



Seasonal Variability in the Zooplankton Community Structure in a Sub-Arctic Fjord as Revealed by Morphological and Molecular Approaches

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Phyto- and zooplankton in Arctic and sub-Arctic seas show very strong seasonal changes in diversity and biomass. Here we document the seasonal variability in the mesozooplankton community structure in a sub-Arctic fjord in Northern Norway based on monthly sampling between November 2018 and February 2020. We combined traditional morphological zooplankton identification with DNA metabarcoding of a 313 base pair fragment of the COI gene. This approach allowed us to provide the most detailed mesozooplankton species list known for this region across an entire year, including both holo- and meroplankton. The zooplankton community was dominated by small copepods throughout the sampling period both in terms of abundance and relative sequence counts. However, meroplankton was the most diverse group, especially within the phylum polychaeta. We identified four distinct periods based on the seasonal analysis of the zooplankton community composition. The pre-spring bloom period (February–March) was characterized by low abundance and biomass of zooplankton. The spring bloom (April) was characterized by the presence of *Calanus* young stages, cirripedia and krill eggs. The spring-summer period (May–August) was characterized by a succession of meroplankton and a relatively high abundance of copepods of the genus *Calanus* spp. Finally, the autumn-winter period (September–December) was characterized by a high copepod diversity and a peak in abundance of small copepods (e.g., *Oithona similis*, *Acartia longiremis*, *Pseudocalanus acuspes*, *Pseudocalanus elongatus*, *Pseudocalanus moultoni*, *Pseudocalanus minutus*). During this period, we also observed an influx of boreal warm-water species which were notably absent during the rest of the year. Both the traditional community analysis and metabarcoding were highly complementary and with a few exceptions showed similar trends in the seasonal changes of the zooplankton community structure.

Keywords: metabarcoding, sub-arctic, seasonal community dynamics, zooplankton, meroplankton, copepods

INTRODUCTION

Marine ecosystems in Arctic and sub-Arctic regions are governed by strong seasonality in incoming solar radiation, leading to distinct seasonal peaks in primary production. Additionally, nutrient availability, relevant to algal growth, is governed by stratification and mixing of water masses, which again are affected by the seasonality in snow and ice melt, river run-off, wind mixing and solar radiation, in addition to algal nutrient uptake dynamics. Herbivorous zooplankton, which plays an essential role in marine ecosystems at high latitudes, tunes their life cycle to the seasonality in primary production, often using lipid stores to survive the non-productive period. The relatively short and intense growing season necessitates a good synchronization between life history events in zooplankton grazers (such as reproduction and growth) and the productive periods of the primary producers. This synchronization allows the acquisition and accumulation of energy and an efficient energy transfer to higher trophic levels. The dark winter season is particularly poorly studied for activity of phyto- and zooplankton, although recent research demonstrated that this season is by no means a period of inactivity, and several trophic levels remain active and complete important parts of the life cycles in the dark season (Berge et al., 2020; Johnsen et al., 2020).

Mesozooplankton is a key link in the energy transfer between primary producers and higher trophic levels (Steele, 1974; Arnkvaern et al., 2005). They include animals that permanently live in the water column (holoplankton) and those who only spend their larval stage as plankton (meroplankton). Zooplankton abundance, diversity and distribution are considered good indicators of the state of marine ecosystems (Hughes, 2000; Taylor et al., 2002; Hays et al., 2005). They are strongly influenced by hydrography and currents, with advection being an important mode of transport and dispersal, and any changes in the hydrographic regime may affect their distribution and fitness dramatically. Most zooplankton species are not commercially harvested, so changes in distribution and abundance reflect changes in fitness due to environmental forcing (e.g., changes in food availability, predator pressure, and abiotic factors) rather than exploitation, although they can also be influenced by eutrophication and pollution. Furthermore, planktonic life cycles are often short and their population dynamics are not affected by the individual's ability to persist over many years, so plankton populations rapidly respond to environmental changes (Hays et al., 2005).

Fjords are semi enclosed systems that are a characteristic feature of the Norwegian coastline (Stone, 1980; Cottier et al., 2010). Despite being coastal locations, they can have depths of 200–2000 m and provide habitats for deep-sea communities. Fjords that are separated from the open ocean by a shallow sill are more influenced by local processes, as advection from outside the fjord is reduced. Northern Norwegian fjords can be highly affected by freshwater inflow from either glacial or river discharges and snow melt, causing periods of partial coverage of sea ice. Many northern Norwegian fjords, however, are characterized by weak stratification and are also often influenced by Atlantic water masses (Eilertsen et al., 1981a;

Reigstad and Wassmann, 1996) allowing them to remain mostly ice free. Due to their unique properties and often easy accessibility by small vessels, fjords provide excellent long-term sites to study seasonality in community composition and population structure of marine fauna. Most studies on fjord populations have, however, focused on either only single seasons or on specific groups or species, such as *Calanus* spp., or krill (e.g., Matthews et al., 1978; Bagoien et al., 2000; Niehoff and Hirche, 2005; Skreslet et al., 2015), and there are surprisingly few studies describing the seasonal variability in the zooplankton communities of Norwegian fjords or sub-Arctic fjords elsewhere.

The pelagic ecosystem of Balsfjord is one of the best studied among northern Norwegian fjords (Hopkins et al., 1989) mostly due to numerous studies conducted there in the 1980s (e.g., Eilertsen et al., 1981a; Falk-Petersen and Hopkins, 1981; Tande and Hopkins, 1981; Hopkins et al., 1984). Although located above the Arctic Circle, Balsfjord is not influenced by Arctic water masses and can be regarded as a sub-Arctic fjord. However Balsfjord is one of the coldest fjords in northern Norway due to the presence of a sill at the mouth of the fjord that limits the exchange of deep water (Oug and Høisøeter, 2000). Since the 1990's, seasonal studies of zooplankton in this region have been limited (Wexels Riser et al., 2010; Svensen et al., 2018; Barth-Jensen et al., 2020; Trudnowska et al., 2020; Ershova et al., In revision). The mesozooplankton community in Balsfjord has been defined as poor in diversity but high in biomass (Hopkins, 1981; Hopkins et al., 1989). It was found to be dominated by copepods in terms of species numbers and abundance (Hopkins, 1981), but euphausiids can also be abundant, forming large sound scattering layers (Hopkins et al., 1978) and play an important role in the vertical carbon flux (Wexels Riser et al., 2010). However, despite being a relatively well studied fjord system, seasonal zooplankton investigations in Balsfjord, as elsewhere, have been significantly biased toward a few organisms that are easily identified, i.e., large copepods and euphausiids. For example, the seasonal variability in the population structure, sex-ratio and gonad maturation, body weight, carbon and nitrogen content, and enzyme activities have been well studied for *Calanus finmarchicus* (Tande and Hopkins, 1981; Tande and Slagstad, 1982; Tande, 1982; Tande and Gronvik, 1983) and *Metridia longa* (Tande and Gronvik, 1983; Grønvik and Hopkins, 1984; Hopkins et al., 1984; Båmstedt et al., 1985), as have the seasonal changes in lipid composition (Falk-Petersen, 1981; Sargent and Falk-Petersen, 1981; Falk-Petersen et al., 1982; Falk-Petersen, 1985) and population dynamics (Falk-Petersen and Hopkins, 1981) in euphausiids in Balsfjord. However, only a few studies have focused on other parts of the zooplankton community in Balsfjord, such as population dynamics and overwintering strategies in small copepod species (Norrbin et al., 1990; Barthel et al., 1995; Svensen et al., 2018; Barth-Jensen et al., 2020), or the role of zooplankton in the vertical carbon flux (Reigstad and Wassmann, 1996; Pasternak et al., 2000). Even less is known about the meroplankton community (Falk-Petersen, 1982), as the benthic community, and especially their larval stages, are generally much less studied (Oug, 1977; Michelsen et al., 2017).

One challenge of working with mesozooplankton is the complexity of accurate identification to species level.

Zooplankton species identification is time consuming and requires specialist taxonomic expertise (Pan et al., 2008). In addition, the presence of cryptic species, and difficulties to morphologically identify even the most common copepod species complexes, such as *Calanus* or *Pseudocalanus* (Gabrielsen et al., 2012; Choquet, 2017; Choquet et al., 2017, 2018), severely limit our ability to document zooplankton biodiversity or identify species-specific life history strategies. For example, recent advances using molecular tools have revealed that the *Calanus* communities in Northern Norwegian fjords are not, as previously assumed, largely to exclusively dominated by *C. finmarchicus* (Choquet et al., 2017) but by a mix of *C. finmarchicus* and *Calanus glacialis*, demonstrating our lack of understanding of the *Calanus* species complex in this region. This also raises the question in how far previous studies on population structure and reproductive strategies of *C. finmarchicus* in Balsfjord (and elsewhere) (Tande and Hopkins, 1981; Tande and Slagstad, 1982; Tande, 1982; Tande and Gronvik, 1983) are biased by the undetected presence of other *Calanus* species in the fjord. Morphological species identification, of meroplankton in particular is almost impossible due to the small size and lack of species-specific morphological differences between many larval and juvenile stages. Meroplanktonic organisms are therefore often only identified to phylum and little is known about species-, or even family-, specific seasonal variability within the meroplankton community (Michelsen et al., 2017).

Over the last decades, advances in high-throughput DNA sequencing technology have improved our ability to identify the “hidden” diversity in plankton communities (Lindeque et al., 2013). Metabarcoding allows for a large-scale taxonomic identification of community samples by analysis of one or more barcode regions (Lindeque et al., 2013; Bucklin et al., 2016). Barcoded sequences are grouped in molecular operational taxonomic units (MOTU) and can be identified to the species level when compared to sequences stored in genetic libraries. Metabarcoding has the advantage of being faster than sorting samples under the microscope and is rapidly becoming more cost-effective compared to traditional morphological approaches. It can provide more detailed assessment of species diversity (Lindeque et al., 2013; Gran-StadniczeŃko et al., 2019), including groups that do not retain their morphological features in preservatives or lack them altogether, like most larval forms. Although the quantitative value of metabarcoding is still disputed (Bucklin et al., 2016), protocols are emerging that allow to use the numbers of sequence reads as a semi-quantitative proxy of organism’s biomass (Ershova et al., In revision). This semi-quantitative approach is particularly useful for seasonal studies, allowing to document the succession and seasonal changes in the contribution of different species of both holo- and meroplankton. However, metabarcoding cannot provide details on the developmental stage composition of a population, or the size composition within a zooplankton community. Thus, it appears essential to combine traditional microscopic analysis with metabarcoding to understand the variability in species diversity and zooplankton community structure in relation to seasonal changes in hydrography.

Here we used the combination of both approaches to (1) provide a complete species zooplankton inventory, (2) describe the seasonal variability in zooplankton community structure in relation to seasonal changes in hydrography and the availability of microalgae, and (3) described the population dynamics of sibling species of common copepods species that are difficult to identify based on morphology alone (i.e., *Calanus* spp. and *Pseudocalanus* spp.) in Ramsfjord, a side arm of Balsfjord (Figure 1). A sill at 30 m at Balsfjord mouth separates the Balsfjord system from the open sea limiting the deep-water exchange and enabling us to observe seasonal patterns in the zooplankton community relatively undisturbed by exchange of water and organisms between the Balsfjord system and the open sea.

MATERIALS AND METHODS

Study Area

The study was conducted in Ramsfjord (Figure 1), northern Norway, a 13 km-long and 1 km-wide fjord, which consists of two basins. At their deepest, the innermost and the outermost basins are 50 and 130 m deep, respectively. The fjord can be partly ice-covered as the inner part of the fjord is heavily affected by freshwater inflow between October and April. The sampling station (125 m water depth; location 69°31′49.9N, 19°02′11.9E) was located close to the deepest point of the outer basin, which was ice-free for the entire sampling period.

Field Sampling

Hydrography

Monthly sampling was conducted between November 2018 and February 2020 (Table 1) on board of R/V *Hyas*. Vertical temperature and salinity profiles were measured during each sampling event with a conductivity-temperature-depth (CTD) profiler (CTD SBE 19plus). In addition, temperature, salinity and *in situ* chlorophyll fluorescence (relative values not comparable with fluorescence value from other studies) were measured continuously at hourly intervals from 18th March 2019 to 11th June 2020 from a moored underwater observatory (69°32.005′N, 19°02.904′E, 115 m water depth) which included a CTD (Seabird Electronics SBE 16) at 18 m depth and 10 temperature loggers (SBE 65) at 10–15 m intervals between 17 and 107 m water depth along the mooring cable.

Chlorophyll *a* Concentration and Phytoplankton Community

Chlorophyll *a* (Chl *a*) concentration was measured at 13 sampling events (Table 1, note missing data in August, September 2019 and February 2020) from water samples taken with a 5 L Niskin bottle at 5 and 30 m. About 250 mL triplicate samples were filtered onto GF/F filters (Whatman plc, Maidstone, United Kingdom) in the dark and frozen at –20°C until processing. Chl *a* was extracted in 96% Ethanol for about 24 h at 4°C. The extracts were measured on a Turner Trilogy AU-10 fluorometer (Turner Designs, 2019) before and after acidification with 5% HCl. Chl *a* and phaeophytin concentrations were calculated based on calibrations done with a Chl *a* standard (Sigma S6144).

