INTRODUCTION

Marine pelagic ecosystems sustain large populations of marine mammals, sea birds, and the majority of the large fish stocks. Within the pelagic food web, zooplankton play a key role as the major trophic link between the pelagic primary producers and higher trophic levels (Fenchel, 1988). In addition, their contribution to nutrient regeneration and dissolved organic carbon release supports the growth of phytoplankton and bacterioplankton (Banse, 1995).
After early detailed accounts of zooplankton community composition at high latitudes (e.g., Smidt, 1979; Wiborg, 1954), most zooplankton research today addresses macrozooplankton (krill, pelagic amphipods) or calanoid copepods of the genus Calanus (Orlova et al., 2015; Renaud et al., 2018). The latter is also the only mesozooplankton component considered in some models of ecosystem dynamics (Wassmann et al., 2006). The reason for this focus on a single genus is related to the dominance of Calanus spp. in mesozooplankton biomass during spring and summer (Aarflot et al., 2018; Arashkevich et al., 2002). The life cycle of Calanus, however, involves a descent away from surface waters to deep overwintering habitats from late summer to spring (Kaartvedt, 2000), while a diverse mesozooplankton community remains within the productive surface water throughout most of the year (Eiane et al., 2018; Silberberger et al., 2016). Consequently, a variety of planktonic groups may have an important ecosystem function (Hansen et al., 1999; Pasternak et al., 2008). Since many functional traits are linked to body size, mesozooplankton body size can be used as a proxy for their role in ecosystem functioning (Hébert et al., 2017; Litchman et al., 2013).

Small mesozooplankton (SMZ), such as small copepods and larval stages of planktonic and benthic invertebrates, are by far more abundant than Calanus throughout the year (Arashkevich et al., 2002; Pasternak et al., 2008). They are less studied than Calanus, partly due to methodological constraints and taxonomic uncertainty, though their importance as grazers has been recognized (Morales et al., 1991; Pasternak et al., 2008). Grazing impacts of SMZ on phytoplankton are directly comparable to that of the larger size fraction of the mesozooplankton community (Pasternak et al., 2008), and SMZ has been identified as an important component of the pelagic food webs in tidally mixed waters of the North Sea and the marginal ice-zone of the Barents Sea (Pasternak et al., 2008; Williams et al., 1994). Meroplankton, larvae of benthic organisms, are even less studied than the holoplanktonic component of SMZ, and their potential ecological significance is mostly unknown. So far, most research on meroplankton focuses on their roles in dispersal and recruitment processes from a benthic perspective (Levin, 2006; Silberberger et al., 2016). However, meroplankton has been proposed to affect the pelagic ecosystem in various ways: (a) as grazers of autotrophic and heterotrophic micro- and nano-plankton in direct competition with holoplankton for resources (Pasternak et al., 2008; Turner et al., 2001), (b) as potential prey for higher trophic levels (Michelsen et al., 2017), or (c) through synchronized settlement that directs the assimilated carbon from the water column to the seafloor and reduces the grazing pressure on micro- and nano-plankton (Kirby et al., 2008; Sommer et al., 2000).

On the Lofoten–Vesterålen shelf, the zooplankton community was dominated year-round by copepods (especially Calanus) between 1949 and 1950 (Wiborg, 1954). This study also reported that meroplankton rarely contributed with more than 10% to the total zooplankton abundance, with an annual average contribution of 2%-4%. While the abundance and the seasonal pattern of the numerically dominant holoplankton taxa and cod larvae was similar in 1949/1950 and 2013/2014 (Eiane et al., 2018; Wiborg, 1954), meroplankton has become a more abundant component of the zooplankton community (Silberberger et al., 2016). In 2013/2014, the annual average contribution of meroplankton to the mesozooplankton abundance was approximately 20% closer to the coast and around 5% over the central shelf (Eiane et al., 2018; Silberberger et al., 2016). Accordingly, a more important ecological function of meroplankton in the Lofoten–Vesterålen region can be assumed. Whether this increased abundance of meroplankton is also reflected in the biomass, which is in most cases a more important measure for ecosystem functions, is still unknown.

To fully understand the functioning of pelagic ecosystems, knowledge about the seasonal and spatial distribution of zooplankton biomass and how it is divided among the various zooplankton components is indispensable. Zooplankton biomass-spectra scale with important community processes, such as growth, mortality, or trophic structure (Hébert et al., 2017; Zhou et al., 2009), which have strong implications for the planktonic food web.

In addition to the lack of knowledge about the biomass associated with small and understudied taxa, virtually no study exists that measured the entire mesozooplankton community biomass on taxon level over space and time. In general, most studies use taxon- or stage-specific individual weight data or length–weight relationships (e.g., Arashkevich et al., 2002; Aarflot et al., 2018). However, individual weight within a Calanus stage can vary by one order of magnitude (Aarflot et al., 2018) and different length–weight relationships can be found in the literature that differ by a factor of 5 for Calanus spp. (Cohen & Lough, 1981). No effort to correct for stage or size is normally made for smaller taxa. For Oithona spp., which is often considered the most abundant mesozooplankton taxon in the world's oceans (Gallienne & Robins, 2001), a fixed value of 0.003 mg/ind is used in studies of sub-Arctic and Arctic mesozooplankton biomass (Blachowiak-Samolyk et al., 2008; Mumm, 1991; Richter, 1994; Stübn er et al., 2016). A similar approach has been applied for meroplankton, but with a lower taxonomic resolution. Typically, individual weights are applied for each meroplankton phylum, often ignoring individual growth stage or species identity. Consequently, it is likely that our understanding of seasonal and spatial variations of the mesozooplankton biomass in the sub-Arctic is strongly biased, particularly for SMZ.

