Importance of bacteria and protozooplankton for faecal pellet degradation*

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Nathalie Morata[1,2,⋆]
Lena Seuthe[1]

[1] Department of Arctic and Marine Biology,
University of Tromsø,
N–9037 Tromsø, Norway

[2] Lemar CNRS UMR 6539,
Rue Dumont D'Urville, 29280 Plouzané, France;

e-mail: nathalie.morata@gmail.com

⋆corresponding author

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Abstract

The degradation mechanisms of faecal pellets are still poorly understood, although they determine their contribution to vertical fluxes of carbon. The aim of this study was to attempt to understand the microbial (bacteria and protozooplankton) degradation of faecal pellets by measuring the faecal pellet carbon-specific degradation rate (FP-CSD) as an indicator of pellet degradation. 'In situ' and 'culture' pellets (provided by the grazing of copepods in in situ water and in a culture of *Rhodomonas* sp. respectively) were incubated in seawater from the chlorophyll *a* maximum and 90 m depth, and in filtered seawater. When microbes were abundant (at the chlorophyll *a* maximum), they significantly increased FP-CSD. In addition, culture pellets had a higher FP-CSD than in situ pellets, suggesting that the

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results obtained with culture pellets should be treated with caution when trying to extrapolate to natural field conditions.

1. Introduction

Zooplankton faecal pellets have been found to constitute an important part of the vertical flux of carbon, accounting for up to 100% of total particulate organic carbon (POC) (Urrère & Knauer 1981, Bodungen et al. 1987, Urban-Rich et al. 1999, Wassmann et al. 1999), but can also be quickly degraded and thus contribute little or nothing to the fluxes (Pilskaln & Honjo 1987, Lane et al. 1994, von Bodungen et al. 1995). Zooplankton faecal pellets can therefore play an important role in the global carbon cycle, as they can be responsible for the important export of carbon to the deeper layers and to the seafloor (Wiebe et al. 1979), or conversely, provide organic carbon to surface water through their degradation (Lampitt et al. 1990). The relative importance of zooplankton faecal pellets in sedimentary flux depends on their sinking rates, which can reach >100 m per day, and on their degradation (Turner 2002).

In high latitudes, copepods of the genus *Calanus* comprise up to 70–80% of the zooplankton biomass (Conover 1988, Hirche & Mumm 1992, Błachowiak-Samołyk et al. 2008) and dominate the grazer community during and after blooms (Madsen et al. 2001). *Calanus* spp. are usually dominated by *C. finmarchicus* in sub-Arctic waters and represent a key link between primary producers and higher trophic levels. When *Calanus* ingest food, part of the carbon intake is used for respiration, growth, reproduction and excretion, and approximately 1/3 is egested as faecal pellets (Noji 1991, Møller et al. 2003). Zooplankton grazing in high latitudes determines carbon pathways in the system, and plays a vital role in vertical flux regulation and ecosystem functioning (Andreassen et al. 1996, Bauerfeind et al. 1997, Fortier et al. 2002, Wexels Riser et al. 2002, Caron et al. 2004, Sampei et al. 2004, Lalande et al. 2007, Juul-Pedersen et al. 2010).

Traditionally, it was thought that copepods were the main degraders of copepod faecal pellets (see the review in Turner 2002, Wexels Riser et al. 2002). However, some studies have also shown that their role is questionable and that organisms other than copepods, in particular protozooplankton and bacteria, may play an important role in faecal pellet degradation (Jacobsen & Azam 1984, Noji 1991, Turner 2002, Poulsen & Kiørboe 2006, Poulsen & Iversen 2008). Protozooplankton has been found to play a key role in the degradation of faecal pellets when incubated at 18°C with water from the chlorophyll *a* maximum (chl *a* max) (Poulsen & Iversen 2008). However, it remains unclear whether it can play such an important role in colder waters (Svensen et al. 2012).

