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Impact of *Microsetella norvegica* on carbon flux attenuation and as a secondary producer during the polar night in the subarctic Porsangerfjord

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It is known that *Microsetella norvegica* feed on phytoplankton and provide an important link to higher trophic levels in Arctic fjords, such as fish sprat (*Sprattus sprattus*) and three-spined stickleback (*Gasterosteus aculeatus*). It has recently been suggested that *M. norvegica* may also contribute substantially to carbon flux attenuation during periods of high abundance. However, we still know very little about how seasonal variations in abundance and vertical distribution of *M. norvegica* impact the efficiency of the biological carbon pump in Arctic fjords. We investigated the role of *Microsetella norvegica*, a small harpacticoid copepod, for particulate organic carbon flux attenuation via aggregate feeding in a subarctic fjord. We quantified the vertical distribution and abundance of *M. norvegica*, phytoplankton, and marine snow simultaneously with a Digital Autonomous Video Plankton Recorder in Porsangerfjord, northern Norway, between August 2013 and November 2014. We estimated the highest abundance of *M. norvegica* as 4.86×10^6 individuals m^{-2} in October. Our results suggest that *M. norvegica* preferred diatoms over both marine snow and the prymnesiophyte *Phaeocystis pouchetii* during euphotic bloom conditions. However, during oligotrophic conditions when phytoplankton were scarce, *M. norvegica* switched to marine snow as a food source. *M. norvegica* has the potential to explain 1.4% and 0.29% of the total carbon flux attenuation in October and November, respectively. These results suggest that small copepods feed on settling detritus when no alternative food is available. Detritus feeding by *M. norvegica* may have an ecological impact during the polar night, both via direct carbon flux attenuation, but also as secondary producers in periods with low primary production. Currently small copepods such as *M. norvegica* are not included in carbon budgets or large-scale modelling, but considering their potentially high abundance they may represent an important but overlooked pathway in both the carbon cycle and trophic level interactions.

KEYWORDS

marine snow, aggregates, fjord ecology, vertical distribution, video plankton recorder, flux attenuation

Introduction

Marine snow is prevalent within the world's oceans (Shanks and Trent, 1979; Gorsky et al., 2003), and represents the main form by which material is transported vertically in the water column (Fowler and Knauer, 1986). These organic aggregates may be comprised of dead phytoplankton and zooplankton, faecal pellets, copepod moults and ctenophore tentacles, in addition to mucus discarded by gelatinous and mucus-producing marine organisms, such as larvaceans and pteropods (Green and Dagg, 1997). Marine snow exists as a spectrum of shapes, sizes and composition of organic aggregates, which can constitute a rich food source for pelagic heterotrophs (Kiørboe and Hansen, 1993; Kiørboe et al., 1998; Stemmann et al., 2004; Iversen et al., 2010). Despite rates of marine snow formation in the ocean often being high (Kiørboe et al., 1998), multiple biologically mediated processes degrade and remineralize the organic matter so only a small fraction reaches the deep ocean. This is part of the biological carbon pump (Steinberg et al., 2008; Passow and Carlson, 2012), the role of which in sequestering carbon in the deep ocean is one of Earth's most valuable ecosystem services in terms of global climate change mitigation (Boyd et al., 2019).

Previous research on the biological pump has focused on bacterial remineralisation (where organic matter is broken down into its simplest inorganic forms, e.g. Iversen and Ploug, 2010; Iversen and Ploug, 2013) and zooplankton particle fragmentation (Iversen and Poulsen, 2007; Iversen et al., 2016; Pauli et al., 2021) as the two main processes for carbon re-entering the food web, concluding that both contribute equally to flux attenuation of organic carbon with increasing depth (Koski et al., 2020). Beyond this, marine snow may be an important food source for some zooplankton (Banse, 1990; Steinberg et al., 1997; Steinberg et al., 2008; Wilson and Steinberg, 2010), and zooplankton can act as an intermediate between organic carbon falling to the ocean's depths, where it would otherwise be sequestered, and higher trophic levels where this energy is recovered (Poulsen and Iversen, 2008). Quantifying the processes that control the transport of organic carbon from the surface to the deep ocean is fundamental in understanding the global cycling of carbon and energy sources for deep-sea food webs.

M. norvegica is known to feed on small marine phytoplankton, and has been highlighted as prey for several species of fish in high latitude fjords, including sprat (*Sprattus sprattus)* and three-spined stickleback (*Gasterosteus aculeatus*) (Svensen et al., 2018). It is evident that *M. norvegica* is an important link between lower and higher trophic levels in the food web (Hopkins et al., 1984; Turner, 1984; Uye et al., 2002; Koski et al., 2005). While it has been suggested that this species of pelagic harpacticoid copepod is not able to feed on small dispersed particles (Koski et al., 2005), it has been observed to be affiliated with organic aggregates (Alldredge, 1972; Ohtsuka et al., 1993; Green and Dagg, 1997; Uye et al., 2002), where it seems to feed on the aggregated organic matter (Banse, 1990; Steinberg et al., 1997; Koski et al., 2005; Koski et al., 2007; Steinberg et al., 2008; Koski et al., 2020). Koski et al. (2007) suggested that small differences in *M. norvegica* abundance may have substantial consequences for rates of organic carbon degradation. While it is known that *M. norvegica* does not exhibit

diel vertical migration (Maar et al., 2006), there is a gap in our understanding of their overall abundance and distribution in the water column. Based on the habitat choice theory, it is logical to predict that foraging zooplankton will distribute themselves at a depth where food intake is maximised, while predation risk is minimised (Lima, 2002; Fossheim and Primicerio, 2008). In this study we contribute important data on abundance and distribution of *M. norvegica* in a sub-arctic fjord at high spatial resolution by using non-invasive optical imaging. Furthermore we provide insight into their seasonal changes of depth preference and potential impact on carbon flux attenuation.

Here we study the fine-scale seasonal depth distributions of *M. norvegica*, phytoplankton, and marine snow in a high latitude ecosystem in order to quantify the impact of *M. norvegica* on flux attenuation. The main objectives were to (i) investigate seasonal abundance of *M. norvegica* throughout three locations in Porsangerfjord, (ii) investigate the seasonal association of *M. norvegica* with marine snow, and to (iii) estimate *M. norvegica's* potential contribution to organic carbon flux attenuation throughout the year.
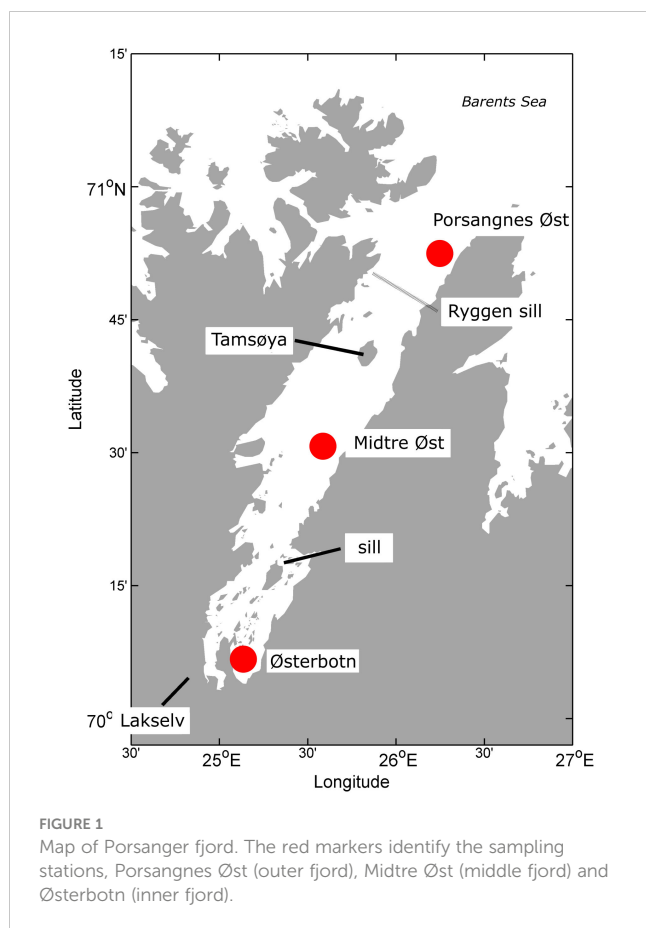
Materials and methods

Study area and sampling design

Our study sites were located in Porsangerfjord (70°52.5′N). With its 100 km length and 10-15 km width, Porsangerfjord is the fourth longest fjord of Norway and located in the northernmost part of the Norwegian mainland. Porsangerfjord extends in a north-easterly direction and opens into the southern Barents Sea. Topographically, Porsangerfjord is divided into three regions, the inner fjord (0-30 km), the middle fjord (30-70 km) and the outer fjord (70-100 km) (Stramska et al., 2016). Each region is separated by a sill and as a result, the three regions have different water flow and exchange with the Barents Sea (Stramska et al., 2016; Figure 1). The inner fjord has little water exchange with the middle and the outer fjord. The outer fjord is strongly influenced by inflow of Atlantic water from the Barents Sea which impacts the middle fjord to a lesser degree. The middle fjord has a strong wind driven circulation that causes an eastern outflow and a western inflow. We sampled at Østerbotn in the inner fjord, at Midtre Øst in the middle fjord, and at Porsangnes Øst in the outer fjord (Figure 1). The inner station is strongly impacted by meltwater, river input, and rain water runoff, with sub-zero temperatures during the winter, and occasionally freezes over during cold periods (Christiansen and Fevolden, 2000). Porsangerfjord is an important site for commercial fisheries, and has recently been under scrutiny after an invasion of the Red King crab, which has altered the food web dynamics in the region (Pedersen et al., 2018).

