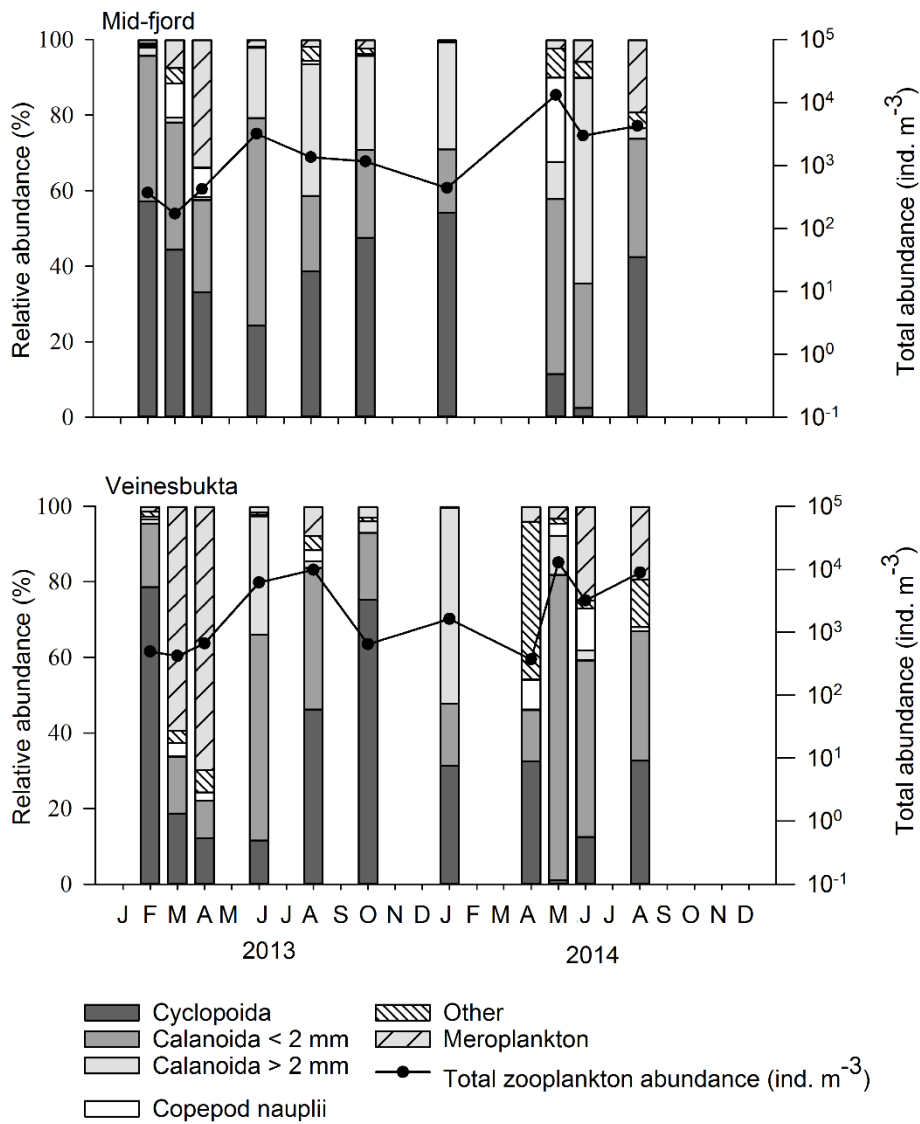
Figure 6. Relative (%) and total abundance (log scale of ind. m^{-3}) of the major zooplankton taxa (holoplankton and meroplankton), at Mid-fjord and Veinesbukta through a 1.5-year period in Porsangerfjord, Norway.