Conversely, while it was previously believed that free-living bacteria were responsible for the colonisation of faecal pellets (Honjo & Roman 1978, Jacobsen & Azam 1984), it was also demonstrated that free-living bacteria play a minor role in faecal pellet colonisation and degradation (Gowing & Silver 1983, Poulsen and Iversen 2008). Pelagic bacteria can penetrate the peritrophic membrane of a faecal pellet in about 6 hours at 20°C (Turner 1979). Bacteria within or attached to faecal pellets may therefore originate from pelagic bacteria but also from copepod guts (Turner 1979, Gowing & Silver 1983, Jacobsen & Azam 1984, Hansen & Bech 1996). It has been found, however, that microbial decomposition of pellets in cold water is slow compared to the high sinking rates of pellets (Honjo & Roman 1978, Svensen et al. 2012). Therefore, Daly (1997) suggested that degradation of whole faecal pellets by bacterial degradation is unlikely at high latitudes.

The aims of this study were: 1) to measure the protozooplankton and bacterial carbon degradation of faecal pellets produced by *Calanus finmarchicus* in cold waters (4–5°C) at different water depths (chl *a* max vs. 90 m), using faecal pellet carbon demand as the indicator of degradation; it was expected that despite the cold temperatures, carbon degradation might be higher in waters with higher concentrations of bacteria and protozooplankton (i.e. at the chl *a* max); 2) to assess whether the results obtained experimentally could be extrapolated to field conditions by using two types of faecal pellets: one produced by copepods grazing in natural in situ water, and the other produced by grazing in a monoalgal culture.

2. Material and methods

2.1. Study area and sampling

Experimental water and copepods were sampled at the Svartnes station in Balsfjord (69°22′N, 19°07′E) in April 2010. Water for the experiments was taken with an acid-washed Go-Flo bottle from the chl *a* max at 13 m depth and from below the pycnocline at 90 m depth. The chl *a* max had a chl *a* concentration of 2 μg l^{-1} and was dominated by *Phaeocystis pouchetii*, while the water from 90 m contained little chl *a* (0.3 μg l^{-1}). Copepods were collected in the upper 100 m with a WP2 zooplankton net (180 μm mesh size) equipped with a non-filtering cod-end. *Calanus finmarchicus* were sorted from the sample in dim light at close to in situ temperatures (4–5°C). The sorted copepods were kept in the dark at 4–5°C overnight in filtered seawater (FSW) for their guts to empty. Subsequently, copepods were either fed ad lib with a culture of *Rhodomonas* sp. (with a chl *a* concentration within the same range as in the in situ water, 1–2 μg l^{-1}), or incubated in in situ water from the chl *a* max, for 6 hours, in

order to produce faecal pellets (referred to as 'culture pellets' and 'in situ pellets' respectively). Samples of in situ water of chl *a* max and 90 m were kept for the determination of protozooplankton and bacterial abundance. Within 12 hours, fresh faecal pellets were collected with a micropipette under a stereoscopic microscope and rinsed three times with 0.2 μm FSW in acid-washed and autoclaved micro-chambers before incubation (Shek & Liu 2010). This procedure ensured the removal of any phytoplankton, protozooplankton or free bacteria, so that only bacteria attached to the pellets remained (coming from copepod guts or attached when faecal pellets were released in the water).

