



Plastics counteract the ability of Antarctic krill to promote the blue carbon pathway in the deep ocean

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ABSTRACT

The Antarctic krill (*Euphausia superba*) play a critical role in promoting the so-called “blue carbon pathway” by producing a large amount of fast-sinking faecal pellets (FPs) which facilitate the transport of CO₂ through the water column. Here we assess how exposure to negatively (PS-COOH) and positively (PS-NH₂) charged polystyrene nanoparticles, impacts degradation of krill FPs (i.e. change in peritrophic membrane state, Carbon concentration and Carbon/Nitrogen ratio). Our findings suggest that exposure of nanoplastics, particularly negatively charged particles, increases krill FP degradation. This can result in a potential loss of FP-sequestered C of up to 27 %, equivalent to up 5.5 Mt. C per productive season (Spring-early Autumn). This study provides new insights into how increasing levels of plastic pollution could affect the natural capital provided by krill FPs. The effect of this emerging anthropogenic contaminant should be considered by international policies focused on climate change mitigation and adaptation.

1. Introduction

In recent years it has become apparent that biodiversity within polar oceans hold an important ‘natural capital’ asset in the blue carbon (C) pathway: the process of C capture, fixation and storage by marine organisms as organic C (for up to 100 years) up to sequestration (which corresponds to the removal of C from the C cycle for >100 years) (Cavanagh et al., 2021). The Southern Ocean (SO) accounts for ~20 % of the global ocean Carbon dioxide (CO₂) uptake (Taro et al., 2002) providing important ecosystem services such as climate regulation.

The Antarctic krill (*Euphausia superba*) has the largest biomass in the SO (Atkinson et al., 2019). This species plays a critical role in the SO blue C pathway, supporting C export and sequestration to the deep ocean through the production of numerous dense faecal pellets (FPs) and shedding of their exoskeleton (Manno et al., 2020). Being one of the largest epipelagic crustaceans, krill in fact produces large and C-rich FPs, which sink at speeds of hundreds of metres per day (Belcher et al., 2019). The rapid sinking of krill FPs together with the occurrence of krill as large swarms in the SO may overcome and escape most of the remineralisation processes along the water column, making krill FPs a fundamental conduit for the C to reach deep-sea sediments (Belcher

et al., 2019; Manno et al., 2020; Cavan et al. 2024). This C export mechanism is particularly relevant in the marginal ice zone (15–80 % ice cover) of the SO (Stroeve et al., 2016), a feeding ground in which krill reaches high densities (Schmidt and Atkinson, 2016).

The Antarctic krill further plays a pivotal role within SO food webs, allowing high energy flow transfer in pelagic systems. For these reasons, the Antarctic krill has long been used as a bioindicator to monitor the health status of the SO in response to environmental and anthropogenic stressors such as emerging contaminants, including micro- and nanoplastics (Corsi et al., 2023).

The indiscriminate feeding tactics coupled with one of the highest grazing rates in the SO pelagic ecosystems (Pakhomov et al., 2002) could make krill particularly prone to microplastic and nanoplastics exposure (Rowlands et al., 2021a, 2021b; Rowlands et al., 2023). Evidence of in situ ingestion of microplastics in Antarctic krill within the Southern Ocean has recently been provided, with microplastics content ranging from 0.10 to 2.13 items ind⁻¹ depending on the reports (Primpke et al., 2024; Zhu et al., 2023; Wilkie-Johnston et al., 2023). Bench-scale experiments show that the consumption and subsequent egestion of micro- and nanoplastics can alter the structural integrity of krill FPs, reducing their density and sinking rates (Bergami et al., 2020; Dawson et al.,

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2018).

The amount of the sequestered C pool in FPs is dictated by the sinking flux of organic C into the ocean interior and its residence time in the deep ocean, which is a function of the depth at which sinking C is remineralized (Kwon et al., 2009), with deeper remineralization leading to increased sequestrations. Therefore, inclusion of low-density plastic particles in krill FPs may increase the remineralisation of C in the water column and in turn the C sequestration potential (Gunaalan et al., 2023). Another factor affecting the downward flux of FPs is the rate at which they are degraded (remineralised) by coprophagous zooplankton and

prokaryotes as they sink. Higher rates of degradation decreases the efficiency of C export to the ocean interior (Svensen et al., 2012). Overall, the impact of micro- and nanoplastics on the degradation rate of FP are, so far, unclear. Potential adhesion of these particles from the ambient environment onto the FP exterior might influence FP stability and/or the capacity of coprophagous organisms to interfere with the FP surface and break up their structure. Such uncertainties limit the application of models (Kvale et al., 2023) and hamper estimates of relevant ecosystem-scale effects on C export.