Video Plankton Recorder

We collected vertical profiles of marine snow and the copepod *Microsetella norvegica* during four cruises with R/V Johan Ruud

FIGURE 1
Map of Porsanger fjord. The red markers identify the sampling stations, Porsangnes Øst (outer fjord), Midtre Øst (middle fjord) and Østerbotn (inner fjord).

(UiT the Arctic University of Norway) between August 2013 and November 2014 (Table 1 and Figure 1). A digital autonomous video plankton recorder (VPR; Seascan Inc., USA) was used to collect 10-16 vertical profiles of zooplankton and aggregates. The VPR is a non-invasive *in situ* camera system (Figure 2) that captures on average 21 frames per second at a vertical speed of ~0.8 meter per second while being yo-yoed for ca one hour. The VPR was equipped with a 1.4 megapixel black and white camera that was illuminated by a Xenon strobe mounted opposite to the camera. The pixel-size

was 24.1 μm per pixel and the water volume captured by each image frame was 26.3 ml in 2013, and 35.2 ml in 2014 (calibration was done in the lab using a grid with precisely spaced markings). The total imaged water volume per vertical profile was calculated by multiplying the number of images by the volume of each image (Table 1). The VPR was equipped with a 16 Hz CTD (SBE49, Seabird Electronics Inc., USA) and an 8 Hz fluorometer (ECO Puck, WET Labs Inc., USA). Fluorescence signals were converted to chlorophyll *a* concentration, Chl *a* (μg L^{-1}) = 0.0125 (X – 55), where X = the registered value from the fluorometer.

Images and physical data were collected as compressed files on detachable flash drives, and later downloaded and decompressed using the Autodeck software (Seascan, Inc.), which detected and extracted in-focus regions of interest (ROIs) from each image based on contrast (Sobel) to the un-illuminated pelagic backdrop. Identification of ROIs was achieved using the Visual Plankton package (C.S. Davis, Woods Hole Oceanographic Institute, USA), where manually sorted images from each sampling period were used to train a season-specific classifier, of the COM-SVM (Co-occurrence Matrix with Support Vector Machine) type (Hu and Davis, 2005), which could automatically identify ROIs using feature extraction algorithms. Automatic classification was suitable for marine snow counts, which were manually validated, but since *M. norvegica* are small, auto classification for this species resulted in significantly underestimated abundances throughout VPR profiles. To achieve accurate abundance estimates for *M. norvegica*, data were used from a single vertical profile in each tow. Each frame of the entire second downward vertical profile was manually counted in each sampling period. Nonetheless, the automatic classification system was used to compare all vertical profiles. This allowed comparison between profiles to verify that the second downward vertical profile was representative of all vertical profiles. Of the objects visually observed in the full frame images, a large majority were *M. norvegica*, but other groups (such as *Pseudocalanus, Oithona, Calanus* and meroplankton) were also present. Additional zooplankton abundances are presented by Priou (2015) for the same deployments at the sample sites based on both VPR data and WP-2 counts.

TABLE 1 Sampling details for the VPR tows.

Date	Sampling Site	Latitude/ °N	Longitude/ °E	Sampling Start (GMT)	Sampling Depth (m)	Number of Images	Total Image Volume (L)
25.08.2013	Østerbotn	70°07.183'	25°10.836'	09:24	110	2249	59.15
22.10.2013	Østerbotn	70°07.125'	25°10.788'	09:16	110	2742	72.12
21.05.2014	Østerbotn	70°07.076'	25°10.869'	09:00	110	2202	77.51
19.11.2014	Østerbotn	70°07.213'	25°10.697'	09:25	106	2043	71.91
21.05.2014	Midtre Øst	70° 30.706'	25° 35.001'	22:30	190	5908	207.96
19.11.2014	Midtre Øst	70° 30.628'	25° 34.925'	19:16	185	3635	127.95
20.05.2014	Porsangnes Øst	70°52.475'	26° 01.071'	09:51	200	4393	154.63
20.11.2014	Porsangnes Øst	70°53.150'	26°15.659'	16:35	210	4140	145.73

The sampling depth is ca. 10 m above the bottom. Number of images and volume refers to one profile only.
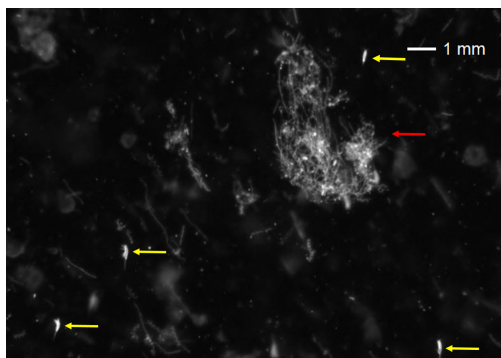
FIGURE 2
Part of a VPR image from Østerbotn, May 2014, showing diatom chains, a loose diatom aggregate (red) and several individuals of *Microsetella norvegica* (yellow).

Marine snow properties

The area of individual aggregates was obtained using the Visual Plankton Matlab package (C.S. Davis, Woods Hole Oceanographic Institute, USA) and the pixel-size from the VPR profile. The aggregate area was converted to equivalent spherical radius (ESR) (Eq. 1) and ESR was used to calculate the equivalent spherical volume (ESV) (Eq. 2).

$$ESR = \sqrt{\frac{area}{\pi}} \tag{1}$$

$$ESV = \left(\frac{4}{3}\right)\pi ESR^3 \tag{2}$$

Aggregates were binned into three logarithmically separated size-ranges; ESR 0 to 250 μm, 250 to 750 μm, and >750 μm. The sinking velocity (U; [m d^{-1}]) of each radius range (a; [mm]) and POC content of aggregates were calculated based on their respective size categories using relationships for size-specific settling and POC content from van der Jagt et al. (2020); (Eq. 3 and 4).

$$U(a) = 48a^{0.85} \tag{3}$$

$$POC = 0.84 \cdot vol^{0.5} \tag{4}$$

Potential aggregate grazing by *Microsetella norvegica*

To estimate the potential aggregate grazing by *M. norvegica* and have an indication of the impact from *M. norvegica* on flux attenuation, we used the behavioural trait values of *M. norvegica* from Koski et al. (2005). These behavioural traits were average residence time of *M. norvegica* on an aggregate (δ^{-1}; [s]), average aggregate carbon-ingestion rate of *M. norvegica* (i; [μg C·individual^{-1}·d^{-1}]), average swimming speed of *M. norvegica* (v; [cm s^{-1}]), average duration of swimming events for *M. norvegica* (τ; [s]) and average duration of pause events of *M. norvegica* (ρ; [s]) (Koski

et al., 2005), see Table 2. These trait values were used to calculate an equivalent diffusion coefficient (D; [cm^2 s^{-1}]) (Eq. 5, Koski et al., 2005), assuming a random isotropic motion pattern (Visser and Thygesen, 2003). As per Koski et al. (2005), we assume a constant residence time according to their estimates based on 2000 μm aggregates. van der Jagt et al. (2020) observed a difference in residence times for *Calanus* attached to aggregates of different sizes, so it is likely that the residence time of *M. norvegica* differs based on aggregate size. Furthermore, the harpacticoid copepod *M. norvegica* might be more adapted to mining aggregates and may have a much longer residence time attached to aggregates compared to the calanoid copepod *Calanus*.

$$D = \frac{v^2 \tau^2}{2(\tau + \rho)} \tag{5}$$

From the diffusion coefficient calculated for *M. norvegica*, the volume of water that an individual *M. norvegica* can search per unit time (β; [ml·d^{-1}]) for a given aggregate radius (a; [cm]) was calculated (Eq. 6, Koski et al., 2005).

$$\beta = 4\pi Da \tag{6}$$

Using β and the *in situ* abundance of *M. norvegica* that we quantified with the VPR, we can then calculate the number of *M. norvegica* that a sinking aggregate with radius (a; [cm]) and a sinking rate ($u(a)$; [cm·s^{-1}]) will encounter (E) during its descent through a water column of depth h (Eq. 7, Koski et al., 2005).

$$E(a) = \beta(a)C\frac{h}{u(a)} = \frac{\beta(a)A_{cop}}{u(a)} \tag{7}$$

Where C is the average ambient concentration of *M. norvegica* integrated per water volume (individuals·m^{-3}) within the depth h, and A_{cop} is the abundance of *M. norvegica* integrated over depth h. E was used to calculate the fractional degradation (k) caused by *M. norvegica* feeding on each sinking aggregate (Eq. 8, Koski et al., 2005).

$$k(a) = \frac{E(a)\delta^{-1} \cdot i}{POC(a)} = \frac{\beta(a)A_{cop} \cdot \delta^{-1} \cdot i}{POC(a) \cdot u(a)} \tag{8}$$

k was calculated for each aggregate size-class, per 10 m depth bin. This gave an estimated fraction of aggregated POC that was degraded by *M. norvegica* for each aggregate size-class, per depth bin. This fraction was then subtracted from the POC content of each aggregate as it entered a new depth bin. This gave an estimate of the POC content of individual aggregates as they sank out of the previous depth bin. This was done for each depth bin throughout the water column, enabling us to estimate the POC export and POC

TABLE 2 Behavioural trait values of *M. norvegica* (Koski et al., 2005).

Average swimming speed, ν (cm s^{-1})	0.06
Swim duration, τ (s)	4.8
Pause duration, ρ (s)	3.6
Average residence time, δ^{-1} (s)	7920
Ingestion rate, i (μg C individual^{-1} s^{-1})	4.63x10^{-6}

loss due to *M. norvegica* of each aggregate size-class through the entire water column. Multiplying these results with the total abundance of aggregates in each respective size-class provided estimates of the total export and attenuation of POC, following grazing by *M. norvegica*.