In this study, we follow the development of the mesozooplankton biomass on a sub-Arctic open continental shelf over a 12-month period. The main objectives were to (a) determine seasonal variation in the contribution of different mesozooplankton taxa to the total plankton biomass in the sub-Arctic Lofoten–Vesterålen region; (b) identify seasonal and spatial patterns in biomass composition of small sized (<1 mm) mesozooplankton; (c) identify whether length–weight relationships can accurately estimate the seasonal development of mesozooplankton at the example of the year-round abundant taxa (Calanus spp. and Oithona spp.). We hypothesize that meroplankton is an important, but so far underexplored, component of the mesozooplankton biomass in the sub-Arctic that might have an important role in the functioning of the highly productive ecosystems in this region.
2 MATERIALS

2.1 Study region

Our study domain was the continental shelf off the coast of the Vesterålen islands, where the Norwegian shelf is at its narrowest (Figure 1). The Lofoten–Vesterålen region is among the most valuable marine regions in Europe, with a high importance for both the Barents Sea and the Norwegian Sea ecosystems (Olsen, 2009). It is an important fish spawning ground and larval drift area where first feeding fish larvae need to encounter suitable prey. The area is north of the Arctic Circle and is subject to strong seasonality in day length, temperature, and primary production (Eiane et al., 2018). Two major northward flowing currents, the Norwegian Atlantic Current (NAC) and the Norwegian Coastal Current (NCC), together with strong tidal forces, shape the hydrography of the region, causing an overall northward transport with retention of planktonic organisms over the shelf (Espinasse et al., 2017; Silberberger et al., 2016). The low salinity NCC overlies the high salinity water of the NAC like a wedge, with the greatest depth of the NCC layer along the coast. The strength, width, and depth of the NCC varies seasonally as it is partly driven by run-off from land (Silberberger, 2017). Coastal regions, shallow banks, and cross-shelf troughs represent the three landscape elements that characterize the region and differ with respect to depth and hydrography (Eiane et al., 2018; Silberberger et al., 2016). Water of the NCC (salinity <34.5) characterizes the relatively shallow coastal region (<50 m depth), which remains mixed for most time of the year. Further offshore, over banks (<100 m depth) and troughs (>200 m depth), a thermohaline vertical structure develops in early summer but typically weakens in late winter and early spring (Eiane et al., 2018). Below 100 m depth, the seasonal variability of salinity and temperature is much reduced compared to shallower waters.

2.2 Sampling

Plankton samples were collected at three stations during eight sampling events between September 2013 and August 2014 (Figure 1). Stations represent the landscape elements in the study region: Coast (C; depth: 40 m), bank (B; depth: 80 m), and trough (T; depth: 215 m). A WP2 closing net (opening = 0.25 m², mesh size = 200 μm) sampled the complete water column in a single vertical tow at station C and B. At the deepest station (T), plankton was collected from two depth intervals: estimated maximum mixed-layer depth (50–0 m) and deeper water (bottom–50 m). These samples were, however, combined for sample processing of this study. Samples were preserved in a buffered 4% formaldehyde-seawater solution until further processing in winter 2017/18.

FIGURE 1 Map of the Lofoten–Vesterålen region. Sampling locations are indicated. Inset: Overview map of Scandinavia with position of study region indicated. Bottom: Timeline with sampling dates.
TABLE 1  List of all taxa with at least one reliable dry weight (DW) measurement. The assigned size class (SMZ or LMZ) is given for each taxon. Applied conversion factors for the calculation of organic carbon content (mg C/mg DW) and energy content (J/mg DW) are given for each taxon together with the source taxa for the conversion factors

| Taxon                     | Size class | mgC/mgDW | J/mgDW | Source taxa in Brey et al. (2010)                                      |
|--------------------------|------------|----------|--------|-----------------------------------------------------------------------|
| **Holoplankton**         |            |          |        |                                                                        |
| *Acartia longiremis*    | SMZ        | 0.453    | 21.595 | Median values for *Acartia* spp.                                       |
| *Calanus spp.*          | LMZ        | 0.502    | 26.889 | Median values for *Calanus* spp.                                       |
| *Centropages typicus*   | SMZ        | 0.395    | 21.949 | Median values for *C. typicus*                                         |
| *Cladocera*             | SMZ        | 0.439    | 17.680 | Median values for marine *Cladocera*                                   |
| *Clausocalanidae*       | SMZ        | 0.497    | 21.222 | Median values for *Pseudocalanidae*                                    |
| *Clione larvae*         | LMZ        | 0.300    | 17.355 | Median values for *Clione* spp.                                        |
| *Copepod nauplii*       | SMZ        | 0.396    | 24.080 | Median values for marine *Copepod* larvae                             |
| *Euphausia larvae*      | LMZ        | 0.395    | 13.915 | Median values for marine *Euphausia* larvae                            |
| *Fritillaria borealis*  | SMZ        | 0.545    | 3.868  | Median C/DW value for *Appendicularia*; Median J/mgDW value for marine swimming *Tunicata* |
| *Hydrozoa*              | LMZ        | 0.101    | 7.864  | Median values for marine swimming *Hydrozoa*                           |
| *Limacina retroversa*   | LMZ\(^a\)  | 0.333    | 15.955 | Median values for *Limacina* spp.                                      |
| *Metridia longa*        | LMZ        | 0.510    | 28.549 | Median values for *M. longa*                                           |
| *Oikopleura*            | LMZ\(^a\)  | 0.504    | 3.868  | Median C/DW value for *Oikopleura* spp.; Median J/mgDW value for marine swimming *Tunicata* |
| *Oithona spp.*          | SMZ        | 0.465    | 18.691 | Median C/DW value for *Oithona* spp.; Median J/mgDW value for marine swimming *Copepod* |
| *Paraeuchaeta spp.*     | LMZ        | 0.587    | 25.100 | Median C/DW value for *Paraeuchaeta* spp.; Median J/mgDW value for marine swimming *Copepod* |
| *Parasagitta elegans*   | LMZ        | 0.399    | 17.366 | Median values for *P. elegans*                                         |
| *Temora longicornis*    | SMZ        | 0.433    | 18.691 | Median values for *T. longicornis*                                     |
| **Meroplankton**        |            |          |        |                                                                        |
| *Amphinomidae*          | SMZ        | 0.373    | 17.800 | Median values for *Polychaeta*                                         |
| *Asteroidea*            | LMZ        | 0.130    | 9.944  | Median values for *Asteroidea*                                         |
| *Bivalvia*              | SMZ        | 0.208    | 7.039  | Median values for *Bivalvia* larvae                                    |
| *Bryozoa*               | SMZ        | 0.402    | 8.721  | Median C/DW value for *Animalia*; Median J/mgDW value for *Bryozoa*    |
| *Cirripedia*            | SMZ        | 0.437    | 17.070 | Median values for *Cirripedia* larvae                                  |
| *Gastropoda*            | SMZ        | 0.335    | 18.335 | Median values for *Gastropoda*                                         |
| *Ophiuroidea*           | SMZ        | 0.142    | 5.425  | Median C/DW value for *Echinodermata*; Median J/mgDW value for *Ophiuroidea* |
| *Polychaeta*            | SMZ        | 0.373    | 17.800 | Median values for *Polychaeta*                                         |
| *Decapoda zoea*         | LMZ        | 0.360    | 12.400 | Median values for *Decapoda* larvae                                    |
| **Ichthyoplankton**     |            |          |        |                                                                        |
| *Fish eggs*             | LMZ        | 0.432    | 22.900 | Median values for *Teleostei* larvae                                   |
| *Cod larvae*            | LMZ        | 0.432    | 22.900 | Median values for *Teleostei* larvae                                   |

\(^a\)Taxa with a size range across both classes.

