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Biofouled microplastics exposure is associated with shifts in late-summer lipid dynamics of juvenile copepod *Calanus hyperboreus*

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Microplastics (MP) are a relevant stressor in Arctic marine ecosystems. Their small size and ubiquity make them readily ingestible by zooplankton, placing copepods at the entry point of MP into high-latitude food webs. *Calanus hyperboreus* is a key Arctic species characterised by exceptionally large lipid reserves that fuel overwinter survival, support higher trophic levels as energy-rich prey, and facilitate carbon sequestration via the lipid pump. Successful lipid accumulation is therefore critical for individual fitness and ecosystem functioning, and MP-driven disruptions may have cascading effects on food-web dynamics and regional carbon sequestration. To address this, we exposed wild-caught *C. hyperboreus* copepodite stage V (CV) from southeastern Greenland to pristine and biofouled MP under feeding and food-deprived conditions during late summer (July–August 2024) aboard RRS Sir David Attenborough. Across experiments, control copepods exhibited seasonal shifts consistent with increasing lipid reserves and changes in fatty-acid composition over time. Responses to MP exposure were strongly context dependent. Pristine MP produced modest and variable changes in lipid content and fatty-acid profiles, whereas the most pronounced shifts were observed during late-summer exposure to biofouled MP under food-replete conditions, including reduced lipid mass and altered fatty-acid composition characterised by lower long-chain monounsaturated fatty acids and higher relative contributions of docosahexaenoic acid. Together, these patterns suggest that MP exposure during periods of active lipid accumulation may interfere with normal energy storage and fatty-acid allocation. These findings also identify a potentially crucial late-summer exposure context in which effects of MP on copepod lipid metabolism are most evident, rather than isolating biofouling as a sole causal factor. Overall, this study highlights the importance of seasonal physiological state and particle conditioning in shaping MP impacts on Arctic zooplankton, with potential implications for food-web dynamics and lipid-driven carbon export.

KEYWORDS
Arctic copepods, biofouling, Greenland, lipids, plastic pollution

1 Introduction

Plastic pollution is a global environmental concern. Since the 1950s, widespread plastic use has delivered substantial societal and economic benefits (Andrady and Neal, 2009), but inadequate waste management has led to large-scale accumulation of plastic in natural systems. In 2022, global plastic production reached 436.66 million tonnes, yet only around 9% of plastic waste is ultimately recycled globally (Houssini et al., 2025). An estimated 75–199 million tonnes of plastic are currently present in the oceans (UNEP, 2021), including 3–11 million tonnes estimated to reside on the ocean floor alone (Zhu et al., 2024). In the marine environment, plastics undergo physical, chemical, and biological degradation (Alimi et al., 2018), fragmenting into microplastics (MP) – plastic particles ranging in size from 5 mm down to 1 µm (Frias and Nash, 2019). MP are transported over long distances by ocean currents (Zhang, 2017) and atmospheric processes (Peries et al., 2024), contaminating environments from surface waters (Dar et al., 2025) to deep-sea sediments (Cunningham et al., 2020) and remote marine protected areas (Rynek et al., 2024). The Arctic is similarly affected, with MP detected in seawater, sediments, snow, and sea ice (Bergmann et al., 2022). Arctic sea ice contamination is particularly severe, with concentrations that can exceed 10, 000 particles L^{-1} (Peeken et al., 2018). Accelerated sea ice loss (Wunderling et al., 2020), therefore, represents a growing risk to Arctic ecosystems via seasonal MP release during ice melt.

The small size of MP makes them readily ingestible by a wide range of aquatic fauna (Thompson et al., 2024). In the Arctic, MP bioaccumulation has been documented across marine invertebrates (Grøsvik et al., 2022), fish (Kögel et al., 2023), seabirds (Taurozzi and Scalici, 2024), and marine mammals (Sletten et al., 2025; Moore et al., 2020; Iyare et al., 2024). MP can also transfer across trophic levels (Cedervall et al., 2012; Nelms et al., 2018), with zooplankton acting as an entry point into food webs due to the overlap between MP particle size and phytoplankton prey (Gunaalan et al., 2023). Given zooplankton's central role in Arctic food webs as a link between primary producers and higher trophic consumers (Graeve et al., 2005), MP-induced perturbations at this level may propagate to community- and ecosystem-scale consequences.

Within zooplankton, copepods are key species in Arctic food webs (Marmillot et al., 2024). Among these, *Calanus hyperboreus* stands out by carrying the largest lipid reserves of Arctic copepods, exhibiting high proportions of monounsaturated lipid compounds such as cetoleic acid (22:1(n-11)) and 22:1(n-11) alcohol, and accumulating energy-rich wax esters (Albers et al., 1996). These lipid reserves also supply predators with essential fatty acids (FAs), particularly long-chain omega-3 (ω-3) and omega-6 (ω-6) polyunsaturated FAs (PUFAs) of microalgal origin (Kattner and Hagen, 2009). Notably, among these, the ω-3 PUFAs docosahexaenoic acid (DHA, 22:6(n-3)) and eicosapentaenoic acid (EPA, 20:5(n-3)) are critical for maintaining membrane fluidity at low temperatures (Pernet et al., 2006), supporting neural function (Persson and Vrede, 2006), and regulating growth, immune responses, and reproduction (Ravet et al., 2010; Pilecky et al., 2021; Kumar et al., 2022).

Higher-trophic level consumers have limited capacity to biosynthesize DHA and EPA *de novo* and depend on dietary supplies provided by their prey (Trushenski and Rombenso, 2020). The amounts of DHA and EPA are essential for the nutritional quality of zooplankton (Rodríguez et al., 1997; Matsunari et al., 2013; Costalago et al., 2020). The DHA/EPA ratio has been used as a prey nutrition quality metric, with higher ratios generally indicating greater DHA availability and higher prey nutritional value, and lower ratios suggesting poorer nutritional quality for consumers with high DHA requirements (Garzke et al., 2023). In zooplankton, DHA/EPA is strongly influenced by phytoplankton prey: DHA-rich flagellates and dinoflagellates tend to increase the ratio, while EPA-rich diatoms tend to lower it (Costalago et al., 2020). As phytoplankton composition varies seasonally, zooplankton DHA/EPA is also expected to vary with season and food quality. Importantly, Deschutter et al. (2019) further suggested that DHA/EPA can act as a sensitive marker of copepod responses to environmental fluctuations and stressors, including changes in temperature and algal food quality that can alter the ratio within zooplankton. We therefore hypothesised that MP ingestion, particularly of biofouled MP, could potentially alter fatty-acid balance in *C. hyperboreus* and reduce their nutritional quality as prey, since this ratio is heavily influenced by the diet.

The lipid-rich reserves of *C. hyperboreus* also support a key ecosystem function: carbon sequestration via the lipid pump. During diapause, *C. hyperboreus* descends to depth and sustains metabolism by catabolizing stored lipids (Baumgartner and Tarrant, 2017), respiring carbon originally fixed by phytoplankton in surface waters and effectively transferring it to the deep ocean (Visser et al., 2017). In regions with high overwintering populations (Fram Strait, Greenland Sea, Iceland Sea), export estimates range from 3.5 to 6.0 g C m^{-2} yr^{-1} at depths of 1000–3000 m, comparable to detrital organic carbon fluxes at similar depths (Visser et al., 2017).