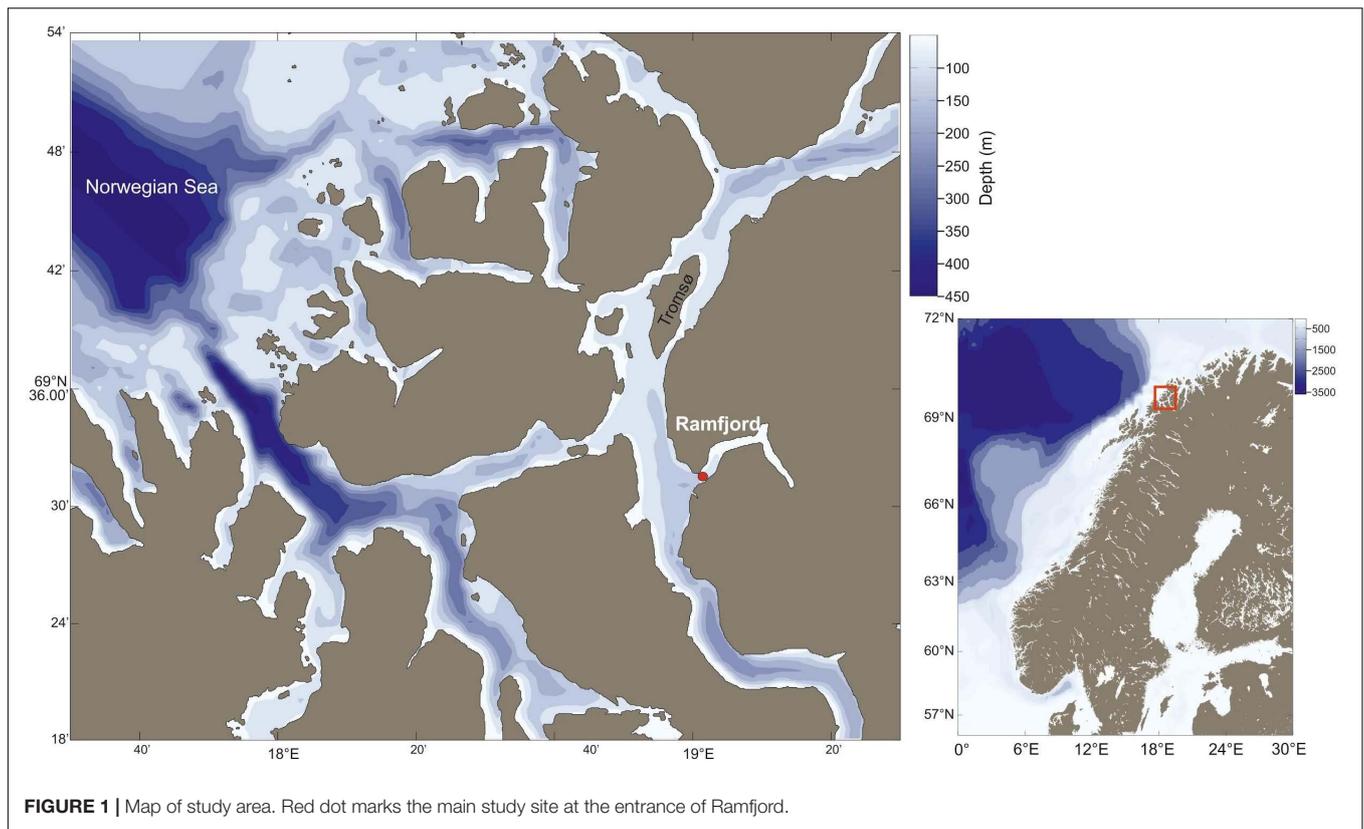


TABLE 1 | Overview of sampling date, method used and data available for each sampling point.

Date	Net meshsize (μm)	Taxonomy	Metabarcoding run	Extraction kit	Chl a conc.	Algae taxonomy	CTD
18.11.2018	64	x	x	E.Z.N.A. Mollusc	x	NA	x
11.12.2018	64	x	x	E.Z.N.A. Mollusc	x	X	x
09.01.2019	64	NA	x	E.Z.N.A. Mollusc	x	NA	x
06.02.2019	64	x	x	E.Z.N.A. Mollusc	x	X	x
13.03.2019	64	x	x	E.Z.N.A. Mollusc	x	X	x
01.04.2019	180	x	x	E.Z.N.A. Mollusc	x	X	x
14.04.2019	180	x	NA	E.Z.N.A. Mollusc	x	X	NA
14.05.2019	180	x	x	E.Z.N.A. Mollusc	x	NA	x
13.06.2019	180	x	x	E.Z.N.A. Mollusc	x	X	x
20.08.2019	180	x	x	E.Z.N.A. Mollusc	NA	NA	x
03.09.2019	180	x	x	E.Z.N.A. Mollusc	NA	NA	x
25.09.2019	180	x	x	E.Z.N.A. Mollusc	x	X	x
14.10.2019	180	X	x	PowerSoil	x	X	x
14.11.2019	180	X	x	PowerSoil	x	NA	x
03.12.2019	180	X	x	PowerSoil	x	NA	x
04.02.2020	180	X	x	PowerSoil	NA	X	x

x indicate that data are available, while *NA* indicate that the data are not available.

Nine phytoplankton samples (Table 1) were taken with a phytoplankton net (KC Denmark) with 10 μm mesh size from 35 to 0 m depth. The samples were fixed in 2% (final concentration) neutral Lugol and stored in a dark borosilicate glass bottle until counting. Phytoplankton taxa were identified in a 2 mL well plate using an inverted microscope (Zeiss Primovert, Carl Zeiss AG, Germany) and taxa were identified using Throndsen et al. (2007).

Zooplankton Sampling

A WP2 net (Hydro-bios, Kiel, Germany) with a closing mechanism and an opening of 0.25 m² was used to sample zooplankton. Between November 2018 and March 2019, a net with a mesh size of 64 μm was used and from April 2019 on the mesh size was changed to 180 μm . Three net hauls were taken at each of the 15 sampling events (Table 1). One sample

was taken from 115 to 50 m and one from 50 to 0 m. Both were preserved in 4% formaldehyde-in-seawater solution. These samples were used to analyze the community composition based on morphology. The third tow was taken from 115 to 0 m and immediately preserved in 96% ethanol. Every net haul was taken with a towing speed ranging between 0.4 and 0.5 m s⁻¹.

Zooplankton Sample Analyses

Morphological Mesozooplankton Community Analysis

For each formalin-preserved sample, the community composition was determined under a Zeiss Discovery V20 stereo microscope (Zeiss, Oberkochen, Germany). First, large (>5 mm) and conspicuous organisms were picked out from the entire sample using fine forceps, identified and counted. Then, the remaining sample was diluted to a known volume and 5 ml subsamples were taken with an automatic pipette with the pipette tip cut at 5 mm diameter to allow free collection of mesozooplankton. The number of subsamples were determined to count at least 100 *Calanus* spp. copepodites which usually corresponded to more than 100 counted individuals of the most common genera in the same sample (*Oithona similis*, *Microcalanus pusillus*, *Pseudocalanus* spp., *Acartia longiremis*). Copepods were identified to the lowest taxonomic level possible based on morphological traits. The developmental stages were determined for *Calanus* spp. individuals. Non-copepods were identified to phylum. Abundance (individuals m⁻²) was estimated by dividing the number of species per sample with the mouth opening area assuming 100% net filtration efficiency.

For further analyses, the abundance from the two depth layers was combined to one depth integrated abundance (115–0 m).

The copepods were classified into two groups, according to their adult prosome length, with copepods with an adult size < 1.5 mm being classified as “small copepods” while the rest were classified as “large copepods” (Table 2).

Dry Weight and Biomass

After being analyzed, each sample was split in two parts using a Motoda box splitter. One half was archived. The other half was used to determine the biomass in terms of dry weight (DW) by removing excess water using a 180 μm sieve, washing the sample with fresh water, drying it for at least 24 h at 50°C and then weighing it with a microbalance (Sartorius BP 615; precision 0.1 mg).

Metabarcoding

The ethanol-preserved sample was split into two parts using Motoda box splitter. One split was homogenized for 30–60 s using a 1000 W blender and allowed to settle for 3–4 h. Excess ethanol was removed by centrifugation and three replicates (±0.3 g) of the homogenized sample were transferred to 2 ml microcentrifuge tubes. DNA was extracted from each replicate using the E.Z.N.A. Mollusc DNA Kit (Omega-Pro) (samples from November 2018 to September 2019) or the PowerSoil DNA Extraction Kit (Qiagen, October 2019–February 2020) (Table 1) following the manufacturer’s protocols. Leray-XT primers containing sample tags (Wangensteen et al., 2018),

including the forward primer mCOIintF-XT 5′-GGWACWRGWTGRACWITITAYCCYCC-3′ and reverse primer jgHCO2198 5′-TAIACYTCIGGRTGICCRAARAAYCA-3′ (Geller et al., 2013) were used to amplify a 313 base pair (b.p.) region of the mitochondrial cytochrome *c* oxidase (COI) gene. The PCR protocol was 10 min at 95°C, followed by 35 cycles of: 94°C for 1 min, 45°C for 1 min, and 72°C for 1 min, and a final extension of 5 min at 72°C. The tagged PCR products were pooled into a single library and cleaned using Minelute PCR purification columns¹. The Illumina library was prepared from the DNA pool using the NextFlex PCR-free library preparation kit (Perkin-Elmer), quantified using the NEBNext Library Quant Kit for Illumina (New England BioLabs) and was sequenced on an Illumina MiSeq using a V3 2 × 250 bp kit.

Bioinformatics

Initial quality filtering of the sequencing data was conducted using OBITools v1.01.22 (Boyer et al., 2016). *Illuminapairedend* was used for aligning paired end sequences and filtering out those with an alignment score < 40. *ngsfilter* was used for demultiplexing and removal of primer sequences. Reads with a length of 299–300 b.p. were selected using *obigrep* and dereplicated using *obiuniq*. Chimeric sequences were then removed using the *uchime_denovo* algorithm (Edgar et al., 2011) in *vsearch* v1.10.1 (Rognes et al., 2016). Step-by-step clustering was performed in SWARM 2.1.13 (Mahé et al., 2015) using a distance value of *d* = 13 (Antich et al., 2021) to cluster individual sequences into Molecular Operational Taxonomic Units (MOTUs). After removing singletons (MOTUs with abundance of 1 read), taxonomic assignment of the representative sequence of remaining MOTUs was then performed using *ecotag* (Boyer et al., 2016) against DUFA-Leray v.2020-06-10, a custom reference database (publicly available from github.com/uit-metabarcoding/DUFA), which includes Leray fragment sequences extracted from BOLD and Genbank, completed with in-house generated sequences. Putative pseudogene sequences in the resulting dataset were then removed using LULU (Frøslev et al., 2017). MOTUs assigned to Prokaryotes and clearly non-planktonic organisms (e.g., insects, mammals) were removed, and a second taxonomy check of the remaining MOTUs was conducted using BOLD (Barcode of Life Database²). A species level identification was assigned with a minimum of 97% similarity. Finally, only MOTUs observed in a minimum of two sample replicates and accounting for at least 0.01% of the total reads of any sample were kept in the final dataset.

Diversity Index

Specific richness was defined as the number of taxa identified by metabarcoding. The specific richness was calculated using the entire metabarcoding data set (total specific richness) as well as using only the data set excluding phytoplankton and fish species (zooplankton specific richness) and the data set including only the copepod species (copepod specific richness).

¹www.qiagen.com

²www.boldsystems.org

TABLE 2 | List of all species identified using metabarcoding, how they were categorized, and if or to what level they were identified in the visual inspection.

Phylum/Subphylum	Class/Order	Species	Category	Visually identified as
Bryozoa	Gymnolaemata	<i>Membranipora membranacea</i>	Meroplankton	Bryozoa larvae
Chaetognatha	Sagittoidea	<i>Eukrohnia hamata</i>	Non-copepod holoplankton	<i>Eukrohnia hamata</i>
Chaetognatha	Sagittoidea	<i>Parasagitta elegans</i>	Non-copepod holoplankton	<i>Parasagitta elegans</i>
Chordata	Ascidiacea	Ascidiacea indet.	Meroplankton	Ascidia larvae
Chordata	Ascidiacea	<i>Ascidiella aspersa</i>	Meroplankton	Ascidia larvae
Cnidaria	Anthozoa	Actiniaria indet.	Meroplankton	Not observed
Cnidaria	Anthozoa	<i>Urticina felina</i>	Meroplankton	Not observed
Cnidaria	Hydrozoa	<i>Clytia hemisphaerica</i>	Non-copepod holoplankton	Not observed
Cnidaria	Hydrozoa	<i>Corymorpha</i> sp.	Non-copepod holoplankton	Not observed
Cnidaria	Hydrozoa	<i>Euphysa aurata</i>	Non-copepod holoplankton	Not observed
Cnidaria	Hydrozoa	<i>Lizzia blondina</i>	Non-copepod holoplankton	Not observed
Cnidaria	Hydrozoa	<i>Melicertum octocostatum</i>	Non-copepod holoplankton	Not observed
Cnidaria	Hydrozoa	<i>Mitrocomella polydiademata</i>	Non-copepod holoplankton	Not observed
Cnidaria	Hydrozoa	<i>Nanomia cara</i>	Non-copepod holoplankton	Not observed
Cnidaria	Hydrozoa	<i>Obelia geniculata</i>	Non-copepod holoplankton	Not observed
Cnidaria	Hydrozoa	<i>Obelia longissima</i>	Non-copepod holoplankton	Not observed
Cnidaria	Hydrozoa	<i>Plotocnide borealis</i>	Non-copepod holoplankton	Not observed
Cnidaria	Hydrozoa	<i>Rathkea octopunctata</i>	Non-copepod holoplankton	Not observed
Cnidaria	Scyphozoa	<i>Aurelia aurita</i>	Non-copepod holoplankton	Not observed
Cnidaria	Scyphozoa	<i>Cyanea</i> sp. RUYNKAR	Non-copepod holoplankton	Not observed
Crustacea	Amphipoda	<i>Themisto abyssorum</i>	Non-copepod holoplankton	Not observed
Crustacea	Cirripedia	Akentronida indet.	Meroplankton	Cirripedia nauplii
Crustacea	Cirripedia	<i>Balanus balanus</i>	Meroplankton	Cirripedia nauplii
Crustacea	Cirripedia	<i>Balanus</i> sp.	Meroplankton	Cirripedia nauplii
Crustacea	Cirripedia	<i>Semibalanus balanoides</i>	Meroplankton	Cirripedia nauplii
Crustacea	Cirripedia	<i>Verruca stroemia</i>	Meroplankton	Cirripedia nauplii
Crustacea	Cladocera	<i>Evadne nordmanni</i>	Non-copepod holoplankton	Not observed
Crustacea	Cladocera	<i>Podon leuckartii</i>	Non-copepod holoplankton	<i>Podon leuckartii</i>
Crustacea	Copepoda	<i>Acartia longiremis</i>	Small copepod	<i>Acartia longiremis</i>
Crustacea	Copepoda	<i>Calanus finmarchicus</i>	Large copepod	<i>Calanus</i> spp.
Crustacea	Copepoda	<i>Calanus glacialis</i>	Large copepod	<i>Calanus</i> spp.
Crustacea	Copepoda	<i>Calanus helgolandicus</i>	Large copepod	Not observed
Crustacea	Copepoda	<i>Calanus hyperboreus</i>	Large copepod	<i>Calanus hyperboreus</i>
Crustacea	Copepoda	<i>Candacia armata</i>	Small copepod	Not observed
Crustacea	Copepoda	<i>Centropages hamatus</i>	Small copepod	Not observed
Crustacea	Copepoda	<i>Centropages typicus</i>	Small copepod	<i>Centropages typicus</i>
Crustacea	Copepoda	Cyclopoida indet.	Small copepod	Cyclopoida indet.
Crustacea	Copepoda	<i>Diaxis hibernica</i>	Small copepod	Not observed
Crustacea	Copepoda	Harpacticoida indet.	Small copepod	Harpacticoida indet.
Crustacea	Copepoda	<i>Longipedia coronata</i>	Small copepod	Not observed
Crustacea	Copepoda	<i>Longipedia</i> sp.	Small copepod	Not observed
Crustacea	Copepoda	<i>Metridia longa</i>	Large copepod	<i>Metridia</i> spp.
Crustacea	Copepoda	<i>Metridia lucens</i>	Large copepod	<i>Metridia</i> spp.
Crustacea	Copepoda	<i>Microcalanus pusillus</i>	Small copepod	<i>Microcalanus pusillus</i>
Crustacea	Copepoda	<i>Microsetella norvegica</i>	Small copepod	<i>Microsetella norvegica</i>
Crustacea	Copepoda	<i>Oithona similis</i>	Small copepod	<i>Oithona similis</i>
Crustacea	Copepoda	<i>Triconia borealis</i>	Small copepod	<i>Oncaea borealis</i>
Crustacea	Copepoda	<i>Paracalanus parvus</i>	Small copepod	Not observed
Crustacea	Copepoda	<i>Paraeuchaeta norvegica</i>	Large copepod	<i>Paraeuchaeta norvegica</i>
Crustacea	Copepoda	<i>Pseudocalanus acuspes</i>	Small copepod	<i>Pseudocalanus</i> spp.
Crustacea	Copepoda	<i>Pseudocalanus elongatus</i>	Small copepod	<i>Pseudocalanus</i> spp.
Crustacea	Copepoda	<i>Pseudocalanus mimus</i>	Small copepod	<i>Pseudocalanus</i> spp.
Crustacea	Copepoda	<i>Pseudocalanus minutus</i>	Small copepod	<i>Pseudocalanus</i> spp.
Crustacea	Copepoda	<i>Pseudocalanus moultoni</i>	Small copepod	<i>Pseudocalanus</i> spp.