4. Discussion

4.1 Meroplankton diversity, abundance and nutritional modes

We identified 56 distinct larval forms belonging to 41 taxa and eight phyla in this study. More taxa were likely present, but due to insufficient identification literature for some high-latitude taxa and difficulties identifying species based on subtle morphological differences, an unknown number of species may be incorrectly grouped together (e.g. veligers of Bivalvia, Prosobranchia and Nudibranchia). However, the number of taxa and phyla found in Porsangerfjord is within the range of other high-latitude Arctic studies: 37 taxa belonging to six phyla in Balsfjord, Norway (69ºN) (Falk-Petersen, 1982a), 42 taxa belonging to eight phyla in a Greenland fjord (82ºN) (Andersen, 1984) and 44 taxa from seven phyla in the Kara Sea (70-76ºN) (Fetzer and Arnts, 2008). These numbers are lower than those found by Silberberger et al. (2016) in Vesterålen, Norway (68ºN), who found 65 taxa in 11 phyla. A direct comparison between surveys is difficult due to differences in the local benthic communities, hydrographical properties, sampling and identification techniques and distinctive inter-annual variability. Yet, the comparable numbers of taxa at high-latitudes indicate that similar reproductive strategies are operating in the Arctic. Interestingly, the number of benthic taxa producing pelagic larvae in the Arctic is lower than comparable high-latitudes in the Antarctic. Stanwell-Smith et al. (1999) suggested that the number of taxa producing pelagic larvae was in the range of 100-150 species in Antarctic waters. Although the proportion of adults with this reproductive strategy is lower in the Antarctic compared to the Arctic (Fetzer and Arntz, 2008; Marshall et al., 2012), a higher benthic diversity on the Antarctic shelf has been suggested as a possible source of this difference (Dayton et al., 1994; Gallego et al., 2015).

In this study, the abundance of meroplankton was, with the exception of a study in Balsfjord, Norway using a 150 µm net (Falk-Petersen, 1982a), lower than those recorded in other coastal areas in the Arctic. In Adventfjorden, Svalbard, Kuklinski et al. (2013) found a peak abundance of 49 000 ind. m^{-3} using a demersal water sampler and a 20 µm sieve, while Stübner et al. (2016) found a maximum abundance of 83 800 ind. m^{-3} using a WP2 with a 63 µm net. Such variation in abundance may reflect the choice of sampling methods or regional differences. A mesh size of 180 µm has been reported to underestimate larvae smaller than 200 µm, which is relevant for early larval stages, particularly of Polychaeta, Bivalvia and trochophores (Hansen et al., 1999; Sastry, 1979). For instance Kuklinski et al., (2013) found several peaks of unidentified trochophores, reaching maximum abundances of 2600 ind. m^{-3}.

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That is in contrast to our findings, where unidentified trochophores reached a maximum abundance of 38 ind. m^3. Our motivation for using a coarser net than the 50 µm mesh recommended by Hansen et al. (1999) was to sample adequately large and fast swimming larvae such as decapod zoea. Kuklinski et al. (2013) did not capture any decapod zoea, while Stübner et al. (2016) found a maximum density of 4 ind. m^{-3}. This is lower than results from a spatial and temporal study on decapod zoea within Posangerfjord using the same sampling procedures as this study, where the maximum abundance of zoea was 12 ind. m^{-3} in April (Michelsen et al., in prep.). Thus, larger meroplankton were more adequately sampled in this study.

The seasonal environment within Porsangerfjord could have an effect on the number of benthic taxa producing planktotrophic and lecithotrophic larvae. In this study, planktotrophy was the dominant nutritional mode, and feeding larvae were very abundant in the water column during spring and summer. Clearly, the most productive period of the year for phytoplankton is an important spawning time for many planktotrophic taxa. Furthermore, the simultaneous presence of both nutritional modes all year around indicates that variability in environmental variables does not select against a planktotrophic reproductive strategy at this latitude. Fetzer & Arntz (2008) found a similarly high abundance of planktotrophic larvae during late summer in the Kara Sea (70-76ºN). Moreover, similar dynamics have been recorded in Antarctic waters, where Gallego et al. (2015) found an overall dominance of planktotrophic larvae at 70-78°S in the Ross Sea, while Bowden et al. (2009) observed a simultaneous presence of both nutritional modes through the whole year at Adelaide Island (67°S). Whether there is a consistent increase in the proportion of lecithotrophic larvae produced at the latitude of this study (70°N), compared to lower latitudes, is beyond the scope of this study. It would require a similar analysis on nutritional modes at several latitudes (e.g. Gallego et al., 2015). It is important to note that due to limitations in our sampling methods and identification techniques there are some artifacts in our findings. Furthermore, the general allocation of nutritional modes based on larval morphology or the most prevalent feeding strategy within a given taxa leads to more uncertainties. During the literature search on nutritional modes, we found a general lack of data on the true reproductive strategies displayed by many Boreal and particularly Arctic species. Thus, whether a high level of planktotrophy holds true among larvae we found to be unassignable (e.g. Mollusca) or for the Arctic as a whole, will require more extensive field and experimental studies on benthic invertebrate reproductive strategies, the identification of meroplankton at species level to correctly allocate nutritional modes and similar analyses at several latitudes.