Several experimental studies on copepod exposure to MP have shown that these particles can negatively affect lipid accumulation and induce stress-triggered moulting (Cole et al., 2019) and spawning (Rodríguez-Torres et al., 2020). Because copepod lipids are critical to Arctic food webs as a source of energy and essential long-chain PUFAs, and to carbon export via the lipid pump, disruptions to lipid accumulation may propagate from individual fitness to population dynamics and ecosystem and biogeochemical functioning. In this context, copepodite stage V (CV – the fifth, pre-adult stage before the final moult) is particularly vulnerable to lipid depletion. This prolonged developmental phase is essential for successful diapause, reproduction, and survival in highly seasonal polar environments, where substantial summer lipid accumulation supports overwintering and transition to adulthood (Sargent and Falk-Petersen, 1988).

Despite the importance of *C. hyperboreus* for prey quality and carbon export in the Arctic, few studies have examined how environmentally realistic MP exposure scenarios affect total lipid reserves and FA composition in this species at the pre-adult stage. Previous work has relied largely on pristine MP, rarely accounting for biofouling, which can alter particle properties and, consequently, the biological effects of MP ingestion *in situ*. There is therefore a need for studies assessing how biofouling, together with MP concentration and feeding conditions, influences copepod lipid accumulation. In

particular, it is essential to determine whether biofilm coatings exacerbate MP-related impacts or whether their nutritional value partially offsets the effects of MP ingestion. To address this gap, we exposed wild-caught *C. hyperboreus* CV from southeastern Greenland to pristine and biofouled MP at two concentrations under feeding and food-deprived conditions during late summer. We focused on total lipid mass and free FA composition as sensitive indicators of changes in energy storage and lipid allocation. By combining freshly collected wild copepods, Arctic seawater, late-season shipboard incubations, and, in the latest experiment, seawater-conditioned biofouled particles, the study was designed to approximate exposure contexts that could plausibly occur *in situ* while retaining experimental control. Rather than testing a fully factorial mechanism, this study aimed to assess whether MP-associated lipid responses vary with ecological context, including seasonal timing, food availability, and particle conditioning.

2 Materials and methods

2.1 Copepod collection

Three independent copepod incubation experiments with MP exposure were conducted during the KANG-GLAC expedition (SD041) aboard RRS Sir David Attenborough in July-August 2024 (British Oceanographic Data Centre (BODC), 2024). To capture late-summer variability, experiments were carried out between late July and late August, using copepods collected from the depth 0–200 m along the southeastern Greenland shelf with a motion-compensated 200 µm Bongo net. Copepods for Experiment I (late July) and Experiment II (early August) were collected from single stations (67.492° N, 33.003° W and 68.107° N, 30.423° W, respectively). For Experiment III (late August), copepods were collected from three stations: two adjacent sites (67.414° N, 32.683° W; 67.411° N, 32.683° W) and a third site ~31 km to the north (67.693° N, 32.577° W), due to late-season conditions in the Arctic seawater, which led to a shortage of this species and developmental stage during collection. The sampling map is presented in Figure 1, produced in QGIS (version 3.30.3-'s-Hertogenbosch; QGIS Development Team, 2024) using the Esri Ocean Basemap, with sampling areas shown as experiment-specific polygons drawn around collection coordinates. Immediately post-capture, individuals were transferred into 1 L beakers with 1.2 µm-filtered arctic seawater and held at 7 °C for 12–24 hours for acclimation. Only active, undamaged individuals were selected for experiments. Copepodite stage CV individuals were identified morphologically by size (≈3 mm or more of the prosome length) and by a four-segmented urosome.

2.2 Experimental setup

Experimental conditions are summarized in Table 1. The study comprised three independent shipboard experiments covering different late-season contexts. Rather than relying solely on laboratory-conditioned animals or pristine particles, the design involved freshly collected copepods with Arctic seawater, seasonal timing, food-present and food-absent settings, and, in Experiment III, particles pre-conditioned in seawater to produce biofouling on MP surface. In Experiment I, copepods were exposed to pristine MP with algal food. Experiment II tested pristine MP under starvation, and Experiment III used biofouled MP with algal food. Each experiment included three treatments: control (0 MP), low MP (20 µg L^{-1}), and high MP (200 µg L^{-1}). Falcon tubes were

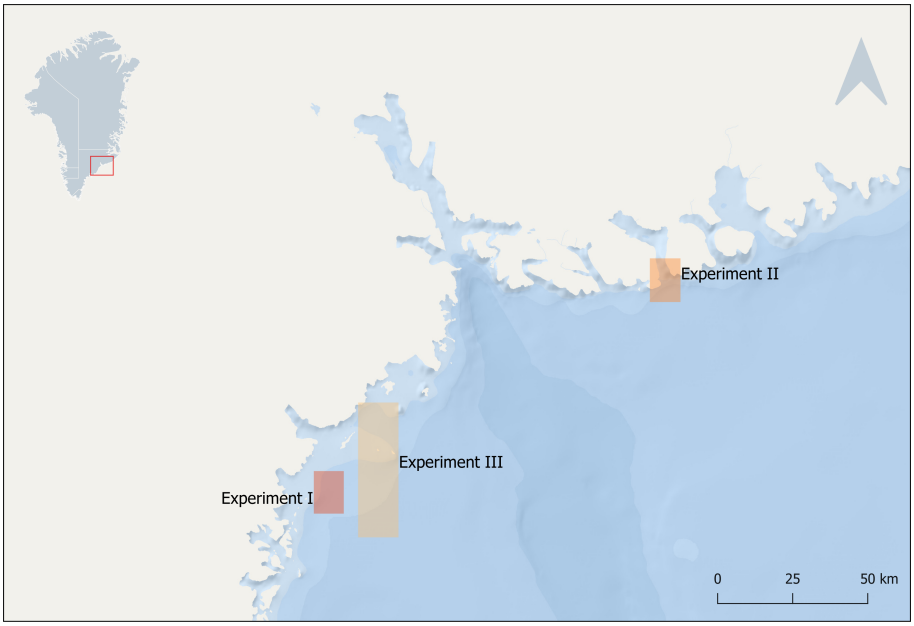

FIGURE 1
Map of the sampling areas used for the three shipboard incubation experiments with *Calanus hyperboreus* CV during the KANG-GLAC (SD041) expedition off south-west Greenland in summer 2024. Coloured polygons indicate the approximate sampling areas for Experiments I–III. The base of the map was created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved. For more information about Esri® software, please visit www.esri.com.

TABLE 1 Overview of experimental conditions across three shipboard experiments with microplastics (MP).