To address this gap, here we assess the impact of exposure to

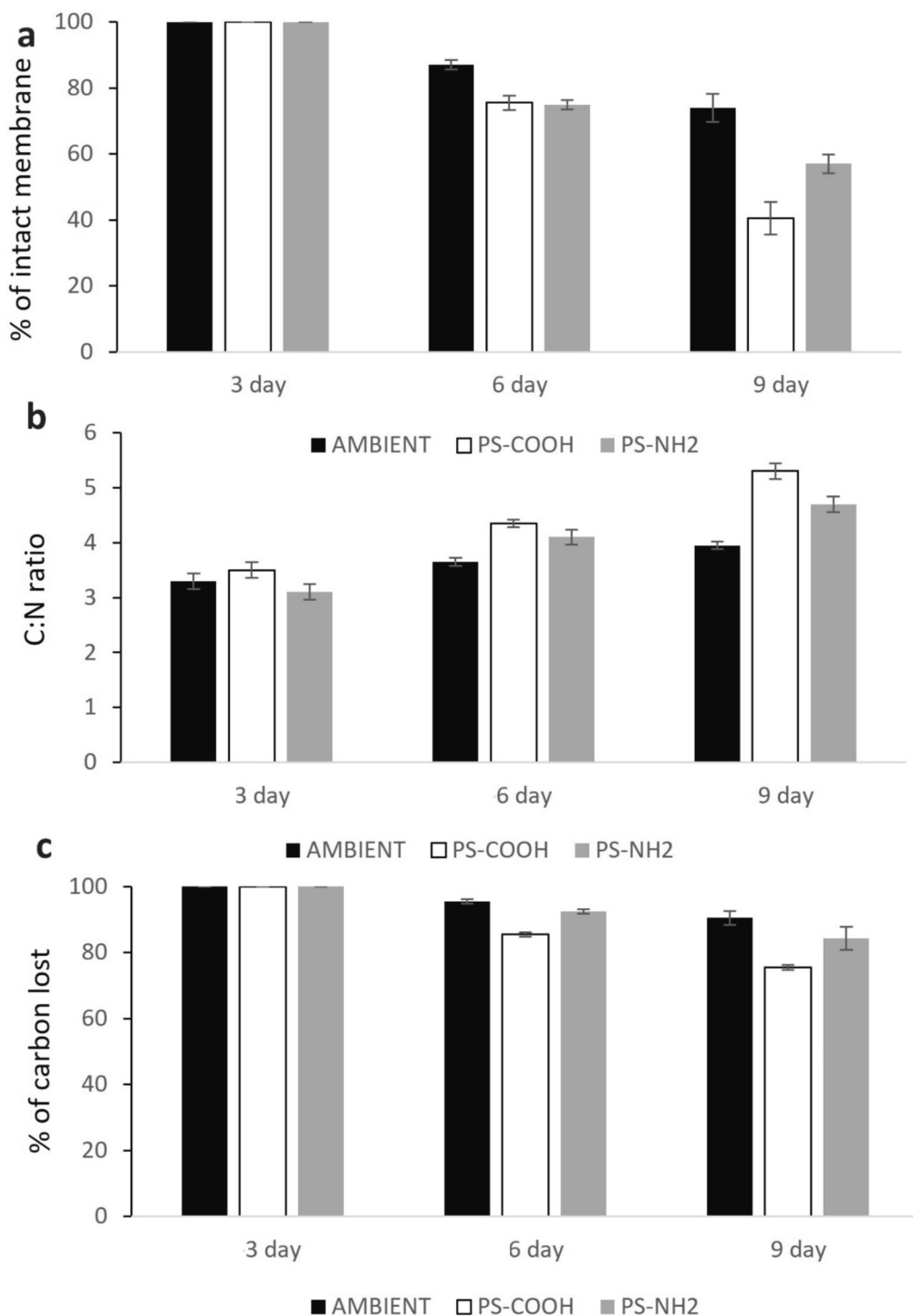


Fig. 1. Antarctic krill FP degradation under control (ambient), PS-COOH and PS-NH₂ exposure after 3, 6 and 9 days; a, % of intact membrane; b, variability of C:N ratio; c, % of C loss.