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4.2 Seasonality of meroplankton

Despite limitations from our coarse mesh size, we observed clear seasonal changes in total abundance and community structure of meroplankton. The existence of this seasonality corresponds well with other year round studies in the Arctic (Kuklinksi et al., 2013; Smidt, 1979; Stübner et al., 2016), sub-Arctic (Falk-Petersen, 1982a; Silberberger et al., 2016) and Antarctic (Bowden et al. 2009; Freire et al., 2006; Sewell and Jury 2011; Stanwell-Smith et al. 1999). Furthermore, the presence of meroplankton throughout the study period indicates that high-latitude fjords such as Porsangerfjord contain a varied benthic community with different reproductive strategies.

The low abundance and few meroplanktonic taxa present during winter suggest that, although winter is not the primary reproductive period, some benthic organisms are still actively spawning. The few larvae present this season are primarily gastropod veligers which has been reported in other winter studies in both the Arctic (Arendt et al. 2012; Falk-Petersen, 1982a; Hirche and Kosobokova, 2011; Stübner et al., 2016) and Antarctic (Sewell and Jury 2011; Stanwell-Smith et al. 1999). However, this is in contrast to conclusions of Thorson (1936), and Fetzer and Arntz (2008), who did not find any gastropod veligers in Franz Joseph Fjord, Greenland or in the Kara Sea, Russia, respectively. Whether this is due to a shift toward fewer taxa producing pelagic larvae at higher-latitudes or an effect of a different adult community of gastropods in these areas is difficult to conclude. Although evidence suggests that a shift toward benthic development at high-latitudes is true for Prosobranch gastropods (Clarke, 1992; Thorson, 1950), further elucidation of latitudinal shifts in reproductive strategies will require better identification of both veligers and benthic adults. The bryozoan cyphonautes and bivalve veligers present in October may be the last larvae released by late-summer and fall spawners. Yet the presence of these taxa in the water column during winter corresponds well with other studies in the Arctic that have used finer mesh sizes (Kuklinski et al., 2013; Smidt 1979; Stübner et al., 2016).

Spring appears to be the start of the reproductive period within the fjord, due to a sharp increase in meroplankton abundance and the appearance of larval Cirripedia and Polychaeta. A large number of other zooplankton studies in the Arctic have found cirripede nauplii in large numbers, often dominating in the zooplankton community just prior to and during the spring phytoplankton bloom (e.g. Arendt et al., 2012; Falk-Petersen, 1982a; Kwasniewski et al., 2013; Smidt, 1979; Stübner et al., 2016). In sub-Arctic waters like Porsangerfjord, their peak abundance comes between late March and May (Falk-Petersen, 1982; Silberberger et al.,

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2016; Smidt, 1979), while the timing is shifted to May-July in high-Arctic waters (Kwasniewski et al., 2013; Stübner et al., 2016; Thorson, 1936). This may be attributed to a later onset of the phytoplankton bloom in the high-Arctic compared to sub-Arctic waters. In contrast, cirripede nauplii are either completely lacking (Bowden et al., 2009; Sewell and Jury, 2011) or are found at very low numbers during spring and summer in Antarctic coastal waters (Gallego et al., 2015; Stanwell-Smith et al., 1999). This may be due to the low abundance of intertidal benthic adults in the Antarctic (Dayton et al., 1994).

The transition between spring and summer was less pronounced, with a majority of the main taxa displaying prolonged spawning through the two seasons. The dominant summer taxa (Bivalvia, Polychaeta and Echinodermata) have been identified as the main constituents of the summer community in many studies in the Arctic and Antarctic (Andersen 1984; Bowden et al., 2009; Falk-Petersen, 1982a; Silberberger et al., 2016; Schlüter and Rachor, 2001; Stanwell-Smith et al., 1999; Stübner et al., 2016). Similar to our study, an increase in number of taxa during summer was also noted in these studies (Bowden et al., 2009; Falk-Petersen, 1982a; Kulikova et al., 2000; Smidt, 1979). Ophiuroid plutei larvae displayed a prolonged presence in the water column, their highest abundances occurring in May and August. Falk-Petersen (1982a, 1982b), found a similar prolonged presence of these larvae in Balsfjord, Norway, and attributed it to early summer spawning by *Ophiopholis* sp. and summer spawning by *Ophiura* spp.. Thus, the plutei larvae recorded in this study may originate from several species with different spawning times. The strong pulse of bivalve veligers in late summer was primarily umbonate- and pediveligers (Michelsen pers. obs.), which are in the final stages of their pelagic phase (Sastry, 1979). Their development typically takes 3-4 weeks or more, meaning that they may have been present in the water column since June/July (Zardus and Martel, 2002). This corresponds well with other studies, which have found strong pulses of small bivalve veligers in June and July (Brander et al., 2016; Kuklinksi et al., 2013; Smidt, 1979; Stübner et al., 2016; Thorson, 1936).