Experiment	Seasonal timing	MP type	Food	MP (µg L^{-1})	Treatment	Replicates per treatment across two rotators
I	Late July (27.07 – 02.08)	Pristine	Yes	0, 20, 200	Control; Low MP; High MP	n=3 (3 copepods pooled)
II	Early August (04.08 – 10.08)	Pristine	No	0, 20, 200	Control; Low MP; High MP	n=3 (3 copepods pooled)
III	Late August (19.08 – 25.08)	Biofouled	Yes	0, 20, 200	Control; Low MP; High MP	n=3 (2 copepods pooled)

mounted horizontally across two vertical rotators at 1 rpm with a 90° tilt to maintain particle suspension. In Experiments I and II, each treatment contained 12 copepods across both rotators, with two individuals per Falcon tube. In Experiment III, lower specimen availability reduced this to six copepods per treatment, with one individual per tube. Tubes were opened every two days for gentle aeration and feeding in the fed treatments. In food treatments (Experiments I and III), copepods were fed every two days with a mixed microalgal suspension (*Nannochloropsis*, *Tetraselmis*, *Pavlova*, *Isochrysis*, and *Thalassiosira weissflogii*; Reefphyto, UK) at 4, 600 cells mL^{-1}. After 7 days, copepods were rinsed with 1.2 µm-filtered Arctic seawater and individually frozen at −80 °C. No mortality or behavioural changes were observed at the end of each experiment. The 7-day exposure was selected to capture any potential early lipid responses within the logistical constraints of shipboard experimentation. Similar exposure durations have been sufficient to detect MP-induced effects in copepods: Cole et al. (2019) exposed *Calanus finmarchicus* CV to small nylon MP for 6 days and reported changes in feeding, lipid accumulation and moulting.

2.3 MP preparation

For MP preparation, all materials were pre-cleaned three times with Milli-Q water and once with ethanol (2 µm-filtered). Experimental MP consisted of polyamide nylon-6 powder (Goodfellow, AM306010). Pristine MP stock was prepared in a clean, plastic-free laboratory at the British Antarctic Survey before shipboard experiments. Particles were size-fractionated to 5–25 µm using a 25 µm nylon mesh sieve. The sieved fraction (0.25 mg) was diluted to 25 mL with 2 µm-filtered Milli-Q water to prepare a stock suspension (0.01 mg mL^{-1}). Before the experiments, defined volumes (100 µL and 1 mL) of the stock were pipetted into 50 mL Falcon tubes and diluted with 1.2 µm-filtered Arctic seawater to reach a final volume of 50 mL, yielding nominal MP concentrations of 20 and 200 µg L^{-1}. Particle abundance in well-mixed subsamples was estimated under light microscopy using a Sedgwick-Rafter counting chamber, confirming approximate target densities of 10 and 100 particles mL^{-1}.

We used MP concentrations of 20 and 200 µg L^{-1}, equivalent to 10 and 100 particles mL^{-1} of small MP (10–25 µm), as these levels fall within the range commonly used in MP ecotoxicology as environmentally relevant exposure concentrations (≤1 mg L^{-1}; Sun et al., 2021) and are comparable to previous copepod studies with nylon MP (Cole et al., 2019). These concentrations are higher than current levels reported for Arctic seawater, with 0–375 particles m^{-3} beneath sea ice of the Central Arctic Basin (Kanhai et al., 2018) and 67–278 particles m^{-3} for MP >10 µm in West Greenland waters (Rist et al., 2020). However, Arctic sea ice can accumulate substantially higher MP loads, reaching up to 12, 000 particles L^{-1} (Peeken et al., 2018). Therefore, our treatments represent environmentally plausible high-exposure scenarios for small, bioavailable MP, particularly under potential warming-driven pulse release from melting sea ice.

For biofouled MP, 1 mg of particles was prepared identically, and transported on-board in pre-cleaned aluminium foil. Particles were incubated in 100 mL of Arctic seawater in a pre-cleaned glass beaker for 27 days with constant mixing at 7 °C to approximate ambient Arctic summer seawater temperature. The presence of biofilm after the incubation has been determined microscopically. Immediately before the experiments, defined volumes of the continuously mixed biofouled MP suspension were pipetted directly into 50 mL Falcon tubes to achieve the same nominal concentrations as in the pristine MP treatments. The aim in the biofouling experiment was to expose copepods to intact microbe-coated particles. Therefore, to preserve these biofilms, we did not isolate, dry, or re-weigh particles after the 27-day conditioning period. Instead, exposures were prepared by volumetric dosing from the continuously stirred biofouled suspension and concentrations were reported as nominal mass concentrations. Similar approaches have been used in other experimental studies with biofouled MP, where conditioned particles were introduced from suspension rather than recovered and reprocessed before the start of the exposure (Polhill et al., 2022; Rades et al., 2022; Kelly et al., 2023). This approach was chosen because filtration or centrifugation of fine conditioned particles risks disturbing the attached microbial layer and altering particle properties before exposure.

2.4 Laboratory analyses

2.4.1 Sample preparation

Copepods were freeze-dried for 24 h before lipid extraction. For each treatment, pooled samples constituted the unit of statistical analysis. Individuals from different Falcon tubes were pooled to meet the FA detection limit and to reduce the influence of inter-individual variability. In Experiments I and II, three individuals were pooled per analytical sample, producing four pooled samples per treatment; three were analysed for FA composition, while one was retained at −80 °C as a backup or for potential further analyses. In Experiment III, all available individuals were used to produce three pooled samples per treatment, with two copepods per sample.

This resulted in a consistent analytical sample size of n = 3 per treatment across all experiments. Pooled samples were weighed on a microbalance to obtain dry weight. Each sample was spiked with 20 µL of the internal standard 5α(H)-cholestane (≥97% purity, Sigma-Aldrich C8003-1G), diluted at 1.29 mg per 15 mL hexane (≈95% n-hexane, Residue Analysis grade, Distol™), to enable absolute FA quantification during GC–MS analysis.

2.4.2 Lipid extraction

For laboratory steps before lipid analysis, only glassware furnaced at 450 °C was used, and two procedural blanks were processed alongside samples throughout the workflow. Lipids were extracted following Rowlands et al. (2023) and Ohman (1988). To each pooled sample, 5 mL of dichloromethane:methanol (9:1 v/v) was added. Samples were sonicated for 5 minutes, incubated at room temperature for 24 hours, then sonicated again for 15 minutes. The solvent was transferred to round-bottom flasks using a glass pipette and evaporated under vacuum at 30 °C (Büchi Rotavapor® R300 with B300 bath and F305 chiller). Dried extracts were re-dissolved in dichloromethane, transferred to glass vials, and re-dried under a gentle stream of nitrogen gas. Lipid content was determined gravimetrically and normalized to dry weight and pooled individual number (µg lipid mg^{-1} DW ind^{-1}).

2.4.3 FA methylation and silylation

Each dried lipid sample was mixed with 3 mL of methanol containing 5% hydrogen chloride (95:5, v/v), sealed, and incubated at 70 °C for 12 hours. After cooling, 4 mL of Milli-Q water and 3 mL of hexane:dichloromethane (4:1, v/v) were added. The upper organic phase was collected, and the extraction repeated twice to maximize recovery. Combined organic phases were dried using a centrifugal evaporator (GeneVac EZ-2 Envi), redissolved in 50 µL dichloromethane, transferred to clean glass vials, and evaporated again under a gentle stream of nitrogen gas.