nanoplastics on the degradation of FPs produced by freshly caught Antarctic krill (*E. superba*) from the SO, with the aim to improve our understanding on the impact of nanoplastic on the ability of FPs to act as a vector of C transport to the deep ocean. To mimic how nanoplastics can interact with krill FPs, we focus on newly synthesised polystyrene nanoparticles (PS NPs), widely used as common proxy for nanoplastics in aquatic ecotoxicity studies (Rowlands et al., 2021b; Corsi et al., 2023). PS is neutrally buoyant in seawater, likely to remain in the water column where Antarctic krill principally feed (Schmidt and Atkinson, 2016). Further, we incorporated our results with previous literature data and estimated the potential reduce amount of C sequestered by the SO because of the interaction of plastics and krill FPs.

To improve predictions of the efficiency of the blue carbon pathway in a world with ever-increasing amounts of plastic (Geyer et al., 2017), studies are needed to assess the implications of plastic debris on oceanic C export. This study provides new insights into how increasing levels of plastic pollution might impact the magnitude of the C export to the deep SO and the potential impact on the natural capital provided by krill FPs. Therefore, the effect of this emerging anthropogenic contaminant should be considered by international policies and strategic plans focused on climate change mitigation and adaptation.

2. Materials and methods

2.1. Specimens collection

Living juveniles of *E. superba* were collected by Rectangular Mid-water Trawl (RMT) in the NW area of South Georgia Island (UK territory) (lat. 53.86.399; long 40.1794), in December 2016, on board of the research vessel RRS James Clark Ross (SI Fig. 1, location map). Soon after collection, krill juveniles were moved to a cold room (at +4 °C) and kept in buckets filled with aerated 0.20 µm filtered sea water.

2.2. Experiment design and analysis

Yellow-green fluorescently labelled PS NPs negatively charged (PS-COOH, 480 nm excitation, 520 nm emission) and unlabelled PS NPs (PS-NH₂ positive charged) were used. Details of the NP stocks and preparation of the NP suspensions have been described in Bergami et al. (2020). The nominal size reported by the supplier (Bangs Laboratories Inc. TechNote 206) was 60 and 50 nm for PS-COOH and PS-NH₂, respectively.

In order to investigate the effects of PS NPs on the FP degradation processes, a FP degradation experiment was performed, where krill faeces were incubated with both negative and positively charged PS nanoplastics at concentration of 2·10¹⁰ NPs/mL (SI Fig. 2, process step diagram).

FPs produced from juveniles of Antarctic krill *E. superba* within 6–12 h from collection were moved from the bucket and incubated in sterile 24-well plates containing PS NP suspensions in filtered natural seawater (NSW) (2 µm mesh) collected from the same area in order to resemble the whole bacterial community naturally occurring in Antarctic seawater and exclude patchy occurrence of large organisms, and the protozooplankton community.

Control (NSW only) and experimental groups (exposed to PS-COOH or PS-NH₂) were run in duplicate, each containing 15 FPs.

To assess the variability of the remineralisation process, FPs from each treatment was collected each 3 days after the start of the experiment up to 9 days and stored in 96 % Ethanol for further analysis.

FP degradation was evaluated in term of damage of peritrophic membrane, and variability in the C and Nitrogen ratio (C/N). Variability in the state of degradation of FPs among the treatments was assessed using a Scanning Electron Microscope (SEM, Hitachi Tabletop TM3000).

To semi-quantify the variability in the state of peritrophic membrane, the % of FP surface presenting absence/damage of membrane to the total FP surface. A total of 30 FPs were investigated for each

treatment (–5 FPs × 2 replicates × 3 time points).

C and N content of the FPs was estimated using a combustion elemental analyzer (CHN, Exeter Analytical Inc. 440CE elemental analyzer, accuracy ±0.15 %). For POC determination, filters were pre-treated with 1 N HCl. Three blank filters were run every 15 samples. Difference between FP_C under control and treatment condition was used as indicative of FP_C loss due to difference remineralization rate with and without the presence of plastic in the sea water.