Statistical analysis

The average number of observations in each VPR image for *M. norvegica* were low, so all data were integrated into 1 m depth bins by summing up individual frame counts. This also reduced the effects of any outlying data points. Using the total sampling volume for all images in each depth interval and the number of *M. norvegica* observed in each image, the number of individuals per m^3 was calculated. Marine snow aggregate observations were also integrated and calculated as the number of aggregates per m^3. Marine snow data had square root transformations applied for the purpose of visualisation, as the number of observations in May were drastically higher than in other sampling periods. The data used for calculations, however, was not transformed. VPR data were processed using Microsoft Excel, and analysed using RStudio 4.0.2 (RStudio Team, 2021).

To investigate differences in vertical distribution of *M. norvegica* during different sampling periods, the mean depth was calculated according to Frost and Bollens' (1992) equation for weighted mean depth (WMD) (Eq. 9).

$$WMD = \frac{\sum n_i d_i}{\sum n_i} \qquad (9)$$

Where n_i is the concentration of individual *M. norvegica* (individuals m^{-3}), and d_i is the water depth (m). The data was non-normally distributed and we used Spearman correlation coefficient (r_s) (Eq 10) to assess the relationships between variables. Results were taken to be significant when r_s was ≤ 0.05.

$$r_s = 1 - \frac{6\sum_X D_X^2}{N - (N^2 - 1)} \qquad (10)$$

Where N is ranks, and D_x is the difference between the X and Y ranks for the xth case.

Results

Seasonal trends in temperature, salinity and chlorophyll *a*

The innermost station, Østerbotn, stood out as a considerably colder site compared to both Midtre Øst in the middle fjord and Porsangnes Øst near the mouth of the fjord (Figure 3). Østerbotn was also more affected by freshwater input in the spring and summer months compared to the middle and outer fjord.

In May, temperatures were 2–2.5°C lower at Midtre Øst and Porsangnes Øst, with similar salinities to November (ca 34.0). Here, the water column was still quite well-mixed, with somewhat warmer temperatures above 10 m depth at both stations (5°C), and a slightly reduced salinity (34.1) at the outer station (Figures 3, 4). At Østerbotn, the temperature was barely above 0°C at 100 m (just above the bottom), increasing to ca 3.8°C near the surface. Salinity decreased from 33.8 in the deeper part of the water column to 33.6
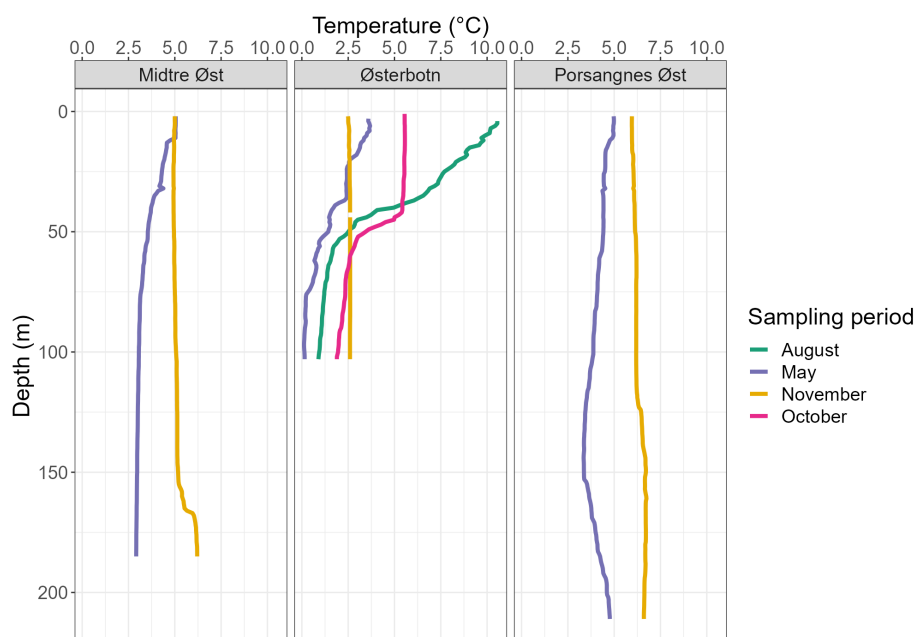

FIGURE 3
Temperature profiles during four sampling periods taken over three sampling stations, integrated into 1 m depth bins.
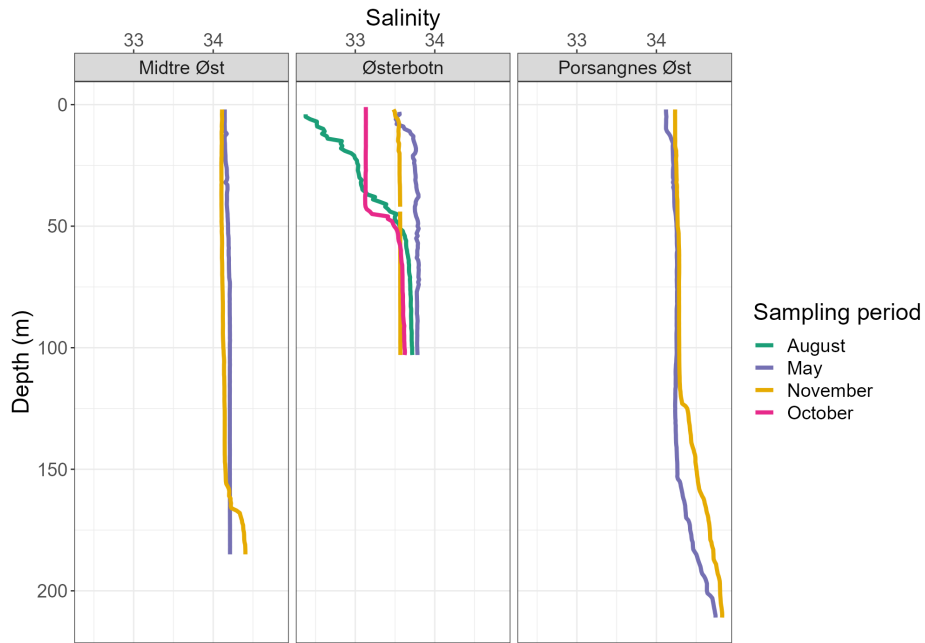
FIGURE 4
Salinity profiles during four sampling periods taken over three sampling stations, integrated into 1 m depth bins.

at the surface. This was prior to the main freshwater input in June, and all three stations had weak pycnoclines. There were subsurface maxima of chlorophyll *a* concentrations at all stations, indicating a post-bloom phase (Figure 5). The chlorophyll *a* maxima were pronounced in Østerbotn (6.4 µg l^{-1} at 23 m) and Porsangnes Øst (5.6 µg L^{-1} at 20 m), while concentrations were 0.8-2.0 µg L^{-1} at Midtre Øst, with higher values found between 20–110 m (Figure 5).

In August, surface waters in Østerbotn had warmed up to 10.4°C, gradually decreasing to 0.93°C at the bottom (Figures 3, 4). There was a broad pycnocline centred around 35 m, with salinity decreasing from 33.7 in the waters below 50 m to 32.4 in the surface. There was a subsurface chlorophyll *a* maximum at 11 m (1.8 µg L^{-1}, Figure 5),

In October, the water column in Østerbotn was strongly stratified with a pycnocline at 42 m. Temperature changed from
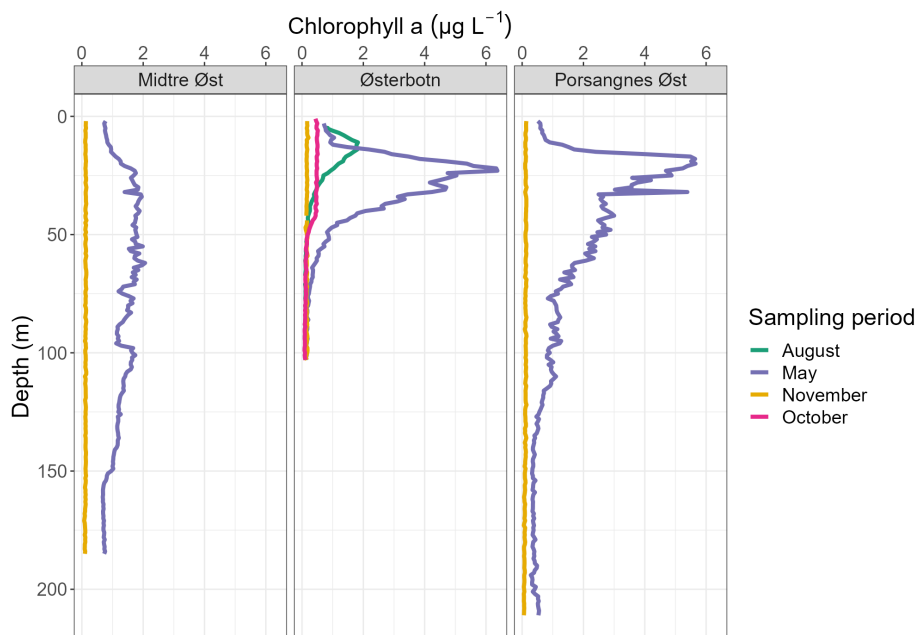

FIGURE 5
Average chlorophyll *a* concentration depth profiles during four sampling periods taken over three sampling stations, integrated into 1 m depth bins.

5.4°C at 42 m to 3°C below 52 m depth, and salinity increased from 33.1 to 33.5 in the same interval (Figures 3, 4). Low chlorophyll *a* concentrations were measured above the pycnocline (Figure 5).

In November, Østerbotn had a well-mixed water column with ca 2.5°C and a salinity of 33.5, while Midtre Øst had ca 5°C and a salinity of 34.2 with a small incursion of slightly warmer and more saline water below 160 m, indicating coastal water of Atlantic origin (Figures 3, 4). At Porsangnes Øst, temperature and salinity were slightly higher (6.0°C and 34.5), with the coastal water intruding below 125 m. Chlorophyll *a* concentrations were negligible at all stations; this was at the beginning of the Polar Night in Porsangerfjord.