For silylation, dried lipids were redissolved in 50 µL dichloromethane, mixed with 50 µL BSTFA (N, O-bis (trimethylsilyl)trifluoroacetamide), and incubated at 70 °C for 1 hour. Samples were then left at room temperature overnight, transferred to gas chromatography-mass spectrometry (GC-MS) vials, dried under nitrogen gas, and stored at 4 °C. Before GC-MS analysis, samples were dissolved in hexane.

2.4.4 GC-MS analysis

Samples were analysed using a Thermo Trace 1300 GC–MS equipped with a RESTEK FAMEWAX column (30 m × 0.25 mm × 0.25 µm). A 0.8 µL aliquot was injected in splitless mode. The oven was programmed from 100 °C (3 min) to 230 °C at 2 °C min^{-1}, with a final hold of 32 min, using helium as the carrier gas at 1 mL min^{-1}. Fatty-acid methyl esters (FAMEs) were identified by retention times and mass spectra using the LIPID MAPS® spectral library and confirmed with a commercial FA standard mix (Supelco 37-component FAME mix, CRM47885, Merck) run under identical conditions. Peaks were manually integrated into the Xcalibur Qual Browser. Due to consistently low internal standard signals, fatty-acid analyses were interpreted on a relative compositional basis only (% total integrated area). Accordingly, apparent increases in individual fatty acids should be interpreted as shifts in relative allocation rather than absolute enrichment. Only FAs contributing >1% to the total FA signal in all replicates were included in statistical analyses. Any FAs detected in both blanks and samples at the same retention time were excluded from final analyses.

2.5 Data analysis

2.5.1 Lipid content

For each treatment, the median, first quartile (Q1), third quartile (Q3), and interquartile range (IQR) were calculated (Supplementary Table 1). Differences among Control, Low MP and High MP were tested using the Kruskal–Wallis test ($\alpha = 0.05$). Effect sizes (ε^2) were reported following Tomczak and Tomczak (2014): 0.01 – small, 0.06 – medium, ≥0.14 – large; negative ε^2 values were treated as negligible (Okada, 2017). Where ε^2 was medium to large, *post hoc* contrasts (Control vs Low MP; Control vs High MP) were performed using Dunn's test with Bonferroni adjustment, and standardized effect size r was calculated using Cohen's benchmarks: $r \approx 0.10$ – small, 0.30 – medium, 0.50 – large (Cohen, 1992).

2.5.2 FA profiles

For each FA, a median, Q1, Q3 and IQR were calculated (Supplementary Table 2). FA proportions were subjected to a centered log-ratio (CLR) transformation to account for the compositional structure of the data (Greenacre, 2021). Differences in overall FA composition were tested using PERMANOVA on CLR-transformed Euclidean distances ($\alpha = 0.05$). Effect sizes were reported as omega-partial (ω^2) and interpreted following Cohen (1988): 0.01 – small, 0.06 – medium, ≥0.14 – large. Multivariate dispersion was assessed using PERMDISP to confirm that PERMANOVA differences reflected group separation rather than variation in dispersion. Where relevant (significant p and/or medium to large ω^2), pairwise PERMANOVA was performed for Control vs Low MP and Control vs High MP with Bonferroni-adjusted p-values, reporting ω^2 for each contrast.

For multivariate visualisation, principal component analysis (PCA) was performed on CLR-transformed FA data, and hierarchical cluster analysis was carried out using Ward's method on the same matrix. PC1 and PC2 loadings and contributions of each FA to principal components were also calculated (Supplementary Table 3).

DHA/EPA ratios with a median, Q1, Q3 and IQR were calculated for each treatment (Supplementary Table 4) and were analysed using Kruskal–Wallis ($\alpha = 0.05$), reporting ε^2 and r (*post hoc*) as effect size measures.

All analyses were conducted in R version 4.3.2 (R Core Team, 2023) using vegan (Oksanen et al., 2025), compositions (van den

Boogaart et al., 2024), ggplot2 (Wickham, 2016), ggrepel (Slowikowski, 2024), ggforce (Pedersen, 2024), ggdendro (de Vries and Ripley, 2024) and base R functions (e.g., kruskal.test(), prcomp(), hclust()).

3 Results

3.1 Dynamics of lipids and FAs across experiments in control treatments

Across the seasonal sampling window, control copepods showed higher lipid mass in later experiments, with median values increasing from Experiment I to Experiment III (Figure 2A). These differences were marginally non-significant (Kruskal–Wallis $p = 0.051$), but were associated with a large effect size ($\varepsilon^2 = 0.66$).

FA composition also shifted across experiments (Figure 2B). PERMANOVA confirmed significant differences in overall FA profiles ($p = 0.027$; $\omega^2 \approx 0.26$), and PERMDISP indicated homogeneous dispersion ($p = 0.655$). The strongest separation occurred between Experiments I and III, not reaching statistical significance ($p = 0.15$), but reflected by the largest effect size ($\omega^2 = 0.51$). FA composition also varied across experiments (Figures 2B, C), including lower 16:0 and higher EPA in later experiments, and a decline in the DHA/EPA ratio from Experiment I to Experiments II–III.

3.2 Change of lipids with MP exposure

Patterns of lipid content differed across experiments and treatments (Figure 3A; Table 2).

3.2.1 Experiment I – pristine MP + food

Under pristine MP exposure with food, copepods showed lower median lipid reserves than controls, but differences were not statistically supported, and the effect size was negligible ($p = 0.561$, $\varepsilon^2 \approx 0$; Table 2).

3.2.2 Experiment II – pristine MP + no food

Under starvation, lipid reserves remained broadly similar across treatments ($p = 0.491$, $\varepsilon^2 \approx 0$; Table 2).

3.2.3 Experiment III – biofouled MP + food

The strongest treatment-associated shifts in lipid reserves were observed in Experiment III. Copepods exposed to biofouled MP showed lower median lipid mass than controls, and the overall comparison indicated a large effect size despite limited statistical support ($p = 0.113$, $\varepsilon^2 = 0.39$; Table 2). Pairwise effect sizes were likewise large at both MP concentrations (Low MP: $r = 0.79$, High MP: $r = 0.67$), consistent with reduced lipid reserves under late-summer biofouled-MP exposure.