2.3. Statistical analysis

Data were checked for normality, and differences in FP membrane fragmentation and C/N ratio for all the treatments were tested for significance using a 2-way ANOVA with time and treatment as factors. Differences between the treatments in the 9 days were tested for statistical differences using paired Student's *t*-test. Differences were considered significant where $\alpha < 0.05$.

2.4. Estimation of potential FP carbon sequestration reduction

The total amount of potential FP C loss due to the interaction with NPs was estimated in combination with available data from the literature using the following equation:

$$FP_{seq_loss} = FP_{seq} - (FP_{seq_PFP} + FP_{seq_PSW}) \quad (1)$$

in which FP_{seq_loss} is the FP C loss, obtained as the difference between FP C sequestered without the presence of plastic (FP_{seq}) and the FP C sequestered when plastic is included in the FPs (FP_{seq_PFP}) and in sea water (FP_{seq_PSW}). FP_{seq} is equal to 20 Mt. C per productive season, previously calculated by Cavan et al. (2024) for krill FP C exported in the SO that would remain sequestered in the oceans for at least 100 years. FP_{seq_PFP} is based on the incubation experiment by Bergami et al. (2020), that show how the incorporation of nanoplastic particle within FPs will halve the sinking speed and consequently FPs will take extra days to cross the remineralisation zone. Assuming an average sinking speed of 200 m d⁻¹ (Belcher et al., 2017) in absence of plastic krill FPs take usually an average of about 2 days to cross the high remineralisation zone (381 m depth average in the SO, based on Cavan et al., 2024). Then with the incorporation of nanoplastics FPs (Bergami et al., 2020), FPs will take extra 2 days to cross the remineralization zone because sinking speed is reduced by 50 %.

Assuming that FPs will lose 10 % of C due to bacteria and protozooplankton degradation activity per every day spent in the remineralization zone (according to incubation experiment by Morata and Seuthe, 2014; Svensen et al., 2012); FP seqPFP can then be write as:

$$FP_{seqPFP} = (FP_{seq} * 10/100) * 2 \text{ days.} \quad (2)$$

The FP_{seq_PSW} can be write as:

$$FP_{seq_PSW} = FP_{seq} * FP_C / 100 \quad (3)$$

where FP_C represent the amount of carbon loss obtained from this study due to the presence of plastic in the sea water.

Then Eq. (1) can be expressed as:

$$FP_{seq_loss} = \left\{ 20 \text{ Mt C} - \left[\left(FP_{seq} * \frac{10}{100} \right) * 2 \right] - (FP_{seq} * FP_C / 100) \right\} \quad (4)$$

3. Results

After 1–3 days of exposure, no significant signal of FP degradation was observed among the treatments, with relatively intact FP membranes and only slight variations in the C/N ratio observed, which were not significant (Fig. 1a,b). After 4–6 d, both PS NPs led to a similar decrease (up to 75 %) in the FP intact membrane surface and to higher C: N ratios (up to 4.35) compared to the FPs exposed to ambient conditions