2.2. Faecal pellet carbon demand

Faecal pellet carbon demand was measured with oxygen micro-respiration chambers (Unisense A/S; Aarhus, Denmark). Only one published study has used the oxygen micro-respiration system for studying faecal pellet respiration (Shek & Liu 2010), and this is the first time it has been used as such in cold waters. For the measurement, 30 faecal pellets (for each of the 4–5 replicates) were transferred to 4 ml glass micro-chambers vials sealed with a glass stopper for preventing bubble formation. The glass stopper had a capillary hole (< 0.7 mm $\times$ 13 mm) allowing the oxygen sensor to pass unimpeded but effectively preventing the diffusion of oxygen. Three incubations were prepared with different types of water: i) 0.2 μm FSW, ii) unfiltered water from the chl *a* max, and iii) 90 m depth, from which larger consumers had been removed by careful gravitational inverse filtration over a 180 μm acid-washed mesh. The incubation of faecal pellets in FSW enabled the measurement of the respiration due solely to the bacteria already present in the faecal pellets, while the incubations from chl *a* max and 90 m allowed the impact of water column microbes (bacteria and protozooplankton) on faecal pellet degradation at different depths to be studied. All vials were acid-washed and autoclaved prior to use in order to eliminate the presence of bacteria or other organisms attached to the vials. The vials were incubated in the dark at 4–5°C on a plankton wheel rotating at 1 rpm keeping the material in suspension (e.g. Reigstad et al. 2005). Blank vials of 0.2 μm FSW and < 180 μm water (chl *a* max and 90 m) without pellets were also incubated in the dark to assess the carbon demand of free-living bacteria, phyto- and protozooplankton present in the < 180 μm water. Oxygen was monitored every 6–8 hours for 24–36 hours with the oxygen microsensor, and never dropped below 15–20% (Renaud et al. 2007). Oxygen consumption rates were calculated as the (negative) slope of the regression line between oxygen concentration and time. Blank values of the respiration due to the free-living bacteria,

phytoplankton and protozooplankton alone, without the presence of faecal pellets, were subtracted in order to obtain the rates of oxygen consumption due only to the presence of faecal pellets (i.e. oxygen consumption by the faecal pellet itself and the increase in oxygen consumption by surrounding microbes because of the presence of the faecal pellet, which stimulated them by providing an alternative food source). Oxygen consumption rates were converted to carbon demand, assuming a respiration factor of 1 mol O_2:1 mol CO_2 (Ploug et al. 2008). Faecal pellet carbon-specific degradation rates (FP-CSD) represents the carbon demand (μg d^{-1}) per faecal pellet carbon contents (μg FP^{-1}) and is expressed as percentage per day (% d^{-1}, Ploug et al. 2008).

2.3. Faecal pellet carbon content

In order to determine the carbon contents of the faecal pellets, about 100 faecal pellets of each type (culture and in situ) were placed on 450°C ash-burned GFF filters for carbon analysis. Filters were fumed with HCl for 24 h and subsequently analysed on a Leeman Lab CEC 440 CHN analyser (Reigstad et al. 2008).

2.4. Protozooplankton and bacterial abundance

Samples (250 ml) for counting phyto- and protozooplankton (i.e. heterotrophic ciliates and dinoflagellates) were fixed with acid Lugol (2% vol. final concentration). Subsamples (12.5 to 100 ml) were counted microscopically after settling in Utermöhl sedimentation chambers for 48 h. The entire chamber or parts of it were examined under an inverted microscope at a magnification of $\times 200$ and $\times 400$.

Samples for bacterial abundance (BA) were fixed with fresh formaldehyde to a final concentration of 2%. BA was determined by direct counts of DAPI-stained filter samples (0.2 μm pore size membrane filters) using an epifluorescence microscope (Porter & Feig 1980). A minimum of 10 frames and 500 cells were counted in each sample.

2.5. Statistical analyses

In order to determine the effects of faecal pellet origin and water type on FP-CSD, these factors were tested using a two-way analysis of variance (ANOVA) followed by an LSD post-hoc test in the case of significant results. Differences in FP-CSD between treatments were tested by one-way ANOVA, followed by a LSD post-hoc test. Normality and homogeneity of variance were subjected to the Bartlett test prior to the application of parametric tests (Fisher Snedecor tests applied through ANOVA). For all the statistical results, a probability of $p < 0.05$ was considered significant.

Statistical analyses were performed using Statgraphics Plus (Manugistics, Inc., Rockville, MD, USA).