There were slight differences in the seasonal meroplankton composition between the two investigated years. An inter-annual variation in meroplankton abundance and composition is common for taxa such as Polychaeta, Echinodermata and Bivalvia, and it may be attributed to varying food and temperature conditions (Kirby et al., 2008). Such yearly variability may have caused the August 2014 samples to contain a higher dominance of Bivalvia and a higher total abundance of meroplankton compared to the preceding year. Alternatively, changing hydrographical conditions may have retained more bivalve veliger within the fjord in 2014 compared to 2013. Sampling frequency may be an additional factor in the observed

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537 community difference. As we did not sample in early spring 2014, we may have missed the

538 dominance of Cirripedia nauplii in the zooplankton community that year. Time series studies

539 with a high sampling frequency could more accurately elucidate inter-annual variation in

540 benthic invertebrate spawning.

541

542 *4.3 Biotic and abiotic factors influencing seasonal meroplankton composition*

543 Our statistical analysis indicates an interaction between seasonal changes in meroplankton

544 composition and changes in environmental variables. This was observed for both years,

545 suggesting that similar benthic spawning behaviors operate each year. The main

546 environmental variables responsible for this transition, i.e. increased chlorophyll *a* and water

547 column temperature, have previously been identified as the primary drivers of meroplankton

548 seasonality in both the Arctic and Antarctic (Freire et al., 2006; Kuklinski et al., 2013; Sewell

549 and Jury 2011; Silberberger et al., 2016; Stübner et al., 2016).

550   The peak phytoplankton bloom within Porsangerfjord occurs later than in other north

551 Norwegian fjords, indicating a more Arctic primary production regime (Eilertsen and

552 Frantzen, 2007; Hegseth et al., 1995). In this study, we may have missed the peak bloom in

553 2013, whereas the May 2014 samples were closer to it. Polychaetes, Echinoids and

554 Ophiuroids were primarily present in the water column through spring and summer and

555 appeared to correlate with the period of peak chlorophyll *a* concentration. A majority of these

556 larvae originate from taxa that produce planktotrophic larvae (Table 3) and are hypothesized

557 to spawn when an optimal combination of photoperiod and temperature have been reached

558 (Olive, 1995). Alternatively, some Echinoderms spawn when they sense heat-stable

559 metabolites released by phytoplankton (Starr et al., 1990). Residing in the water column

560 during summer introduces the danger of predation, as potential predators such as

561 chaetognaths, fish larvae, ctenophores and hydromedusae are present in higher numbers

562 (Table 3 and data not included) (Thorson, 1950). Indeed, bivalve veligers, polychaete larvae

563 and cyphonautes have been found in stomachs of juvenile capelin and herring caught at the

564 mouth of Porsangerfjord (Fossheim et al., 2006; Pedersen and Fossheim, 2008). Yet,

565 spawning in this season may ensure that larvae are present during the period of maximum

566 phytoplankton production and warming surface temperatures, both of which can reduce

567 development time, shortening exposure to both predators and advection toward unsuitable

568 habitats.

569   The sharp increase in meroplankton abundance coincided with an increase in chlorophyll *a*

570 in March and April. The organisms responsible for this strong pulse were primarily the nauplii

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of *Balanus crenatus* and *Balanus* spp., the latter being a mixture of *Semibalanus balanoides* and *Balanus balanus* (Michelsen pers. obs.). Adult *S. balanoides* have been found to initiate spawning when they come in direct contact with foods such as diatoms or other suspended particles (Barnes, 1962; Gyory et al., 2013; Starr et al., 1991). Turner et al. (2001), found nauplii of *B. crenatus* to be highly food dependent when they enter the water column. Thus, spawning in March and April may ensure that these food dependent larvae are present in the water column during the onset of the spring bloom. Although a majority of spionid polychaetes spawn when both temperature and photoperiod are increasing (Blake and Arnofsky, 1999 and references therein), the dominant spring polychaete, *L. cirrata* displays a semiannual reproductive cycle, spawning in late winter (January to March) and again in autumn (September) (Hannerz, 1956). Similarly, Blake (1969) found that members of the spionid genus *Dipolydora* spawn in late winter when temperatures are low, and he hypothesized that they spawn early in order to match the phytoplankton bloom. Thus, it is likely that the spring community consists of a mixture of late winter-spawned larvae and larvae dependent on the onset of the phytoplankton bloom.