(Continued)

TABLE 2 | Continued

Phylum/Subphylum	Class/Order	Species	Category	Visually identified as
Crustacea	Copepoda	<i>Temora longicornis</i>	Small copepod	<i>Temora longicornis</i>
Crustacea	Decapoda		Meroplankton	Decapod larvae
Crustacea	Decapoda	<i>Eualus pusiolus</i>	Meroplankton	Decapod larvae
Crustacea	Decapoda	<i>Hyas coarctatus</i>	Meroplankton	Decapod larvae
Crustacea	Decapoda	<i>Munida sarsi</i>	Meroplankton	Decapod larvae
Crustacea	Decapoda	<i>Pagurus pubescens</i>	Meroplankton	Decapod larvae
Crustacea	Decapoda	<i>Pandalus borealis</i>	Meroplankton	Decapod larvae
Crustacea	Decapoda	<i>Pandalus</i> sp.	Meroplankton	Decapod larvae
Crustacea	Decapoda	<i>Sabinea septemcarinata</i>	Meroplankton	Decapod larvae
Crustacea	Euphausiacea	<i>Meganyctiphanes norvegica</i>	Non-copepod holoplankton	Euphausiacea
Crustacea	Euphausiacea	<i>Thysanoessa inermis</i>	Non-copepod holoplankton	Euphausiacea
Crustacea	Euphausiacea	<i>Thysanoessa raschii</i>	Non-copepod holoplankton	Euphausiacea
Crustacea	Isopoda		Non-copepod holoplankton	Isopoda indet.
Ctenophora	Ctenophora	Ctenophora indet.	Non-copepod holoplankton	Not observed
Echinodermata	Asteroidea	<i>Asterias rubens</i>	Meroplankton	Echinoderm larvae
Echinodermata	Asteroidea	<i>Ctenodiscus australis</i>	Meroplankton	Echinoderm larvae
Echinodermata	Asteroidea	<i>Solaster endeca</i>	Meroplankton	Echinoderm larvae
Echinodermata	Echinoidea	<i>Echinocardium cordatum</i>	Meroplankton	Echinoderm larvae
Echinodermata	Echinoidea	<i>Echinus esculentus</i>	Meroplankton	Echinoderm larvae
Echinodermata	Echinoidea	<i>Strongylocentrotus droebachiensis</i>	Meroplankton	Echinoderm larvae
Echinodermata	Echinoidea	<i>Strongylocentrotus pallidus</i>	Meroplankton	Echinoderm larvae
Echinodermata	Holothuroidea	<i>Cucumaria frondosa</i>	Meroplankton	Echinoderm larvae
Echinodermata	Holothuroidea	<i>Labidoplax buskii</i>	Meroplankton	Echinoderm larvae
Echinodermata	Holothuroidea	<i>Thyonidium drummondii</i>	Meroplankton	Echinoderm larvae
Echinodermata	Ophiuroidea	<i>Ophiocten affinis</i>	Meroplankton	Echinoderm larvae
Echinodermata	Ophiuroidea	<i>Ophiopholis aculeata</i>	Meroplankton	Echinoderm larvae
Echinodermata	Ophiuroidea	<i>Ophiura albida</i>	Meroplankton	Echinoderm larvae
Echinodermata	Ophiuroidea	<i>Ophiura robusta</i>	Meroplankton	Echinoderm larvae
Mollusca	Bivalvia	<i>Hiatella</i> sp.	Meroplankton	Bivalve larvae
Mollusca	Gastropoda	<i>Aporrhais pespelecani</i>	Meroplankton	Gastropod larvae
Mollusca	Gastropoda	<i>Eubranchus exiguus</i>	Meroplankton	Gastropod larvae
Mollusca	Gastropoda	Gastropoda	Meroplankton	Gastropod larvae
Mollusca	Gastropoda	<i>Lacuna vincta</i>	Meroplankton	Gastropod larvae
Mollusca	Gastropoda	<i>Limapontia capitata</i>	Meroplankton	Gastropod larvae
Mollusca	Gastropoda	<i>Microchlamylla gracilis</i>	Meroplankton	Gastropod larvae
Mollusca	Gastropoda	<i>Oenopota</i> sp.	Meroplankton	Gastropod larvae
Mollusca	Gastropoda	<i>Placida dendritica</i>	Meroplankton	Gastropod larvae
Mollusca	Gastropoda	<i>Velutina velutina</i>	Meroplankton	Gastropod larvae
Mollusca	Polyplacophora	<i>Tonicella marmorea</i>	Meroplankton	Not observed
Nematoda			Non-copepod holoplankton	Not observed
Nemertea		<i>Malacobdella grossa</i>	Meroplankton	Not observed
Nemertea		<i>Micrura varicolor</i>	Meroplankton	Not observed
Platyhelminthes			Non-copepod holoplankton	Not observed
Polychaeta	Amphinomida	<i>Paramphinome jeffreysii</i>	Neroplankton	Polychaete larvae
Polychaeta	Capitellida	<i>Capitella capitata</i>	Meroplankton	Polychaete larvae
Polychaeta	Capitellida		Meroplankton	Polychaete larvae
Polychaeta	Eunicida indet.		Meroplankton	Polychaete larvae
Polychaeta	Eunicida	Dorvilleidae indet.	Meroplankton	Polychaete larvae
Polychaeta	Eunicida	<i>Nothria conchylega</i> CMC02	Meroplankton	Polychaete larvae
Polychaeta	Maldanidae	<i>Euclymene zonalis</i>	Meroplankton	Polychaete larvae
Polychaeta	Maldanidae	<i>Maldane sarsi</i>	Meroplankton	Polychaete larvae
Polychaeta	Orbiniidae	<i>Scoloplos armiger</i>	Meroplankton	Polychaete larvae
Polychaeta	Phyllodocida		Meroplankton	Polychaete larvae

(Continued)

TABLE 2 | Continued

Phylum/Subphylum	Class/Order	Species	Category	Visually identified as
Polychaeta	Phyllodocida	<i>Aglaophamus malmgreni</i>	Meroplankton	Polychaete larvae
Polychaeta	Phyllodocida	<i>Antinoella finmarchica</i>	Meroplankton	Polychaete larvae
Polychaeta	Phyllodocida	<i>Bylgides sarsi</i>	Meroplankton	Polychaete larvae
Polychaeta	Phyllodocida	<i>Eunoe oerstedii</i>	Meroplankton	Polychaete larvae
Polychaeta	Phyllodocida	<i>Gyptis mackiei</i>	Meroplankton	Polychaete larvae
Polychaeta	Phyllodocida	<i>Harmothoe sarsi</i>	Meroplankton	Polychaete larvae
Polychaeta	Phyllodocida	<i>Harmothoe</i> sp. CMC01	Meroplankton	Polychaete larvae
Polychaeta	Phyllodocida	<i>Lepidonotus squamatus</i>	Meroplankton	Polychaete larvae
Polychaeta	Phyllodocida	<i>Nereimyra punctata</i>	Meroplankton	Polychaete larvae
Polychaeta	Phyllodocida	<i>Pholoe baltica</i>	Meroplankton	Polychaete larvae
Polychaeta	Phyllodocida	<i>Phyllodoce grenlandica</i>	Meroplankton	Polychaete larvae
Polychaeta	Phyllodocida	<i>Phyllodoce</i> sp.	Meroplankton	Polychaete larvae
Polychaeta	Phyllodocida	<i>Tomopteris</i> sp.	Non-copepod holoplankton	<i>Tomopteris</i> sp.
Polychaeta	Sabellida	<i>Hydroides elegans</i>	Meroplankton	Polychaete larvae
Polychaeta	Sabellida		Meroplankton	Polychaete larvae
Polychaeta	Scalibregmatidae	<i>Scalibregma inflatum</i>	Meroplankton	Polychaete larvae
Polychaeta	Spionida	<i>Spionidae</i> <i>indet.</i>	Meroplankton	Polychaete larvae
Polychaeta	Spionida		Meroplankton	Polychaete larvae
Polychaeta	Spionida	<i>Laonice cirrata</i>	Meroplankton	Polychaete larvae
Polychaeta	Spionida	<i>Scolelepis</i> sp.	Meroplankton	Polychaete larvae
Polychaeta	Spionida	<i>Spio</i> sp.	Meroplankton	Polychaete larvae
Polychaeta	Spionida	<i>Spiophanes kroyeri</i>	Meroplankton	Polychaete larvae
Polychaeta	Spionida	<i>Spiophanes</i> sp.	Meroplankton	Polychaete larvae
Polychaeta	Terebellida	<i>Ampharete finmarchica</i>	Meroplankton	Polychaete larvae
Polychaeta	Terebellida	<i>Amphitrite cirrata</i>	Meroplankton	Polychaete larvae
Polychaeta	Terebellida	<i>Chaetozone setosa</i>	Meroplankton	Polychaete larvae
Polychaeta	Terebellida	<i>Flabelligera affinis</i>	Meroplankton	Polychaete larvae
Polychaeta	Terebellida	<i>Lanassa venusta</i>	Meroplankton	Polychaete larvae
Polychaeta	Terebellida	<i>Melinna elisabethae</i>	Meroplankton	Polychaete larvae
Polychaeta	Terebellida	<i>Neoamphitrite grayi</i>	Meroplankton	Polychaete larvae
Polychaeta	Terebellida	<i>Pectinaria koreni</i>	Meroplankton	Polychaete larvae
Polychaeta	Terebellida	<i>Pista maculata</i>	Meroplankton	Polychaete larvae
Polychaeta	Terebellida	<i>Polycirrus medusa</i>	Meroplankton	Polychaete larvae
Polychaeta	Terebellida	<i>Polycirrus</i> sp.	Meroplankton	Polychaete larvae
Polychaeta	Terebellida	<i>Terebellidae</i> <i>indet.</i>	Meroplankton	Polychaete larvae
Polychaeta	Terebellida	<i>Thelepus cincinnatus</i>	Meroplankton	Polychaete larvae
Polychaeta	Terebellida		Meroplankton	Polychaete larvae
Rotifera	Ploima		Non-copepod holoplankton	Not observed
Pisces	Gadiformes	<i>Melanogrammus aeglefinus</i>	Fish	Not observed
Pisces	Pleuronectiformes	<i>Hippoglossoides platessoides</i>	Fish	Not observed
Pisces	Pleuronectiformes	<i>Microstomus kitt</i>	Fish	Not observed
Chlorophyta	Mamiellales	<i>Bathycoccus prasinos</i>	Phytoplankton	NA
Haptophyta	Prymnesiophyceae	<i>Phaeocystis</i> spp.	Phytoplankton	NA
Ochrophyta	Bacillariophyceae	<i>Chaetoceros</i> spp.	Phytoplankton	NA
Ochrophyta	Bacillariophyceae		Phytoplankton	NA
Pyrrophytophyta	Dinophyceae <i>indet.</i>		Phytoplankton	NA
Pyrrophytophyta			Phytoplankton	NA

The iNEXT R package (Hsieh et al., 2016) was used to ensure that the richness saturation plateau was reached for all samples (Supplementary Figure 3).

Data Analysis

We used the metabarcoding data as a semi-quantitative estimate of relative biomass of zooplankton taxa

(Ershova et al., In revision) by multiplying the total zooplankton biomass with the proportion of the sequence reads for each species for each corresponding month to calculate biomass-weighted sequence reads (BWSR, mg DW m⁻²).

Multivariate analyses of the community composition were performed on morphological identification data (abundance). An estimation of the abundance of *C. finmarchicus*, *C. glacialis*, *C. helgolandicus*, *P. acuspes*, *P. elongatus*, *P. minutus*, and *P. moultoni* was calculated based on the relative composition obtained with metabarcoding, by multiplying the genus abundance by the proportion of the targeted species, and add to the data set used for the multivariate analysis. As metabarcoding data were missing in mid-April, the abundances estimation at this sampling point was estimated as the average of estimated abundance over the entire period. Abundance data were fourth-root transformed in order to reduce the impact of super abundant and rare species. Copepod nauplii, *Microsetella norvegica* and rare copepods species were excluded from the analyses since abundance estimates of these taxa were likely biased due to the change of the net mesh size over the study period. Chi-squared distances were calculated and used to perform hierarchical cluster analysis.

To elucidate the relationships between zooplankton community structure across seasons and environmental parameters, a Canonical Correspondence Analysis (CCA) was performed using the previously described data set. Explanatory variables included average water column temperature salinity and algal fluorescence obtained from the CTD profile as well as the Chl *a* concentrations from water samples. The significance of the overall model and individual terms was calculated using permutation tests [ANOVA function in the R package *vegan*; Oksanen et al., 2020] at a significance level of $p < 0.05$ and only significant constraining factors were retained. Missing CTD data in mid-April were assumed to be similar to the ones obtained 14 days before in early April. Missing measurements of Chl *a* concentrations in August, early September and February 2020 were replaced by the average Chl *a* concentration over the study period. All analyses were performed using R (version 4.0.1) (R Core Team, 2020) and the package *vegan* (Oksanen et al., 2020).