3. Results

3.1. Phytoplankton, protozooplankton and bacteria

All the investigated plankton groups (i.e. bacteria, phyto- and protozooplankton) had higher abundances at the chl *a* max than at 90 m (Figure 1). Phytoplankton at the chl *a* max was dominated by *Phaeocystis pouchetii*, which was absent at 90 m depth. Diatoms were less abundant but with 7100 cells l^{-1} at the chl *a* max were about 3.6 times more abundant than at 90 m. Heterotrophic dinoflagellates were more abundant than ciliates at both depths.

The carbon demand of the microbial community, used as a blank for measuring the FP-CSD, was 42.4 ± 6.0 SD μg C l^{-1} d^{-1} and 5.5 ± 0.9 SD μg C l^{-1} d^{-1} for water from the chl *a* max and 90 m respectively. In the vials with faecal pellets, these blank values represented between 22 and 50% of the total carbon demand. Once the FP carbon demand is withdrawn, this represents an increase of the chl *a* max microbial carbon demand by

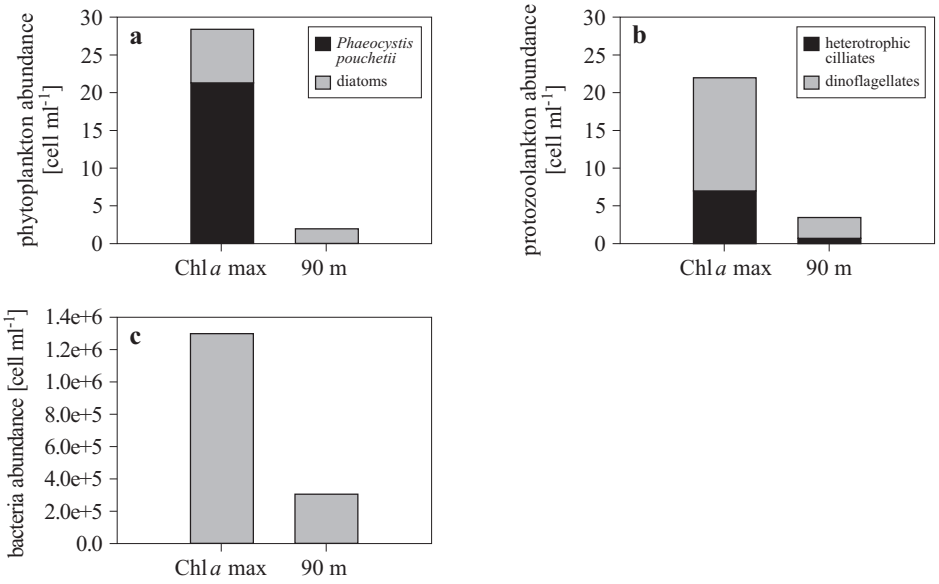

Figure 1. Abundances of a) phytoplankton, b) protozooplankton and c) bacteria at the chlorophyll *a* maximum (chl *a* max) and at 90 m depth. Note that these microbe abundances were not determined in the 0.2 μm filtered sea water (FSW) as this filter size prevents the passage of any phyto- and protozooplankton or bacteria, which are therefore absent in FSW

a factor of 1.8 to 8, and an increase of the 90 m microbial carbon demand by a factor of 1.1 to 5.

3.2. Faecal pellet carbon-specific degradation rate

When incubated in 0.2 μm FSW, the FP-CSD was 2.0% d^{-1} for in situ pellets and 5.9% d^{-1} for culture pellets (Figure 2). We interpret this FP-CSD as the respiratory result of bacteria from the faecal pellet matrix. Both treatments – water type and faecal pellet origin – had significant effects on the FP-CSD, although their interaction did not have a significant effect (two-way ANOVA, water type $F_{2.23} = 8.783$, $p < 0.05$, chl *a* max significantly higher than FSW and 90 m, LSD post-hoc both $p < 0.05$, no difference between FSW and 90, $p = 0.966$; faecal pellet origin $F_{1.23} = 10.030$, $p < 0.05$, culture significantly higher, LSD post-hoc test $p < 0.05$, Table 1). For both pellet types, FP-CSDs in water from the chl *a* max were significantly higher than in 0.2 μm FSW or 90 m water (one-way ANOVA, LSD post-hoc test all $p < 0.05$, Figure 2). Since the FP-CSD in 0.2 μm FSW is due to the activities from the bacteria of the faecal pellet matrix, the difference between

