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Nematode community dynamics in the Arctic deep sea in response to experimental alterations in organic matter quantity and quality

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ABSTRACT

Successional dynamics of deep-sea nematode communities are shaped by environmental conditions, resource availability, and ecological processes such as species interactions, dispersal, and disturbance. This study investigates the in-situ response of free-living nematodes to artificial organic matter enrichment at the deep-sea floor in the Arctic Ocean. The experiment was conducted at 1265 m depth at the LTER HAUSGARTEN observatory in Fram Strait. We created azoic sediments with a grain size composition similar to natural deep-sea sediments and applied three treatments: (1) azoic sediment (control), (2) azoic sediment treated with fresh *Phaeocystis*, and (3) azoic sediment treated with decaying *Phaeocystis*. The organic content of the artificial sediments was adjusted to match that of natural sediments. The experimental setup was deployed for three months with a bottom lander and compared to natural sediment samples for reference.

Despite similar organic carbon content, artificial sediments exhibited lower nematode abundance and diversity compared to natural sediments, indicating an early successional state dominated by opportunistic taxa. Organic enrichment influenced community composition, with fresh *Phaeocystis* favouring epistrate feeders and decaying *Phaeocystis* supporting later-stage colonisers. Natural sediments, characterized by long-term stability and organic accumulation, supported higher nematode abundance, functional diversity, and a balanced trophic structure. These findings indicate that a mature community requires more time to develop than the three-month duration of the experiment.

Our findings emphasize the role of organic matter retention and long-term sediment accumulation in shaping deep-sea nematode communities and highlight the potential ecological consequences of anthropogenic-driven changes in organic matter deposition, which could affect deep-sea biodiversity and ecosystem resilience.

1. Introduction

Deep-sea ecosystems in polar regions, particularly the Arctic Ocean, are among the most extreme and least explored environments on Earth. These habitats are characterised by low temperatures, high hydrostatic pressure, limited food availability, and perpetual darkness (Thiel et al., 1996). Despite these challenging environmental conditions, Arctic deep-sea sediments harbour diverse benthic communities, with free-living nematodes being among the most abundant and ecologically significant meiobenthic metazoans (Jensen, 1988; Schratzberger et al., 2019; Tietjen, 1992). Nematodes play crucial roles in sediment bioturbation, nutrient cycling, and organic matter decomposition, making them integral to deep-sea ecosystem functioning (Górska et al., 2014; Soltwedel et al., 2020; Vanaverbeke et al., 1997; Schratzberger and Ingels, 2018; Pape et al., 2013a).

Organic matter availability in the Arctic deep sea is primarily driven by seasonal phytoplankton blooms, which influence the deposition of organic material from surface waters to the seafloor (Sakshaug 2004; Bourgeois et al., 2017). The seasonal availability of organic matter from surface waters has a direct impact on benthic life (Grebmeier et al., 2015; Cautain et al., 2024).

While Arctic sea ice continues to decline due to climate change, resulting shifts in primary productivity and organic matter export may alter the structure and functioning of these deep-sea ecosystems

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(Wassmann, 2015; Negrete-García et al., 2024). Observational studies report increasing net primary production (NPP) across the Arctic over recent decades, with gains of up to 57% between 1998 and 2018 (Lewis et al., 2020) and a 19% increase from 2003 to 2024, particularly in the Eurasian Arctic and Barents Sea (Frey et al., 2024). While these trends suggest enhanced export of organic material to the seafloor, future trajectories remain uncertain due to regional variability and potential nutrient limitation (IPCC et al., 2022).

Changes in the amount and quality of organic matter reaching the seafloor can influence benthic patterns and processes, affecting community dynamics, structural diversity, population densities, and biomasses from micro-to megafauna (Doney et al., 2012; Grebmeier et al., 2006; Schnier et al., 2025c). In this context, meiofaunal organisms such as free-living nematodes offer a useful model for assessing ecological responses to such variations in food supply, due to their abundance, diversity, and functional importance in benthic systems. Understanding nematode responses to differences in organic matter availability and lability is therefore essential for evaluating the resilience of Arctic deep-sea ecosystems to environmental change.

Nematode community responses to food availability manifest in species composition, diversity patterns, and functional traits. Studies have shown that nematode biomass and diversity correlate with organic matter availability, such as settled phytodetritus (McClain and Barry, 2010; McClain and Rex, 2015). While nematode densities generally decline with increasing water depth due to reduced food supply (Mokievskii et al., 2007), taxonomic diversity exhibits a unimodal pattern, peaking in the lower bathyal zone (2500–3500 m) (Górska et al., 2014; Schnier et al., 2023). Food availability also influences trophic interactions, feeding types, and life-history traits (Dos Santos et al., 2008, 2020; Grzelak et al., 2020).