RESULTS

Hydrography

The water column was cold, and well mixed from January to mid-May. The lowest temperatures were observed between March and May (0–2°C) (Figure 2A). The surface started to warm in mid-May, and from mid-May to August, the water column was stratified with warm water (5–10°C) in the uppermost 40 m and colder water (around 4°C) below 70 m. By September, the entire water column had warmed to >6°C and highest surface temperatures (12°C) were observed in early September. The water column started to cool down in November, and for the rest of the year the water was well mixed. From mid-December the water temperature was between 2 and 4°C (Figure 2A). Salinity varied between 32 and 33.5 throughout the year in most samples (Figure 2B). A relative fresh surface layer (salinity < 25)

was observed starting in mid-May, coinciding with the onset of snowmelt on land resulting in increased freshwater runoff.

Chlorophyll and Phytoplankton Community

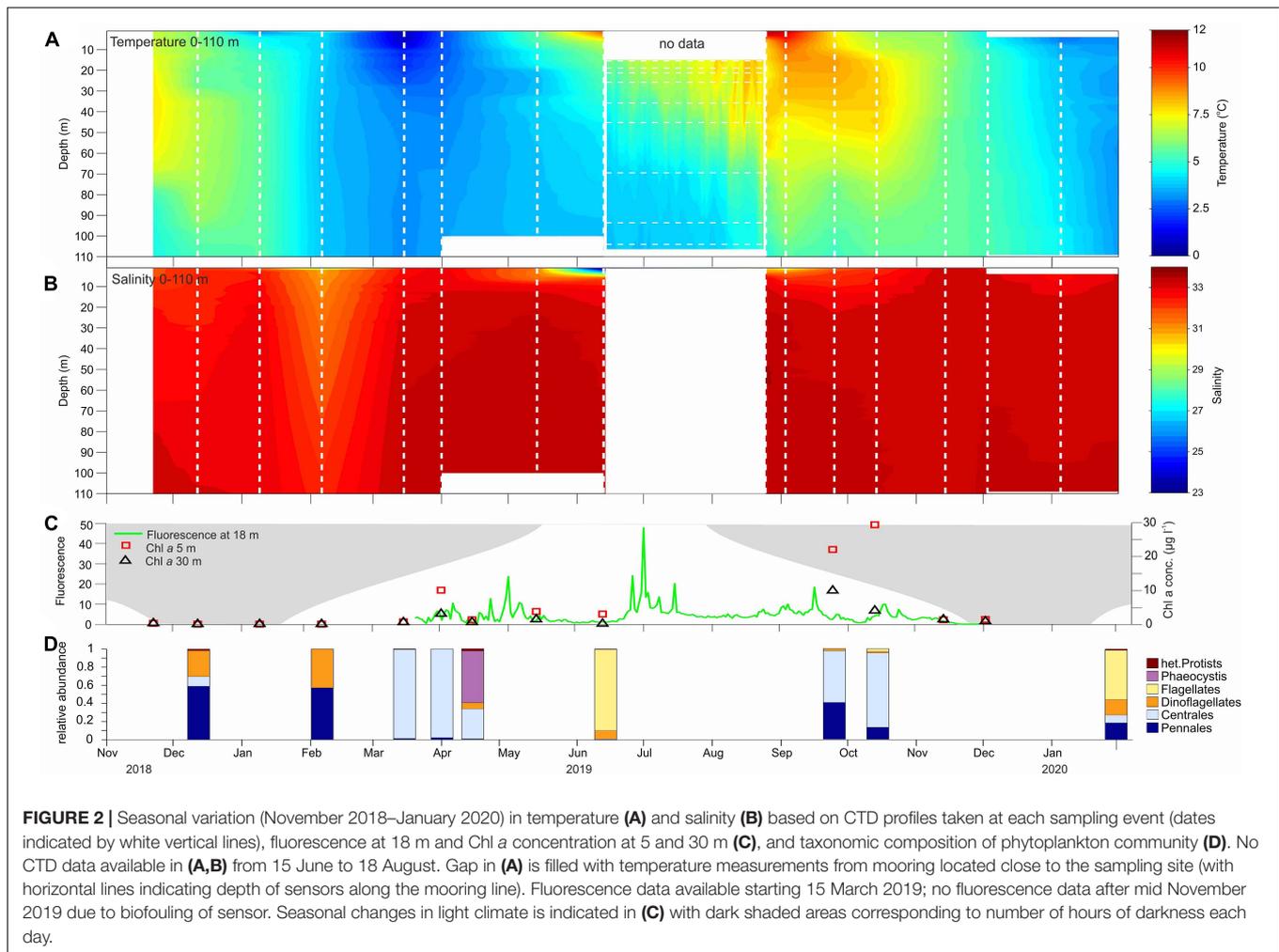
In situ concentrations of Chl *a* were low from November to March (Figure 2C). The abundance of microalgae was low, and the community consisted mainly of pennate diatoms and dinoflagellates during the polar night and in February 2019, while flagellates dominated in February 2020 (Figure 2D). Chl *a* concentration and fluorescence increased strongly in early April (10.2 mg m⁻³ at 5 m) and the algae community was dominated by centric diatoms (mainly *Chaetoceros socialis*; Figure 2D). By mid-April, the prymnesiophyte *Phaeocystis pouchetii* dominated, but Chl *a* concentration and fluorescence were low. Fluorescence at 18 m depth peaked in early May (~20 mg m⁻³), coinciding with the onset of stratification, and in July (~50 mg m⁻³). However, no Chl *a* and phytoplankton data are available in those periods. In June, flagellates, mainly *Chrysochromulina* sp. dominated the phytoplankton community, and the fluorescence and Chl *a* concentrations (3 mg m⁻³) were relatively low (Figures 2C,D). Very high Chl *a* concentrations at the end of September (22 mg m⁻³) and in October (29 mg m⁻³) at both depth, indicate the occurrence of an intense autumn phytoplankton bloom dominated by centric diatoms (*Chaetoceros* sp.). Interestingly, this signal was not caught by the fluorescence sensors on the mooring in 18 m depth. From late November 2019 the fluorescence sensor did not provide reliable readings due to biofouling and *in situ* Chl *a* concentrations were low.

Seasonal Variability in the Zooplankton Community

Mesozooplankton Diversity

Thirty-five unique taxa were identified morphologically over the study period. Of these, 25 belonged to holoplankton, including 13 species of copepods: nine species or genera of small copepods and four species or genera of large copepods (Table 2). Ten taxonomic groups (class or phylum) of meroplankton were identified. The highest specific richness was observed in late April, and the lowest in February (2020). Only five copepod taxa were present throughout the entire study (i.e., *Calanus* spp., *Pseudocalanus* spp., *Microcalanus pusillus*, *Oithona similis*, *Acartia longiremis*), while all other taxa were absent during some months.

Metabarcoding revealed a total of 490 MOTUs, which corresponded to 154 unique taxa (Table 2). Hundred and fourteen of these were identified to species level, 17 to genus, and 22 to family or broader. Of the 154 unique identified taxa, 121 were present in more than four samples (Supplementary Table 1). Twenty-six species were present during every month, but only two of them (*Pseudocalanus acuspes* and *M. pusillus*) represented more than 1% of the sequence reads every month. Seven species represented at least 1% of the sequence reads during most of the months. These included *A. longiremis*, *Calanus finmarchicus*, *C. glacialis*, *O. similis*, *Pseudocalanus moultoni*, *Nanomia cara*, and *Parasagitta elegans*.



Of the 154 identified taxa, 36% (55) belonged to the holoplankton, while 58% (90) are known as benthic species and were therefore categorized as meroplankton. The remaining nine belong to fish and phytoplankton groups. Polychaeta presented the highest species richness with 46 taxa identified. Copepods were second in terms of number of taxa with 27 taxa identified over the study period (Table 2). Cnidaria and echinodermata were well represented as well, with respectively 15 and 14 taxa identified (Table 2). However, half of the identified cnidarians were present during only 1–4 months. Other groups such as bivalvia, amphipoda, ctenophora or chitonida were only detected as single taxa, generally identified at taxonomic levels above species (Table 2). Metabarcoding indicated that species richness was highest between December 2018 and February 2019 with a maximum number of species (110) in February (Table 3). It is noteworthy that during this period, sampling was conducted using a smaller mesh size. Between April and late September, the species richness varied between 80 and 104. Species richness was lowest between October 2019 and February 2020, when a different DNA extraction kit was used (Table 1 and Supplementary Figure 2B), with around 50 taxa identified, while between 80 and 110 taxa were identified in the other months

(Table 3). The use of a different DNA extraction kit reduced the diversity that we were able to identify (Supplementary Figure 2). However, it did not impact the diversity of Copepoda taxa that we were able to detect (Supplementary Figure 2B). A maximum Copepoda species richness of 26–28 was reached between November 2018 and February 2019 (Table 3) when we used the smallest net mesh size (Table 1). However, it reached the same number in September (Table 3) when the largest net mesh size was used (Table 1).

Mesozooplankton Biomass, Abundance, and Community Structure

Total mesozooplankton abundance and biomass in Ramfjord varied between 1.2×10^4 to 23×10^4 ind m^{-2} and 174 to 2609 mg DW m^{-2} , respectively. Lowest abundance and biomass were measured between December and March during both winter seasons, while the highest values were recorded in summer/early autumn between August and October (Figures 3A,B). The mesozooplankton community was dominated in terms of abundance and biomass by small copepods (adult size < 1.5 mm) all year-round (Figures 3C,D). Small copepods represented up to 97% of the community in terms of abundance and up to

TABLE 3 | Species richness in Ramfjord based on metabarcoding analysis.

Date	Total species richness	Zooplankton species richness	Copepod species richness
18.11.2018	89	80	26
11.12.2018	108	99	27
09.01.2019	107	98	28
06.02.2019	109	100	26
13.03.2019	94	85	23
01.04.2019	103	94	24
14.04.2019	NA	NA	NA
14.05.2019	92	83	24
13.06.2019	84	75	24
20.08.2019	79	90	21
03.09.2019	90	81	26
25.09.2019	100	91	25
14.10.2019	52	43	22
14.11.2019	57	48	22
03.12.2019	55	46	20
04.02.2020	47	38	19

The total species richness included all species or taxa identified. For the zooplankton species richness phytoplankton and fish species were removed.

94% in terms of sequence read (Figures 3C,D). Non-copepod holoplankton (Figure 3 and Table 2), consisting mainly of chaetognaths and krill, dominated in terms of sequence reads in November and December 2018, although their abundance was negligible (<1%). In late April, a high number of krill eggs was observed (64920 ind m⁻²). The estimated BWSR of non-copepods varied between 0.44 mg DW m⁻² in November 2019 and 690.96 mg DW m⁻² in late September, which accounts for <0.1% to 55% of the total biomass (Figure 3D).

Large copepods (>2 mm at adult stage) were present year around, with highest abundance observed between April and June (Figure 3C). In terms of abundance, they represented a maximum of 27% of the zooplankton community in May, but only 2% in early September (Figure 3C). High abundances of copepod nauplii were recorded in February and March, accounting for up to 49% of the total abundance (Figure 3C). The highest BWSR of large copepods was observed in June (253 mg DW m⁻²), and their contribution to the sequence reads varied between 1 and 25%, in November 2019 and June, respectively (Figure 3D).

Small copepods

The lowest proportion of small copepods, in terms of abundance, was observed in late April when only 20% of the community consisted of small copepods, while they represented between 50 and 90% of the community during the rest of the year (Figure 3C). The BWSR of small copepods varied between 0.35 mg DW m⁻² in early April and 1359 mg DW m⁻² in late September. The small copepods community had a relatively high diversity with nine species identified morphologically and 24 species detected using metabarcoding (Table 2). *Acartia longiremis*, *M. pusillus*, *O. similis* and four species of *Pseudocalanus* (*P. acuspes*, *P. elongatus*, *P. minutus*, *P. moultoni*) were present in Ramfjord year-round (Supplementary Table 1). These species represented more than 1% of all the sequence reads, together with *Paracalanus parvus* and *Temora longicornis*. We combined these species as the main representatives of the small copepod community (Figure 4). *Paracalanus parvus* was not observed visually, likely due to its morphological similarity to *Pseudocalanus* spp. at juvenile stages (Table 2 and Figure 4).

The abundance of small copepods was relatively low between November and May (<3.10⁴ ind m²) (Figure 4). Only

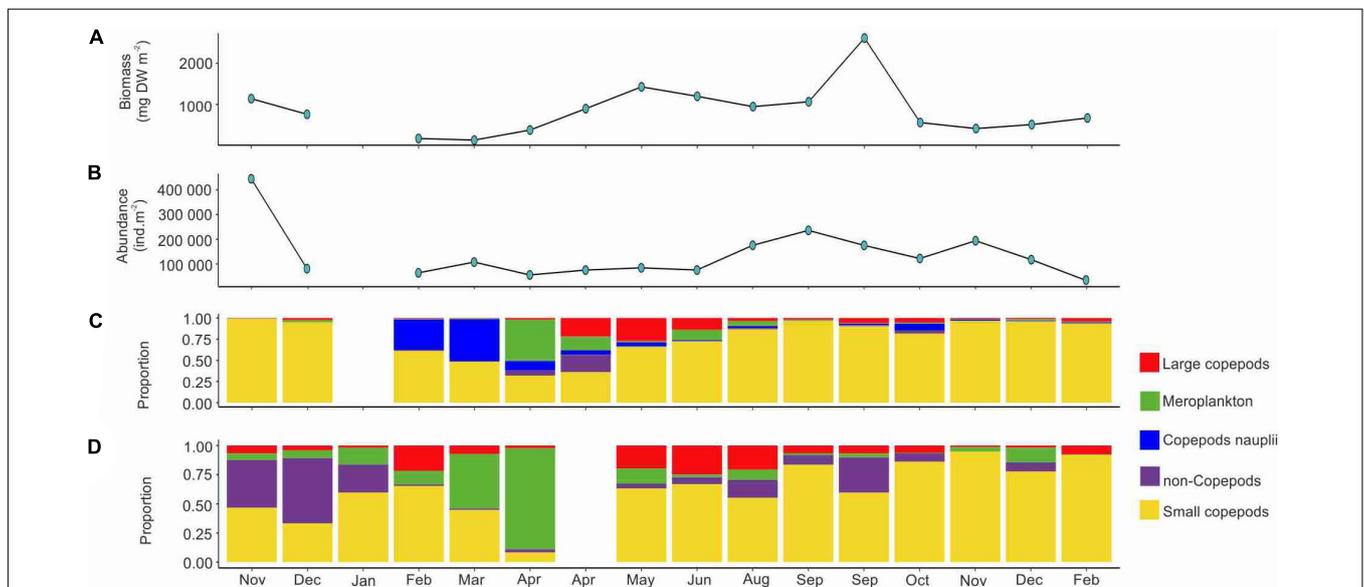


FIGURE 3 | Seasonal changes in the total zooplankton biomass (A), total zooplankton abundance (B), proportions of main taxonomic groups based on morphological analysis (C), and metabarcoding (D) in Ramfjord during November 2018–February 2020.