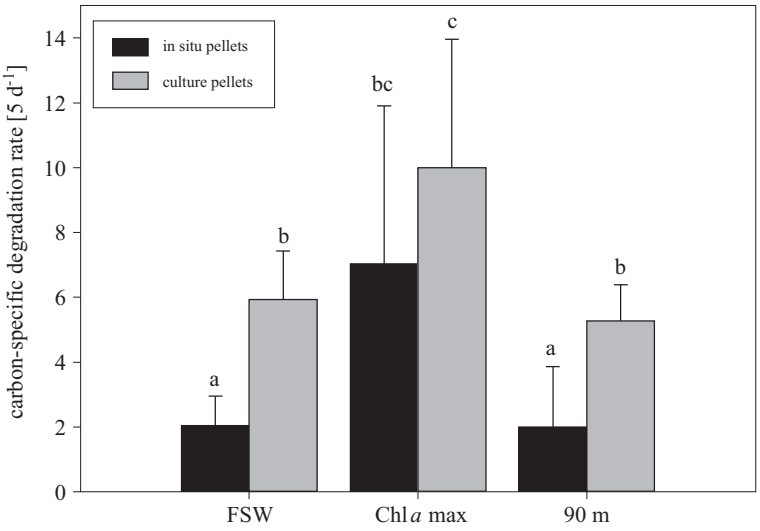

Figure 2. Carbon-specific degradation rate per day (CSD% d^{-1}) of in situ and culture pellets produced by *Calanus finmarchicus* and incubated in filtered sea water (FSW), < 180 μm water from the chlorophyll *a* maximum (chl *a* max) and < 180 μm water from 90 m depth at station 1. Note that the CSD of FSW, < 180 μm chl *a* max and 90 m have already been withdrawn. The values presented here are therefore the CSD due to the presence of faecal pellets (FP-CSD). The different letters indicate significant differences among treatments (one-way ANOVA, LSD post-hoc test, $p < 0.05$); (average $\pm$ SD, $n = 4$ or 5)

Table 1. Two-way ANOVA table of faecal pellet carbon-specific demand, with faecal pellet (FP) origin (culture or in situ) and water type (FSW, chl *a* max, 90 m) as the main factors, and their interactions

	Df	SS	MS	*F*	*p*
FP origin	1	0.00820	0.00820	10.030	**0.004***
water type	2	0.0144	0.00718	8.782	**0.001***
FP origin × water type	2	0.000121	0.0000606	0.0741	0.929
residual	23	0.0188	0.000817		
Total	28	0.0421	0.00151		

chl *a* max FP-CSD and FSW FP-CSD provides information on the FP-CSD due to the free-living bacteria and protozooplankton, which represents about 40% and 70% of the total FP-CSD from the culture and in situ faecal pellets respectively. FP-CSD of the culture pellets were statistically higher than for the in situ pellets when incubated in FSW and 90 m (factors of 2.3 and 2.6 respectively, one-way ANOVA $p < 0.05$ for both, Figure 2), and had a tendency to be higher for chl *a* max, though not significantly (Figure 2).