Although our experiment was not designed to simulate climate change directly, it reflects potential shifts in organic matter flux and composition that may occur under future Arctic conditions, such as increased dominance of *Phaeocystis* blooms, changes in phytoplankton size classes, or faster sinking rates. Such changes could modify the quality and freshness of organic matter delivered to the deep sea, which is particularly relevant for benthic nematodes. Investigating these responses allows us to explore how community structure, diversity, and functional traits may respond to variations in organic matter lability.

To address these questions, this study examines the ecological response of free-living nematodes to artificial organic matter enrichment in the Arctic Ocean. An in-situ experiment was conducted at 1200 m depth at the LTER observatory HAUSGARTEN in the Fram Strait. Artificial sediments were enriched with fresh and decayed *Phaeocystis*, simulating variations in organic matter quality (Orkney et al., 2020; Assmy et al., 2017; Sugie et al., 2020), while natural sediments provided a reference for established communities containing organic material from multiple phytoplankton sources. By analysing key aspects of nematode communities, species composition, diversity, functional traits, and trophic interactions, we aim to assess how differences in organic matter quality influence benthic communities, thereby providing insights into the resilience of Arctic deep-sea ecosystems to alterations in carbon flux and composition.

2. Material & methods

2.1. Study site and experimental deployment

The experiment was conducted at the deep-sea long-term observatory HAUSGARTEN, located in the Fram Strait between 78°N and 80°N and 05°W-11°E off the Svalbard archipelago and Greenland (Soltwedel et al., 2005). During the Polarstern expedition PS85 in June 2014 (Schewe, 2015), the bottom lander based long-term biological experiment was deployed at 1265 m depth near HAUSGARTEN station HG-I

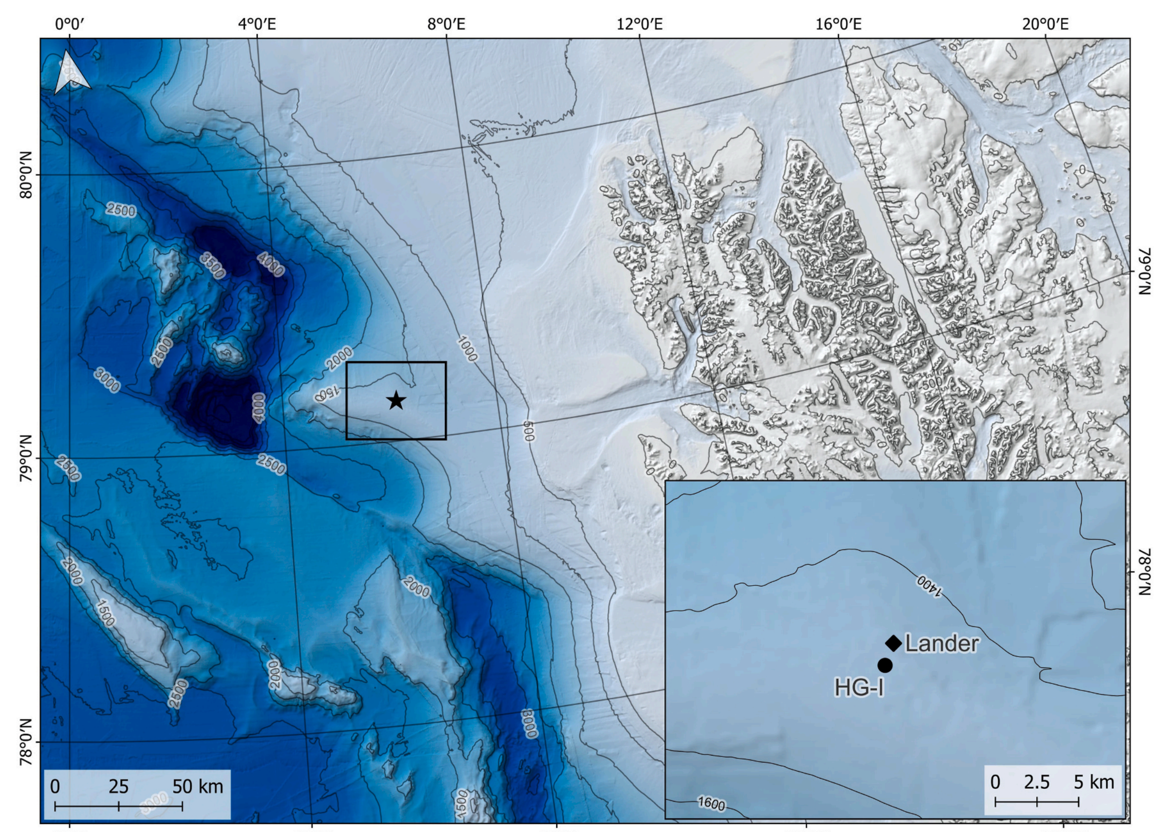

Fig. 1. Map of the general location and the position of the experimental lander and MUC deployment at station HG-I (approx. 1200 m depth) of LTER HAUSGARTEN observatory (© Böhringer, 2025).