Distribution of marine snow and *Microsetella norvegica*

Østerbotn had the highest concentrations of marine snow as well as the highest abundances of *M. norvegica* of the three investigated locations.

In Østerbotn, the abundance of marine snow aggregates was 50 times higher in May than in any other sampling period, with a maximum aggregate density of 6.1×10^5 aggregates m^{-3} at 42 m depth (Figure 6). The other sampling periods had more uniform abundances of marine snow throughout the water column, with the lowest abundance in November. Similarly, in Midtre Øst and Porsanges Øst, the abundance of marine snow peaked in May (Figure 6). A very low abundance of marine snow was observed in November, with the highest aggregate abundance observed toward the bottom of the water column.

The abundance and depth distribution of *M. norvegica* varied drastically throughout the year in Østerbotn (Figure 7). *M. norvegica*
was most abundant in October, with a maximum estimated abundance of 2.31×10^5 individuals m^{-3} at 87 m and a total abundance of 4.86×10^6 individuals m^{-2}. The WMD was shallower, at 78 m. This was similar to the depth at which the maximum concentration of marine snow was observed. The lowest abundance of *M. norvegica* was observed in November, with the highest density recorded as 5.01×10^4 individuals m^{-3}. During this sampling period, the concentration of *M. norvegica* increased with increasing depth from the surface to the bottom, hence the WMD was observed at a lower depth than the maximum concentration of *M. norvegica* (99 and 80.6 m, respectively; Table 3). In May and August, the maximum number of *M. norvegica* (1.4×10^5 individuals m^{-3} and 1.3×10^5 individuals m^{-3}, respectively) was nearer the surface (14 and 13 m, respectively) than the observed WMD's (23.6 and 25.8 m, respectively; Figure 7). The WMD's were similar to the depths at which the chlorophyll *a* maximum was recorded during these months. At the locations Midtre Øst and Porsangnes Øst, more individuals of *M. norvegica* were observed during November than in May, but there was a low abundance of *M. norvegica* observed during both sampling periods (Figure 7). The WMD of *M. norvegica* was deeper in November than in May for both sampling periods (Table 3). There was no clear similarity between WMD of *M. norvegica*, chlorophyll *a* maximum or marine snow maximum.

In May and August in Østerbotn, there were statistically significant positive correlations between the distribution of chlorophyll *a* and *M. norvegica* ($R^2 = 0.76$, $p = 0.0000$ and $R^2 = 0.94$, $p = 0.0000$, respectively). The correlations between the distribution of marine snow and *M. norvegica* were negative. This was not statistically significant in May, but was in August ($R^2 = -0.07$, $p = 0.5025$ and $R^2 = -0.37$, $p = 0.0002$, respectively). In October and November, there were statistically significant
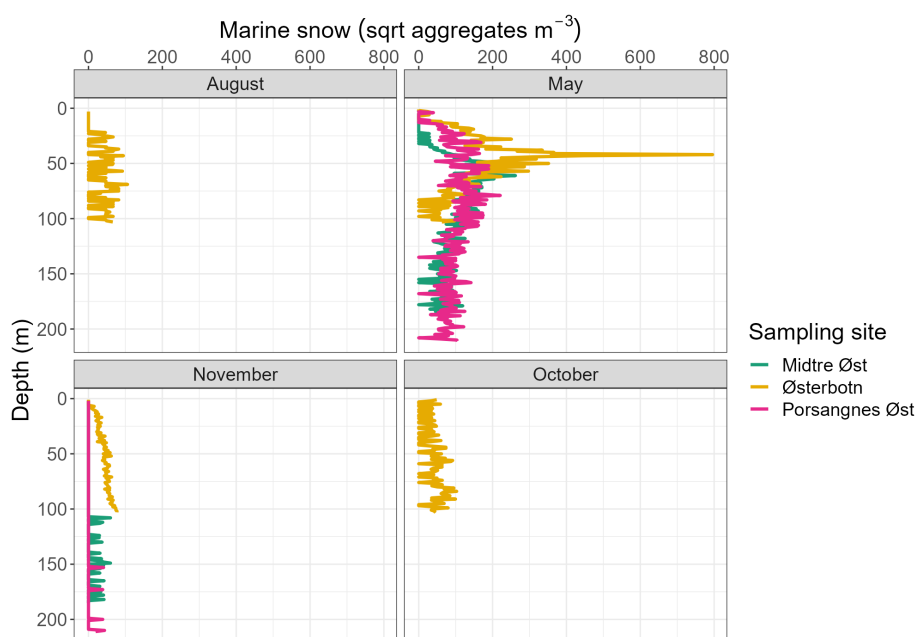

FIGURE 6
Vertical distribution of the square root of marine snow aggregates during four sampling periods, sampled using the Video Plankton Recorder and integrated into 1 m depth bins. Marine snow aggregates are presented as abundance (aggregates m^{-3}).
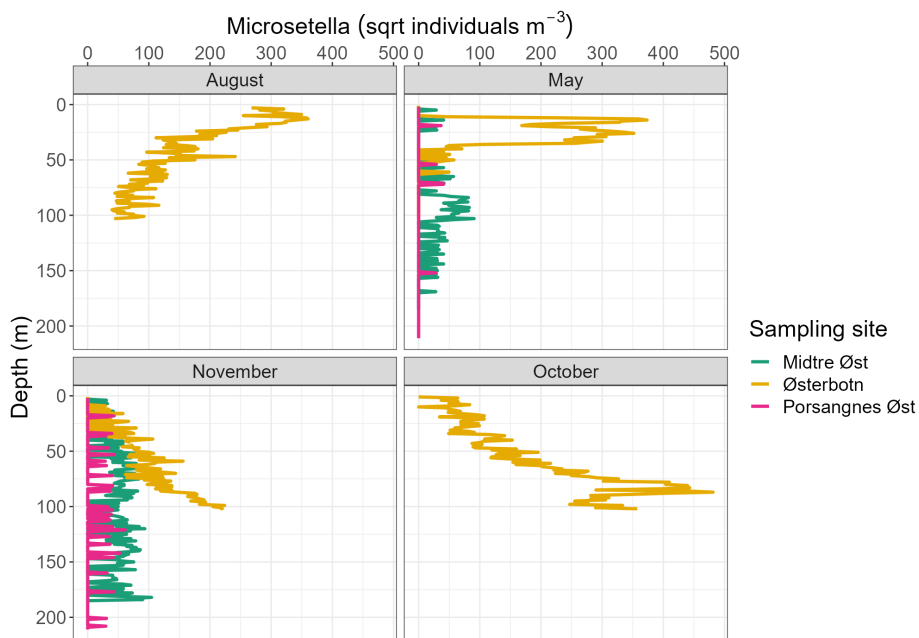
FIGURE 7
Vertical distribution of the square root of *M. norvegica* individuals during four sampling periods, sampled using the Video Plankton Recorder and integrated into 1 m depth bins. *M. norvegica* individuals are presented as abundance (individuals m^{-3}).

positive correlations between the distribution of marine snow and *M. norvegica* ($R_2 = 0.49$, p = 0.0000 and $R^2 = 0.86$, p = 0.0000, respectively). In October, there was a statistically significant negative correlation between the distribution of chlorophyll *a* and *M. norvegica* ($R^2 = -0.71$, p = 0.0000). In November, there was a weak statistically significant correlation between the distribution of chlorophyll *a* and *M. norvegica* ($R^2 = 0.16$, p = 0.0205 (Table 4).

Effect of aggregate size on flux attenuation by *Microsetella norvegica*

To evaluate the potential impact of *M. norvegica* on the vertical POC flux, we estimated the fraction of aggregated POC that was ingested by *M. norvegica* for each aggregate size-class. The estimated degradation fraction (*k*) of aggregates varied with aggregate size, and with ambient abundance of *M. norvegica*. As

TABLE 3   Weighted mean depth (WMD) of *Microsetella norvegica*, abundance of *M. norvegica* in the entire water column, and estimated maximum values and depths for *M. norvegica* density, chlorophyll *a* maximum and marine snow density during eight sampling occasions.

Month	Sampling site	*M. norvegica* abundance (individuals m^{-2})	WMD *M. norvegica*.	Max. *M. norvegica* (individuals m^{-3}) [depth (m)]	Chlorophyll *a* max. (µg L^{-1}) [depth (m)]	Max. marine snow (aggregates m^{-3}) [depth (m)]
May	Østerbotn	2.0x10^6	23.6	1.4x10^5 [14]	6.37 [23]	6.1x10^5 [42]
May	Midtre Øst	1.4x10^5	94.8	8.2x10^3 [103]	2.06 [62]	6.9x10^4 [61]
May	Porsangnes Øst	6.3x10^3	68.3	1.7x10^3 [72]	1.25 [20]	4.9x10^4 [79]
August	Østerbotn	3.1x10^6	25.8	1.3x10^5 [13]	1.82 [11]	1.1x10^4 [69]
October	Østerbotn	4.9x10^6	78.0	2.3x10^5 [87]	0.52 [6]	1.1x10^4 [84]
November	Østerbotn	1.2x10^6	80.6	5.0x10^4 [99]	0.21 [9]	6.0x10^3 [102]
November	Midtre Øst	4.2x10^5	109	1.1x10^4 [182]	0.15 [44]	3.6x10^3 [80]
November	Porsangnes Øst	4.5x10^4	102	3.8x10^3 [121]	0.15 [30]	1.9x10^3 [210]

TABLE 4 Spearman correlation coefficients (R^2) of *Microsetella norvegica* abundance versus chlorophyll *a* concentrations, marine snow abundance and marine snow aggregate size for four sampling periods.