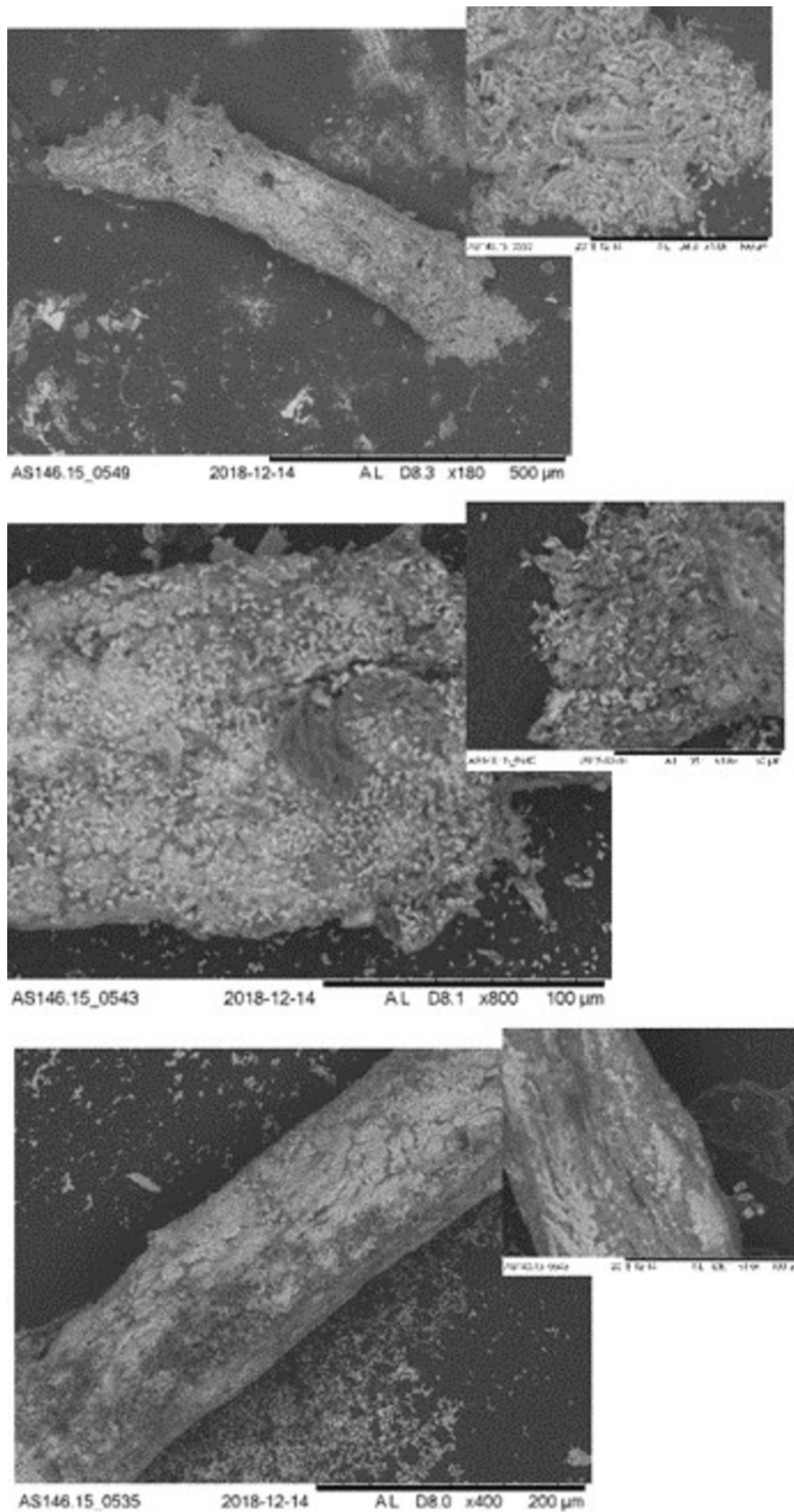


Fig. 2. Scanning Electron Microscope images show the state of Antarctic krill FPs at the end of the experiment (9 days). The arrows highlight the higher damage/degradation of membranes under exposure to PS-COOH and PS-NH₂ (top and middle image respectively), than control (bottom image).

(87 % and 3.65 %, respectively). At the end of the experiment, such discrepancy between PS NP treatments and the control group further increased (Fig. 1a,b). For both parameters, FP membrane degradation and C/N ratio, a significant difference over the time was observed after 7–9 days (FP membrane, $Z = 24,532$, $p < 0.05$, FP C/N ratio, $Z = 25,411$, $p < 0.05$). FP membrane damage, C loss and C/N data are provided in the supplementary material (SI Table 1). Both nanoplastics significantly promoted the degradation of krill FPs, with altered surface and cracks compared to ambient conditions. Overall, PS-NH₂ and PS-COOH led to a decrease in the FP intact surface membrane of 40 % and 57 %, respectively, compared to the FPs at ambient conditions (up 74 %) (Fig. 1a). Similarly, exposure to PS NPs affected C/N ratio, with a significant increase (to 5.3 for PS-NH₂ and to 4.7 for PS-COOH) than at ambient conditions (3.9) (Fig. 1b). SEM images are representative of the state of FPs at the end of the experiment and highlight the damage of the membrane (Fig. 2).