(79° 8,69′N 6° 8,23′E) (Fig. 1). The lander carried colonisation cores filled with azoic, organically enriched artificial sediments to investigate the response of meiofauna organisms, in particular nematode communities to azoic, organically enriched artificial sediments intended to mimic freshly deposited but biologically uncolonized material. After three months, the lander was recovered by the Norwegian Coast Guard icebreaker KV Svalbard in August 2014.

In addition, sediment samples were collected during expedition PS85 with a multiple corer (MUC) at the HAUSGARTEN station HG-I (79° 8.01′N 6° 6.39E, 1244 m depth) as a reference for the study of natural nematode communities. The reference and experimental sites are approximately 1.48 km apart, both located at similar water depths (~1250 m) on the Arctic continental slope. Given the close proximity and shared oceanographic and ecological conditions, we consider the reference station to be representative of the natural nematode community at the experimental site (Table S1).

2.1.1. *Experimental setup*

A free-fall lander served as the platform for the experimental setup (Fig. 2). This type of device is designed for use at depths of up to 6000 m and can carry different payloads.

For this experiment, twelve penetrating units were mounted on a carrier plate in the lower section of the lander (Fig. 3). Each unit consisted of a plastic tube with an outer diameter of 50 mm and an average inner diameter of 43.5 mm. To allow water exchange and colonisation by meiofauna, the cylinders were open at the top and perforated along the sides, with the openings covered with titanium mesh (500 μm mesh size). To facilitate penetration into the seabed, each tube was equipped with a removable, acute-angled tip, secured using a bayonet catch. This design allowed for easy removal and reattachment, simplifying the filling and sampling process.

Before deployment, the tubes were filled with artificial sediment designed to replicate the grain size distribution of natural HAUSGARTEN sediments (Table 1). The artificial sediment was prepared from commercially available, natural clay-based materials. The fine fraction (<63 μm) was derived from *Rapido Universallehmputz*, and the coarse fraction (>63 μm) from *Claytec Lehmputz Mineral 16*, both of which are free of organic additives. To ensure consistency and remove any remaining organic residues, the sediment fractions were calcined at 500 °C for 20 h in a muffle furnace before mixing.

The composition of the artificial sediment was based on the sediment-to-water ratio and organic carbon (C-org) content of natural samples. The required sediment volume was calculated to match the capacity of the experimental cylinders. For each experimental unit, 140 g of sediment was mixed with 60 ml of water, resulting in a total sample mass of 200 g per cylinder. Sediment-to-water ratio:

- Sediment content: 70% of total mass (140 g)

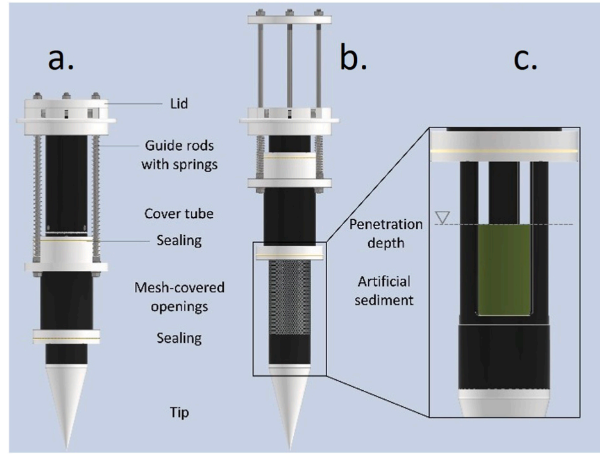

Fig. 3. Schematic illustration of the penetrating units. **[a.]** Closed state for the passage through the water column during the descent and ascent phase. **[b.]** Open state during the residence time in the seabed. **[c.]** Open state without showing the mesh cover to visualise the filling height and penetration depth.

Table 1
Grain size distribution in natural and artificial sediment. **(a)** Average percentage grain size composition in natural sediments (0 - 5 cm) from HAUSGARTEN observatory. **(b)** Mass of grain size fractions in natural sediments, adjusted to match experimental sample volume of artificial sediment (30% water content). **(c)** Mass composition of custom-mixed artificial sediment by fraction. **(d)** Percentage distribution of grain sizes in the artificial sediment.