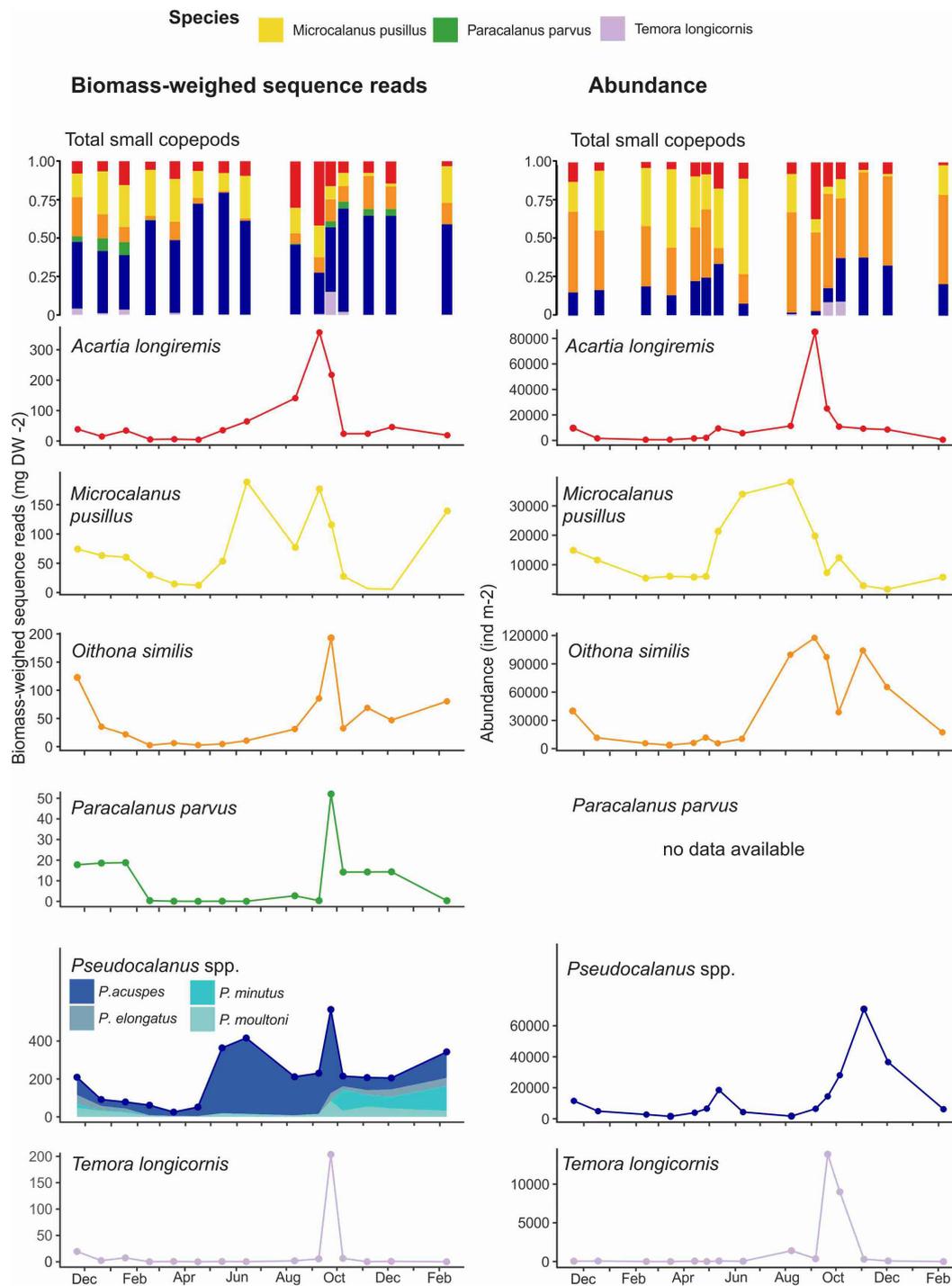


FIGURE 4 | Seasonal changes in small copepod BWSR (mg DW m^{-2} , left column) and abundance ($\text{individuals m}^{-2}$, right column) in Ramfjord between November 2018 and February 2020. The first row represents the relative proportion of the main small copepod species to the small copepod community remaining rows represent the seasonal variation of the main small copepod species.

Microsetella norvegica had a peak in abundance during this time, dominating the community in terms of abundance in February and March 2019 with up to 39×10^3 ind m^2 . However, the number of sequence reads of *M. norvegica* was

negligible (less than 1% of the total sequence reads) during the entire study period.

From May, the abundance of small copepods increased and reached its maximum in September (23×10^4 ind m^{-2}).

O. similis dominated the small copepod community throughout most of the study period in terms of abundance, contributing up to 65% and with a maximum abundance of 11×10^4 ind m^{-2} in September (Figure 4). In terms of sequence reads, *O. similis* represented a low portion of the small copepod community, with a maximum of 20% in November 2019 (Figure 4), and its BWSR varied from 1 mg DW m^{-2} to 192 mg DW m^{-2} .

Between November 2018 and January 2019, the small copepod community as estimated by BWSR was represented by all the main species depicted in Figure 4. The contribution of *O. similis* and *M. pusillus* BWSR was slightly higher, contributing 24 and 27%, respectively, while the other species contributed 1–15% to the small copepod BWSR (Figure 4). Between February and August *P. acuspes* dominated the community in terms of BWSR (up to 73%), which varied between 33 mg DW m^{-2} and 441 mg DW m^{-2} (Figure 4). The rest of the BWSR was composed of *A. longiremis* (between 5 and 41%) and *M. pusillus* (between 1.7 and 28%) (Figure 4). From late September to the end of the study, copepods of the genus *Pseudocalanus* dominated the small copepod community in terms of the BWSR (Figure 4). *P. minutus* had the highest proportion of sequence reads, up to 35% in October, with a BWSR varying from 1.94 mg DW m^{-2} to 113 mg DW m^{-2} . *Pseudocalanus elongatus* contributed least to the *Pseudocalanus* biomass, representing only between 2 and 12% of the small copepod BWSR between late September and December 2019 (Figure 4).

Meroplankton community

Eight groups of meroplankton, the six presented in Figure 3 plus Bryozoa and Decapoda, were identified during the entire study period.

Meroplankton accounted for only 0.5–12% of the total zooplankton abundance between November 2018 and August 2019, and the abundance was negligible during the study period except in April when Chl *a* concentrations were high (Figure 3C). However, meroplankton BWSR varied between 1.81 mg DW m^{-2} in late September and 312 mg DW m^{-2} in March, which represented respectively 3.1 and 46% of the BWSR. The highest proportion of meroplankton, in terms of BWSR, was observed in early April when it accounted for 86% of the total BWSR (Figure 3C).

The composition of the meroplankton community estimated by metabarcoding followed the overall trends provided by morphological analysis, but with a higher taxonomic resolution. Polychaeta larvae and juveniles were present year-round in Ramfjord (Figure 5) and made up a high proportion of the meroplankton community in terms of abundance, contributing between 9% in October and 82% in December 2019 (Figure 5). The highest abundance of polychaeta larvae was observed in mid-April (4360 ind m^{-2}) (Figure 5). They dominated the meroplankton community in terms of BWSR between November 2018 and March 2019 and between October and December 2019 when they accounted for 14–80% of the meroplankton BWSR (Figure 5). Cirripedia larvae dominated the meroplankton community in terms of abundance and BWSR in April with a peak in abundance (19×10^3 ind m^{-2}) in mid-April

(Figure 5). In June, echinoderm larvae accounted for 89% of the meroplankton abundance and 70% of the meroplankton BWSR (Figure 5). Their maximum abundance, 8.2×10^3 ind m^{-2} , was also observed in June (Figure 5).

Juveniles bivalves dominated the meroplankton community between November 2018 and February 2019 (23–68% of meroplankton) (Figure 5), and between August and November 2019 (up to 70%; Figure 5), with a peak in abundance in August (62×10^2 ind m^{-2}). However, their BWSR was low or negligible over the entire study period (Figure 5). Likewise, the BWSR of gastropod larvae was low, never contributing more than 7% to the meroplankton community (Figure 5). However, in terms of abundance they represented up to 43% of the community in February 2019 (Figure 5).

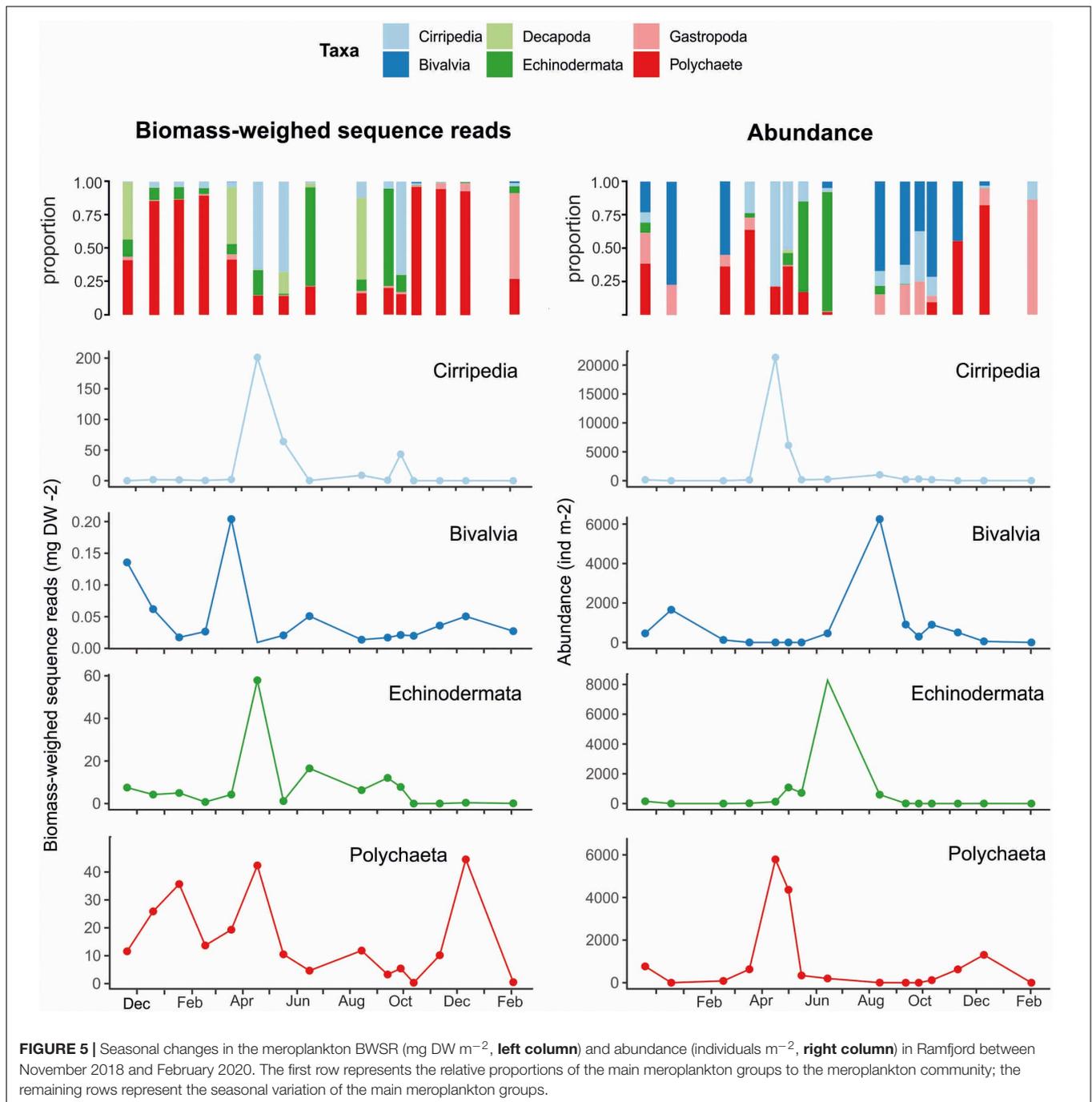
Calanus spp. species and stage composition

Based on morphological characteristics, only *Calanus hyperboreus* copepodite stage III (CIII)-adults could be identified with confidence and their abundance was overall very low (maximum 80 ind. m^{-2} in May). We did not identify other *Calanus* individuals to species morphologically and defined them as *Calanus* spp. Abundance of *Calanus* spp. was relatively low between November and early April (around 1000 ind. m^{-2}) and reached a maximum of 20 820 ind. m^{-2} in May (Figure 6A). In March and April, adult stages dominated the *Calanus* spp. population, with females contributing 77% in March and 66% in early April (Figure 6B). In mid-April, males were the dominating stage, representing 50% of the population (Figure 6B). Young copepodite stages (CI, CII, and CIII) started to appear in March, and were dominating the population in May (Figure 6B). Older copepodite stages (CIV and CV) were present in later winter (February–March), reappeared in higher proportions in May and were dominating the population from June on for the rest of the year (Figure 6B). CVs contributed up to 93% of the population between June and October (Figure 6B). A second peak in *Calanus* spp. abundance (10428 ind. m^{-2}) was observed in late September (Figure 6A). In October and November, CIIIs were detected again, representing 20 and 40% of the population, respectively (Figure 6B).

Metabarcoding detected the presence of four species of the genus *Calanus*: *C. hyperboreus*, *C. finmarchicus*, *C. glacialis*, and *C. helgolandicus* (Figure 6C). *C. finmarchicus* and *C. glacialis* dominated the *Calanus* community in Ramfjord for most part of the year, contributing equally in September, while *C. finmarchicus* dominated in February and March, and from October to December, and *C. glacialis* in January, and from April to June. In contrast to the low abundance observed, *C. hyperboreus* BWSR was relatively high between November 2018 and January 2019 and from April to August, when they represented between 0.3 and 64% of the *Calanus* sequence reads (Figure 6C). The contribution of *C. helgolandicus* to the *Calanus* community was low year-round (from 0 to 19%), with higher proportion observed during autumn-winter months (between 0.1 and 19%) (Figure 6C).