A detailed account of the holoplankton and meroplankton community in connection with environmental parameters collected during this field investigation is provided by Eiane et al. (2018) and Silberberger et al. (2016), respectively.

2.3 Sample processing

Depending on zooplankton density, samples were split to four, eight, or sixteen parts, depending on the concentration of organisms, with
a Motoda plankton splitter. One part was diluted to 200 ml and used for the analysis. A fixed volume pipette was then used to collect 2 ml subsamples, and all individuals were identified under an Olympus SZX16 stereo microscope equipped with an Olympus SC180 digital camera that was connected to a computer with the image analysis software Olympus stream. Individuals of each taxon were transferred to 4 ml distilled water in preweighed aluminum weighing boats, which have been heated to 200°C for 3 hr prior to preweighing to remove any volatile residue and reach a stable mass. In addition, the length of each individual was measured (prosome length for copepods, longest extension of the body without appendages for all other taxa). Length measurements were made for up to 100 individuals of the most abundant taxa in a sample. For other taxa, length measurements were made for approximately 300–400 individuals per sample, which allowed to assess the length distribution of each taxon that was abundant enough for DW measurements. To ensure the establishment of unbiased length distributions, length measurements for a started 2 ml subsample were always completed.

We chose the taxonomic resolution at the lowest level that allowed for a close to complete representation of the plankton community in the DW measurements (>95% individuals in each sample). If enough individuals of one taxon for dry weight measurement were collected, this taxon was disregarded in the remaining subsamples taken from that net haul. The weight of the collected plankton was determined after drying at 50°C for 18–26 hr (Stübner et al., 2016). Weighing boats were transferred to a desiccator to cool down to room temperature, before the mass was determined with a Mettler Toledo XS205 analytical balance with a precision of 0.01 mg. Temperature, humidity, and air pressure in the laboratory were monitored during preweighing and weighing to ensure accurate measurements.

To estimate our measurement error, three preweighed boats containing 4 ml of distilled water were dried as controls for each sample (i.e., 72 controls in total = 3 controls × 3 stations × 8 sampling dates). The average error was 0.016 mg, which was significantly different from 0 (t(71) = 12.269, p < .001). In comparison, the median weight gain of the containers with plankton was 0.2 mg (range: 0.01–26.46 mg).

### 2.4 Data processing

All biomass measurements were corrected by subtraction of the measurement error. Afterwards, all biomass values that did not exceed a weight gain of 4 standard deviations of the control samples (4 × SD = 0.043 mg) were discarded as unreliable (i.e., 25 of 223 measurements). These unreliable measurements were obtained when the sample size of uncommon species was small.

Preservation of mesozooplankton in formaldehyde may cause a biomass loss in the range from 37%–43% depending on size and species (Giguère et al., 1989; Williams & Robins, 1982); thus, we assumed a loss of 40% for all taxa and corrected the measured biomass accordingly by multiplying by a factor of 1.67. Biomass loss during formalin preservation is typically large in the first weeks of preservation, after which it decreases gradually until a stable weight is reached after a few months (Schram et al., 1981; Wetzel et al., 2005). Since all samples were preserved for over three years, we assume that the biomass changes had stabilized. Finally, biomass estimates were standardized to 1-m² surface area by correcting for the used fraction of the total sample (split), the number of 2 ml subsamples used to collect the individual taxa, and the area sampled by the net (0.25 m²). Data were not corrected for tow depth, because zooplankton species are typically not distributed equally throughout the water column and occupy typically narrow depth ranges at any time (Eiane et al., 2018; Unstad & Tande, 1990). For comparison with volume-specific data (per m³) in other studies, the presented values can be divided by the station depth. Biomass measurements per m² surface area at the three sampling stations (C, B, T) in the ratio 1:2:5.4, therefore, indicate equal biomass per volume (averaged over the entire water column).

In addition, the average individual biomass for each taxon was calculated by dividing the corrected, but not standardized, biomass by the number of individuals that was collected for the measurement. All reported results are based on biomass or average individual biomass per m². Based on the biomass measurements, we used taxon-specific conversion factors (Brey et al., 2010) to estimate organic carbon and energy content of the zooplankton community (Table 1).

### 2.5 Data analysis

All multivariate statistical analyses were performed twice: once on the complete mesozooplankton biomass data, and once on a subset that included taxa smaller than 1 mm. This separate analysis of small taxa was performed for two reasons: (i) Body size is an important trait that has strong implications on food web structure and ecosystem functioning (Ye et al., 2013; Zhou et al., 2009), and (ii) only taxa smaller than 1 mm are commonly underrepresented in comparison with larger taxa in samples collected with a mesh size of 200 μm (Riccardi, 2010). Due to this sampling bias, the data for the smaller size fraction have to be considered nonquantitative and need to be interpreted with care.

The separation of the studied taxa in large and small was done according to their mean length (Table 1). *Limacina retroversa* and *Oikopleura* spp., however, displayed a large size variety between and within samples. Although their mean size was below 1 mm, we decided to exclude these two taxa from the small taxa for two reasons: (i) The size measurements of preserved samples (shell height of *L. retroversa* and head length of *Oikopleura* spp.) are underestimating the actual in situ size for both taxa. (ii) Some individuals were much larger than 1 mm, and we assume that our biomass measurements reflect primarily these big individuals. Since multiple individuals of one taxon from one sample were pooled to estimate biomass, we were not able to distinguish the weight of specific size classes of a single taxon and had to assign the entire biomass to the large or small size fraction. *Calanus* represented a third taxon that was represented by
individuals in the small and large size fraction in our data. However, in contrast to the other two taxa, Calanus nauplii and copepodite stages were collected separately and accordingly the biomass associated with the different size fractions could be assigned correctly.

Each data set was subjected to a Hellinger transformation to make the data suitable for the Euclidean space (Legendre & Gallagher, 2001). The Hellinger transformation is defined as:

$$y_j^i = \sqrt{\frac{y_{ij}}{\sum_j y_{ij}}}$$

where $y_{ij}$ is the abundance of species $j$ in sample $i$, and $y_{ij}$ is the total abundance in sample $i$. Principal component analysis (PCA) and hierarchical clustering were used to identify patterns in the biomass data. To select a suitable clustering method and identify meaningful clusters, we used an explorative approach following methods described by Borcard et al. (2018). Cophenetic correlations and Gower distance were used to select the clustering method that represented the Hellinger transformed data best. The evaluated clustering methods were single linkage, complete linkage, unweighted pair-group method using arithmetic averages (UPGMA), and Ward's minimum variance clustering. Fusion level values, average silhouette widths, and matrix correlations between original dissimilarity matrix and binary matrices were used to identify the optimal numbers of clusters for the previously selected clustering method.