4. Discussion

4.1. Importance of bacteria and protozooplankton

Although previous studies have used microbial volumes of bacteria and protozooplankton for assessing their carbon demand (i.e. Shinada et al. 2001), in the present study at the same temperature, the same microbial community (chl *a* max or 90 m) increased its carbon demand by a factor up to 8 in the presence of 30 faecal pellets in the 5 ml vials. In natural conditions, it is unlikely that 30 faecal pellets may occur at the same time in such a small volume; however, it is important to consider that respiration and carbon demand depend on the available carbon sources, and in particular the presence of faecal pellets. It was previously thought that because of the low temperature in high latitudes, the respiration of microbes and microbial decomposition of faecal pellets were also low (Honjo & Roman 1978, Daly 1997), and that the low planktonic respiration and low faecal pellet degradation were responsible for the increased vertical export with respect to lower latitudes (Urban-Rich 1999, Rivkin & Legendre 2001), leading to a strong pelagic-benthic coupling in cold waters (Petersen & Curtis 1980, Carroll & Carroll 2003). However, the present study agrees with recent studies suggesting that respiration is not only controlled by temperature, but that the food availability is an important factor for microbial, zooplankton and benthic respirations (Takahashi et al. 2002, Renaud et al. 2007).

Protozooplankton biomass has been found to increase along with phytoplankton biomass in both temperate and polar areas (Froneman & Perissinotto 1996, Sherr et al. 2003, Seuthe et al. 2011). In accordance with these results, both protozooplankton and free-living bacteria abundances were higher at the chl *a* max than at 90 m in the present study (Figure 1). It was also at the chl *a* max that the FP-CSD was higher by a factor of 1.6 to 3.4 with respect to the incubations in 0.2 μm FSW or 90 m (Figure 2). These results suggest that the important abundance of bacteria and protozooplankton at the chl *a* max may be responsible for an increase in the FP-CSD and therefore for faecal pellet degradation.

The impact of free-living bacteria and protozooplankton on the degradation of faecal pellets seems, however, to depend on their abundances. Indeed, when incubated with deeper water at 90 m with lower abundances of free-living bacteria and protozooplankton (Figure 1), FP-CSD remained similar to the rates measured in the 0.2 μm FSW, which is due only to the bacteria present in the faecal pellet matrix (about 2% d^{-1} for in situ pellets). Most of the bacteria associated with copepod faecal pellets have been found to come from the inside of the pellet matrix, and to be enteric and digestion-resistant bacteria, which were passed onto faecal pellets (Gowing & Silver 1983, Tang 2005). Interestingly, the FP-CSD rates observed in the present study are similar to the FP-CSD of in situ faecal pellets from an entire zooplanktonic community ($\sim$1.1% d^{-1}), incubated over 22 days at 5°C in water containing only free-living bacteria (Roy & Poulet 1990). Although Roy & Poulet (1990) did not measure the abundance of free-living bacteria in their experiment, it could be suggested that the bacteria and protozooplankton abundances observed at 90 m in our samples, and their bacteria abundance, were not sufficient to increase the FP-CSD from the matrix bacteria. The faecal pellet FP-CSD in <180 μm water from 90 m is therefore most likely to be due only to matrix bacteria from copepod intestines, while degradation by the free-living bacteria and protozooplankton present at 90 m is negligible because of their lower abundances at this depth.

Recent studies have shown that in cold waters, free-living bacteria and protozooplankton play an important ecological role as phytoplankton grazers and food sources for higher trophic levels (Levinsen et al. 2000, Calbert & Landry 2004, Seuthe et al. 2011). The present study shows their importance for the degradation of faecal pellets: here, the microbial community <180 μm is responsible for 40 and 70% d^{-1} of the total FP-CSD (in situ pellets and culture pellets respectively), which is in a range similar to that of the rates measured in temperate waters ($\sim$57% d^{-1} for the fraction 2–200 μm, Poulsen & Iversen 2008). However, when incubated in FSW, faecal pellets incubated at higher temperatures (15–22°C) were found

to range from 6 to 28% d^{-1} for in situ pellets (Turner 1979, Roy & Poulet 1990) and from 8 to >100% d^{-1} for culture pellets (Olsen et al. 2005, Ploug et al. 2008, Poulsen & Iversen 2008), while it was about 2% d^{-1} and 6.9% d^{-1} at 5°C for in situ and culture pellets respectively in the present study at 4–5°C. While the microbial community seems to depend mainly on food availability, activity of the bacteria within the pellet matrix seems to be lower at lower temperatures. Potential climate-induced increases in water temperature and primary productivity in the North Atlantic (Zhang et al. 1998, Arrigo et al. 2008) may therefore enhance pellet matrix bacterial activities and protozooplankton abundances, and therefore increase faecal pellet degradation.