Seasonality of zooplankton community in Ramfjord

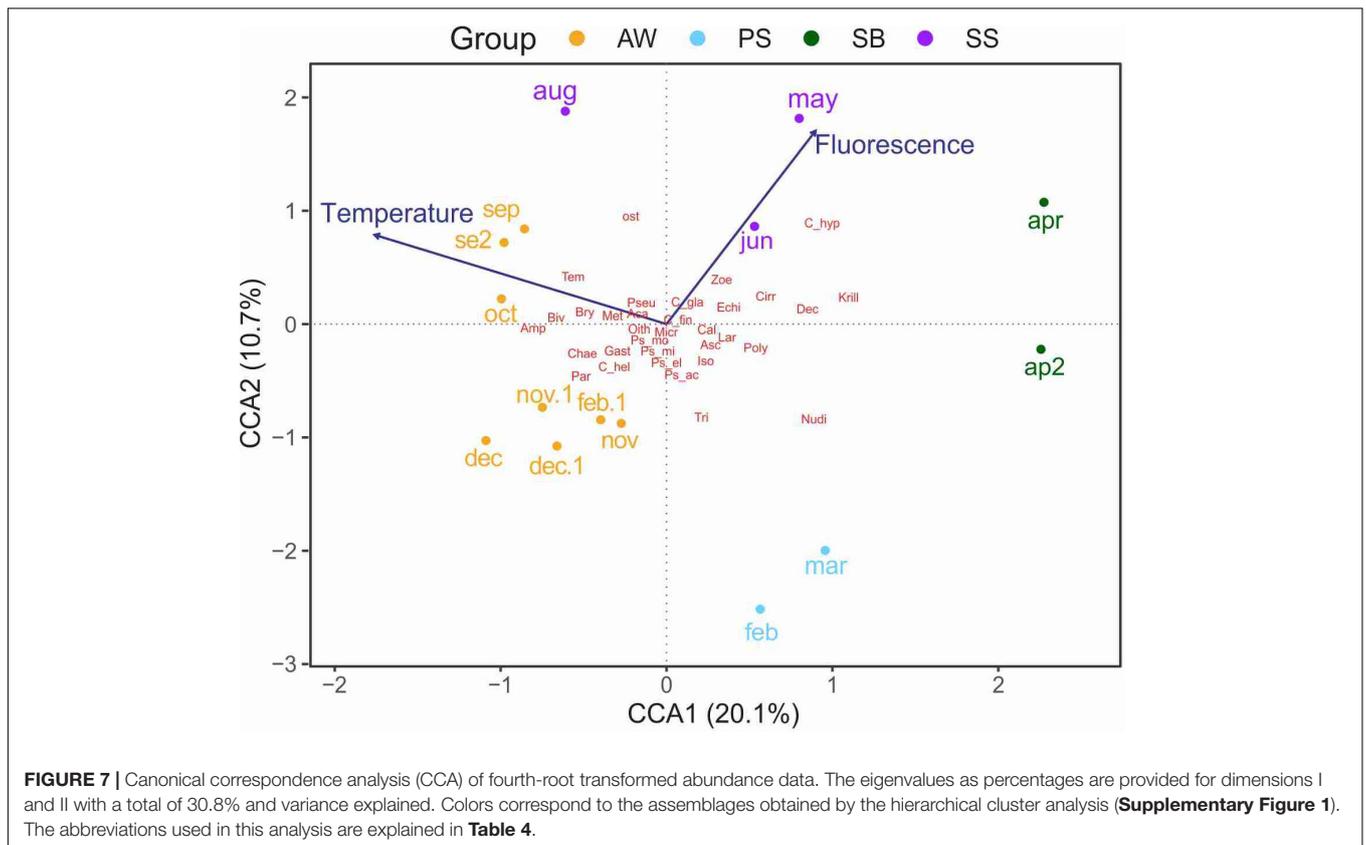
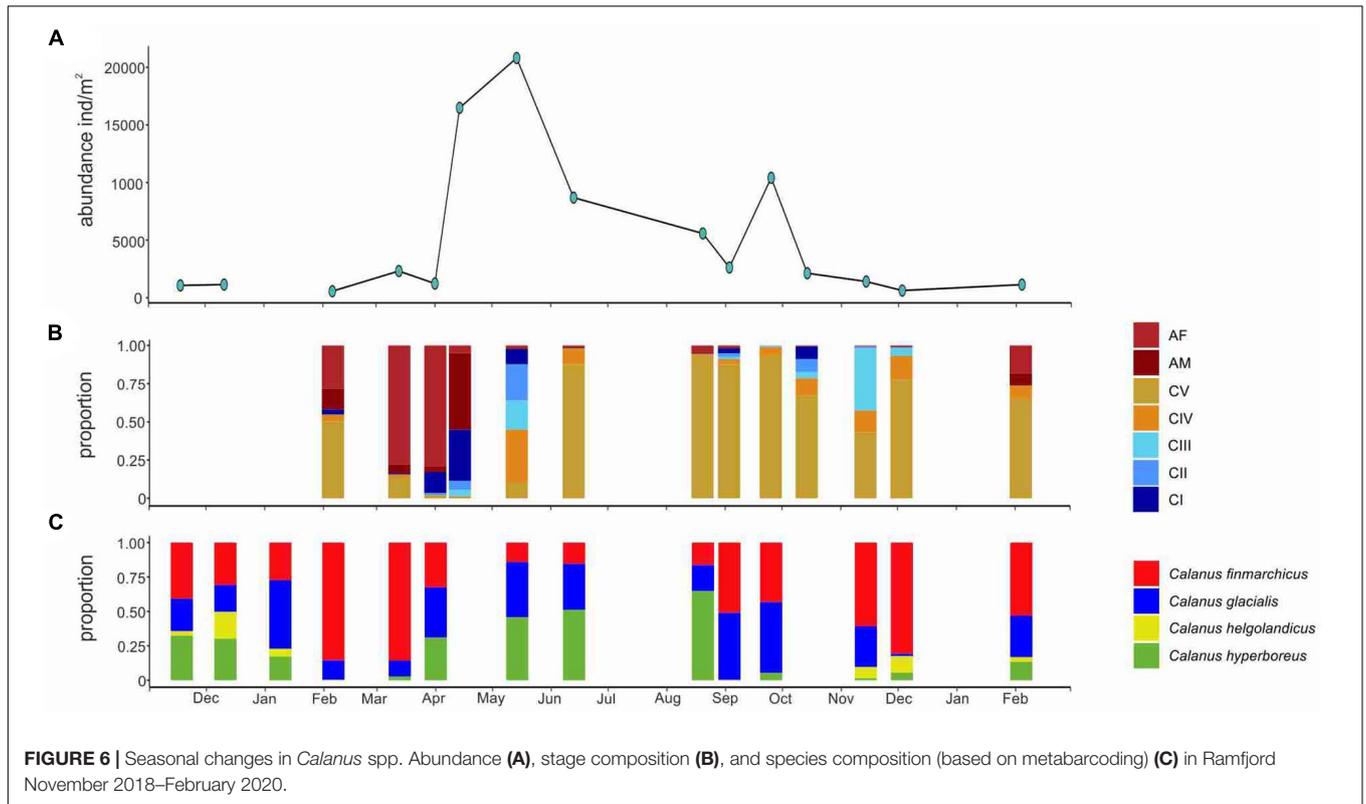
Hierarchical cluster analysis of abundance data of the entire zooplankton community, identified four main assemblages:



spring bloom (SB), spring/summer (SS), Autumn/winter (AW), and pre-spring bloom (PS) (**Supplementary Figure 1**).

The CCA models was significant ($p < 0.05$) with temperature and fluorescence as significant constraining factors ($p < 0.05$), while salinity and Chl *a* were insignificant. The resulting CCA model for abundance explained 29% of the total inertia (variance) in the abundance data, with 21% accounted for by the first axis (**Figure 7**). The results of the CCA were consistent with the cluster analysis, showing a clear separation of the samples based on season. The two April samples formed their own

group (SB), being distinguished by the presence of cirripedia nauplii, euphausiid larvae and decapod larvae (**Figure 7**), and a high abundance of krill eggs (1333 ind m^{-2}) The SB and PSB assemblages were most distinct on the ordination, while SS and AW grouped closer together (**Figure 7**). The SS group was distinguished by relatively high fluorescence and water temperatures (**Figure 7**), and a higher abundance of *Calanus* spp. (**Figure 7**), particularly *C. hyperboreus* and *C. glacialis* (**Figure 7**), as well as echinoderm larvae and *A. longiremis*. The AW group was characterized by a wide range of water temperatures and low



fluorescence. Furthermore, high abundance of small copepods (e.g., *O. similis*, *Pseudocalanus* spp., *M. pusillus*), *Metridia longa*, *Paraeuchaeta norvegica*, gastropoda larvae, chaetognatha and a relatively low abundance of *Calanus* spp. were characteristic

for AW. The PS group, which included February and March samples, was characterized by low temperatures and fluorescence. Zooplankton abundance was overall low within this group, with a higher relative contribution of nudibranch larvae and *Triconia* sp. Although they were not included in the multivariate analyses, during this season we also registered a high abundance of copepod nauplii (23348 ind m⁻² in February and 53908 ind m⁻² in March).

TABLE 4 | List of abbreviation used in the CCAs and their meaning.

Abbreviation	Meaning
C_fin	<i>Calanus finmarchicus</i>
C_gla	<i>Calanus glacialis</i>
C_hel	<i>Calanus helgolandicus</i>
Oith	<i>Oithona similis</i>
Micr	<i>Microcalanus pusillus</i>
Pseu	<i>Pseudocalanus</i> spp.
Ps_el	<i>Pseudocalanus elongatus</i>
Ps_mi	<i>Pseudocalanus minutus</i>
Ps_mo	<i>Pseudocalanus moultoni</i>
Ps_ac	<i>Pseudocalanus acuspes</i>
Tri	<i>Triconia</i> sp.
Met	<i>Metridia</i> spp.
Aca	<i>Acartia longicornis</i>
Par	<i>Paraeuchaeta</i> spp.
Tem	<i>Temora longiremis</i>
C_hyp	<i>Calanus hyperboreus</i>
Amp	Amphipoda
Lar	Appendicularia
Asc	Ascidia
Biv	Bivalves juvenile
Bry	Bryozoa
Chae	Chaetognatha
Cirr	Cirripedia
Ost	Ostracoda
Dec	Decapod
Echi	Echinodermata
Gast	Gastropoda
Iso	Isopoda
Krill	Krill larvae
Nudi	Nudibranche
Poly	Polychaeta larvae
Zoe	Zoea
nov	November 2018
dec	December 2018
jan	January 2019
feb	February 2019
mar	March 2019
apr	Early April 2019
ap2	Mid-April 2019
may	May 2019
jun	June 2019
aug	August 2019
sep	Early September 2019
se2	Late September 2019
oct	October 2019
nov.1	November 2019
dec.1	December 2019
feb.1	February 2020

DISCUSSION

The present study is one of only a few studies combining metabarcoding and morphological identification to study the seasonal variability of a zooplankton community with relatively high temporal resolution (Gran-Stadniczeňko et al., 2019; Schroeder et al., 2020). This approach enabled us to describe the seasonal variability of the zooplankton community in Ramfjord with high quantitative and taxonomical accuracy, while at the same time also linking the detected changes to environmental variables.

The Zooplankton Community Diversity

Using metabarcoding, we identified 154 taxa in Ramfjord over the study period, which was four times as many taxa as using the morphological identification alone. The mesozooplankton diversity in this fjord system has previously been described as low (Hopkins, 1981) although the authors did not specify compared to what this assessment was made. Mesozooplankton diversity is rarely fully described, but compared to other well-studied high latitude fjords, such as Kongsfjorden (97 taxa over 20-year-long time series, Hop et al., 2019b), Rijpfjorden (42 taxa over 8 months) (Weydmann et al., 2013) and Dolgaya Bay (33 taxa in July, Dvoretzky and Dvoretzky, 2010), the zooplankton community in Ramfjord does not appear to be particularly low in diversity. However, the majority of taxa identified in our study can be categorized as meroplankton (i.e., larvae and juveniles of 90 benthic adult taxa), which are usually not identified to lower taxonomic level. Of the 55 holoplanktonic taxa, copepods accounted for 27, which is low compared to Kongsfjorden (52 species), but diverse compared to Rijpfjorden and Dolgaya Bay as well as Hudson Bay (Estrada et al., 2012) (13, 15, and 13 species, respectively). The lower number of copepod species from studies relying on visual identification are, however, only comparable to the number of copepod species we identified morphologically (13), strongly supporting the concept of combining metabarcoding with morphological identification.

Meroplankton diversity in Ramfjord exceeded estimates from other northern Norwegian locations (including Balsfjord) that were based on morphology. Here, meroplankton species richness varied between 37 (Porsangerfjord) and 65 taxa (Vesterålen) (Falk-Petersen, 1982; Andersen, 1984; Fetzer and Arntz, 2008; Silberberger et al., 2016; Michelsen et al., 2017). Meroplankton diversity was also higher than the diversity of benthic organisms previously assessed in Ramfjord (Oug, 1977), particularly with regard to polychaetes and echinoderms. However, the benthic communities of Ramfjord and Balsfjord are poorly studied

(Oug and Høisøeter, 2000), which makes it difficult to conclude whether the meroplankton species identified in Ramfjord were part of local populations or present due to advection. Among meroplankton, polychaetes were the most diverse group. This is not surprising, since polychaetes are the most diverse group of benthic organisms in other Arctic, sub-Arctic and Norwegian fjords (Holte, 1998; Ellingsen and Gray, 2002; Bluhm et al., 2011). Oug and Høisøeter (2000) found that polychaetes represented 97% of all species of the soft-bottom macrofauna community in Balsfjord (of a total of 78 species). Little is known about the biodiversity of taxa usually associated with hard bottom communities in our study area. The presence of larval stages of cirripedia and ascidia has been reported previously in this fjord system (Falk-Petersen, 1982). Sandnes and Gulliksen (1980) identified the sea urchins *Strongylocentrotus droebachiensis* and *S. pallidus* as key species in the system, controlling the abundance of sessile organisms such as the barnacle *Semibalanus balanoides* and the limpet *Testudinalia testudinalis*. Larval stages of these species were present in our study (Table 2 and Supplementary Table 1) while the gastropods and bivalves mentioned by Sandnes and Gulliksen (1980) did not show up in our species inventory. Bivalvia were the only group whose diversity of larval stages was lower than the diversity of adult forms previously described in the study area (Oug, 1977; Sandnes and Gulliksen, 1980; Vahl, 1980; Drent, 2002) with only one MOTU of bivalve identified. For juvenile bivalves we also found the largest difference between the visual analysis and metabarcoding. While high abundance was observed in summer, bivalves hardly featured in the BWSR. This underestimation of bivalve diversity can be explained by a lack of relevant data in the reference database, PCR bias using our chosen primer set, or problems with DNA extraction. Molluscs are notoriously hard to extract DNA from Pereira et al. (2011) presumably due to the presence of polysaccharides that inhibit DNA polymerase, and although we used an extraction kit tailored for molluscs during most of our study period, this demonstrates the ongoing challenges for this taxonomic group.