Presence of some meroplankton did not correlate with environmental variables. Considering the scarcity of phytoplankton during winter, it is likely that some larvae present then have a lecithotrophic nutritional mode. Ascidian tadpole larvae are lecithotrophic, and the adults of all species produce such larvae (Young et al., 2002). Furthermore, some gastropods produce lecithotrophic veligers (Thorson, 1936, 1950). Having larvae independent of external sources of nutrition means that the adults can utilize a larger part of the year for spawning. However, some planktotrophic larvae were observed in winter (e.g. asteriodean brachiolaria and bipinnaria larvae). Detritus, bacteria and protozoans are thought to be the main food sources during winter within Arctic and sub-Arctic fjords surrounding the Barents Sea (Dvoretsky and Dvoretsky, 2015), all of which serve as important sources of nutrition for gastropods, polychaetes, echinoderms and bivalves (Boidron-Fétairon, 1995 and references therein). Dissolved organic material has been identified as an alternative source of nutrition during the early development of planktotrophic and some lecithotrophic larvae (Jaeckle and Manahan, 1989; Shilling and Bosh, 1994). Thus, meroplanktonic larvae may be actively feeding outside the main primary production period. A spawning strategy that is de-coupled from the spring bloom would provide less competition for space when settling and an increased juvenile survival rate due to high food concentrations becoming available to the benthos during the phytoplankton bloom (Bowden et al., 2009; Kuklinski et al., 2013).

604 However, low temperatures often lead to a longer pelagic developmental time, increasing the

605 danger of transport away from suitable habitats (O'Connor et al., 2006).

606

607 *4.4 Zooplankton dynamics*

608 Copepods were the dominant component in the zooplankton community for a majority of the

609 study period and, like meroplankton, displayed reduced reproduction during winter. The

610 primary residents during that season were cyclopoid copepods and calanoid copepods in the

611 smallest size fraction. Small copepod taxa, such as *Oithona* spp., *Microcalanus* spp. and

612 *Pseudocalanus* spp. remain active and are often abundant during winter (Hopkins et al., 1984;

613 Madsen et al., 2008). A different strategy is found for *Calanus* spp., where immature

614 copepodite stages (CIV- CV) descend to deeper waters for overwintering (Arashkevich et al.,

615 2002; Tande, 1989). Two recent zooplankton studies within Porsangerfjord reached similar

616 findings, that late copepodite stages of *Calanus finmarchicus* start to descend in August and

617 are all at depth by November (Priou, 2015; Varela, 2015). The early appearance of larvae and

618 nauplii of both benthic invertebrate and copepod origins in March and April coincided with

619 increased chlorophyll *a* concentrations, suggesting that organisms with larvae relying on

620 phytoplankton as their main food start spawning at the onset of the spring bloom within the

621 fjord. Although we did not identify the copepod nauplii to species, *C. finmarchicus* females

622 have been found to synchronize their spawning with the onset of the spring phytoplankton

623 bloom (Tande 1982, 1989). The high contribution of meroplankton in the zooplankton

624 community during spring corresponds well with other high-latitude studies in the Arctic

625 (Arendt et al., 2012; Falk-Petersen, 1982a; Kuklinski et al., 2013; Kulikova, 2000;

626 Kwasniewski et al., 2013; Smidt, 1979; Stübner et al., 2016). This abundant contribution of

627 meroplankton and the high proportion of planktotrophic larvae suggest that meroplankton

628 could be of trophic importance in the pelagic ecosystem during this time, both as grazers on

629 phytoplankton and as prey for other organisms. Their large contribution also points their

630 particular importance in shallow, strongly retentive areas such as Veinesbukta. The peak

631 abundance of all zooplankton in summer was dominated by calanoid copepods, pointing to

632 their key role in the mesozooplankton community during that season. Similarly to other high-

633 latitude areas, the community shifted from dominance of calanoid copepods to a dominance

634 of cyclopoid copepods and small copepods in late summer (Hansen et al., 1999; Smidt, 1979).