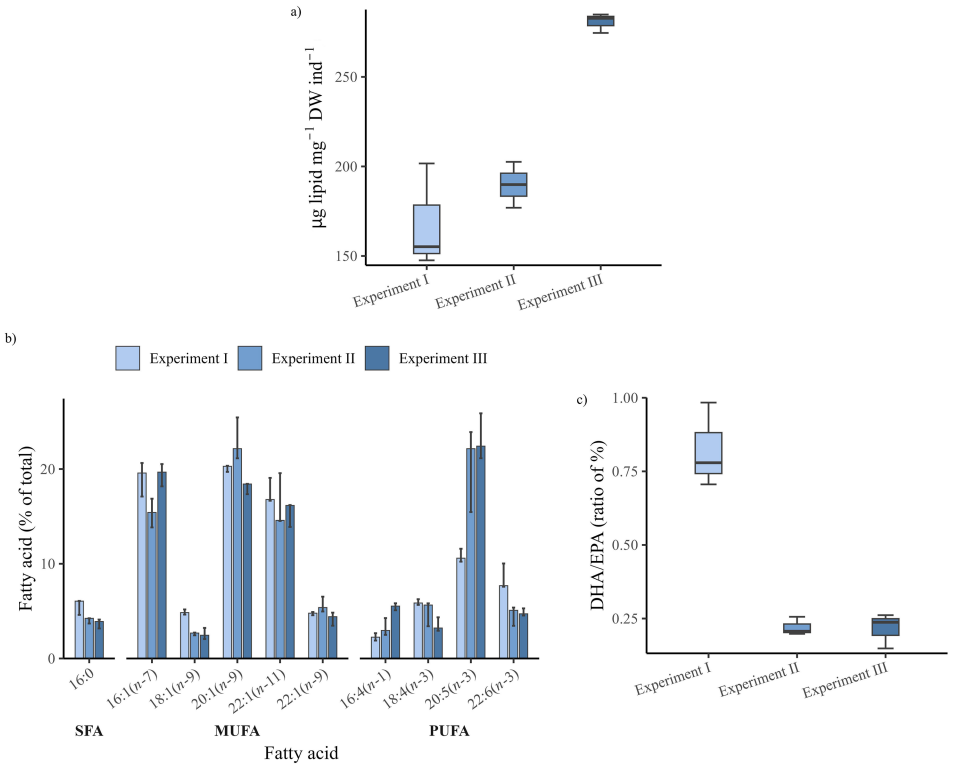

FIGURE 2
Seasonal changes in lipids of *Calanus hyperboreus* CV not exposed to microplastics (MP) across Experiments I – III: **(A)** total lipid mass; **(B)** fatty-acid (FA) composition; **(C)** DHA/EPA ratio.

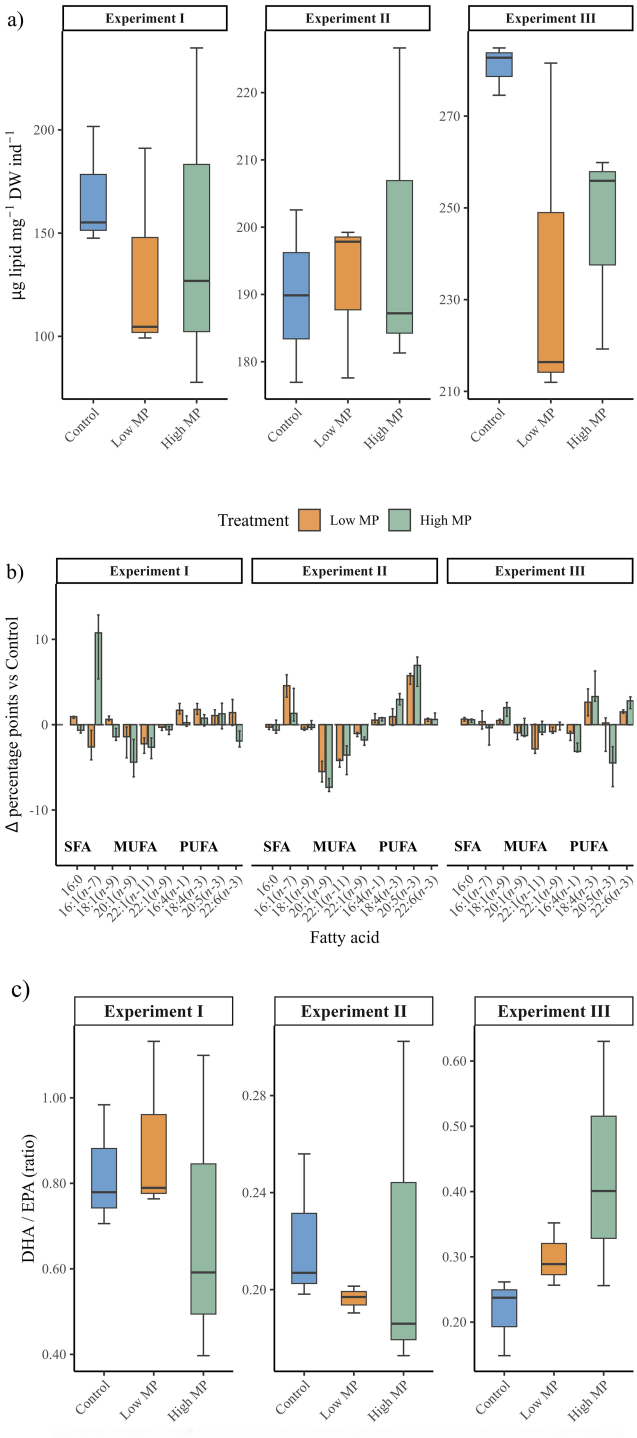

FIGURE 3
Effects of microplastics (MPs) exposure on lipids in *Calanus hyperboreus* CV across Experiments I – III: **(A)** total lipid mass; **(B)** fatty-acid (FA) composition deviations relative to controls. **(C)** DHA/EPA ratio.

3.3 Change of FA composition with MP exposure

FA responses and DHA/EPA ratios varied across experiments and were strongly context dependent (Figures 3B, C; Table 3). Multivariate dispersion did not differ among treatments in any experiment (PERMDISP: Experiment I – $p = 0.657$; Experiment II – $p = 0.065$; Experiment III – $p = 0.974$), indicating that PERMANOVA results reflected treatment-related structure rather than differences in within-group variance.

3.3.1 Experiment I – pristine MP + food

FA responses to pristine MP with food were modest. Relative to controls, MP-exposed copepods tended to show lower long-chain MUFAs together with shifts in several PUFAs with the medium

TABLE 2 Summary of lipid responses (median µg mg^{-1} DW ind^{-1}) to microplastics (MP) exposure across experiments.

Experiment	Treatment	Control	Low MP	High MP	Kruskal–Wallis (p, ε^2)	Pairwise effect size (vs Control)
I	Pristine MP + food	155.2	104.6	126.9	p = 0.561, $\varepsilon^2 \approx 0$	–
II	Pristine MP + no food	189.9	197.8	187.2	p = 0.491, $\varepsilon^2 \approx 0$	–
III	Biofouled MP + food	282.7	216.4	255.9	p = 0.113, ε^2 = 0.39	Low MP: r = 0.79 High MP: r = 0.67

effect size, but treatment differences were not statistically significant overall (p = 0.202, $\omega^2 \approx$ 0.11; Table 3). PCA and cluster analysis indicated only subtle treatment structuring in Experiment I, with partial but overlapping separation among groups (Figures 4A, B). The DHA/EPA ratio showed no consistent response in Experiment I (p = 0.491, $\varepsilon^2 \approx 0$; Table 3).