The % of C loss of the total FPs (Fig. 1c) after 4–6 and 7–9 d was significantly higher under both PS NP treatments (up 10 % and 23 % respectively) than at ambient conditions (11 %) ($Z = 26,884$, $p < 0.05$; $Z = 23,923$, $p < 0.05$). Overall, the FP degradation was always higher following exposure to PS-COOH than to PS-NH₂.

Considering the C sequestered by Antarctic krill FPs in the entire SO equal to 20 Mt. C per productive season (Cavan et al., 2024) and assuming a concentration of 2.10^{10} NPs/mL in seawater as for our incubation experiment (corresponding to 2.40 mg/L for 60 nm PS-COOH and 1.375 mg/L for 50 nm PS-NH₂, Bangs Laboratories Inc. TechNote 206), we estimated (as for Eqs. (1) and (2)–(4), see Materials and methods section) that the increase in krill FP degradation, due to the interaction between FP and nanoplastic in the seawater, corresponds to a reduction in FP-sequestered C of 1.5 Mt. C (based on the calculation 20 Mt. C * 7.5/100). To be conservative, we selected the lowest value of carbon loss (7.5 %) corresponding to the FP_C loss due to the exposure of PS-NH₂ occurring from day 4–6. Further, we calculated an additional reduction in FP-sequestered C of 4 Mt. C due to the inclusion of nanoplastic in krill FPs (based on the calculation 20 Mt. C * 0.1*2), using previous results of Bergami et al., 2020 (see Eqs. (1), (3), (4)).

4. Discussion

4.1. Impact of nanoplastics on FP degradation

Nanoplastics have been shown to negatively impact marine organisms including Antarctic ones (Corsi et al., 2023). Surface charges of PS NPs drive the outcome of toxicity with positive one (PS-NH₂) more detrimental as for instance able to disrupt cell membranes upon contact (as reviewed in Corsi et al., 2021), while those negatively charged (PS-COOH) more prone to accumulation but less toxic. This has recently been observed also for Antarctic zooplankton species (Manno et al., 2022; Bergami et al., 2020; Rowlands et al., 2021b), confirming that surface charge of PS NPs is responsible for their reactivity, nano-bio-interactions and ecotoxicological impact (Corsi et al., 2020, 2021).

Although the interactions of nanoplastics and marine bacteria are still poorly understood, available literature tends to confirm such paradigm: exposure to PS-NH₂ can lead to cell toxicity through increase in oxidative stress and cell death, while PS-COOH mostly cause negative effects on bacterial populations only at high concentrations (e.g. 200 mg/L, Okshevsky et al., 2020). Sun et al. (2018) investigated the toxic effects of charged PS NPs on the marine bacterium *Halomonas Alkaliphila* showing that nanoplastics promoted the bacterial growth when exposed to a relatively low concentration of PS NPs ($<< 80$ mg/L). Further, Okshevsky et al. (2020) showed that biofilm community structure by marine bacteria is affected by the surface functionalization of PS NPs, with neither positive nor negative charged NPs impairing the overall ability of marine bacteria to form biofilm but changing species relative abundance in a species-specific manner.

Antarctic krill has an important role in modelling the marine

bacterial assemblages of the SO, with distinct bacterial groups found in their digestive tract, moults, FPs and surrounding water (Clarke et al., 2019). Bacteria within or attached to zooplankton FPs may thus originate from pelagic bacteria or from the guts of the organisms from which they are produced (Jacobsen and Azam, 1984; Hansen and Bech, 1996). Once released, FPs are generally heavily colonized by bacteria, at population densities much higher than those that are free-living (Tang, 2005). These bacteria attached to the FP surface are principally responsible for their natural degradation (i.e. Honjo and Roman, 1978).

We found that the presence of nanoplastics, and in particular negatively charged ones, promoted the ability of bacteria to decompose organic material, which, in turn, increase krill FP degradation process. Specifically, after 6 and 9 d of incubation, the peritrophic membranes of the FPs exposed to both PS NPs were less intact (PS-COOH > PS-NH₂) than those kept in NSW and subject to natural degradation. Furthermore, a significant higher C/N ratio in the FPs exposed to PS NPs (PS-COOH > PS-NH₂) compared to those in NSW was found, which is a further indicator of increased levels of degradation. Although here we did not investigate the microbial community associated to krill FPs in the different treatments, we previously showed that the presence of PS NPs can alter the composition and abundance of bacteria in SO seawater (Bergami et al., 2020).