A species contribution analysis (SCA) was performed to identify taxa contributing to the differences among the identified clusters (van Son & Halvorsen, 2014).

Redundancy analysis (RDA) was used to partition the variation in the Hellinger transformed data on spatial and seasonal predictor variables (Borcard et al., 2018), thereby quantifying the spatial and seasonal component in the data. We used a factor variable, including variables (Borcard et al., 2018), thereby quantifying the spatial and seasonal predictor in the variation partitioning. This circular predictor was chosen to ensure that samples from September 2013 and August 2014 were considered seasonally similar.

Three length–weight relationships for Calanus spp. and 4 length–weight relationships for Oithona spp. were applied to calculate individual DW for these two taxa (Table 2). We calculated the individual DW for each Calanus and Oithona with a prosome length measurement and consecutively used them to calculate the average individual DW in each sample. The calculated average individual DWs were then compared to the measured average individual DWs in each of our samples. Since neither formula for Oithona was developed for species in the north Atlantic or Arctic, the commonly used individual dry weight of 0.003 mg (Blachowiak-Samolyk et al., 2008 and references therein) was also included in the comparison.

All statistical analyses were performed in R, version 3.5.0, making use of the vegan (Oksanen et al., 2018), veganUtils (Vihtakari, 2018), cluster (Maechler et al., 2018), and dendextend packages (Galili, 2015).

### 3 | RESULTS

In total, we obtained biomass data for 28 taxa, representing 17 holoplankton and 9 meroplankton taxa, as well as two different developmental stages of ichthyoplankton (Table 1).

The relationships between measured biomass (mg DW/m²), calculated organic carbon (mg C$_{org}$/m²), and energy content (J/m²) differed somewhat between the different plankton components. The C$_{org}$/DW ratio and energy:DW ratio were higher in holoplankton and ichthyoplankton than in meroplankton, and thus, the contribution of meroplankton to the sample C$_{org}$ and energy content was...
slightly lower than to the sample dry weight (Table 1, Appendix S1). However, this difference was small (maximum difference 4%, compare Appendix S1) and accordingly, general patterns of dry weight composition can be transferred to $C_{org}$ or energy content.

3.1 | Total biomass patterns

Averaged over the whole study period, a distinct spatial pattern with total low biomass near the coast (2,547 mg DW/m²), intermediate biomass over the bank (5,116 mg DW/m²), and highest biomass over the cross-shelf trough (13,921 mg DW/m²) was observed. This pattern was caused by the holoplankton, which accounted for >90% of the total zooplankton biomass at all locations (Figure 2; Appendix S1).

The meroplankton biomass component, however, showed an opposite pattern, with highest values at the coast (174 mg DW/m²), intermediate values over the bank (125 mg DW/m²), and lowest values at the deep station (76 mg DW/m²). Accordingly, the relative contribution of meroplankton to the total biomass differed from 6.8% at the coast-near station to 2.6% and 0.5% over the bank and at the deep station, respectively. However, this was just an average trend and no consistent spatial pattern emerged across all sampling dates for biomass or the number of taxa that contributed to the biomass (Figure 2). Ichthyoplankton (mainly cod eggs and larvae) was present in samples from early April to mid-May, with a biomass peak in early May. No consistent spatial pattern of ichthyoplankton distribution was observed throughout this period (Appendix S1). This general lack of a consistent spatial pattern was further confirmed by variation partitioning that showed station ID could not explain any variation in the complete data set (adj. $R^2 = -0.04$, Figure 3a).

Temporal succession of the plankton biomass followed a seasonal pattern with low values during winter and early spring (January-April), highest values in late spring and early summer (May-July), and intermediate values in late summer and autumn (August-October) (Figure 2a). A seasonal pattern was also confirmed by variation partitioning results, which indicated that the sampling date explained 40% of the variation in the data (Figure 3a).

Overall, Calanus spp. dominated the zooplankton biomass on the Vesterålen shelf, accounting for 81% of the total biomass in this study (Figure 4). Furthermore, Calanus was the dominant taxon in 21 out of 24 samples. In the remaining three samples, the pteropod Limacina retroversa (St. C & B, 23.10.2013) and the copepod Metridia longa (St. C, 22.01.2014) dominated. Accordingly, PCA and hierarchical clustering identified three distinct clusters representing the samples of different species dominance (Figure 3a). Species contribution analysis (SCA) and species loadings of the PCA identified Calanus and L. retroversa as characteristic for clusters 1 and 2, respectively (Figure 3a, Figure 4). Station C in January (cluster 3), however, was rather characterized by the very low biomass of only two taxa that could be collected in necessary amounts to measure the biomass. This low number of taxa separated it clearly from all other samples that contained at least six taxa with sufficient biomass (Figure 2b).

FIGURE 2 Barplots depicting total mesozooplankton biomass (a), total number of mesozooplankton taxa (b), biomass associated with small mesozooplankton (SMZ; < 1 mm) (c), and number of SMZ taxa (d). Color indicates the fraction that was associated with taxa larger and smaller than 1 mm (a, b) or with holoplanktonic and meroplankton taxa (c, d). Sampling stations are abbreviated: C, Coast; B, Bank; T, Trough.
Small mesozooplankton

The seasonal pattern of SMZ biomass development followed the general trend that was observed for the total mesozooplankton biomass (Figure 2). The on-average elevated total biomass over the deep trough, however, was not reflected in the SMZ fraction. SMZ biomass was in general more equally distributed throughout the study area (Figure 2).

Meroplankton accounted for 34.2% of the total SMZ biomass. The majority of this biomass was associated with amphinomid polychaete larvae in samples from July. However, a considerable amount of meroplankton was found from April to September and their relative contribution to SMZ biomass was high in some samples (range: 0%–85%; Figure 2c).

Hierarchical clustering and PCA identified six distinct clusters (Figure 3b). We identified Oithona spp. as the only small taxon that contributed to the biomass of all six clusters (Figure 4). Three meroplankton taxa, Cirripedia, Gastropoda, and Bryozoa, contributed to four clusters, while the remaining taxa contributed to three (1 taxon), two (4 taxa), or one (5 taxa) cluster. However, the contribution of Cirripedia, Gastropoda, and Bryozoa was below 2% for one cluster each, and thus, only Oithona spp. contributed considerably to more than three clusters. With few exceptions, samples from the same sampling date were assigned to the same cluster (Figure 3b) and, therefore, a significant part of the variation was explained by the sampling date, but not by the sampling station (Figure 3b).