Size fraction [μm]	(a) [%]	(b) [g]	(c) [g]	(d) [%]
>2000	2.4	3.3	0.0	0.0
1000 - 2000	1.0	1.3	2.0	1.4
500 - 1000	1.0	1.4	2.0	1.4
250 - 500	1.8	2.4	4.0	2.9
125 - 250	5.9	8.2	8.5	6.1
63 - 125	11.0	15.3	15.5	11.2
32 - 63	13.6	19.0	19.0	13.7
<32	63.3	88.2	88.0	63.3
Sum	**100.0**	**139.2**	**139.0**	**100.0**

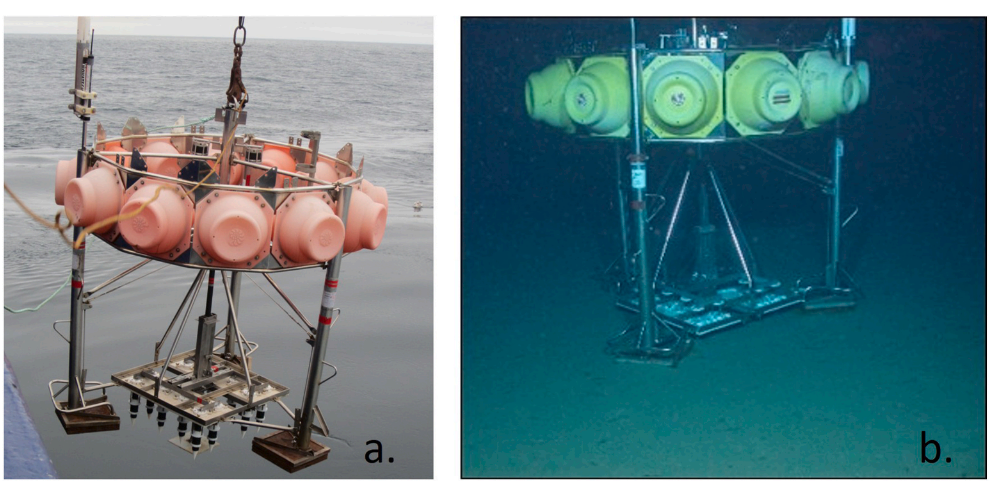

Fig. 2. Free-falling experimental lander equipped with penetration units. On its way into the water and **[a.]** on the seafloor **[b.]**. Image **b.** was taken during an earlier first deployment in 2007 by the ROV 'Quest 4000'. © MARUM.

- Water content: 30% of total mass (60 g)

Within the 60 ml of water, 5 ml of *Phaeocystis* suspension (either fresh or decayed) was included, with a C-org concentration of 200 mg/ml. This contributed 1 g of C-org per cylinder. The final mass composition per cylinder was calculated as follows:

- Mass contribution from seawater (55 ml): ~55 g
- Mass contribution from *Phaeocystis* suspension (5 ml, 200 mg/ml C-org): 5 g, with 1 g of C-org

For control cylinders, 60 ml of 0.2 µm-filtered seawater without *Phaeocystis* was used, ensuring no additional organic carbon input (Table 2).

Phaeocystis starter cultures were maintained at 3 °C and cultivated in 100% F/2 medium (Guillard, 1975; Guillard and Ryther, 1962), obtained from the Provasoli-Guillard National Center for Marine Algae and Microbiota (NCMA, https://ncma.bigelow.org/). Cultures were grown in 50 ml Corning flasks. The C-org content of the culture was determined using a EuroVector CHNS-O Elemental Analyzer. To achieve the target concentration, the culture was concentrated by centrifugation, resulting in a final C-org concentration of 200 mg/ml. This concentration translates to an addition of approximately 1 g C-org per cylinder, corresponding to the natural sediment organic carbon content of about 0.7% at the study site.

A total of twelve cylinders were prepared and divided into three experimental groups (Fig. 4):

- Enriched sediment treatments (8 cylinders)
    - 4 cylinders received fresh *Phaeocystis* suspension (FP)
    - 4 cylinders received decayed *Phaeocystis* suspension (DP)
- Control treatments (4 cylinders)
    - 4 cylinders with no organic enrichment (control)

The prepared sediment mixtures were poured into the cylinders and frozen at −20 °C to maintain structural integrity. After thawing, the sediment reached a height of 70 mm within the cylinders. The frozen cylinders were then attached to the lander shortly before deployment. For the arrangement of control and enriched (fresh and decayed *Phaeocystis*) sediments, refer to Fig. 4.

Table 2
Theoretical composition and properties of artificial sediment (weight, volume, and organic carbon content).