	Month	Sampling Site	Temperature (R^2) [p-value]	Salinity (R^2) [p-value]	Chlorophyll *a* concentration (R^2) [p-value]	Marine snow abundance (R^2) [p-value]
M. norvegica abundance	May	Porsangnes Øst	0.02 [0.7873]	-0.06 [0.3596]	0.12 [0.0786]	0.06 [0.3809]
		Midtre Øst	-0.21 [0.0038]	0.25 [0.0006]	0.13 [0.0796]	0.21 [0.0049]
		Østerbotn	0.55 [0.0000]	-0.06 [0.5618]	0.76 [0.0000]	-0.07 [0.5025]
	August	Østerbotn	0.86 [0.0000]	-0.85 [0.0000]	0.94 [0.0000]	-0.37 [0.0002]
	October	Østerbotn	-0.91 [0.0000]	0.87 [0.0000]	-0.71 [0.0000]	0.49 [0.0000]
	November	Porsangnes Øst	-0.06 [0.3526]	-0.12 [0.0899]	0.16 [0.0205]	-0.06 [0.4224]
		Midtre Øst	0.10 [0.1733]	0.11 [0.1438]	-0.04 [0.5762]	0.10 [0.1944]
		Østerbotn	0.41 [0.0000]	0.43 [0.0000]	-0.07 [0.5081]	0.86 [0.0000]

such, the POC content of aggregates varied according to sampling period and depth. The overall fraction of POC that was consumed was largest in Østerbotn, and lower in Midtre Øst and Porsangnes Øst. In Østerbotn, we observed the highest aggregate grazing in October, and the lowest in August and November. In Midtre Øst and Porsangnes Øst, there were no significant differences in aggregate grazing by *M. norvegica* between the sampling periods.

Estimates of total aggregate grazing by *Microsetella norvegica*
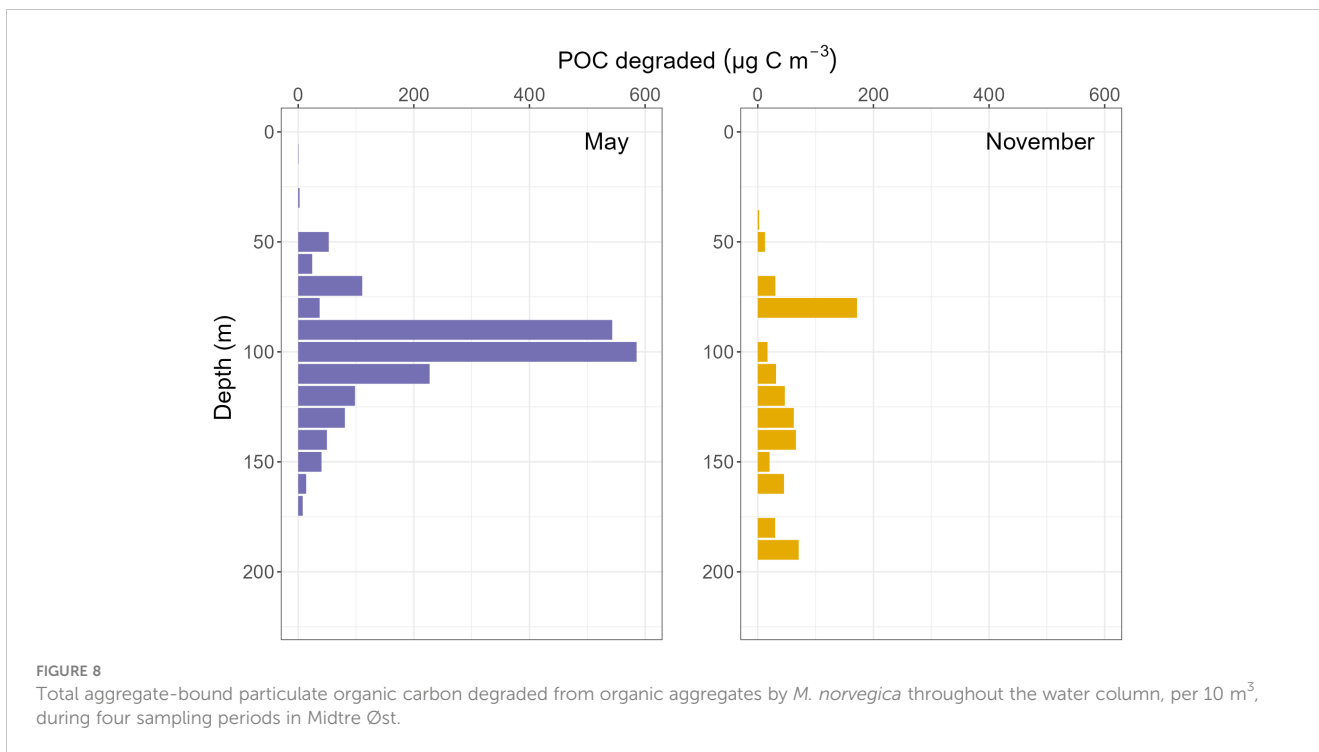
The amount of aggregated POC varied with depth and between sampling periods and locations. The total aggregated POC that was consumed by *M. norvegica* was higher in Østerbotn than at the other locations for each sampling period (Table 5 and Figures 8–10). The most intense aggregate grazing by *M. norvegica* at Østerbotn was in October, where 1.4% (Table 5) of the total aggregated POC was consumed. The lowest aggregate grazing by *M. norvegica* was in May, at Porsangnes Øst. Here, 3.8×10^{-4}% (Table 5) of the total aggregated POC was consumed.

Comparisons can be made between all three stations for May and November. *M. norvegica* consumed more aggregated POC in May at Midtre Øst and Porsangnes Øst, but not at Østerbotn. Here, the most POC was instead consumed in October. However, there was a higher amount of aggregated POC available during May compared to November; this suggested that the higher aggregate grazing was not caused by increased fractional grazing of each aggregate, but due to more aggregate-copepod encounters during May compared to November (Table 5 and Figures 8–10).

TABLE 5 Total organic carbon bound to aggregates in the entire water column, total organic carbon degraded from aggregates by *Microsetella norvegica* and the total grazing potential of *M. norvegica* on aggregate-bound organic carbon throughout the entire water column.

Month	Sampling site	Total biomass of aggregate-bound carbon (µg C)	Total organic carbon degraded by *M. norvegica* (µg C)	Total grazing potential of *M. norvegica* (%)
May	Porsangnes Øst	2.3×10^7	87	3.8×10^{-4}
	Midtre Øst	1.4×10^7	1.9×10^3	1.4×10^{-2}
	Østerbotn	9.5×10^6	3.5×10^4	0.37
August	Østerbotn	3.8×10^6	1.6×10^4	0.41
October	Østerbotn	3.7×10^6	5.2×10^4	1.4
November	Porsangnes Øst	1.6×10^5	4.5	2.9×10^{-3}
	Midtre Øst	9.2×10^5	6.1×10^2	6.6×10^{-2}
	Østerbotn	2.9×10^6	8.5×10^3	0.29