Most of the holoplankton taxa identified using metabarcoding (Table 2 and Supplementary Table 1) are species common to boreal and Arctic zooplankton communities (e.g., Dvoretzky and Dvoretzky, 2010; Estrada et al., 2012; Weydmann et al., 2013; Hop et al., 2019b). Particularly for *Calanus* and *Pseudocalanus*, metabarcoding provided a more detailed insight into the species composition than previous studies. Since life cycles and life strategies may differ even in closely related species within the same genus (McLaren et al., 1989; Lischka and Hagen, 2005; Ershova et al., 2021), correct species identification is crucial for describing species specific life history strategies and for documenting changes in population dynamics (see below). *Pseudocalanus* lacks easily distinguishable morphological features that would aid species identification, particularly when it comes to the early life stages, and they are therefore often reported as *Pseudocalanus* spp. Only two species of *Pseudocalanus*, i.e., *P. acuspes* and *P. minutus* (Norrbin, 1993, 1994) and one species of *Calanus*, i.e., *Calanus finmarchicus* (Hopkins et al., 1989) have previously been reported from Ramfjord/Balsfjord, while we revealed the presence of four species of each genus coexisting in Ramfjord, (i.e.,

C. finmarchicus, *C. glacialis*, *Calanus helgolandicus*, *Calanus hyperboreus*, *Pseudocalanus acuspes*, *Pseudocalanus elongatus*, *Pseudocalanus minutus*, *Pseudocalanus moultoni*, Table 2 and Supplementary Table 1).

While morphological features such as size (e.g., Daase and Eiane, 2007) or coloration (Nielsen et al., 2014) may enable species identification of *Calanus* spp. with some degree of accuracy in the high Arctic, they are not reliable in populations along the Norwegian coast (Choquet et al., 2017). This can lead to an under representation of *C. glacialis* in particular and explains the lack of records of these species in Norwegian fjords (included Balsfjord) in most previous studies. The Arctic *C. hyperboreus* on the other hand, is easily distinguishable from the other *Calanus* species due to its large size and a clear morphological feature (a spine on the last prosome segment) in the older copepodite stages and in adults. Metabarcoding revealed a relatively high proportion of *C. hyperboreus* in Ramfjord, while only very few individuals were recorded by visual identification. This discrepancy between molecular and visual tools could be explained by the fact that the number of sequence reads is a proxy of the biomass (Lindeque et al., 2013; Ershova et al., In revision). Because of its large size, *C. hyperboreus* (prosome length up to 5 mm) can represent a substantial part of the biomass, even if the abundance is low. However, we only identified very few *C. hyperboreus* individuals per sample visually (1 or 2 per sample) compared to *Calanus* in the size range of *C. finmarchicus* and *C. glacialis* (2–4 mm, 100–5000 per sample), thus even in terms of BWSR *C. hyperboreus* should not contribute to the *Calanus* weighted sequence reads in such high proportion. If *C. hyperboreus* was present in high numbers as young copepodite stages (CI–II) they could have been misidentified, as size differences of young stages are less pronounced between the different *Calanus* species. However, the sequence reads indicate highest relative contribution of *C. hyperboreus* in June and August when the *Calanus* population was dominated by late copepodite stages and young stages were rare. Thus, further studies are needed, e.g., using mock samples, to investigate the relationship between *C. hyperboreus* biomass, abundance and relative sequence reads.

Seasonality in the Zooplankton Community in Ramfjord

Long term data on hydrographic conditions are not available for the Ramfjord/Balsfjord system. However, the hydrographic conditions we observed in Ramfjord during our study were similar to observations from Balsfjord in 1976–1977 (Eilertsen et al., 1981a) and 2013–2014 (Svensen et al., 2018), with temperature peaking between 8 and 12°C in the surface during summer, and otherwise varying between 2 and 4°C at depth during summer and throughout the water column during winter and spring. We also observed salinity in a similar range to observations from Balsfjord (32–33), with lower salinity in surface waters during snow melt and heavy snow fall (Eilertsen et al., 1981a; Svensen et al., 2018). We concluded that no strong differences in hydrographic settings was evident between the current and historical data.

A tight coupling of seasonal changes in zooplankton community structure and the strong seasonality in phytoplankton biomass and production, driven by the light regime, is typical for polar and sub-polar areas (e.g., Pertsova and Kosobokova, 2003; Weydmann et al., 2013; McKinstry and Campbell, 2018). In Ramfjord, the seasonal variability in the zooplankton community structure was manifested in four distinct periods (Figure 8), characterized by differences in overall abundance, presence of meroplankton, and shifts in diversity.

The pre-spring bloom (PS) period (February–March) was characterized by increasing day length but low water temperatures and an overall low phytoplankton and zooplankton abundance. However, the high abundance of copepod nauplii indicates that reproduction had started and given the low Chl *a* concentration, most of this effort was likely fueled by internal energy reserves, indicating a dominance of capital breeders among the reproducing copepods (Varpe, 2009).

April was initiated with a peak in Chl *a* concentration, marking the start of the spring bloom (SB). A succession from a dominance of diatoms such as *Chaetoceros socialis* and *Thalassiosira* spp. to a dominance of *Phaeocystis pouchetii* has previously been observed in Ramfjord and other areas including, e.g., the Barents Sea and the marginal ice zone in the

Greenland sea (Eilertsen et al., 1981b; Tande and Bamstedt, 1987; Gradinger and Baumann, 1991; Orkney et al., 2020). We did not observe *P. pouchetii* beyond late April and thus lack data to assess how long it dominated the spring bloom in Ramfjord and its importance during the rest of the year as we may have underestimated the presence of the single cell stage of *P. pouchetii* for most parts of the year using a 10 μm phytoplankton net, which may only collect larger colonies that form during periods of high abundance.

The spring bloom fueled reproduction and development in the zooplankton and benthos community, as indicated by an increasing dominance of nauplii and juvenile stages. Adults and early developmental stage of *Calanus* spp. were abundant as well, as were krill nauplii and eggs, and within the meroplankton community, cirripedia nauplii and polychaete larvae reached their peak abundance. The SS period, starting in May, was characterized by low Chl *a* concentration and fluorescence, indicating a post bloom situation, dominated by flagellates as previously observed by Gaarder (1938) and Eilertsen et al. (1981b). We unfortunately lack data on Chl *a* and microalgae taxonomy from July to September to properly describe seasonal changes in the phytoplankton community throughout summer. The fluorescence measurements at 18 m depth indicate the

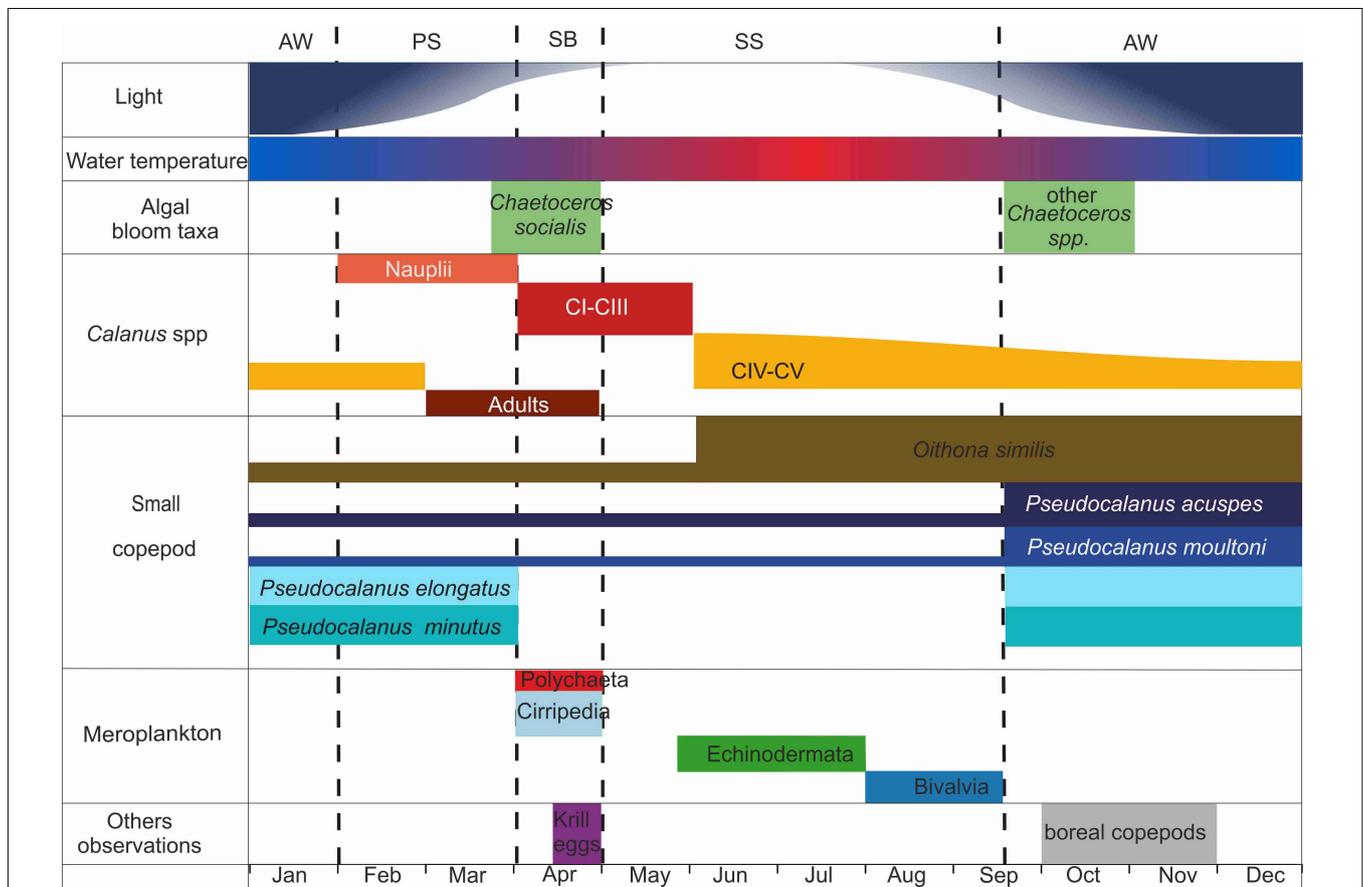


FIGURE 8 | Conceptual understanding of the seasonality variability in the zooplankton community in Ramfjord. The size of the boxes is proportional to the abundance of the organisms, but size of boxes is not comparable between the different compartments.

presence of microalgae throughout summer with a potential bloom event in July. Thus, algal food was available throughout summer, and a succession of different meroplankton taxa characterized the SS period. Cirripedia nauplii and polychaete larvae had disappeared from the water column by June, while the abundance of echinoderm larvae increased in June followed by an increase of juvenile bivalves in August. A similar succession in meroplankton has previously been described in Ramfjord (Falk-Petersen, 1982) and corresponds to observations from Arctic fjords in Svalbard (Kuklinski et al., 2013; Kwasniewski et al., 2013; Stübner et al., 2016) and Greenland (Nielsen et al., 2007).

Algal bloom dynamics in boreal and sub-Arctic regions typically include at least two seasonal peaks, one in spring and one in autumn (Eilertsen et al., 1981b; Eilertsen and Frantzen, 2007), and the AW period (AW, mid-September–January) in Ramfjord commenced with an autumn bloom dominated by diatoms (a mix of *Chaetoceros* species) similar to observations by Eilertsen et al. (1981b). Particularly high Chl *a* concentration measured in October far exceeded those during the spring bloom. This autumn bloom coincided with highest copepod diversity and peak in zooplankton abundance but also a steep decline in zooplankton biomass from September to October, largely driven by the decrease in abundance of the large *Calanus* species. Small copepods thus became the main contributors to the zooplankton community not only in terms of abundance but also in terms of BWSR, and biomass remained relatively constant throughout the AW period, even when temperature and light decreased, and Chl *a* concentration remained low. Hansen et al. (1999) hypothesized that the descent to overwintering depth of the large *Calanus* species creates a free niche in upper water layers that benefits small copepods, such as *Oithona similis*, *Microcalanus pusillus*, *Acartia longiremis*, and *Pseudocalanus* spp. These predominately omnivorous species (Saiz and Kjørboe, 1995; Castellani et al., 2005; Cleary et al., 2016) thus become the dominating functional group in the zooplankton community during AW.

The occurrence of species regarded as Atlantic/boreal, such as the copepods *C. helgolandicus*, *P. elongatus*, *Temora longicornis*, *P. minutus*, and *P. elongatus* and other species such as *Themisto abyssorum* and *Evadne normanni*, was restricted to AW when strong south-west winds often prevail in the Tromsø area (Eilertsen et al., 1981a), forcing water of Atlantic origin into the fjord system. Those species were likely advected into the fjord system and do not have established populations in the fjord.

Life History Strategies of Common Copepods

Except for *Calanus* spp., we did not identify copepodite stages of most common copepod species, thus we lack data to discuss the population dynamics of these species. However, changes in the total and relative abundance throughout the seasons nevertheless allow us to draw some conclusions about their life history strategies in Ramfjord. As observed in Disko Bay, Greenland (Madsen et al., 2008), the small copepods peak in Autumn in Ramfjord. This abundance peak of small copepod was prior or simultaneously to the second phytoplankton bloom, while it occurred after the algal bloom in Disko Bay (Madsen et al., 2008).

The ubiquitous *O. similis* is known to actively feed and reproduce all year-round (Svensen et al., 2011; Zamora-Terol et al., 2014). Similar to observations from Kongsfjorden (Lischka and Hagen, 2005; Hop et al., 2019b), Greenland (Digby, 1954; Madsen et al., 2008), Malangen (Falkenhaus et al., 1997), and Kola Bay (Dvoretzky and Dvoretzky, 2009), we observed the highest abundance between August and December with peaks in September and November, thus coinciding with periods of relative warm water temperature that may affect recruitment and development rates positively (Svensen et al., 2011; Zamora-Terol et al., 2014). The life cycles and life history strategies of *A. longiremis*, *T. longicornis*, and *M. pusillus* are overall not well studied. *A. longiremis* is a neritic species commonly observed in Arctic and sub-arctic zooplankton communities (e.g., Hopcroft et al., 2010; Estrada et al., 2012; Ershova and Kosobokova, 2019; Hop et al., 2019a). In Ramfjord, *A. longiremis* was present year-round, indicating that it has established a population here, although its abundance sharply peaked during October. Falkenhaus et al. (1997) also observed a peak of *Acartia* spp. at the same period in Malangen, however the authors did not discuss this increase of abundance. We suggest a possible advective source as well. *T. longicornis*, a temperate, brackish water weakly selective herbivorous species whose reproduction is coupled to the phytoplankton spring bloom (Peters et al., 2013), appeared only during the autumn bloom, suggesting that the population was not established in Ramfjord but was the result of advection. *M. pusillus* represented a substantial proportion of the small copepod community particularly in spring and summer, with a peak of abundance in August. This is similar to *Microcalanus pygmaeus* in west Greenland (Digby, 1954) but in contrast to observations from Kongsfjorden (Hop et al., 2019b), east Greenland (Ussing, 1938) and the Amundsen Gulf (Darnis and Fortier, 2014), where *Microcalanus* spp. abundance peaked in later autumn and winter, indicating different strategies in the sub-Arctic *Microcalanus* populations compared to the high Arctic.