Parameter	Value	Unit
General Composition		
Water Content	30	wt%
Sediment Content	70	wt%
Density of Water	1.0	g/cm^3
Density of Sediment	2.2	g/cm^3
Sample Properties		
Sample Diameter	4.35	cm
Sample Height (Thawed)	7.00	cm
Sample Volume (Thawed)	122.93	cm^3
Sample Height (Frozen)	8.27	cm
Weight and Volume Distribution		
Component	Weight (g)	Volume (cm^3)
Water	59.66	59.66
Sediment	139.20	63.27
Total	198.86	122.93
Organic Carbon Content		
Target C-org	0.7	wt%
C-org (absolute)	0.97	g

To prevent the artificial sediment from being washed out during the descent and ascent phase of the lander through the water column, the openings were covered by a protective tube. The upper open end of the sample tube was also closed by a lid, and spring force kept the protective tube and lid closed during descend. Once the lander reached the seabed, the openings were cleared by a mechanism (not shown) to allow the tubes to penetrate the sediment. The penetration depth depended on the properties of the surrounding sediment. Through preliminary tests and the evaluation of underwater images from previous deployments, the set-up was adjusted so that the sample tubes penetrated to approximately half of the openings. This corresponded approximately to the filling level of artificial sediment.

At the beginning of the ascent process, the mechanical system first pulled the sample tubes out of the seabed and closed them. The lander then rose to the sea surface. After recovery, the penetrating units were removed on deck and prepared for sampling. To do this, the lower sections of the sample tubes were separated and the tips were removed. The artificial sediment to be sampled was pressed to the edge of the sample tube using a piston of appropriate diameter. Sediment subsamples were obtained using syringes.

2.2. Sample collection for nematode analysis

Subsamples for nematode analysis were collected using 2.2 cm diameter cut-off syringes. The top 3 cm of sediment from each core were subsampled, as this interval encompasses the ecologically most relevant fraction of deep-sea nematode communities, with most individuals concentrated in the upper 1–3 cm (e.g. Leduc et al., 2012; Górska et al., 2014; Schnier et al., 2023). Due to the shorter, conically tapered design of the experimental cores compared to multicorer samples, subsampling was limited to 3 cm to ensure consistent recovery across replicates. Each subsample was sectioned into 1 cm layers and fixed in 4% borax-buffered formalin prepared with filtered seawater.

2.2.1. Nematode preparation, determination and investigation

Nematode samples were rinsed with freshwater through a 32 µm sieve to remove excess formalin. Nematodes, along with other meiofauna taxa, were separated from sediment by density gradient centrifugation using LUDOX® TM-50 colloidal silica (specific gravity 1.18 g/cm^3, Sigma-Aldrich 420778), following Heip et al. (1985). Samples were centrifuged at 75×*g* (900 RPM) using a Thermo Scientific Heraeus Megafuge 16R with an F15-6 × 100 fixed-angle rotor. Centrifugation was performed for 15 min, with each sample processed twice to ensure thorough separation of the metazoan meiofauna organisms from the sediment. After each centrifugation, the supernatant was rinsed through a 32 µm sieve with freshwater to remove LUDOX®, and the retained meiofauna were transferred to a Petri dish with freshwater and Rose Bengal stain for easier visualization. Nematodes were sorted under an OLYMPUS SZX16 stereomicroscope and subsequently transferred to anhydrous glycerine for preservation. Following glycerine infiltration, all specimens were hand-picked and mounted on permanent slides for further morphological examination (Pfannkuche and Thiel, 1988).

Each nematode specimen was identified to genus level and measured for both length (excluding the filiform tail) and width (at the widest body region) using high-resolution light microscopy in order to calculate their biomass (see below for equipment and software details). Life stage (juvenile or adult) was identified for each specimen, with juveniles typically differing from adults in size and body proportions.

Classification into feeding types followed Wieser's (1953) scheme, which divides nematodes into four feeding types based on their buccal morphology and presumed feeding behaviour: 1. Selective deposit feeders (1A) – Nematodes with small, unarmed buccal cavities, primarily feeding on bacteria and organic detritus. 2. Non-selective deposit feeders (1B) – Nematodes with larger, unarmed buccal cavities, capable of ingesting a wider range of organic particles, including bacteria and detritus. 3. Epistrate feeders (2A) – Nematodes with small, armed buccal