3.3.2 Experiment II – pristine MP + no food

Under starvation, pristine MP exposure was associated with lower long-chain MUFAs, particularly 20:1(n-9) and slightly higher EPA and 16:1(n-7), while DHA remained relatively stable. Overall FA composition changed little among treatments, and statistical support for treatment effects was limited (p = 0.364, $\omega^2 \approx$ 0.03, Table 3). PCA and cluster analysis likewise showed minimal separation among treatments in Experiment II (Figures 4C, D). The DHA/EPA ratio showed no meaningful trend in Experiment II (p = 0.430, $\varepsilon^2 \approx 0$; Table 3).

3.3.3 Experiment III – biofouled MP + food

The strongest FA shifts were observed in Experiment III. Biofouled MP exposure was associated with lower long-chain MUFAs and higher relative contributions of DHA and 18:4(n-3), while EPA showed a mixed response and was lower at High MP. Overall treatment differences were not statistically significant, but the effect size indicated a large shift (p = 0.168, $\omega^2 \approx$ 0.17), driven mainly by separation between Control and High MP (Low MP: ω^2 = 0.03, High MP: ω^2 = 0.288; Table 3).

PCA indicated clearer treatment structuring in Experiment III than in the pristine-MP experiments, with High MP samples tending to separate from controls along a PUFA–MUFA gradient together with reduced relative contribution of long-chain storage MUFAs (Figures 4E, F). The DHA/EPA ratio tended to increase with MP exposure in Experiment III (p = 0.177, ε^2 = 0.183), particularly at High MP (Low MP: r = 0.55, High MP: r = 0.73; Table 3), although statistical support was limited by low replication.

4 Discussion

This study shows that microplastics (MP) exposure can be associated with changes in lipid reserves and FA allocation in juvenile *Calanus hyperboreus*, but that these responses are strongly dependent on seasonal timing, feeding context, and particle conditioning. Across three shipboard experiments from late July to late August, the most pronounced lipid depletion and fatty-acid (FA) restructuring occurred during late summer under food-replete conditions in the presence of biofouled MP. In contrast, pristine MP tested earlier in the season, with and without food, produced weaker and more variable responses. Because MP type, food regime, and seasonal timing were not fully crossed experimentally, the observed responses cannot be attributed to particle conditioning alone. Instead, they should be interpreted as context-dependent responses emerging from the combined effects of exposure type, feeding conditions, and seasonal physiological state. The results point to a late-summer exposure context in which MP effects on

TABLE 3 Summary of major fatty-acid (FA) responses to microplastics (MP) exposure across experiments.

Experiment	Treatment	Key FA changes vs control	PERMANOVA FA (p, ω^2 and pairwise effect size vs control)	DHA/EPA values (Kruskal–Wallis p, ε^2 and pairwise effect size vs control)
I	Pristine + food	**Low MP** 20:1(n-9): 20.3→18.5%, 22:1(n-11): 16.8→16.0% **High MP** 20:1(n-9): 20.3→15.5%, 22:1(n-11): 16.8→15.6%.	p = 0.202, $\omega^2 \approx$ 0.11 **Low MP** ω^2 = 0.163 **High MP** $\omega^2 \approx 0$	**Control**: 0.78; **Low MP**: 0.79; **High MP**: 0.59 p = 0.491, $\varepsilon^2 \approx 0$
II	Pristine + no food	**Low MP** 20:1(n-9): 22.2→18.2%, EPA: 22.2→24.6%, 16:1(n-7): 15.4→19.9% **High MP** 20:1(n-9): 22.2→16.3%, EPA: 22.2→25.8%	p = 0.364, $\omega^2 \approx$ 0.03	**Control**: 0.21; **Low MP**: 0.20; **High MP**: 0.19 p = 0.430, $\varepsilon^2 \approx 0$
III	Biofouled + food	**Low MP** DHA: 4.7→6.5%, 18:4(n-3): 3.2→6.4%, 22:1(n-11): 16.2→11.8% **High MP** DHA: 4.7→7.8%, 18:4(n-3): 3.2→7.1%, EPA: 22.4→19.4%, 20:1(n-9): 18.4→16.4% 22:1(n-11): 16.2→13.8%	p = 0.168, $\omega^2 \approx$ 0.17 **Low MP** ω^2 = 0.03 **High MP** ω^2 = 0.288	**Control**: 0.237; **Low MP**: 0.289; **High MP**: 0.401 p = 0.177, ε^2 = 0.183 **Low MP** r = 0.55; **High MP** r = 0.73

Bold text identifies treatment, treatment-specific values and pairwise treatment comparisons within each experiment. Statistical support is shown by the reported p-values and effect sizes.