Overall data let us to formulate the following hypotheses: the presence of PS NPs did not affect the bacterial attachment on the FP surface regardless of surface charges; the microbial community was generally favoured by both PSNPs although in a different way related to their distinct behaviour in seawater (see Bergami et al., 2020): PS-COOH tend to form large agglomerates, which may actively contributing to the biofilm growth (and thus bacterial activity), while PS-NH₂, although able to impair bacterial growth (Sun et al., 2018) may still favour cell-cell aggregation between negatively charged bacteria through electrostatic interactions (Okshevsky et al., 2020). This could explain the increase in FP degradation (as a result of the enhanced bacterial activity) observed for both PS NPs, with the most pronounced effect for negatively charged PS-COOH.

Our results highlight that the nanoplastic pollution can foster FP-bacterial interaction in the seawater generating a negative feedback mechanism on C export.

4.2. Implication for the carbon export

The potential implication of reducing the efficiency of the biological carbon pump relative to the pre-plastic era have been recently a matter of great attention, where several studies showed that the incorporation of microplastic caused marine aggregate to sink slower than they would without the presence of this pollutant (e.g., salp and copepod FPs (Wieczorek et al., 2019, Cole et al., 2016) and marine snow (Roberts et al., 2024).

In our previous study we showed that PS NPs reduce the sinking rate of Antarctic krill FPs and agglomerates were spotted inside the faeces using labelled PSNP (Bergami et al., 2020). Such lower sinking rates increase the retention time of the FPs through the water column and thus their exposure to bacteria, protozoa and smaller coprophagous organisms (Poulsen and Iversen, 2008), which in turn promote FP remineralization. Here we demonstrate that nanoplastics may have cumulative impact on krill FPs fate due to the presence of nanoplastics in both seawater and FPs (Fig. 3) resulting in a lower capability to act as a vector of C export.

We suggest that the assessment of the cumulative effect of micro- and nanoplastic load on zooplankton FPs is fundamental to fully understand the impact of such emerging contaminants on the deep C export.

Kvale et al. (2020, 2023) estimated by numerical analysis the high potential of marine aggregates (such as zooplankton FPs) to remove microplastic from the ocean. In other words, the zooplankton FPs can pump plastic particles from the surface to the oceanic depth. Here we show that (at the experimental conditions considered) this “krill plastic