Meroplanktonic taxa dominated the biomass in clusters D and E (i.e., >50% of SMZ biomass) and contributed 13%–16% to the SMZ biomass of clusters B, C, and F (Figures 3b and 4). Cluster A (September) contained only 7% meroplankton and was dominated by five small holoplanktonic copepod taxa. Two species which were virtually absent from all other samples, Centropages typicus and Temora longicornis, accounted for approximately 45% of the SMZ biomass in cluster A. Similarly, samples from July (cluster E) were characterized by a particularly high biomass of amphinomid polychaetes (55%), which did not contribute to the biomass of any other month. These two clusters, which were dominated by taxa that were exclusively collected on a single sampling date, were the two clusters with the highest SMZ biomass.

Cluster C represents the spring community and contains all but one sample from 1 April and all samples from 1 May. Although Oithona spp. and Clausocalanidae were the dominant small taxa in these samples, cluster C was clearly distinguished from all other clusters by abundant cirriped and copepod nauplii (Figures 3b and 4). In April, both types of nauplii were found in similar numbers and accounted for a similar total biomass (Table 3). Regarding their length and individual biomass, cirriped nauplii were smaller than copepod nauplii in early spring. Within a month, both groups increased their total biomass similarly. The median length of cirriped nauplii increased from 392 𝜇m to 703 𝜇m and the individual weight increased by one order of magnitude, while their abundance did not change from April to May. In contrast, copepod nauplii increased in numbers, but individual size stayed very similar. The mean individual weight of the copepod nauplius even decreased slightly from April to May.

Length–weight relationships

Overall, comparisons between calculated (based on published length–weight relationships) and measured average individual biomass of Calanus spp. and Oithona spp. indicated significant variability and rarely resulted in a satisfactory estimation (±20%) of the measured biomass (Figure 5). For Calanus spp., the three employed
length–weight relationships all had a strong seasonal bias. The two exponential formulas (method i and iii) reflected the measured biomass well from April to July. The log-linear model according to Hirche (1991), however, performed more poorly than the exponential formulas during this period and overestimated Calanus biomass by more than 20% during 3 (out of 4) sampling events. For the rest of the year, the biomass was consistently underestimated by all methods.

**TABLE 3** Abundance, individual biomass, total biomass, and length for cirriped nauplii and copepod nauplii in samples collected 1. April and 1. May

| Cluster A | Cluster B | Cluster C | Cluster D |
|----------|----------|----------|----------|
| b17 mgDW/m² | 95 mgDW/m² | 259 mgDW/m² | 46 mgDW/m² |
| 1. Centropages typicus (0.34) | 1. Clauropsalisae (0.24) | 1. Clauropsalisae (0.24) | 1. Clauropsalisae (0.24) |
| 2. Temora longicornis (0.26) | 2. Copepod nauplii (0.23) | 2. Copepod nauplii (0.23) | 2. Copepod nauplii (0.23) |
| 3. Clausocalanidae (0.15) | 3. Crithiid nauplii (0.20) | 3. Crithiid nauplii (0.20) | 3. Crithiid nauplii (0.20) |
| 4. Oithona spp. (11.3%) | 4. Bryozoa (4.3%) | 4. Bryozoa (4.3%) | 4. Bryozoa (4.3%) |

**TABLE 3** Abundance, individual biomass, total biomass, and length for cirriped nauplii and copepod nauplii in samples collected 1. April and 1. May

| 1. April 2014 | 1. May 2014 |
|---------------|-------------|
| Coast | Bank | Trough | Coast | Bank | Trough |
| Abundance [ind./m²] | | | | | |
| Cirriped nauplii | 4,128 | 3,136 | 0* | 4,000 | 2,880 | 1,200 |
| Copepod nauplii | 1,120 | 5,248 | 753* | 12,400 | 30,933 | 21,688 |
| Individual biomass [mg DW/ind.] | | | | | |
| Cirriped nauplii | 0.0030 | 0.0029 | - | 0.0208 | 0.0101 | 0.0435 |
| Copepod nauplii | 0.0054 | 0.0035 | - | 0.0029 | 0.0027 | 0.0023 |
| Total biomass [mg DW/m²] | | | | | |
| Cirriped nauplii | 12,496 | 8,993 | - | 83,179 | 28,963 | 61,811 |
| Copepod nauplii | 6,096 | 18,593 | - | 35,718 | 83,827 | 49,959 |
| Length [μm] | | | | | |
| Cirriped nauplii | 385 (83) | 434 (67) | - | 748 (119) | 725 (35) | 632 (460) |
| Copepod nauplii | 500 (54) | 546 (42) | 548 (49) | 496 (37) | 489 (47) | 506 (77) |

**Note:** * indicates sample with too little material for biomass determination. Abundance estimates for this sample are based on the initial size measurement. Length measurements are presented as means (1 SD).
The choice of conversion method for *Oithona* had a huge impact on estimates all year round. For *Oithona* spp., the exponential formula for *O. hebes* according to Ara (2001) performed clearly better than all other methods (Figure 5). The other length–weight relationships either consistently overestimated or consistently underestimated the biomass. The application of a fixed individual weight of 3 μg performed well during spring (April–May) but lead to a strong overestimation of the *Oithona* spp. biomass in autumn and winter.

**4.1 Large mesozooplankton**

We found an overall dominance of *Calanus* spp. in the Lofoten–Vesterålen region that was comparable to other studies of zoo plankton biomass in high latitude systems (Arashkevich et al., 2002; Blachowiak-Samolyk et al., 2008) and points toward *Calanus* spp. as the key taxon supporting the large stocks of marine mammals, sea birds, and adult fish, and also seems to justify the general focus of ecosystem models on *Calanus* spp. (Renaud et al., 2018; Wassmann et al., 2006). However, 69% of the *Calanus* biomass was collected over the deep trough, indicating that *Calanus* spp. is specifically important over troughs (this study) and further offshore regions (Basedow et al., 2019).

Furthermore, our results highlight a particularly high biomass of *Limacina retroversa* at the end of the productive season (July–October). A similar high contribution of mollusks (primarily *L. retroversa*) to total zooplankton biomass is also known from the North Sea where Hay et al. (1991) report high mollusk biomass in October with an additional increase in November/December, before a drop in January. We were not able to collect samples between October and January, and accordingly, we do not know when *L. retroversa* disappeared from the study area. Meinecke and Wefer (1990), however, reported sedimentation of *L. retroversa* shells in the Lofoten basin from August to November with a peak in October, and therefore, we assume that most *L. retroversa* disappeared from the study region shortly after our sampling in the end of October. Hay et al. (1991) pointed out that a considerable part (up to 50%) of mollusk DW represents the shell and accordingly the measured DW should be considered an overestimate of the biomass. Nonetheless, the high biomass of *L. retroversa* from July to October and the extreme dominance of *L. retroversa* in October in the shallow parts of our study region (Figure 4; 81.5% of biomass in cluster 2) indicates a potentially important role as prey species for higher trophic levels at shallow shelf regions in autumn, similar to the importance of the more Arctic species *L.*
helicina (Karnovsky et al., 2008) or their Southern Ocean counterparts L. retroversa australis and L. rangii (Hunt et al., 2008).