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636 *4.5 The benthic community and advection*

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Knowledge of the diversity and distribution of benthic organisms, the hydrographical conditions within an area and the specific identities of larvae are crucial for determining the true origins of meroplanktonic larvae. In this study, both stations are located in areas of soft bottom containing similar benthic communities (Bjørge and Jørgensen, 2013; Fuhrmann et al., 2015). In a recent study, Fuhrmann et al. (2015) found that Polychaeta followed by Bivalvia are the most abundant and productive components of the soft bottom macrofauna in Porsangerfjord, representing more than 90% of the benthos in the middle basin. A majority of identified polychaete larvae have adult representatives, with Oweniidae, Spionidae, Nephtyidae and Plynoidae being well represented (Fuhrmann et al., 2015; Oug and Fuhrmann, 2013). The fjord also supports large beds of bivalves, including the scallop *Chlamys islandica* and the horse mussel *Modiolus modiolus* (Wiborg, 1962; Wiborg and Bøhle, 1968), and high-densities of ophiuroids and the echinoid *Strongylocentrotus droebachiensis* (Fuhrmann et al., 2015; Sivertsen and Bjørge, 2015). Thus, the proportions of the dominant meroplanktonic taxa may reflect the local benthic communities within the fjord.

The currents and circulation of water masses within fjords, estuaries and bays are complex and planktonic larvae risk being transported out of or into fjords. These areas also produce barriers to advection due to eddy formations, tides, and temperature and salinity gradients (Fetzer, 2003; Scheltema, 1986), all of which can promote retention of larvae (Fetzer, 2003). The advective properties of drifting particles within and outside Porsangerfjord have been simulated. In a 30 day transportation model of cod eggs within the fjord (Myksvoll et al., 2012), the eggs primarily circulated within the middle basin with few eggs drifting into the fjord. The bays surrounding and including Veinesbukta were also identified as retention hotspots, receiving eggs in the model from the inner part of the fjord and from neighboring bays (Myksvoll et al., 2012). Pedersen et al. (2006), found in a 110-day simulation of advection of red king crab zoea that a majority are transported from the west along the north Norwegian coast, where they enter fjords (including Porsangerfjord). In the model they settled primarily along the fjord's western shorelines. Additionally, model zoea released within fjords had a tendency to remain there (Pedersen et al., 2006). A majority of taxa found in this study have members with developmental times lasting between 30 and 110 days (Young et al., 2002), and they may follow similar dispersal patterns to those described by the modeling. Thus, the available literature suggests that a majority of pelagic larvae within the fjord may be produced locally. The observed seasonality may, therefore, be representative for high-latitude fjords and coastal areas containing a similar benthic community.

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5. Conclusion and perspectives

The meroplankton community displayed strong seasonality in abundance and numbers of taxa that were comparable to other studies in the Arctic and Antarctic. Distinct seasonal communities of meroplankton may be linked to seasonal changes in chlorophyll *a* concentration and temperature triggering adults to spawn. The large number of planktotrophic larvae and high proportion of meroplankton in the spring and summer zooplankton community suggest that larvae could act as important members of the zooplankton community, both as grazers on phytoplankton and as prey for other organisms.

Due to limitations in sampling methods and identification techniques, a greater number of meroplanktonic taxa are likely to be present in the fjord that implied by our samples. In order to understand different reproductive strategies displayed by benthic invertebrates, and as components in the pelagic ecosystem at high-latitudes, future focus should be put on detailed identification of adults and their larvae, on the timing and durations of their pelagic phases based on better temporal and spatial sampling of both the pelagic and benthic communities. More precise identifications will require a combination of molecular (e.g. Webb et al., 2006) and morphological determination.

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903

904   **Table 1.** Overview of stations at which zooplankton and environmental parameters were sampled
905   between February 2013 and August 2014 in Porsangerfjord.

Station name	Position	Sampled depth (m)	Equipment	Year	Sampling date	Julian day
Mid-fjord	70.31˚N 25.35˚S	190	WP2 CTD	2013	Feb. 19	50
					March 20	79
					April 12	102
					June 4	155
					Aug. 22	237
					Oct. 22	295
				2014	Jan. 14	379
					May 21	506
					June 24	540
					Aug. 21	597
Veinesbukta	70.23˚N 25.08˚S	60	WP2 (CTD April)	2013	Feb. 19	50
					March 20	79
					April 12	102
Inner-west	70.21˚N 25.14˚S	160	CTD		June 4	155
					Aug. 22	237
					Oct. 22	295
				2014	Jan. 14	379
					April 25	480
					May 21	506
					June 24	240
					Aug. 21	597

906

907   **Table 2.** Identification scheme for the enumeration of holoplankton in the samples.