Pseudocalanus Species Complex

The peak in *Pseudocalanus* abundance in October coincided with a change in the *Pseudocalanus* species composition, although we cannot discount the possibility of a bias related to a change in DNA extraction kit coinciding with this change. While *P. acuspes* dominated in spring/summer and only *P. moultoni* was found in addition, *P. minutus* and *P. elongatus* appeared in autumn when all four species were found in more or less equal proportions. A similar succession has been recently observed in Svalbard (Ershova et al., 2021) indicating species specific differences in life history strategies. The pronounced annual cycle in abundance in *P. acuspes*, peaking during summer and declining in winter, indicates a dependence on the spring bloom for growth and development. This is in agreement with recent observations from Svalbard (Ershova et al., 2021) and previous studies in the Baltic sea (Peters et al., 2006; Renz and Hirche, 2006), Balsfjord (Norrbin, 1991) and Nova Scotia (McLaren et al., 1989). *P. acuspes* life cycle is described as mostly annual, but the *P. acuspes* population can also produce a second generation (McLaren et al., 1989; Norrbin, 1991; Peters et al., 2006) and such a second reproductive effort could explain the second peak

in BWSR in autumn. It has been suggested that *P. moultoni* has a more boreal distribution where it reproduces year-round (McLaren et al., 1989), but little is known of *P. moultoni* life cycle in Arctic and sub-Arctic waters as it has been misidentified for a long time (Aarbakke et al., 2017; Hop et al., 2019b). Our study confirmed that this species is established in Ramfjord year-round, and thus likely can reproduce successfully in sub-Arctic fjords. *P. minutus* the largest of the observed species, has a strictly annual life cycle in other parts of the world, spending most of its life as C4–C5 copepodites and relying on lipid stores more than its sibling species (McLaren et al., 1989). The distribution of *P. minutus* is generally restricted to ice-covered Arctic shelf seas (Melnikov et al., 2005; Persson et al., 2012; Ershova and Kosobokova, 2019) or the deep Atlantic Ocean (Wiborg, 1955; Aarbakke et al., 2017). In Isfjorden, a Svalbard fjord heavily influenced by Atlantic advection and lacking a seasonal ice cover, *P. minutus* failed to complete its life cycle and was only advected into the fjord during the summer months (Ershova et al., 2021). Similarly, we observed *P. minutus* in Ramfjord only between September and March, together with other non-resident species, suggesting an Atlantic origin. Likewise, *P. elongatus* is a warm water boreal species (Unal et al., 2006) and was present in Ramfjord only during the fall and the winter, likely due to advection.

Calanus Life Cycle

The co-existence of several *Calanus* species is not unusual for Arctic and sub-Arctic locations where sympatric populations of *C. glacialis*, *C. finmarchicus* and *C. hyperboreus* are common (e.g., Madsen et al., 2001; Arnkvaern et al., 2005; Darnis and Fortier, 2014; Choquet et al., 2017). These species differ in life history strategies such as timing of reproduction, life cycle duration and overwintering stages (Tande et al., 1985; Arnkvaern et al., 2005; Falk-Petersen et al., 2009) even when living in the same habitat. Our data do not allow us to distinguish life history strategies of the different *Calanus* species in Ramfjord. Higher sampling resolution around the spawning event as well as genetic identification of nauplii and the young copepodite stages are needed to describe the life cycles of the different *Calanus* species in Ramfjord more precisely.

Development from egg to nauplii and CV takes around 60 days at temperatures observed in Ramfjord (McLaren, 1978; Campbell et al., 2001; Daase et al., 2011). Since we observed high abundance of copepod nauplii in February and March, and CI were recorded in high abundance in early April, spawning of *Calanus* spp. probably started in February and thus before the phytoplankton spring bloom. Spawning prior to the spring bloom is common in *C. glacialis* (Daase et al., 2013), while *C. finmarchicus* is often described to follow an income breeding strategy (i.e., being dependent of the spring bloom for gonad maturation and reproduction (Varpe et al., 2009). Previous studies from Balsfjord described a close synchronization of spawning with the phytoplankton bloom in *C. finmarchicus* (Tande and Hopkins, 1981; Tande, 1982; Grønvik and Hopkins, 1984; Hopkins et al., 1984). However, Hirche et al. (2001) observed CI and CII *C. finmarchicus* in the water column before the spring bloom in the Norwegian Sea, indicating that

C. finmarchicus is able to start reproduction ahead of the bloom, and we suggest that nauplii and young copepodites likely consisted of both *C. glacialis* and *C. finmarchicus* in Ramfjord.

An increase in abundance of young copepodites prior to the autumn bloom in October suggested a second spawning event, most likely by *C. finmarchicus* who can produce a second generation as previously described in the Scotian shelf (McLaren et al., 2001) and the Norwegian Sea (Wiborg, 1954; Marshall and Orr, 1955; Matthews et al., 1978; Strand et al., 2020).

We suggest that the *C. finmarchicus*/*glacialis* population in Ramfjord has a 1-year life cycle as the population was dominated by CV for large parts of the year, a common overwintering stage of both *C. finmarchicus* and *C. glacialis* (Tande, 1982; Arnkvaern et al., 2005). For *C. glacialis*, a 1–2 years life cycle (e.g., Kosobokova, 1999; Arnkvaern et al., 2005; Daase et al., 2013) and for *C. finmarchicus* a 1-year life cycle is commonly described for Svalbard fjords (Kwasniewski et al., 2003; Arnkvaern et al., 2005), the Barents Sea (Tande et al., 1985), as well as in sub-Arctic locations (Wiborg, 1954; Marshall and Orr, 1955; McLaren, 1978; Gislason and Astthorsson, 1998; Astthorsson and Gislason, 2003) including Balsfjord (Tande, 1982). In Ramfjord, *Calanus* spp. had disappeared from the upper 50 m by August (data not shown) except for the young stages observed in October and November 2019. The generally low abundance of *Calanus* throughout the water column in autumn and winter suggests that the population either suffered high mortality already at the start of the overwintering period, or that they do not overwinter in Ramfjord but seek refuge elsewhere. Relatively low abundance and high mortality of *C. finmarchicus* have been observed in other Norwegian fjords during winter (Bagoien et al., 2001; Skreslet et al., 2015), although deep fjords can be suitable for overwintering (Hirche, 1983; Espinasse et al., 2016). Due to its shallowness, Ramfjord is likely not a good overwintering habitat for *Calanus* spp., whose overwintering population is generally found at greater depth, particular in oceanic populations of *C. finmarchicus* and *C. hyperboreus* (600–2000 m, Hirche, 1991; Heath et al., 2004). These deep habitats provide not only refuge from predation and physiological advantages (lower metabolic cost in cold water), but also affect the buoyancy of lipid rich copepods with implications on their energy budget during diapause. Changes in wax ester chemistry reduces the buoyancy when descending below 500 m (Pond and Tarling, 2011), thus affecting buoyancy control during overwintering. *Calanus* spp. in shallow waters such as Ramfjord cannot reach a depth where they are neutrally buoyant, thus may have to work actively to remain at depth, which can be energetically demanding and reduce fitness.

Methodical Considerations

While metabarcoding provides a much more detailed species inventory than visual inspection, how the proportion of frequency reads relates to the actual proportion of species in the community and how sequences reads can be used to quantify species biomass is still in debate. A meta-analysis of 22 studies looking at a wide variety of biological communities ranging from land plants to fish investigated to which degree metabarcoding is quantitative (Lindeque et al., 2013; Lamb et al., 2019) and showed a weak correlation between the number of reads and

biomass with a large degree of uncertainties. However, only two of those examined studies looked at marine zooplankton, and neither of those used the primer set that we employed in this work. The quantitative value of our approach is described in detail in Ershova et al. (In revision) and has shown robust correlations between relative biomass and sequence read counts in high latitude marine zooplankton communities, although with biases toward certain taxonomic groups. The higher quantitative value of this method is obtained by the application of universal primers with a high level of degeneracy and the absence of a second PCR step at the library preparation stage. However, it is important to highlight that the BWSR measure that we use in this study remains semi-quantitative, meaning that it is useful in the context of seasonal comparisons of taxa-specific biomass in a single study, but likely not for comparing biomass estimates using other methods. It is noteworthy that in our study taxonomy and metabarcoding generally showed similar trends in the seasonal changes of the zooplankton community structure. BWSR captured the same seasonal peaks in *O. similis*, *Microcalanus* spp., *A. longiremis*, and *T. longicornis* as the abundance estimates. Only for *Pseudocalanus* and *M. norvegica* did the two methods show different patterns. The high BWSR of *P. acuspes* between May and August contradicted the low abundance of *Pseudocalanus* spp. in that period, although this could have been biased by the presence of nauplii which also peak during this time period (Vazyulya et al., 2001) and were not identified to genus. Low abundance but high BWSR would indicate a dominance of older stages and adults (few individuals but high individual biomass), but given *P. acuspes* life history (see above) the population should have been composed mainly of young stages with low individual biomass during that time period, and high abundance of those would have been recognized during the visual inspection. *Microsetella norvegica* is not sampled effectively by traditional zooplankton nets (Svensen et al., 2018) and was likely underestimated, especially after the change in mesh size when abundance decreased markedly. Despite its low individual biomass, we would have expected a higher proportion of sequence reads at the early part of the study when we used the smaller mesh size, but the number of sequence reads of *M. norvegica* were almost negligible year-round.

The increase in mesh size from April did not only result in an underestimation of *M. norvegica* but likely also other smaller organisms, such as small meroplankton and young copepodite stages, particularly those of small copepods (Vinogradov and Shushkina, 1987; Nielsen and Andersen, 2002; Tseng et al., 2011). Consequently, their abundances and the species richness between November 2018 and April are not directly comparable with the rest of the study. There is however little evidence that larger copepods and older life stage of smaller copepods (including copepodites stage CIII-adults of *Calanus* and *Pseudocalanus*) are caught less efficiently with a mesh size of 64 μm compared to 180 μm (e.g., Nichols and Thompson, 1991; Di Mauro et al., 2009; Altukhov et al., 2015; Chen et al., 2016). Thus, we are confident that the seasonal patterns we observed in the morphological data are not severely biased by the change in mesh size, especially when we take the change of mesh size into consideration in our data interpretation. Furthermore, despite the use of the 180 μm

mesh, we did observe a strong increase of the abundance of most of the small copepod. Even if their abundance is underestimated, our data provide clear evidence of seasonal changes, such as a strong increase in abundance in autumn. Finally, the application of two different DNA extraction kits during the course of the study highlights the biases that can be introduced at this stage of the analysis. The EZNA Mollusc DNA Kit recovered, on average, 44% higher diversity than the Qiagen PowerSoil Kit, especially among the meroplankton and non-crustacean taxa (Supplementary Figure 2). Unfortunately, the lack of a temporal overlap in the application of the two kits precludes a more concrete analysis of the taxonomic biases of either and remains to be resolved in future studies.

One of the main concerns of the effect of climate warming on plankton communities is the potentially negative effect of changes in the algal bloom phenology related to zooplankton life history strategies. These changes may alter the energy transfer through the pelagic food web and potentially also impact benthic invertebrates through their pelagic early life stages. Furthermore, biogeographical distributional shifts may change community composition with repercussions on energy transfer and ecosystem structure (Beaugrand et al., 2009; Chust et al., 2013). In order to document changes and to be able to distinguish between natural seasonal variability and climate change impacts on ecosystems structure and functioning, we need to establish baselines, such as detailed species inventories and how community composition varies seasonally. Species specific changes in life histories can only be observed if species are correctly identified, as even closely related species may vary in their annual routines and their role in the ecosystem structure. Our study demonstrates that the combination of both morphological and metabarcoding approaches is providing the necessary quantitative and qualitative detail to document seasonal changes in community composition and population structure. While our study focused on mesozooplankton, future studies are needed to fully describe the community composition of the microplankton and macrozooplankton community.

CONCLUSION

There are few studies from sub-Arctic locations describing the seasonal variability in the zooplankton community structure. The combination of traditional methods of identification and state-of-the-art molecular tools allowed us to provide high-resolution data on seasonal variability in zooplankton abundance and diversity at a much higher taxonomic resolution. Both methods were highly complementary, with metabarcoding providing the most extensive species list of mesozooplankton from a Norwegian fjord to date, particular in terms of the meroplankton which are rarely identified to species in most zooplankton studies. 154 unique taxa were identified in Ramfjord over the study period, 58% were meroplankton organisms. Seasonality in the zooplankton community structure was driven by the seasonal changes in temperature and algae biomass and was manifested not only by changes in abundance and biomass but also by changes in diversity, although methodological shortcomings

limits our ability to identify seasonal changes in diversity to some extent. The succession of meroplankton was an important factor driving the seasonal changes in the mesozooplankton community over summer. An assessment of the diversity of the benthic community is needed to determine the role of advection and local production of the meroplankton community in the Ramfjord/Balsfjord system, and how seasonal changes in meroplankton composition and abundance are linked to difference in the life history strategies of the various species.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: <https://www.gbif.org/dataset/b4804f19-8a8a-49e7-8dc2-79b528635696>. The raw sequencing datasets presented in this study are publicly 882 available in the Sequence Read Archive (SRA) repository of NCBI. Bioproject ID: PRJNA742507. 883 <https://www.ncbi.nlm.nih.gov/bioproject/742507>.

AUTHOR CONTRIBUTIONS

EE, MD, RG, TV, and EC designed the study. EC, TV, and EE realized the sampling. EE and OW did the metabarcoding analysis and the bioinformatic. EC, MD, and EE did the zooplankton visual identification and wrote the first draft of the manuscript. TV did the phytoplankton cell count and the measure of the chlorophyll *a* concentration. MD, EC, and EE did the data analysis and data visualization. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.705042/full#supplementary-material>

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