4.2. Methodology discussion

Experimental studies of faecal pellet degradation have often been carried out by using phytoplankton cultures as food sources in order to control the food ingested by the copepods (e.g. Olsen et al. 2005, Reigstad et al. 2005, Ploug et al. 2008). Indeed, when feeding copepods with in situ water, it is impossible to know what type of food they ingest as they can feed selectively (Levinsen et al. 2000, Yang et al. 2010). In addition, changes in food quantity and quality (e.g. algal species, C:N ratio, lipid content) have been found to influence the size, composition and robustness of copepod faecal pellets (Turner 2002, Ploug et al. 2008). Changes in algal species as food sources have also been found to lead to changes in the production and enzymatic activities of the bacteria surrounding the pellets (Thor et al. 2003). Faecal pellets were found to be more fragile when copepods fed at low food concentrations, less dense when they fed on diatoms, and more compact when they fed on flagellates (Dagg & Walser 1986, Urban et al. 1993, Hansen et al. 1996). It is therefore tempting to use a high concentration of food and certain type of algae in order to collect robust faecal pellets for experiments. The results from the present study show, however, that pellet origin had a significant effect on FP-CSD (ANOVA, Table 1), the FP-CSD of the culture pellets being higher by a factor of ~ 2 than that of the in situ pellets (Figure 2). In addition, the standard deviations were much higher when using in situ pellets (from 44 to 100%) than culture pellets (from 25 to 43%, Figure 2). Using culture pellets may provide better control over experimental conditions and may yield more reliable results. The results obtained, however, may not reflect natural in situ conditions, as in the present case, where FP-CSD was overestimated when culture pellets were used (Figure 2). Although we do not have an explanation for this overestimate, future studies should endeavour to use in situ pellets. If this is not possible and culture pellets are used, their characteristics should

resemble those of in situ ones (e.g. similar algae for feeding, similar textures, C:N ratios, lipids contents, etc.).

Interestingly, it was recently argued that degradation by bacteria and protozooplankton of culture (*Rhodomonas* sp.) faecal pellets of *C. finmarchicus* incubated in cold waters takes three days to be significant (32% after 3 days) (Svensen et al. 2012). In the present study, FP-CSD by bacteria and protozooplankton was measured over the first two days of incubation (about 10.1% d^{-1} for culture pellets, Figure 2). Assuming a constant carbon to volume ratio, the degradation would thus be about 30% in 72 h, which is comparable to the results of Svensen et al. (2012). Those authors used a different method, where microscopic measurements were performed in order to estimate faecal pellet volume changes and therefore degradation. It seems, however, that this microscopic method did not make it possible to determine statistical differences in volume during the first two days, in contrast to the respiration method used in the present study. The use of micro-respiration chambers may therefore be more sensitive. In addition, the method used in the present study is less subjective and less time-consuming than the microscopic method.

5. Conclusion

Despite the limited data set, the novel use of micro-respiration chambers for faecal pellet FP-CSD in the present study highlights the importance of bacteria from the pellet matrix, free-living bacteria and protozooplankton for faecal pellet degradation. Bacteria and protozooplankton play an important role in faecal pellet degradation at the chl *a* max compared to deeper water, and it most likely an important factor in areas where primary production is high, as the abundance of bacteria and protozooplankton is correlated with primary production. Few studies have addressed the importance of protozooplankton in Arctic areas, but this knowledge will be crucial for our understanding of the role of protozooplankton for the vertical flux of faecal pellets, which have been underestimated in the past owing to the low temperatures.

In addition, the comparison between in situ and culture pellets addresses the importance of using in situ pellets if we wish to extrapolate results to natural field conditions. The results obtained from the experiments with culture pellets should be treated with caution, as they may overestimate the degradation rates.

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