FIGURE 8

Total aggregate-bound particulate organic carbon degraded from organic aggregates by *M. norvegica* throughout the water column, per 10 m³, during four sampling periods in Midtre Øst.
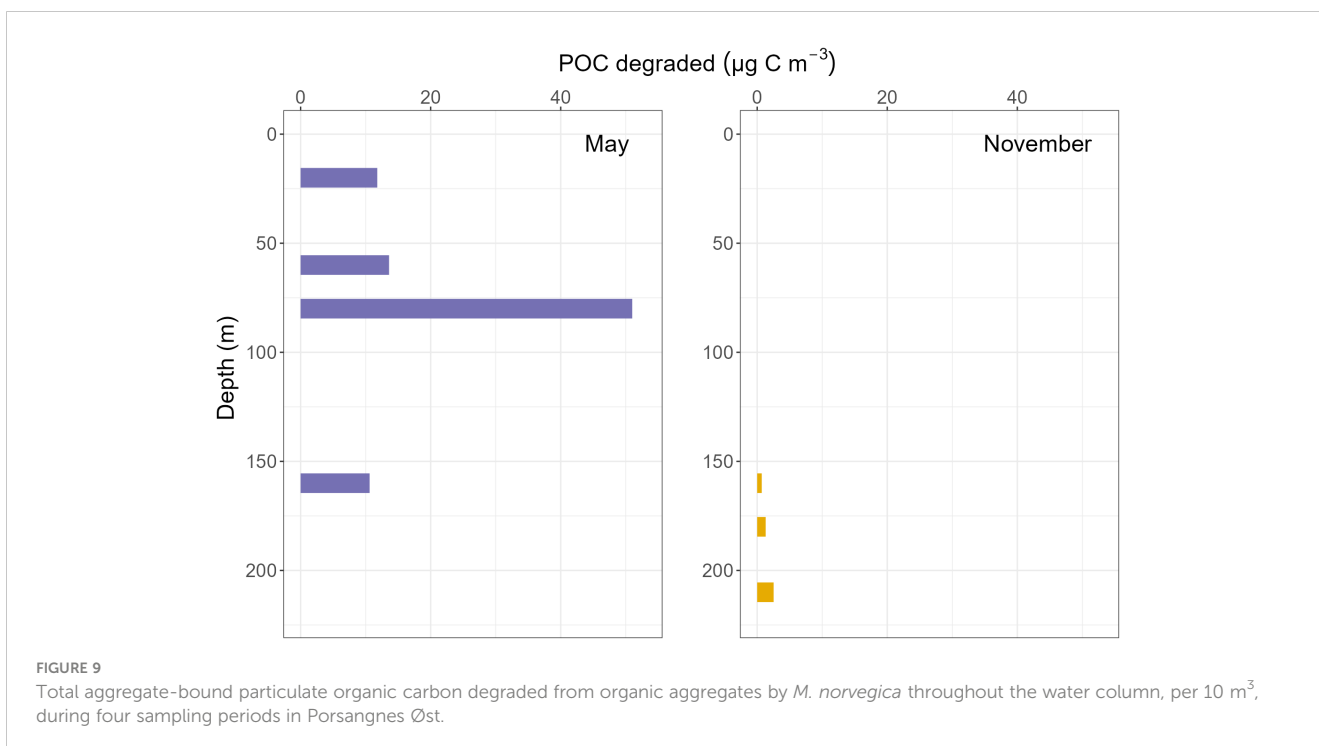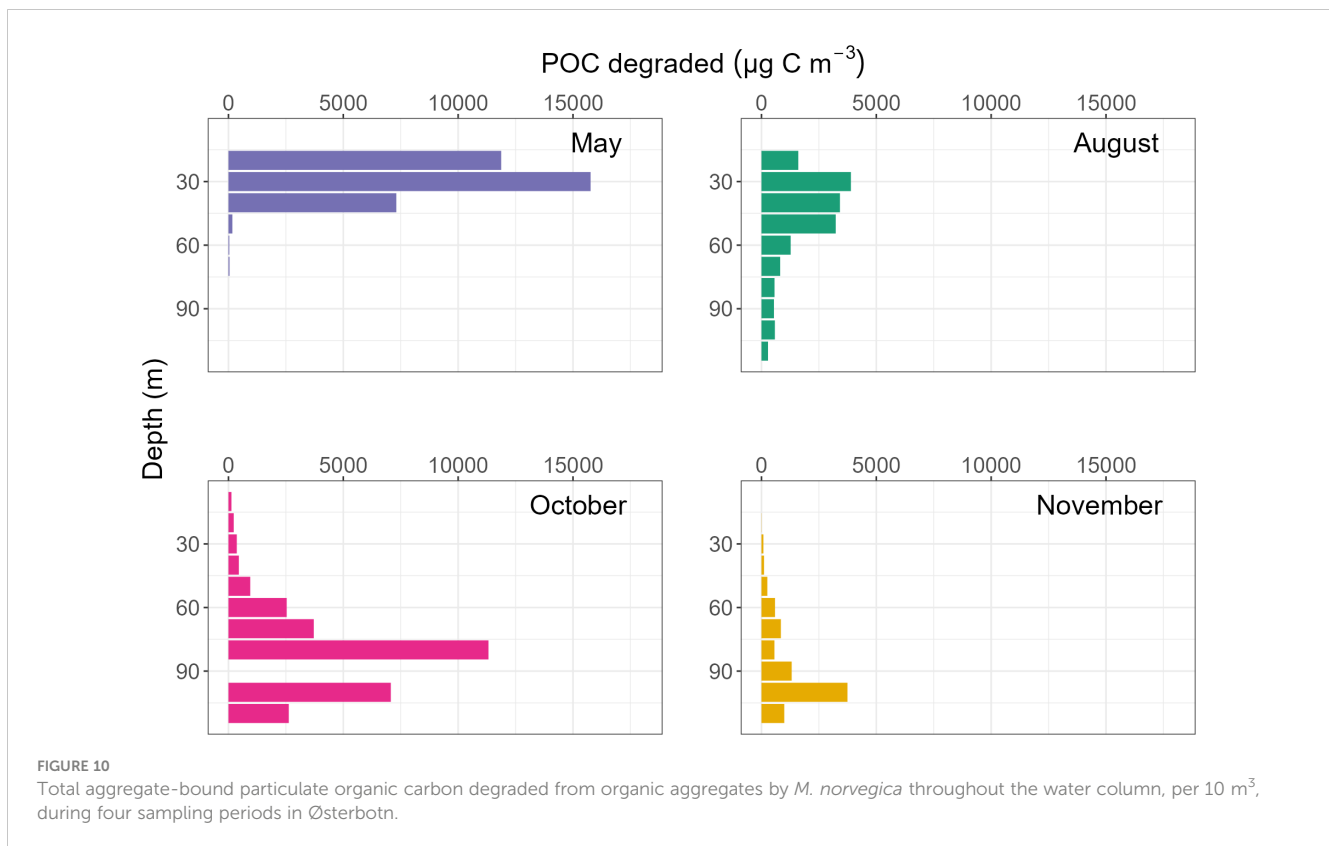
Discussion

Our study demonstrated the potential for *M. norvegica* to feed on settling aggregates and, thus, impact the amount of downward carbon flux in a sub-arctic North Norwegian fjord. In the following we will discuss the potential for, and possible factors influencing the role of, *M. norvegica* in affecting POC flux. We will focus on the geographical, seasonal and vertical distribution of aggregate grazing by *M. norvegica* and discuss the potential ecological impact from *M. norvegica* for flux attenuation in the ocean.

Seasonal and geographic abundance of *Microsetella norvegica*

The amount of POC that falls through the water column towards the seafloor is a function of organic matter production rates and

FIGURE 9

Total aggregate-bound particulate organic carbon degraded from organic aggregates by *M. norvegica* throughout the water column, per 10 m³, during four sampling periods in Porsangnes Øst.

FIGURE 10
Total aggregate-bound particulate organic carbon degraded from organic aggregates by *M. norvegica* throughout the water column, per 10 m^3, during four sampling periods in Østerbotn.

aggregate formation in the shallow, sunlit waters. Sub-arctic ecosystems exhibit strong seasonality in phytoplankton blooms, displaying significantly higher biomass during summer compared to the dark winter. The results of this study showed a clear seasonal variation in the abundance of *M. norvegica* in Porsangerfjord. Although abundances were high during May 2014 and August 2013, the highest abundance of *M. norvegica* in Østerbotn was observed during October 2013. This is a later seasonal peak in *M. norvegica* abundance compared to a previous study in Balsfjord in 2014, where *M. norvegica* abundance peaked during May and observed a population of older copepodite stages and adults until September (Svensen et al., 2018). Svensen et al. (2018) quantified *M. norvegica* using WP-2 nets and Go-Flow bottles, which allowed quantifications of nauplii and young copepodites, which were not easily identifiable in the VPR images. It should therefore be noted that our *M. norvegica* abundances from the VPR images are mainly based on older copepodite stages and adults. During October, this population may have been sustained by efficient water mixing, which could have caused resuspension of POC from the seafloor to the water column and provided a food source in the shallow Østerbotn. WP-2 net counts from the same study period showed that *M. norvegica* abundances also peaked during October in the other two fjord regions (Prat Varela, 2015; Priou, 2015). Here we assume that the water depth was too deep to have caused resuspension of POC and it seems more likely that the population development of *M. norvegica* was delayed in 2014 and *M. norvegica* peaked in late May or June, i.e. after our sampling campaign. Judging from previous studies, there seem to be strong variations in the

population dynamics of *M. norvegica* between years; Svensen et al. (2018) observed very different abundances of *M. norvegica* between May 2013 and May 2014 in the North Norwegian Balsfjord. Despite the limitations in detecting nauplii and smaller copepodite stages by the VPR, the abundance of *M. norvegica* reported in this study is in line with previous observations. Studies using water bottles or zooplankton nets with appropriately small mesh sizes (≤100 µm) to sample *M. norvegica* have reported high abundances at different latitudes (34° N - 69° N), ranging from 2.0×10^4 individuals m^{-3} to 5.0×10^5 individuals m^{-3} (Uye et al., 2002; Arendt et al., 2013; Demchuk et al., 2015; Svensen et al., 2018). The maximum abundance recorded in this study was 2.3×10^5 individuals m^{-3}, suggesting that the VPR did provide accurate abundances of adult *M. norvegica* during our study.

The most obvious contrast in *M. norvegica* abundances was that between the inner fjord (Østerbotn) and the middle and outer fjord; the abundance per m^{-2} was approximately two orders of magnitude higher in Østerbotn than at the outer station, with the middle station intermediate. It is clear that *M. norvegica* thrived especially in the inner fjord, which is known to have a local diatom community emerging from overwintering spores each spring (Hegseth et al., 1995). This diatom bloom is restricted to the inner fjord by the shallow sill and the circulation of the waters within the middle fjord. The division between a diatom-dominated phytoplankton community (especially *Chaetoceros socialis*) in the inner fjord and a *Phaeocystis pouchetii*-dominated phytoplankton community in the outer fjord has been observed in earlier years during May (Hegseth et al., 1995; Priou, 2015). Diatoms are known

to be a preferred food choice for *M. norvegica* (Uye et al., 2002), and they seem to prefer aggregates made up of diatoms (Koski and Lombard, 2022), which may explain the dominance of *M. norvegica* in the inner fjord.

Vertical distribution of *Microsetella norvegica*

The use of the video plankton recorder (VPR) allowed the fine scale vertical distribution of *M. norvegica* to be described for the first time. A strong seasonal variation in vertical distribution of *M. norvegica* was found throughout Porsangerfjord. Maar et al. (2006) suggested that *M. norvegica* is distributed within or just below pycnoclines. While aggregates have been observed to accumulate in these layers because of density gradients (Alldredge et al., 2002), this study did not identify any relationship between *M. norvegica* or marine snow depth distribution with any stratified layers in any sample period. Some correlations between temperature, salinity and *M. norvegica* abundance were significant (Table 4), but the only strong significant correlation was between temperature and *M. norvegica* abundance in August. These correlations are unlikely to be explained by either temperature or salinity driving the distribution of *M. norvegica*. Instead, it is more likely that covariances observed between *M. norvegica* and other factors, such as food availability from either phytoplankton or marine snow aggregates, drove their vertical distribution during our study.

Seasonal sampling provided insight into the role of *M. norvegica* in the ecosystem throughout the year. May and August are productive periods with high chlorophyll *a* concentrations in the surface water, indicating the occurrence of phytoplankton blooms. Comparing *M. norvegica's* vertical distribution with chlorophyll *a* profiles revealed a statistically significant correlation in Østerbotn. Marine snow was also in high abundance here during May, but *M. norvegica* were not distributed at the same depths as the marine snow during May and August even though it has previously been observed to feed on marine snow (Koski et al., 2005; Koski et al., 2007; Steinberg et al., 2008). The distribution of *M. norvegica* in the upper euphotic zone during summer also highlights their importance as grazers of phytoplankton, serving as a trophic link between primary producers and higher levels of the food web.