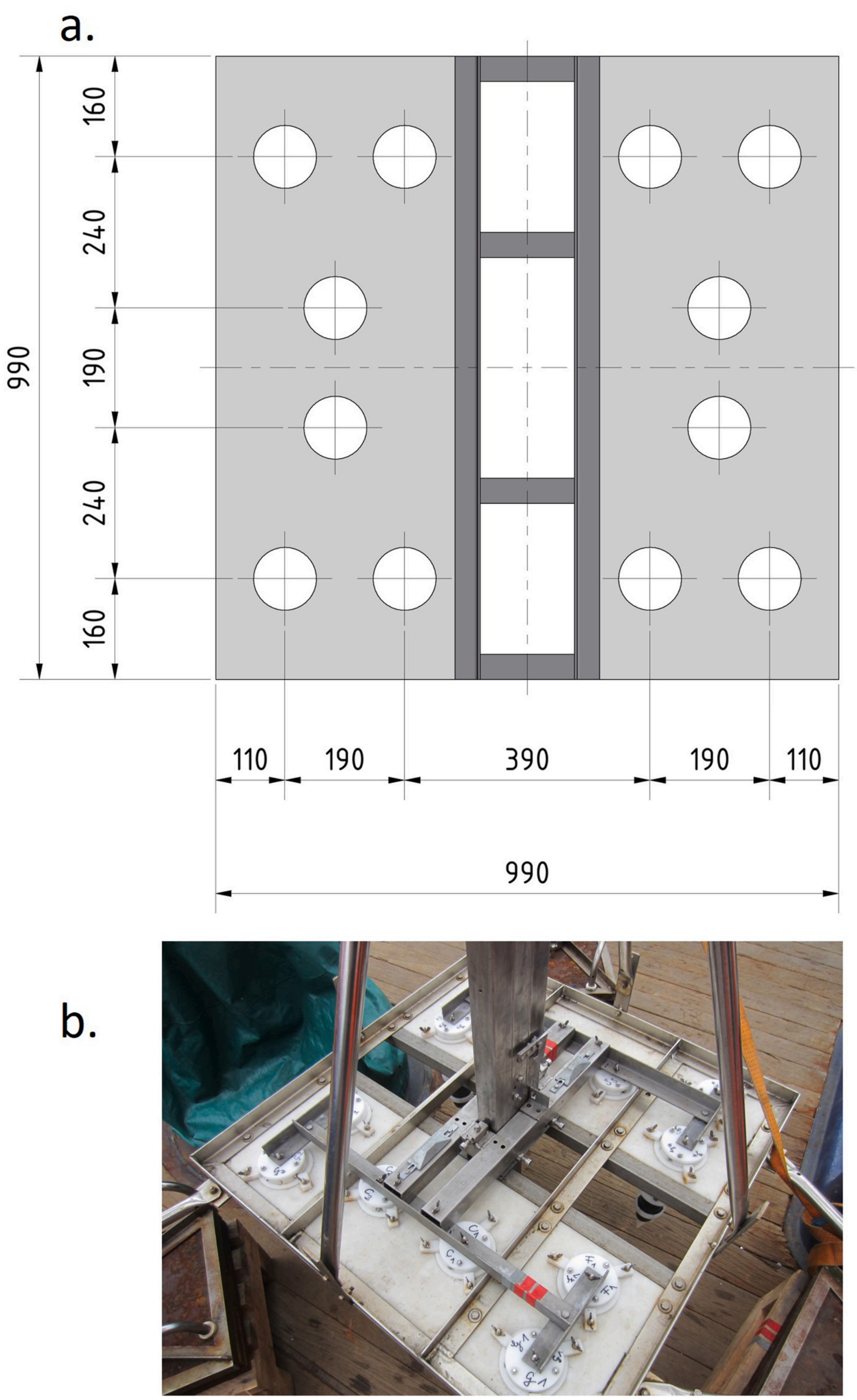

Fig. 4. Arrangement and positioning of the twelve penetration units on the mounting plate of the free-falling lander, with distances provided in millimeters **[a.]**. The units are organized into four groups, each containing three units: one control unit (labelled with C: filled with unenriched sediment), one FP unit (labelled with F: filled with sediment enriched with fresh *Phaeocystis*), and one DP unit (labelled with G: filled with sediment enriched with decayed *Phaeocystis*) **[b.]**.

cavities, grazing on diatoms, fungi, and other biofilm-associated microorganisms. 4. Predators/omnivores (2B) – Nematodes with large, strongly armed buccal cavities, preying on other small invertebrates or consuming a variety of food sources. Trophic diversity was calculated using the Index of Trophic Diversity (ITD) as described by Heip et al. (1985), using the formula ITD $= \sum \theta_i^2$, where θ_i is the relative proportion of individuals belonging to feeding type *i*. Lower ITD values indicate higher trophic diversity.