4.2 Methods of plankton biomass estimation

We used direct measurements of dry weights of formalin fixed samples. This approach is tedious and has the shortcoming that rare taxa can only be included at low taxonomic resolution. We were, however, able to describe the seasonal development of the biomass of 17 holoplankton and 9 meroplankton taxa, and 2 developmental stages of ichthyoplankton. Accordingly, our data attained a similar taxonomic resolution for holoplankton and ichthyoplankton as used in previous studies of these community components in our study region (Eiane et al., 2018). The nine meroplanktonic taxa with biomass data, however, were far below the 65 meroplankton taxa known to occur in the same community (Silberberger et al., 2016). This large discrepancy was a result of most meroplankton being rather small or low in abundance, and accordingly, meroplankton had to be aggregated on a higher taxonomic level to ensure that our biomass measurements were not biased against meroplankton. While this is a shortcoming for the taxonomic resolution of meroplankton in comparison to holoplankton in our study, we achieved a similar taxonomic resolution as other studies that used conversion factors for meroplankton biomass estimation (e.g., Coyle & Paul, 1990; Stübner et al., 2016).

Furthermore, it is likely that the weighing of such small organisms involves comparatively high measurement errors, and that the applied correction factor for the formalin fixation is not equally suitable for all taxa. Accordingly, the discrepancy between our measured and calculated weights for Calanus and Oithona could stem from the use of formalin preserved samples in our study. However, only Uye (1982) clearly states that fresh zooplankton was used in his study. All other studies seem to either have used formalin preserved samples or supplemented literature data based on formalin preserved samples with data from fresh samples. While the zooplankton material is not well described in all the publications, a predominant use of formalin preserved samples is apparent, especially for Calanus. Mumm (1991) and Hirche (1991) wrote that they used formalin preserved samples to develop their formulas. Furthermore, Mumm (1991) reports that a formalin weight loss of 38% was assumed for copepods. Accordingly, our data are directly comparable to Mumm (1991). No mentioning of correction for formalin preservation was made in Hirche (1991), and we do not know how the material for the formula in Cohen and Lough (1981) was treated. However, due to the similarity of the calculated weights of Calanus across all three methods, we consider it most likely that all formulas were developed on formalin preserved samples with a correction for formalin preservation similar to the 40% weight loss assumed in our study. In contrast, Oithona was treated differently to develop the formulas. Uye (1982) used fresh material. Ara (2001) used formalin preserved samples, but did not correct for formalin preservation. Accordingly, the formulas from Uye (1982) and Ara (2001) are not directly comparable to our data. Nonetheless, our analysis showed that the formula for Oithona hebes in Ara (2001) can be used to satisfy estimate year-round Oithona biomass in the Lofoten-Vesterålen region for formalin preserved samples after formalin correction. The widely used individual weight of 0.003 mg per individual in Blachowiak-Samolyk et al. (2008) is based on an average of three other studies (Hanssen, 1997; Mumm, 1991; Richter, 1994). However, Richter (1994) and Hanssen (1997) refer back to Mumm (1991) and accordingly it is based on formalin preserved samples and above mentioned correction. Since the individual Oithona weight of 0.003 mg is applied in virtually all sub-Arctic studies (e.g., Richter, 1994; Blachowiak-Samolyk et al., 2008; Stübner et al., 2016) and Calanus weight-length relationships were established on formalin preserved samples, we conclude at this point that our understanding of sub-Arctic mesozooplankton biomass is based on formalin preserved and corrected data. Although this is an observation that is not related to our results, we consider it important to highlight this fact as both reviewers expressed their concern about the use of formalin preserved zooplankton samples for biomass determination and questioned whether they could be compared with weight-length relationships from the literature.

Our application of length-weight relationships for Calanus spp. and Oithona spp. demonstrated that the commonly used biomass estimation methods for the two most common mesozooplankton taxa in the sub-Arctic introduce huge seasonal biases. For Calanus spp., we found a consistent underestimation of the biomass from late August to January, the period with large copepodite stages (prosome length >2 mm) dominating the samples. From April to July, the period with various size classes present in the same samples, the exponential length-weight relationships according to Cohen and Lough (1981) and Mumm (1991) performed well. However, since the winter samples demonstrated that biomass of large individuals is underestimated with these formulas, we consider it likely that the formulas overestimate the weight of the small copepodite stages. This overestimation of the biomass of small Calanus must be even stronger for the log-linear weight-length relation according to Hirche (1991) as it consistently overestimated the biomass in the spring/summer samples.

Similar to the observations for Calanus, we found the commonly applied individual biomass of 3 μg for Oithona spp. to perform best during spring (April–May), while the Oithona biomass was strongly overestimated throughout the rest of the year. Consequently, we suggest that our knowledge about the mesozooplankton biomass in the sub-Arctic is most accurate for spring and early summer, while considerable differences between true and calculated biomass for autumn and winter have to be expected.

We applied length-weight relationships only to the two most common taxa in the study region and worldwide. Accordingly, species- or genus-specific length-weight relationships were available for Calanus and Oithona. Since such taxon-specific length-weight relationships are not available for most other taxa, we assume that literature-based conversion factors retrieved from higher taxonomic levels for other taxa are likely more biased. Since the calculated biomass was already strongly biased for Calanus and Oithona, we argue
that an increased effort to measure mesozooplankton biomass is needed. In general, the commonly used approach to use a variety of taxon-specific conversion factors (Arashkevich et al., 2002; Richter, 1994; Stübben et al., 2016) comes with several drawbacks: (a) Conversion factors for most taxa are based on relatively few studies with relatively few replicates. (b) Conversion factors are not available for all taxa and conversion factors from similar taxa at different locations are used as surrogates. This is especially problematic for meroplankton taxa with a typically low taxonomic resolution, which results often in a single individual dry mass value being applied for a complete class, like Polychaeta or Bivalvia (e.g., Stübben et al., 2016). (c) Conversion factors are not adjusted for season. (d) Conversion factors from different studies are not truly comparable as they result in sometimes very different biomass estimates (our study, Blachowiak-Samolyk et al., 2008). (e) Taxonomic uncertainties with many planktonic species, even for the dominant Calanus spp. (Choquet et al., 2018), may affect biomass estimates based on conversion factors.