During October and November, the amount of phytoplankton in the water was negligible at all sampling stations. At Østerbotn, *M. norvegica* was not found at shallow depths, but in deeper water where it was significantly positively correlated to the vertical distribution of marine snow. This suggests that *M. norvegica* preferred marine snow as a food source during October and November, when phytoplankton were scarce, while they were preferentially feeding on phytoplankton during bloom periods in May and August. Isari et al. (2013) suggested that copepods might choose more nutritious food items under conditions with high prey availability. From an evolutionary point of view, it is advantageous to be less selective when food is scarce (White, 1978) and to select nutritious food during times of plenty. Given that phytoplankton have a higher fatty acid, protein and particulate organic nitrogen

content compared to organic detritus, such as marine snow (Roman, 1984), *M. norvegica's* preference toward phytoplankton as a food source, when available, is not surprising. This supports the concept presented by Uye et al. (2002), where *M. norvegica* was found to be associated with and feeding on marine snow in oligotrophic environments, similar to our conditions during October and November.

At Midtre Øst and Porsangnes Øst, no significant correlation was found between the vertical distribution of *M. norvegica*, chlorophyll *a*, or marine snow. This may be explained by the low abundances of both *M. norvegica* and marine snow at both sampling stations in May and November, which reduces the difference between a presence and absence of objects from a statistical point of view.

Potential aggregate grazing by *Microsetella norvegica*

If we assume that *M. norvegica* was indeed feeding on marine snow during October and November, we can use previously measured ingestion rates to evaluate the impact from aggregate grazing by *M. norvegica* on flux attenuation (Koski et al., 2005; van der Jagt et al., 2020). It is important to note that these are rough estimations and more accurate calculations would have been obtained if we had measured life-history traits directly on *M. norvegica* collected from the same site as the VPR samples were taken. Similarly, our estimates for POC content of marine snow aggregates are based on measurements taken from Hornsund, Svalbard. While also a arctic fjord similar to Porsangerfjord in depth, Hornsund is located at a higher latitude. However, our POC estimates for settling organic aggregates were similar to those measured by Walker et al. (2022). They took physical samples using sediment traps in Kaldfjord, Norway, which is similar to Porsangerfjord in latitude, climate and depth, and is also a north-south facing fjord. To improve estimates, properties of organic aggregates should be based on *in situ* experiments using sediment traps at the same site sampling takes place.

The majority of the potential POC consumption by *M. norvegica* occurred in the lower half of the water column during October and November since most of the marine snow was located at that depth. *M. norvegica* grazing on aggregates has the potential to explain 1.4% and 0.29% of the total carbon flux attenuation during October and November, respectively (Table 5). In comparison, 12% of total carbon flux attenuation is likely to be explained by microbial degradation at 15°C (Iversen and Ploug, 2010; Iversen et al., 2010). However, when temperature is lowered to 4°C, microbial degradation is reduced to explaining 2-3% of carbon flux attenuation (Iversen and Ploug, 2013; van der Jagt et al., 2020; Pauli et al., 2021).

Our estimates of carbon flux attenuation by *M. norvegica* are considerably more modest than those made by Koski et al. (2005), but with *in situ* measurements of life history traits and organic aggregates it might be the case that carbon flux attenuation is higher. We used a conservative estimate for the residence time of *M. norvegica* on the

aggregates, which is directly proportional to the aggregate carbon ingestion and, hence, the flux attenuation. Often small copepods are ignored in carbon budgets and model studies, yet *M. norvegica* may play a role in the biological carbon pump, both via carbon turnover and as a link to higher trophic levels. Observations by Svensen et al. (2018) emphasised the importance of *M. norvegica* as an important prey for a variety of fish species. This suggests that *M. norvegica* may be an important species in many ecosystems throughout the year, especially due to its potential to feeding on marine snow during periods with low productivity and thereby convert detritus into eukaryotic biomass during oligotrophic conditions, such as arctic winters. This may explain how this small copepod without lipid storage is able to maintain a large overwintering population, which often exceeds that of calanoid copepods that are well documented to retain just a fraction of their summer population over the winter (Hind et al., 2000). *M. norvegica's* relatively high population throughout the winter demonstrates their importance as secondary producers, especially when the abundance of primary producers becomes less in the autumn and winter months. In other words, *M. norvegica* represents an important source of food to higher trophic levels in times of otherwise scarce food supply. So, in addition to their, at times, modest, but still contributing role as gatekeepers for carbon flux, *M. norvegica* may be a key trophic link in Arctic ecosystems during the low-productive season. As the oceans warm, the impact of *M. norvegica* on flux attenuation is likely to increase owing to temperature dependant metabolic rates and carbon demand (Heinle, 1969; Heine et al., 2019).

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

BM and MN contributed to conception and design of the study. MN was involved with sampling and data acquisition. BM organized the database and performed statistical analysis. BM and MI contributed to modelling. BM wrote the first draft of the manuscript. MN wrote sections of the manuscript. All authors contributed to the article and approved the submitted version.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

Alldredge, A. L., Cowles, T. J., MacIntyre, S., Rines, J. E. B., Donaghay, P. L., Greenlaw, C. F., et al. (2002). Occurrence and mechanisms of formation of a dramatic thin layer of marine snow in a shallow pacific fjord. *Mar. Ecol. Prog. Ser.* 233, 1–12. doi: 10.3354/meps233001

Alldredge, A. L. (1972). Abandoned Larvacean Houses: A Unique Food Source in the Pelagic Environment. *Science* 177, 885–887. doi: 10.1126/science.177.4052.885

Arendt, K. E., Juul-Pedersen, T., Mortensen, J., Blicher, M. E., and Rysgaard, S. (2013). A 5-year study of seasonal patterns in mesozooplankton community structure in a sub-Arctic fjord reveals dominance of *Microsetella norvegica* (Crustacea, copepoda). *J. Plankton Res.* 35, 105–120. doi: 10.1093/plankt/fbs087

Banse, K. (1990). New views on the degradation and disposition of organic particles as collected by sediment traps in the open sea. *Deep Sea Res. Part A. Oceanographic Res. Papers* 37, 1177–1195. doi: 10.1016/0198-0149(90)90058-4

Boyd, P. W., Claustre, H., Levy, M., Siegel, D. A., and Weber, T. (2019). Multi-faceted particle pumps drive carbon sequestration in the ocean. *Nature* 568, 327–335. doi: 10.1038/s41586-019-1098-2

Christiansen, J. S., and Fevolden, S.-E. (2000). The polar cod of Porsangerfjorden, Norway; revisited. *Sarsia* 85, 189–193. doi: 10.1080/00364827.2000.10414571

Demchuk, A., Ivanov, M., Ivanova, T., Polyakova, N., Mas-Martí, E., and Lajus, D. (2015). Feeding patterns in seagrass beds of three-spined stickleback gasterosteus

aculeatus juveniles at different growth stages. *J. Mar. Biol. Assoc. United Kingdom* 95, 1635–1643. doi: 10.1017/S0025315415000569

Fossheim, M., and Primicerio, R. (2008). Habitat choice by marine zooplankton in a high-latitude ecosystem. *Mar. Ecol. Prog. Ser.* 364, 47–56. doi: 10.3354/meps07483

Fowler, S. W., and Knauer, G. A. (1986). Role of large particles in the transport of elements and organic compounds through the oceanic water column. *Prog. Oceanography* 16, 147–194. doi: 10.1016/0079-6611(86)90032-7

Frost, B. W., and Bollens, S. M. (1992). Variability of diel vertical migration in the marine planktonic copepod *Pseudocalanus newmani* in relation to its predators. *Can. J. Fisheries Aquat. Sci.* 49, 1137–1141. doi: 10.1139/f92-126

Gorsky, G., Le Borgne, R., Picheral, M., and Stemmann, L. (2003). Marine snow latitudinal distribution in the equatorial pacific along 180°. *J. Geophysical Res.* 108, 146–192. doi: 10.1029/2001JC001064

Green, E. P., and Dagg, M. J. (1997). Mesozooplankton associations with medium to large marine snow aggregates in the northern gulf of Mexico. *J. Plankton Res.* 19, 435–447. doi: 10.1093/plankt/19.4.435

Hegseth, E. N., Svendsen, H., and von Quillfeldt, C. H. (1995). "Phytoplankton in fjords and coastal waters of northern Norway: environmental conditions and dynamics of the spring bloom," in *Ecology of fjords and coastal waters* (Amsterdam: Elsevier Science), Pp 45–Pp 72.