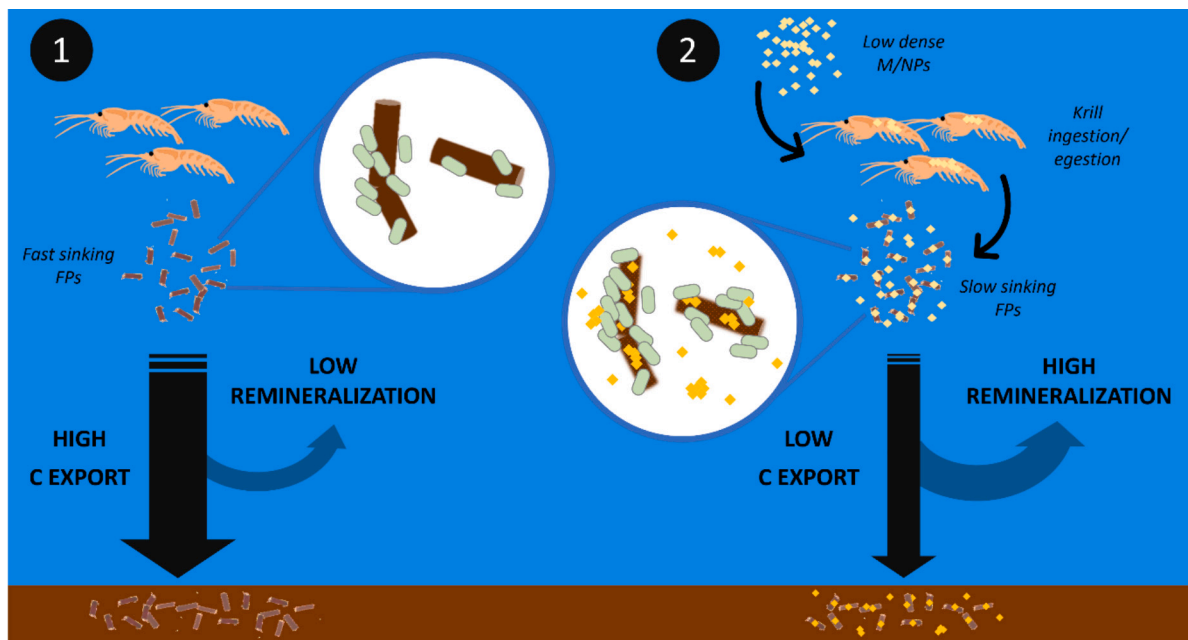


Fig. 3. Schematic of the Krill FPs carbon pump and the effect of plastic on Krill FP carbon export highlighting the interaction with Krill Faecal Pellets and nano-plastics: 1-nanoplastics are not present in seawater, 2- nanoplastics are present in both seawater and FPs. Yellow square: nanoplastics, light green cylinder: bacterial. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

pump” might counteracts the capability to support the oceanic krill C pump, with a reduction up 27 % corresponding to 5.5 Mt. C per productive season of the total krill C sequestered in the SO.

We are aware that, in addition to bacteria, protozooplankton grazers may also strongly contribute to the natural FP degradation process in seawater (Morata and Seuthe, 2014; Poulsen and Iversen, 2008). To this aim, the design of future FP degradation experiments should include this larger organisms' fraction to fully understand the impact of nanoplastics on the whole microbial community of SO seawater.

It is important also to note that our calculations might represent an overestimation of the potential loss in krill C sequestration because they are based on experimental data (present study and Bergami et al., 2020), in which krill were exposed to relatively high concentrations of nanoplastics (in the range of 1.4–2.4 mg/L for EXP-1), considering only one polymer (PS) and a small particle size range (nominal: 50–60 nm). On the other hand, such laboratory-controlled conditions even not reflecting natural exposure scenarios (Caruso et al., 2022) allow us to recognize the need to further disclose the plastic budget/contamination in the SO due to several unpredictable negative outcomes. Although our calculations are based to one component (FPs) and one zooplankton species (*E. superba*) only, the loss in C sequestration in the SO may be much larger than the one estimated considering that plastic reaching the SO is predicted to increase in the near future if no actions are taken either globally or locally (<https://council.science/current/blog/plastic-at-the-end-of-the-earth/>). Jambeck et al. (2015) predicted an increase in the input of plastic in the ocean by one order of magnitude by 2025, thus our estimations can be indicative of a near future worst-case scenario in which marine plastic leakage and accumulation in the oceans continue to raise along with its exponential production. Potentially, in addition to ingestion and repackaging into FPs, krill promote the transport of C below the thermocline by daily vertical migrations (swimming to the surface at night to feed and then returning to depth during the day) and seasonal descent to overwinter at depth (Boyd et al., 2019) as well as through the rapid sinking of their moults and carcasses (Manno et al., 2020). Scaling up, the value of the C loss can become even more relevant taking into account zooplankton global biomass higher than that of humans (Strömberg et al., 2009).

5. Conclusion

This study provides new insights into how increasing levels of plastic pollution could significantly affect the magnitude of the C export in the SO, and particularly the natural capital provided by Antarctic krill in promoting the blue carbon pathway in the deep ocean. We show that the interaction of nanoplastics reduce the sinking and increase degradation of Krill faecal pellets, resulting in an overall reduction in C export. International policy and strategy on climate change mitigation and adaptation rely on the most robust possible projections of future changes to CO₂ uptake and storage. Thus, the investigation of the main mechanisms regulating the interaction between ocean C export, zooplankton dynamics and plastic debris is critical to understand the impact of an emerging anthropogenic disturbances (such as plastic pollution) on the ability of the ocean to sequester C into its deeper layer. This aspect is particularly relevant in the Antarctic regions where Krill population is already undertreated by human-induced multi-stress (Cavanagh et al., 2021) such as ocean warming, ocean acidification and increase of fishery.

CRedit authorship contribution statement

C. Manno: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **I. Corsi:** Writing – review & editing, Funding acquisition. **E. Rowlands:** Writing – review & editing, Writing – original draft, Visualization, Supervision. **E. Bergami:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2024.117238>.

Data availability

All data are available at NERC EDS UK Polar Data Centre (DOI-XX) and presented in the supplementary material.

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