In our study area, a dominance of C. finmarchicus can be assumed (Choquet et al., 2017). However, C. glacialis and even C. hyperboreus or C. helgolandicus can be advected onto the northern Norwegian shelf from fjords and the northern North Sea (Choquet et al., 2017). Since these species cannot be separated according to prosome length in our study region (Choquet et al., 2018), we do not know which species contributed to the Calanus biomass in our study. Nonetheless, this did not lead to problems with the application of length-weight relationships. Hirche (1991) and Mumm (1991) developed their length-weight relationship for a mix of C. finmarchicus and C. glacialis. The formula from Cohen and Lough (1981) was developed for C. finmarchicus. However, species identification in these studies was done morphologically and accordingly our Calanus would have been identified as C. finmarchicus when the same classification would be applied.

4.3 Potential ecological functions of small mesozooplankton

4.3.1 Prey for larval fish

Spring is the period when first-feeding fish larvae are abundant (Fossum & Ellertsen, 1994; Fossum & Moksnes, 1993) over the Lofoten–Vesterålen shelf. Although our sampling method did not target ichthyoplankton, the presence of cod eggs and larvae in the plankton during April and May 2014 (Appendix S1, Eiane et al., 2018) supports the assumption that the spring SMZ community represents potential prey items available for fish larvae. Knowledge about the prey composition of fish larvae of species spawning in sub-Arctic Norway is largely limited to some early studies that found copepod nauplii dominating the gut content of larval herring and cod (Bjørke, 1978; Fossum & Ellertsen, 1994; Tilsseth, 1984). On this basis, more recent studies often limited their efforts to the identification of a spatio-temporal overlap between fish larvae and Calanus nauplii as key prey and therefore as a basis for estimating/predicting larval success (Espinasse et al., 2016, 2017; Sundby, 2000). The low total SMZ biomass in early April (Figure 2), however, indicates that fish larvae cannot afford selective feeding in early spring and that the entire SMZ community could be important prey items for fish larvae. A strong increase of the total SMZ biomass from early April to May indicates that a possible oversupply of suitable food in early May might allow for selective feeding. Studies that found Calanus nauplii dominating in stomachs of first-feeding cod larvae were typically conducted in late April or May (Fossum & Ellertsen, 1994).

Mesocosm experiments have shown that first feeding cod larvae generally select for copepod nauplii, but prey opportunistically on other less nutritious small taxa if copepod nauplii with a suitable size are low in abundance (van der Meer & Naess, 1993). Overall, prey size tends to be the primary determinant of diets of first feeding fish larvae (Blaxter, 1963; Fossum & Ellertsen, 1994; Kane, 1984). For example, cod is limited to prey sizes of 120–400 μm for the first 30 days posthatching, after which the size range of prey increases to 200–2000 μm (Fossum & Ellertsen, 1994). We assume, therefore, that the entire spring SMZ biomass (and also a part of the larger size fraction) in our study is suitable prey for older cod larvae (>30 days posthatching). Due to the overall low mesozooplankton biomass in April, we suggest that cod larvae that hatched in February and early March are likely to feed nonselectively on the entire SMZ biomass. Larvae that hatched during March, however, will be limited to prey that is smaller than 400 μm. We measured the length of a total of 136 individuals smaller than 400 μm for early April, and the majority of these individuals belonged to three taxa/groups: ophiopluteus larvae (46%), cirripedia nauplii (26%), and Fritillaria borealis (20%). Due to their low weight, however, DW data of Ophiopluteus larvae were considered unreliable (i.e., weight gain less than 4 × SD of measurement error) and excluded from the analysis. A single Calanus nauplius smaller than 400 μm was measured in April (392 μm), and only one additional Calanus nauplii had a length between 400 and 450 μm.

The copepod nauplii in our study had an average size of approximately 500 μm (Table 3), which indicates that these nauplii most likely represent Calanus nauplii (stages N4–N6) throughout the spring (Campbell et al., 2001; Hygum et al., 2000). One could argue that this absence of early Calanus nauplii is most likely related to the sampling efficiency of the chosen mesh size. The sampling efficiency of a 200-μm mesh has to be considered nonquantitative for such small taxa and abundances of taxa below 500 μm are likely underestimated by 90% or more in our samples (Riccardi, 2010). Indeed, we assume that our sampling was biased toward the collection of specific small taxa that are more likely to get stuck in the mesh with their appendages (like ophiopluteus larvae, cirripedia nauplii, and Fritillaria borealis). However, in contrast to the earlier naupliar stages of Calanus, other taxa with no appendages were collected in samples from late spring to autumn. The bivalve veliger larvae we measured as part of this study were on average 328 μm long, and 23% of the gastropod veliger were smaller than 300 μm. We consider this as an indication that some smaller Calanus nauplii should have been caught in our net (although not quantitatively) if they were present in high
numbers. However, only 6% of the measured *Calanus* nauplii in our study were smaller than 400 µm, with the shortest individual being 329 µm. *Calanus* naupliar stage 3 is shorter than 300 µm (Hygum et al., 2000), and accordingly, we only measured stages N4–N6. Based on this consideration, we suggest that the complete lack of earlier naupliar stages of *Calanus* in our samples suggests that they were not abundant in our study region. This absence could reflect the distance of our study region to the *Calanus* overwintering population in the inner part of Vestfjorden (shortest distance: ~75 nm; distance along main dispersal pathway: ~150 nm) and the time it takes for the *Calanus* eggs and nauplii to be advected to the outside of the Lofoten and Vesterålen islands (over 20 days) (Espinasse et al., 2016, 2017; Silberberger et al., 2016). Advection of nauplii from offshore waters is low in most years (Espinasse et al., 2017) and particle-tracking suggests a shelf origin of spring nauplii in 2014, when our samples were collected (Silberberger et al., 2016). Although this is speculation, we suggest that other prey than *Calanus* nauplii may be important alternative prey for first-feeding cod larvae in early spring in our study region.