Holoplankton taxon groups	Size fraction	Species
Cyclopoida		*Oithona* spp.
Calanoida	< 2 mm	*Pseudocalanus* spp., *Microcalanus* spp., copepodite stages of all Calanoid copepods
	≥ 2 mm	*Calanus finmachicus* (CIV-CVI)*, Metridia longa, Paraeuchaeta* sp.
Copepod nauplii		All copepod species
Other		Krill, Chaetognath, pelagic gastropods, harpacticoida, cladocera, tunicates

908

909

Table 3. The meroplanktonic and holoplanktonic taxa recorded at Mid-fjord and Veinesbukta in Porsangerfjord in 2013 and 2014, with the abbreviations used in the CCA plot, their maximum abundance (ind. m^{-3}), the month with the maximum abundance for each species and the nutritional mode (NM) of each larvae (P, planktotrophic; L, lecithotrophic; ?, not assigned to nutritional mode). n.o.: not observed.

Taxa	Taxa/species	Abbrev. (Fig. 5)	Mid-fjord Maximum Abundance (ind. m^{-3})	Month	Veinesbukta Maximum Abundance (ind. m^{-3})	Month	NM
Meroplankton							
Arthropoda	*Paralithodes*						
Decapoda	*camtschaticus*	Pa_ca	1	February	2	April	P
	Hyas sp.	Hyas	1	May	1	June	P
	Pagurus pubescens	Pa_pu	1	June	2	June	P
	Pagurus bernhardus	Pa_be	2	August	0	n.o.	P
	Pagurus spp.	-	1	March	1	March	P
	Munida rugosa	-	0	n.o.	1	August	P
	Munida sp.	-	1	June	0	n.o.	P
Cirripedia	Cirripedia nauplii early stage	Ci_ery	16	April	72	August	P
	Cirripedia nauplii late stage	Ci_lt	1	June	66	August	P
	Balanus crenatus	Ba_cr	35	April	247	April	P
	Balanus spp.	Baln	82	April	562	April	P
	Cyprid	Cyp	10	August	10	June	P
Annelida	Polychaete undetermined	-	2	June	12	May	?
	Trochophore polychaete	-	1	October	3	April	?
	Metatrochophore undetermined	-	3	March	3	February	?
	Spionidae	Spa	25	April	9	June	P
	Laonice cirrata	La_ci	2	March	133	March	P
	Spio sp.	Spi	0	n.o.	20	May	P
	Polydora spp. early stage	-	0	n.o.	1	April	P
	Polydora spp. late stage	-	0	n.o.	3	May	P
	Dipolydora sp.	Dpol	1	April	59	April	P
	Scolelepis sp.	Scol	15	May	2	April	P
	Phyllodoce spp. early stage	Py_ery	10	May	22	August	P
	Phyllodoce spp. late stage	-	10	May	0	n.o.	P
	Phyllodoce mucosa	-	1	June	0	n.o.	P
	Nephthys sp.	Nep	0	n.o.	46	May	P
	Oweniidae	Own	11	June	33	May	P
	Amphinomidae	Amp	4	June	0	n.o.	P
	Pectinaria sp.	Pek	26	May	30	May	P
	Harmothoe sp.	Harm	50	May	111	May	P
	Harmothoe sp. juvenile	-	0	n.o.	3	June	P
	Echiura	-	1	March	1	February	P
	Undetermined 1 (metatrochophore)	-	0	n.o.	27	August	P
Echinodermata	Ophiuroidea pluteus	Op_pl	91	May	192	August	P
	Ophiuroidea juvenile	Op_ju	3	August	7	August	?
	Echinoidea pluteus	Ec_pl	24	May	16	May	P
	Echinoidea juvenile	-	3	June	0	n.o.	?
	Pluteus indet.	-	3	August	0	n.o.	P
	Asteroidea brachiolaria	-	1	February	1	February	P
	Asteroidea bipinnaria	-	1	August	1	February	P