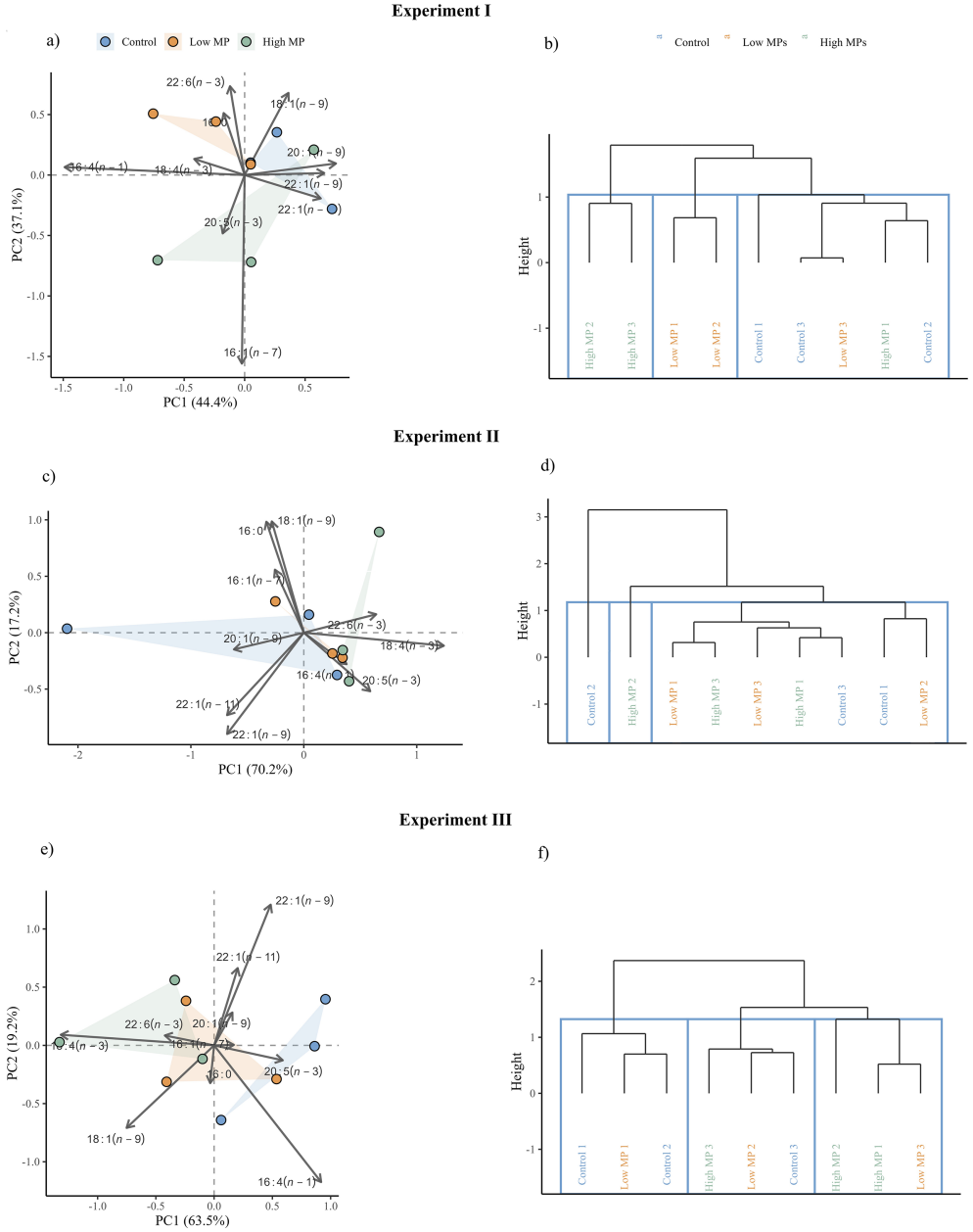

FIGURE 4
Fatty-acid (FA) composition response of *Calanus hyperboreus* to microplastics (MP) exposure across experiments: **(A, C, E)** principal component analysis (PCA) of centered log-ratio (CLR)-transformed FA data; **(B, D, F)** hierarchical clustering of samples based on FA profiles.

lipid metabolism were most evident, with biofouling potentially contributing to this response but requiring direct testing in future fully crossed experiments.

Across the experiments, copepods not exposed to MP showed a gradual seasonal increase in lipid mass (Supplementary Table 1), 16:4(*n*-1) and eicosapentaenoic acid (EPA), fluctuating monounsaturated FAs (MUFAs), and a decline in docosahexaenoic acid (DHA) and 18:4(*n*-3) (Supplementary Table 2) as they approached autumn and diapause, irrespective of food availability. These key patterns observed generally align with previous seasonal studies of Arctic *Calanus*: increasing lipid mass and EPA are consistent with summer lipid accumulation in *C. hyperboreus* described by McMeans et al. (2012), while higher 16:4(*n*-1) and lower 18:4(*n*-3) values are consistent with patterns observed in the autumn season by Falk-Petersen et al. (2009). These trends are also in agreement with long-term seasonal patterns described for another cold-water calanoid, *C. finmarchicus*, where diatom-associated FAs such as 16:4(*n*-1) and EPA typically peak from May to October, while 18:4(*n*-3) declines towards autumn and DHA remains low outside early spring (Hill, 2009). The observed decrease in 16:0 contributions across control individuals though should be interpreted cautiously, because this FA is commonly associated with storage lipid metabolism (Lee et al., 2006; Yamada et al., 2016) and yet its decline across control individuals disagrees with the overall increase in lipid mass (Figure 2A). However, our 16:0 record reflects proportional changes in the broader FA pool as other lipid classes

and long-chain FAs accumulated; it is possible that the absolute concentrations of 16:0 increased with time as others have observed (Yamada et al., 2016) but is masked here by the more pronounced shifts in other lipid components.

4.1 Pristine MP effects across experiments I and II

Responses to pristine MP were modest across Experiments I and II, which are broadly consistent with previous copepod studies reporting limited short-term effects of pristine particles on lipid reserves (Cole et al., 2019; Almeda et al., 2024). Under food-replete conditions, this pattern may reflect partial tolerance to inert particles and the capacity of copepods to reject or rapidly egest non-food items when they co-occur with prey (Xu et al., 2022).

Under starvation, the limited response in total lipid mass is also biologically plausible. *Calanus* spp. are adapted to periods of food limitation through large wax-ester reserves and decreased metabolic demand (Hirche, 1996). Under starvation, its metabolic rates may decline to ~10–20% of normal levels, with individuals relying primarily on internal energy stores (Hirche, 1996). Previous observations also indicate that starvation- related mortality often reflects physiological exhaustion rather than complete lipid depletion, and that lipid reserves remain relatively stable during early starvation (Hatlebakk et al., 2019). Roncalli et al. (2023) showed that unfed *Neocalanus flemingeri* maintained lipid stores during the first week of starvation, with declines occurring only after the second week, highlighting the strong resilience to starvation in calanoids. In our study, lipid mass under pristine MP exposure remained broadly stable relative to controls, consistent with this general resilience reported in literature. However, despite this apparent stability, starvation combined with pristine MP exposure induced subtle shifts in FA composition, characterised by depletion of MUFAs and a slight elevation of EPA and DHA. This response contrasts with typical starvation physiology in *Calanus* spp., where EPA and DHA generally decline as wax-ester reserves are mobilised (Mayor et al., 2015). For instance, Mayor et al. (2015) reported that short-term food deprivation increased free MUFAs (20:1 and 22:1) and decreased PUFAs, a pattern opposite to that observed here. This divergence from established responses suggests that MP ingestion during starvation may alter the usual trajectory of lipid mobilisation, potentially through disruption of digestive processes or stress-induced lipid remodelling. While Mayor et al. (2015) showed that ocean acidification and warming induced only minor effects on lipid metabolism compared to starvation, likely reflecting the adaptive capacity of *Calanus* spp. to environmental variability, our results suggest that MP may represent a more direct and unnatural stressor that can interfere with FA composition.

Although replication was low and ingestion of MP was not measured directly, this divergence from expected starvation physiology is consistent with the idea that MP exposure may modify the usual trajectory of lipid mobilisation under food-limited conditions. These patterns should therefore be interpreted cautiously, but they support the view that even though *Calanus* spp. are relatively resilient to natural abiotic stressors, MP may uniquely disrupt lipid metabolism under food-limited conditions.

4.2 Biofouled MP exposure and seasonal lipid dynamics of *C. hyperboreus*

In the biofouled MP exposure experiment, copepods diverged from the lipid and FA dynamics observed in the corresponding controls. Because the biofouled MP experiment was conducted at the end of August, the observed deviations in lipid dynamics occurred during a period when *C. hyperboreus* CV would be expected to maximise lipid reserves in preparation for diapause. This was also the exposure context in our study that most closely leaned toward conditions plausible *in situ*, as wild-caught copepods were incubated shipboard in Arctic seawater and encountered particles that had been conditioned in the Arctic seawater rather than remaining pristine. Although the present design does not allow biofouling effects to be separated from seasonal physiological state, the data suggest that this late-summer lipid-accumulation window may be a period of greater sensitivity to MP exposure, especially with biofouling factor present.