Similarly, the early spring community also represents the available prey for first-feeding larvae of Norwegian spring spawning herring during March and the first days of April (Fossum & Moksness, 1993). Fossum and Moksness (1993) reported a mismatch between first-feeding herring and their assumed prey (copepod nauplii and eggs) that displayed a low abundance throughout the first half of April. Herring larvae, however, can survive for up to three weeks when fed with early naupliar stages of *Cirripedia* (Dempsey, 1978). Furthermore, herring larvae show increased activity when presented with washings and extracts of *Semibalanus balanoides* (Dempsey, 1978), the dominant cirriped in the plankton community in the Lofoten–Vesterålen region in early April (Silberberger et al., 2016), even before they started feeding. Based on this suitability of *Cirripedia* nauplii as a prey for first-feeding herring larvae and their high contribution to the total mesozooplankton biomass at the coast in early spring (17% or 19% when ichthyoplankton is excluded), we suggest that *Cirripedia* can act as an alternative prey item for first-feeding herring larvae that drift close to the coast. Herring larvae that drift further offshore, however, seem more likely to rely on small sized copepods, copepod nauplii, and other small-sized holoplankton like *F. borealis*.

4.3.2 | Meroplankton as a vector of vertical carbon flux

We encountered high meroplankton biomass (up to 1,084 mg DW/m²) during July, which contributed with 12.7%, 9.8%, and 1.7% to the total mesozooplankton biomass close to the coast, over the shallow bank, and over the deep trough, respectively (Figure 2c). The majority of this biomass was accounted for by larvae of amphipod polychaetes (490–885 mg DW/m²). This high contribution of benthic polychaete larvae at the coast and over the shallow bank in summer is comparable to reports of Hickel (1975) from the Wadden Sea of Sylt, where he found polychaete larvae to contribute on average 15% of the zooplankton biomass. Pelagic larvae of benthic invertebrates have subsequently been confirmed as an important component of the summer zooplankton community in the North Sea (Franco-Santos et al., 2019; Kirby et al., 2007, 2008).

We suggest that the high summer meroplankton biomass in our study indicates a similar importance of meroplankton in the Lofoten–Vesterålen region during summer. Benthic macrofauna communities on the Lofoten–Vesterålen shelf have an average abundance of 1,047 individuals per m² (Silberberger et al., 2019). This is considerably lower than the average of over 50,000 meroplankton individuals per m² surface area on 22 July 2014 (Silberberger et al., 2016). Furthermore, amphipod polychaetes are not abundant on the Lofoten–Vesterålen shelf (Silberberger et al., 2019). Accordingly, the vast majority of the summer meroplankton biomass must have a different fate than successful recruitment. A similar mismatch between meroplankton and adult populations is known from the Chukchi Sea (Ershova et al., 2019). Ershova et al. (2019) concluded that this means that the meroplankton is consumed either by pelagic or benthic predators. Lalande et al. (2020) found that daily sinking rates of polychaete larvae in the Chukchi Sea exceed 10,000 individuals per m² in the second half of September. Similarly, we consider it likely that the majority of summer meroplankton reaches the sediment, since the primary summer feeding grounds of herring, mackerel, and blue whiting are located further offshore (Bachiller et al., 2016). The carbon demand of epibenthic communities (the potential consumers of settling larvae) in our study region has not been assessed. However, assuming a total epibenthic carbon demand in the range of 6 to 70 g C m⁻² y⁻¹ as found on Svalbardbanken in the Barents Sea (Kędra et al., 2013), the average 278.6 mg C m⁻² associated with the settlement of all meroplankton in our samples from July could account for 0.4 to 5% of the epibenthic annual carbon demand. While this contribution might seem small, we consider it a better food source for benthic carnivores and omnivores than other forms of organic matter that reach the seafloor. Microalgae, zooplankton fecal pellets, and detritus first have to be consumed by primary consumers, while settled meroplankton is directly available to benthic carnivores and omnivores that are typical for our study region (Silberberger et al., 2018).

We suggest that this rapid (relative to sinking phytodetritus) and active transport of pelagically derived carbon directly to the benthic zone could potentially become more important in Arctic and sub-Arctic regions in the future. In a warmer future Arctic/sub-Arctic, it is likely that meroplankton biomass will increase due to northward range expansion of southern species (Narayanaswamy et al., 2010), whose life history involves planktotrophic larvae more frequently than that of Arctic species (Clarke, 1992; Thorson, 1950). This may, then, lead to an increased carbon export via settling meroplankton with potential consequences for trophic interactions of the whole ecosystem. Whereas this prediction is largely speculative at this point, ignoring a potentially important vector like meroplankton may hinder a better understanding of ecosystem functioning of high latitude ecosystems.
5 | CONCLUSION

Our study confirmed the dominance of *Calanus* spp. in the mesozooplankton biomass and an overall rather small contribution of meroplankton to this biomass on an annual basis. Nonetheless, we found meroplankton representing a considerable fraction of the SMZ biomass in early April (prior to the *Calanus* nauplii peak) and a meroplankton biomass peak in July contributing approximately 10% of the total net caught mesozooplankton biomass at the coast and over the shallow part of the shelf.

We suggest that the complex succession of SMZ (holoplankton and meroplankton) indicates recruitment of the large boreo-arctic fish stocks may be less tightly coupled to the early life cycle of *Calanus* spp. than previously assumed, as they may utilize small holoplanktonic and meroplanktonic taxa as an alternative source of food throughout the spring and early summer. This could be advantageous in the context of the ongoing climate change, since variable changes in phenology of different components of pelagic food webs are expected to result in increased trophic mismatch situations and reduced recruitment success of fish in the future (Rijnsdorp et al., 2009). In general, the availability of multiple SMZ taxa originating from two different ecosystem components (plankton–benthos) with relatively high biomass ensures a longer time-window with suitable prey for first-feeding fish larvae over the northern Norwegian continental shelf and might reduce the risk of mismatch situations.

High abundances in meroplankton biomass can comprise an important and virtually unstudied bidirectional vector of carbon transport between pelagic zone and benthos. On the one hand, a potential importance of meroplankton in fish diets suggests shunting of benthic carbon to the pelagic food web. On the other hand, settling meroplankton may contribute significantly to vertical flux during summer (the time when benthic carbon demand is highest) and provide a high-quality food source for the benthos. Overall, our findings indicate that roles of functionally different components of the mesozooplankton community need to be better described and quantified. Specifically, we suggest that benthic populations as the source of meroplanktonic larvae should receive more attention to fully understand the functioning of pelagic systems.

We recommend the increased use of direct mesozooplankton biomass measurement in future studies when possible, since the currently applied conversion factors are highly biased, and only allow for incomplete understanding of ecosystem processes and prediction of ecosystem-wide responses to ongoing climate change.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTION

Marc J. Silberberger: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing-original draft (lead); Writing-review & editing (lead). Paul E. Renaud: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (equal); Methodology (supporting); Writing-original draft (supporting); Writing-review & editing (equal). Ketil Eiane: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (equal); Methodology (supporting); Writing-original draft (supporting); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT

Mesozooplankton biomass and length measurements can be accessed on DataverseNO: https://doi.org/10.18710/07JT6E

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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