To classify nematode life strategies, Bongers (1990) and Bongers et al. (1995) developed the coloniser-persister scale (cp-scale). This scale assigns nematodes to categories ranging from cp-1 (highly opportunistic colonisers) to cp-5 (highly specialized persisters):

- cp-1: Includes fast-growing, highly resilient genera (e.g., bacterial feeders in disturbed environments).

- cp-2 to cp-3: Represents intermediate life strategies with varying degrees of adaptability.
- cp-4 to cp-5: Comprises slow-growing genera adapted to stable, undisturbed conditions.

Identification and measurements were carried out using an OLYMPUS BX53 light microscope, equipped with an OLYMPUS DP28 digital camera, and processed with OLYMPUS cellSens Entry v3.2 software for high-precision imaging. Genera were identified based on morphological keys provided by Platt and Warwick (1983, 1988), Warwick et al. (1998), and Schmidt-Rhaesa (2014).

2.3. Data analysis

Nematode biomass was measured as the De Man ratio *a* (body length: width) for each individual nematode (Platt and Warwick, 1983). Total wet weight of nematodes was calculated using the formula of Andrássy (1956): $wt = L*W^2/1,600,000$; where L is the nematode body length in μm (excluding filiform tails) and W is the maximum body width in μm. Wet weight was converted to dry weight (dwt μg/10 cm^2), assuming a dry to wet weight ratio of 0.25 (Wieser, 1960). To reveal the distribution of biomass across differently sized nematodes, we log_2-transformed the nematode dry weight and rounded to the nearest decimal. This resulted in log_2-size classes, which were plotted against the nematode dry weight in μg per log_2-size class in scatterplots (Schwinghamer, 1981, 1983). Using the available morphometric data and histogram analysis of the nematode length/width (L/W) ratio, nematodes were categorised into different morphotypes based on their length and width. For length, individuals were classified as 'short' if their measurements were below the first quartile (<Q1), 'medium' if they were between the first and third quartiles (Q1-Q3), and 'long' if they exceeded the third quartile (>Q3). Similarly, nematodes were categorised by width as 'slender' (<Q1), 'medium' (Q1-Q3) and 'thick' (>Q3) (Grzelak et al., 2020). The relative abundance of each morphotype and selected subgroups in the artificial and natural sediments were compared using a chi-square ($\chi 2$) test for independence.

Nematode community composition in artificial (control, FP, DP) and natural (MUC) sediments was analysed using non-metric multi-dimensional scaling (nMDS), ANOSIM (Analysis of Similarity), and SIMPER (Similarity Percentage) based on a Bray-Curtis similarity matrix. Prior to analysis, data were square-root transformed to account for the high number of singletons, and a dummy variable was added for samples with no recorded nematodes.

ANOSIM was applied to assess the influence of sediment depth and artificial (control, FP, DP) and natural (MUC) sediment on nematode community composition, while SIMPER analysis determined the percentage of similarity and dissimilarity of the community within and between artificial (control, FP, DP) and natural (MUC) sediment. Additionally, BIOENV (Biota-Environment Matching) analysis identified correlations between nematode community structure and functional traits (feeding types and cp-classes), with significant relationships visualized using vector overlays.

Differences in descriptors of nematode assemblages, including mean individual biomass, length, and width, were evaluated using analysis of variance (ANOVA). To identify specific differences between nematode communities from the different artificial sediments (control, FP, DP) and those from natural sediments (MUC), a post hoc test (two-sample *t*-test) was applied. The resulting p-values were Bonferroni-corrected to account for multiple comparisons. To quantify the magnitude of treatment effects independently of sample size, Cohen's f (Cohen, 1988) is calculated as effect size measure for ANOVA, derived from Eta-Squared (η^2). Cohen's d (Cohen, 1988) measures the standardised mean difference between two groups and was calculated for effect size for pairwise comparisons (*t*-test). Effect sizes complement statistical significance by providing insight into the biological relevance of observed differences. Interpretation of effect sizes followed the thresholds proposed by Cohen (1988) for d: 0.2 = small, 0.5 = medium, 0.8 = large; for f: 0.1 = small, 0.25 = medium, 0.4 = large. Given the subtle but ecologically meaningful responses typical of deep-sea ecosystems, effect sizes offer valuable context for understanding the biological importance of our findings (Ramirez-Llodra et al., 2010).

Additionally, diversity metrics were calculated to characterise the nematode community structure. These included Pielou's evenness (J′) (Pielou, 1966), ShannonWiener diversity (H′) based on log_2 (Shannon, 1948; Shannon and Weaver, 1963), total genera number (G), and rarefied genus richness ($EG_{(50)}$) (Hurlbert, 1971).