Heine, K. B., Abebe, A., Wilson, A. E., and Hood, W. R. (2019). Copepod respiration increases by 7% per °C increase in temperature: a meta-analysis. *Limnology Oceanography Lett.* 4 (3), 435–447. doi: 10.1002/lol2.10106

Heinle, D. R. (1969). Temperature and zooplankton. *Chesapeake Sci.* 10, 186–209. doi: 10.2307/1350456

Hind, A., Gurney, W. S. C., Heath, M., and Bryant, A. D. (2000). Overwintering strategies in *Calanus finmarchicus*. *Mar. Ecol. Prog. Ser.* 193, 95–107. doi: 10.3354/meps193095

Hopkins, C. C. E., Tande, K. S., Grønvik, S., and Sargent, J. R. (1984). Ecological investigations of the zooplankton community of balsfjorden, northern Norway: an analysis of growth and overwintering tactics in relation to niche and environment in *Metridia longa* (Lubbock), *Calanus finmarchicus* (Gunnerus), *Thysanoessa inermis* (Krøyer) and *T. raschi* (M. sars). *J. Exp. Mar. Biol. Ecol.* 82, 77–99. doi: 10.1016/0022-0981(84)90140-0

Hu, Q., and Davis, C. (2005). Automatic plankton image recognition with co-occurrence matrices and support vector machine. *Mar. Ecol. Prog. Ser.* 295, 21–31. doi: 10.3354/meps295021

Isari, S., Antó, M., and Saiz, E. (2013). Copepod foraging on the basis of food nutritional quality: can copepods really choose? *PloS One* 8, e84742. doi: 10.1371/journal.pone.0084742

Iversen, M. H., Nowald, N., Ploug, H., Jackson, G. A., and Fischer, G. (2010). High resolution profiles of vertical particulate organic matter export off cape blanc, Mauritania: degradation processes and ballasting effects. *Deep-Sea Research part I: Oceanographic Research Papers.* 57, 771–784. doi: 10.1016/j.dsr.2010.03.007

Iversen, M. H., Pakhomov, E. A., Hunt, B. P., v Jagt, H., Wolf-Gladrow, D., and Klaas, C. (2016). Sinkers or floaters? contribution from salp pellets to the export flux during a large bloom event in the southern ocean. *Deep-Sea Research part II: Topical Studies in Oceanography.* 138, 116–125. doi: 10.1016/j.drs2.2016.12.004

Iversen, M. H., and Ploug, H. (2010). Ballast minerals and the sinking carbon flux in the ocean: carbon-specific respiration rates and sinking velocities of macroscopic organic aggregates (marine snow). *Biogeosciences* 7, 1–30. doi: 10.5194/bg-7-2613-2010

Iversen, M. H., and Ploug, H. (2013). Temperature effects on carbon-specific respiration rate and sinking velocity of diatom aggregates. potential implications for deep ocean export processes. *Biogeosciences*. 10, 4073–4085. doi: 10.5194/bg-5110-5191-2013

Iversen, M. H., and Poulsen, L. K. (2007). Coprorhexy, coprophagy, and coprochaly in the copepods *Calanus helgolandicus, Pseudocalanus elongatus*, and *Oithona similis*. *Mar. Ecol. Prog. Ser.* 350, 79–89. doi: 10.3354/meps07095

Kiørboe, T., and Hansen, J. L. S. (1993). Phytoplankton aggregate formation: observations of patterns and mechanisms of cell sticking and the significance of exopolymeric material. *J. Plankton Res.* 15, 993–1018. doi: 10.1093/plankt/15.9.993

Kiørboe, T., Tiselius, P., Mitchell-Innes, B., Hansen, J. L. S., Visser, A. W., and Mari, X. (1998). Intensive aggregate formation with low vertical flux during an upwelling-induced diatom bloom. *Limnology Oceanography* 43, 104–116. doi: 10.4319/lo.1998.43.1.0104

Koski, M., Kiørboe, T., and Takahashi, K. (2005). Benthic life in the pelagic: aggregate encounter and degradation rates by pelagic harpacticoid copepods. *Limnology Oceanography* 50, 1254–1263. doi: 10.4319/lo.2005.50.4.1254

Koski, M., and Lombard, F. (2022). Functional responses of aggregate-colonizing copepods. *Limnology Oceanography* 67, 2059–2072. doi: 10.1002/lno.12187

Koski, M., Møller, E., Maar, M., and Visser, A. W. (2007). The fate of discarded appendicularian houses: degradation by the copepod, *Microsetella norvegica*, and other agents. *J. Plankton Res.* 29, 641–654. doi: 10.4319/lo.2005.50.4.1254

Koski, M, Valencia, B., Newstead, R., and Thiele, C. (2020). The missing piece of the upper mesopelagic carbon budget? biomass, vertical distribution and feeding of aggregate-associated copepods at the PAP site. *Prog. Oceanography* 181, 102–243. doi: 10.1093/plankt/fbm046

Lima, S. L. (2002). Putting predators back into behavioral predator–prey interactions. *Trends Ecol. Evol.* 17, 70–75. doi: 10.1016/S0169-5347(01)02393-X

Maar, M., Visser, A. W., Nielsen, T. G., Stips, A., and Saito, H. (2006). Turbulence and feeding behaviour affect the vertical distributions of *Oithona similis* and *Microsetella norvegica*. *Mar. Ecol. Prog. Ser.* 313, 157–172. doi: 10.3354/meps313157

Ohtsuka, S., Kubo, N., Okada, M., and Gushima, K. (1993). Attachment and feeding of pelagic copepods on larvacean houses. *Journal of Oceanography* 49, 115–120. doi: 10.1007/BF02234012

Passow, U., and Carlson, C. A. (2012). The biological pump in a high CO_2 world. *Mar. Ecol. Prog. Ser.* 470, 249–272. doi: 10.3354/meps09985

Pauli, N.-C., Flintrop, C. M., Konrad, C., Pakhomov, E. A., Swoboda, S., Koch, F., et al. (2021). Krill and salp faecal pellets drive the carbon flux at the Antarctic peninsula. *Nat. Communication.* 12, 7168. doi: 10.1038/s41467-021-27436-9

Pedersen, T., Fuhrmann, M. M., Lindstrøm, U., Nilssen, E. M., Ivarjord, T., Ramasco, V., et al. (2018). Effects of the invasive red king crab on food web structure and ecosystem properties in an Atlantic fjord. *Mar. Ecol. Prog. Ser.* 596, 13–31. doi: 10.3354/meps12548

Poulsen, L. K., and Iversen, M. H. (2008). Degradation of copepod fecal pellets: key role of protozooplankton. *Mar. Ecol. Prog. Ser.* 367, 1–13. doi: 10.3354/meps07611

Prat Varela, A. (2015). *Vertical distributions of zooplankton using the video plankton recorder in two high-latitude fjords. a case study on diel migration in Billefjorden, Svalbard, and seasonal migration in Porsangerfjord, northern Norway* (Tromsø Norway: UiT Arctic University of Norway). Available at: https://hdl.handle.net/10037/8271. MSc thesis.

Priou, P. (2015). *Associations between herbivorous zooplankton, phytoplankton and hydrography in Porsangerfjord, northern Norway* (Tromsø Norway: UiT Arctic University of Norway). Available at: https://hdl.handle.net/10037/8270. MSc thesis.

Roman, M. R. (1984). Utilization of detritus by the copepod, *Acartia tonsa*. *Limnology Oceanography* 29, 949–959. doi: 10.4319/lo.1984.29.5.0949

RStudio Team (2021). *RStudio: integrated development environment for r* (Boston, MA: RStudio, PBC). Available at: http://www.rstudio.com/.

Shanks, A. L., and Trent, J. D. (1979). Marine snow: microscale nutrient patches. *Limnology Oceanography* 24, 850–854. doi: 10.4319/lo.1979.24.5.0850

Steinberg, D., Silver, M. W., and Pilskaln, C. H. (1997). Role of mesopelagic zooplankton in the community metabolism of giant larvacean house detritus in Monterey bay, California, USA. *Mar. Ecol. Prog. Ser.* 147, 167–179. doi: 10.3354/meps147167

Steinberg, D. K., Van Mooy, B. A. S., Buesseler, K. O., Boyd, P. W., Kobari, T., and Karl, D. M. (2008). Bacterial vs. zooplankton control of sinking particle flux in the ocean's twilight zone. *Limnology Oceanography* 53, 1327–1338. doi: 10.4319/lo.2008.53.4.1327

Stemmann, L., Jackson, G. A., and Gorsky, G. (2004). A vertical model of particle size distributions and fluxes in the midwater column that includes biological and physical processes – part II: application to a three year survey in the NW Mediterranean Sea. *Deep-Sea Res. I* 51 (7), 885–908. doi: 10.1016/j.dsr.2004.03.002

Stramska, M., Jankowski A., A., and Cieszyńska A., A. (2016). Surface currents in the Porsanger fjord in northern Norway. *Polish Polar Res.* 37, 337–360. doi: 10.1515/popore-2016-0018

Svensen, C., Antonsen, M. T., and Reigstad, M. (2018). Small copepods matter: population dynamics of *Microsetella norvegica* in a high-latitude coastal ecosystem. *J. Plankton Res.* 40, 446–457. doi: 10.1093/plankt/fby019

Turner, J. T. (1984). The feeding ecology of some zooplankters that are important prey items of larval fish. *Natl. Oceanographic Atmospheric Administration* 7:13–19.

Uye, S., Aoto, I., and Onbé, T. (2002). Seasonal population dynamics and production of *Microsetella norvegica*, a widely distributed but little-studied marine planktonic harpacticoid copepod. *J. Plankton Res.* 24, 143–153. doi: 10.1093/plankt/24.2.143

van der Jagt, H., Wiedmann, I., Hildebrandt, N., Niehoff, B., and Iversen, M. H. (2020). Aggregate feeding by the copepods *Calanus* and *Pseudocalanus* controls carbon flux attenuation in the Arctic shelf Sea during the productive period. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.543124

Visser, A. W., and Thygesen, U. F. (2003). Random motility of plankton: diffusive and aggregative contributions. *J. Plankton Res.* 25, 1157–1168. doi: 10.1093/plankt/25.9.1157

Walker, E. Z., Wiedmann, I., Nikolopoulos, A., Skarðhamar, J., Jones, E. M., and Renner, A. H. H. (2022). Pelagic ecosystem dynamics between late autumn and the post spring bloom in a sub-Arctic fjord. *Elementa: Science of the Anthropocene* 10, 00070. doi: 10.1525/elementa.2021.00070

White, T. C. R. (1978). The importance of a relative shortage of food in animal ecology. *Oecologia* 33, 71–86. doi: 10.1007/BF00376997

Wilson, S., and Steinberg, D. (2010). Autotrophic picoplankton in mesozooplankton guts: evidence of aggregate feeding in the mesopelagic zone and export of small phytoplankton. *Mar. Ecol. Prog. Ser.* 412, 11–27. doi: 10.3354/meps08648