915

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Table 3. Continued

Taxa	Taxa/species	Abbrev. (Fig. 5)	Mid-fjord Maximum Abundance (ind. m^{-3})	Month	Veinesbukta Maximum Abundance (ind. m^{-3})	Month	NM
Meroplankton							
Echinodermata	Asteroidea juvenile	-	1	August	0	n.o.	?
	Holothuroidea pentactula	Hol_pen	2	June	22	June	L
Mollusca							
Gastropoda	Prosobranchia veliger	Ga_ve	200	August	217	August	?
	Nudibranch veliger	Nu_ve	3	August	14	April	?
	Velutina sp.	Velt	1	April	1	May	?
Bivalvia	Bivalvia veliger	Bi_ve	485	August	1239	August	?
	Anomia sp.	Anm	239	August	224	August	P
Bryozoa	Cyphonautes undetermined	Cy_ui	10	August	257	August	L
	Electra pilosa	El_pi	8	June	6	June	P
	Membranipora membranacea	Me_me	23	October	10	October	P
Chordata	Ascidiacea larvae	Asc	1	April	7	August	L
	Unknown fish larvae		0	n.o.	1	March	-
	Mallotus villotus		1	May	1	June	-
	Gadus sp.		1	May	1	June	-
Nemertea	Pilidium larvae	Pil	3	May	3	May	P
Platyhelminthes	Müller larvae	-	1	June	1	June	P
Cnidaria	*Cerianthus* sp.	-	1	June	1	April	P
Other	Trochophore undetermined	Trc_ui	1	June	38	April	?
Holoplankton							
Crustacea	Cyclopoida		2223	August	4949	August	
	Calanoida < 2 mm prosome length		6239	May	10711	May	
	Calanoida > 2 mm prosome length		1709	June	1963	June	
	Copepod nauplii		3002	May	470	June	
	Euphausiacea nauplii		500	May	11	April	
	Unknown crustacea nauplii		0	n.o.	6	April	
	Podon sp.		128	August	791	August	
	Evadne sp.		0	n.o.	336	August	
	Harpacticoid		3	October	38	August	
	Euphausiacea		68	June	164	May	
	Parathemisto		1	June	1	January	
	Amphipoda		0	n.o.	1	August	
	Isopoda		7	August	0	n.o.	
	Mysidacea		1	January	31	June	
	Unknown crustacea		1	April	1	April	
Chaetognath	Chaetognath		58	June	18	August	
Mollusca	*Limacina* spp.		1	March	3	January	
	Clione spp.		0	n.o.	46	June	
Chordata	Appendicularia		530	May	158	August	
Annelida	*Tomopteris* spp.		0	n.o.	1	January	

918 **Table 4.** The relative contributions (percentage ± standard deviation) of the main meroplankton taxa
919 averaged for three seasons (winter, spring and summer) at two stations in Porsangerfjord and the
920 number of larval types assigned to each nutritional mode (P, planktotrophic; L, lecithotrophic),
921 excluding larvae that could not be assigned a nutritional mode (Table 3). Dominant taxa are given in
922 bold. Based on n = 6 samples in winter, n = 4 samples in spring and n = 11 samples in summer.

	Winter			Spring			Summer		
	Relative contribution	Nutritional mode		Relative contribution	Nutritional mode		Relative contribution	Nutritional mode	
Taxa		P	L		P	L		P	L
Cirripedia	4 ± 9	1	0	**72 ± 18**	4	0	9 ± 6	2	1
Polychaeta	7 ± 5	3	0	**22 ± 9**	10	0	**21 ± 24**	12	0
Echinodermata	1 ± 1.5	3	0	0.5 ± 0.5	2	0	**18 ± 15**	5	1
Gastropoda	**60 ± 36**	0	0	5 ± 8	0	1	11 ± 6	0	1
Bivalvia	2 ± 4	1	0	0.01 ± 0.02	1	0	**34 ± 30**	1	0
Bryozoa	**24 ± 38**	2	0	0	0	0	6 ± 5	3	0
Crustacea	5 ± 8	2	0	0.5 ± 0.6	4	0	1 ± 1	6	0
Other	1 ± 1	1	1	0.4 ± 0.4	2	3	0.2 ± 0.3	2	4
Sum		12	1		23	4		30	7

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924 **Table 5**. Results from the permutational ANOVA test for the significance of environmental variables
925 in the CCA (Figure 5).

Variable	F	p	
Surface salinity	1.9	0.05	*
Seafloor salinity	1.9	0.07	
Surface temperature	2.0	0.003	**
Seafloor temperature	3.3	0.0005	***
60 m temperature	2.7	0.0006	***
Chlorophyll *a*	2.2	0.01	*
Axis 1	5.0	0.0001	***
Axis 2	3.3	0.0004	***
Axis 3	2.7	0.0017	**
Axis 4	1.6	0.1	

Significance level indicated by * = 0.05,
** < 0.01, *** < = 0.001

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