The reductions in lipid reserves and long-chain MUFAs in Experiment III coincide with weaker accumulation of storage lipids under this exposure context. In *Calanus* spp., these MUFAs are closely linked to wax-ester storage (Albers et al., 1996; Kattner & Hagen, 2009), and lower relative contributions may therefore reflect reduced storage investment or greater mobilisation of existing reserves. In the same experiment, MP-exposed copepods also diverged from the FA trajectory seen in controls, with DHA enrichment, lower EPA at high exposure, and elevated DHA/EPA ratios. Together, these shifts point to a potential shift from the FAs profile expected during late-summer diapause preparation. Although individual variability was high, the direction and consistency of these patterns support the interpretation that lipid allocation may be negatively affected by biofouled MP during a physiologically sensitive and seasonally constrained period.

This difference from the control seasonal pattern was also evident in the balance of long-chain PUFAs. The changes were most pronounced when control copepods accumulated the largest lipid reserves for diapause, suggesting that MP exposure during this period may alter PUFA allocation rather than simply reduce total lipid quantity. DHA is primarily associated with membrane phospholipids, contributing to membrane stability, flexibility, and signalling, and is often retained under stress to preserve membrane integrity and limit oxidative damage (Stillwell and Wassall, 2003; Hishikawa et al., 2017; Bie et al., 2020; Brenna and Diau, 2007). EPA, which is more closely associated with storage lipids and eicosanoid production, has been shown to be strongly conserved in some studies (Sargent and Henderson, 1995; Sargent and Whittle, 1981; Stübing et al., 2003), whereas others have shown that EPA may be more readily mobilised under energetic imbalance or stress (Simopoulos, 1999; Funk, 2001).

Within this context, the FA patterns observed here are consistent with a biologically meaningful shift in PUFA allocation under biofouled MP exposure, with preferential DHA retention alongside EPA depletion pointing to lipid reorganisation rather than simple lipid loss. This response may relate to microbial conditioning and alteration of particles in seawater. During biofouling, MP can become more irregular and develop microbial films that adsorb

organic material (Andrady, 2011; Lobelle and Cunliffe, 2011; Zettler et al., 2013; Oberbeckmann et al., 2015). These films may release chemical cues such as dimethyl sulphide (DMS) that resemble prey signals, potentially reducing sensory discrimination between plastic and food and reinforcing MP ingestion (Savoca et al., 2016). Consequently, behavioural avoidance observed for pristine MP may be weakened, with biofouled particles becoming more difficult to distinguish from natural prey. Sustained ingestion could then lead to dietary dilution and physical interference in the gut, as proposed more broadly for marine MP exposure (Wright et al., 2013). The biochemical patterns observed here are consistent with this interpretation, with declines in long-chain MUFAs, higher DHA/EPA ratios, and lower lipid reserves suggesting a real energetic cost under biofouled MP exposure. The reduction in MUFAs and total lipid reserves may also be compounded by alterations to gut microbiota and digestive function (Hou et al., 2022; Théry et al., 2023). MP exposure has been linked to gut dysbiosis, oxidative stress, and reduced digestive enzyme activity across taxa, including processes involved in lipid and FA assimilation (Hou et al., 2022; Zhang et al., 2023). In copepods, the gut microbiome plays an important role in lipid digestion and transformation, and its disruption could constrain lipid absorption and alter host lipid metabolism (Yoon et al., 2023; Martin et al., 2025). Although these mechanisms were not measured directly in the present study, they provide a possible explanation for why biofouled MP exposure coincided with weaker lipid accumulation and altered FA allocation in late summer.

Some methodological limitations should also be considered when interpreting these patterns. Sample sizes were necessarily small because the experiments were conducted under shipboard conditions, and FA analyses were based on pooled individuals to obtain sufficient material for analysis. Pooling reduced the influence of inter-individual variability, including possible sex-related differences, but it also limited statistical power and prevented assessment of individual- or tube-level variability. Therefore, the treatment responses observed here should be interpreted cautiously, particularly where within-treatment variability was high. Yet, even with these constraints, the recurring alignment between lower lipid mass, reduced storage-associated MUFAs, and altered DHA/EPA ratios under late-summer biofouled MP exposure supports the interpretation that the observed responses are biologically meaningful. These findings highlight the need for targeted follow-up studies that directly compare pristine and biofouled MP exposure across feeding regimes and seasonal stages, and that link lipid disruption to diapause performance in *C. hyperboreus*, as well as to its nutritional quality and carbon export potential.

5 Conclusions and future directions

The study demonstrates that MP exposure can alter lipid accumulation and fatty acid allocation in juvenile *C. hyperboreus*, but that the magnitude and direction of these responses depend strongly on exposure context. Across the three shipboard experiments, the clearest effects emerged in late August under food-replete conditions with biofouled particles, when copepods would normally be maximising lipid storage prior to diapause. In this setting, lower lipid mass, reduced storage-associated MUFAs, and shifts in DHA/EPA ratios point to a disruption of normal late-summer lipid dynamics rather than a simple uniform response to plastic presence alone. This suggests that seasonal physiological state and particle conditioning may interact to amplify MP effects during a particularly sensitive pre-diapause window. Overall, these results show that biochemical indicators such as storage MUFAs and DHA/EPA ratios can reveal subtle but potentially important disruptions to lipid metabolism in a key Arctic copepod. This timing is ecologically important. Late summer is the period when pre-adult *C. hyperboreus* are expected to build the lipid reserves needed for successful diapause, and disruption at this stage could extend beyond short-term biochemical change. If similar responses occur *in situ*, fewer individuals may reach lipid levels associated with successful overwintering, while their value as prey may also decline. As a species with large lipid stores and high long-chain PUFA content, *C. hyperboreus* is a major source of energy and essential fatty acids for Arctic consumers. Reductions in lipid mass and changes in FA composition could therefore lower prey energy density and nutritional quality, with possible consequences for predator growth and reproduction, particularly during PUFA-sensitive life stages. These findings also have biogeochemical relevance. Because *C. hyperboreus* contributes to carbon sequestration through the lipid pump, even modest disruption of late-summer lipid storage could influence lipid-driven carbon export and, potentially, Arctic carbon cycling more broadly.

The present design does not isolate biofouling as a sole causal driver, but it highlights the importance of considering both realistic seasonal context and particle conditioning when assessing MP effects in polar zooplankton. Future work should test these interactions more directly using fully crossed designs comparing pristine and biofouled MP across seasonal states and feeding conditions. Longer-term experiments linking MP exposure to ingestion, digestion, lipid assimilation, diapause performance, and gut microbial dynamics would be especially valuable, as would studies assessing combined effects with other climate change-related stressors such as warming and ocean acidification.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material and are available at the UK Polar Data Centre: https://doi.org/10.5285/0298edcf-93b1-4a6c-9a81-d9c785149b39. Further inquiries can be directed to the corresponding authors.

Ethics statement

The requirement of ethical approval was waived by Non-exclusive licence No. G24-105 for utilisation of Greenland

resources, issued by the Government of Greenland, Ministry of Foreign Affairs, Business and Trade. Studies on zooplankton were approved by the above-mentioned licence as part of the KANG-GLAC expedition. The studies were conducted in accordance with the local legislation and institutional requirements.

Author contributions

AS: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft. EM: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing. ER: Conceptualization, Methodology, Supervision, Writing – review & editing. CM: Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work 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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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2026.1866517/full#supplementary-material

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