The length/width relationship plots were constructed using R (version 4.4.1; R Core Team, 2024) and the RStudio environment (Posit team, 2024), with the following R packages: tidyverse (Wickham et al., 2019), ggplot2 (Wickham, 2016), ggpmisc (Aphalo, 2022), ggpubr (Kassambara, 2023), ggtext (Wilke and Wiernik, 2022), forcats (Wickham, 2023), svglite (Wickham et al., 2023), gridextra (Auguie, 2017), paletteer (Hvitfeldt, 2021). All other statistical analyses were performed using the PRIMER-E software (version 7.0.24) with the PERMANOVA + add-on (Anderson et al., 2008; Clarke and Gorley, 2015) and Microsoft Excel (Office Professional Plus, 2019).

3. Results

3.1. Nematode community structure

A total of 2071 nematode specimens were identified, representing 71 genera. In the natural sediments from the MUC, an average of 1177 individuals per 10 cm^2 were distributed among 54 genera. The artificial control sediments (control) from the experiment contained an average of 207 individuals per 10 cm^2 across 27 genera. Artificial sediments enriched with fresh *Phaeocystis* (FP) contained an average of 357 individuals per 10 cm^2 across 31 genera, while sediments enriched with decayed *Phaeocystis* (DP) contained an average of 193 individuals per 10 cm^2 across 30 genera.

Interestingly, 28% of the genera found in the natural sediments (MUC) were also present in the artificial sediments of the experiment after three months. Furthermore, 18 genera identified in the artificial sediments were absent from the natural sediments. These 18 genera represent 25% of all genera identified across both the natural and artificial sediments.

The MUC sediments were dominated (≥5%) by seven genera, while five genera dominated the unenriched control sediments. Six genera dominated the FP sediments, and seven genera dominated DP sediments (Table 3). Among these, *Monhystrella* was the only genus consistently dominant across all sediment types (artificial and natural).

The six additional dominant genera in the MUC sediments were exclusive to this site and not dominant in the artificial sediments. Conversely, eight genera were dominant only in the artificial sediments: three (*Leptolaimus, Mologolaimus, Sabatieria*) were dominant in the natural sediment (control, FF, DP) across all three experimental treatments; one (*Trefusia*) was dominant solely in the control sediments; one (*Amphimonhystrella*) was dominant only in the enriched sediments (FP and DP); one (*Microlaimus*) was dominant in FP sediments; and two (*Campylaimus, Daptonema*) were dominant in DP sediments (Table 3).

In artificial sediments, the majority of nematode individuals were concentrated in the uppermost sediment layer (0 – 1 cm), ranging from 58% to 80% of the total population (control: 80%, FP: 78%, DP: 58%). The second sediment layer (1 – 2 cm) contained between 13% and 29% of the nematodes (control: 13%, FP: 17%, DP: 29%), while the lowest proportion was found in the deepest sediment layer (2 – 3 cm; control: 7%, FP: 5%, DP: 13%). In contrast, nematodes in natural sediment (MUC) were more evenly distributed across the sediment depth, with approximately equal proportions in each layer (0 - 1 cm: 31%, 1 - 2 cm: 35%, 2 - 3 cm: 33%).

Regarding vertical community composition, *Monhystrella* was the dominant genus in the uppermost sediment layer of the control (56%)

Table 3
Dominant genera (≥5%) of the nematode communities within the artificial sediments (control, FP, DP) and the natural sediment (MUC). Data are based on sediment samples from the 0–3 cm depth range.

control (≥5%)		FP (≥5%)		DP (≥5%)		MUC (≥5%)	
Monhystrella	48.5%	*Leptolaimus*	28.6%	*Monhystrella*	22.6%	*Amphimonhystera*	11.5%
Molgolaimus	8.1%	*Monhystrella*	12.9%	*Sabatieria*	12.3%	*Desmoscolex*	9.8%
Sabatieria	8.1%	*Sabatieria*	9.6%	*Amphimonhystrella*	9.9%	*Acantholaimus*	9.7%
Trefusia	7.7%	*Microlaimus*	8.5%	*Daptonema*	9.1%	*Tricoma*	8.7%
Leptolaimus	5.0%	*Amphimonhystrella*	7.6%	*Leptolaimus*	7.4%	*Aegialoalaimus*	7.7%
		Molgolaimus	5.4%	*Molgolaimus*	7.4%	*Halalaimus*	6.7%
				Campylaimus	5.3%	*Monhystrella*	6.5%

and DP sediments (31%). However, in FP sediments, *Leptolaimus* dominated this layer (32%). In all three artificial sediment treatments, the deeper layers (1 - 2 cm and 2 - 3 cm) were predominantly inhabited by *Sabatieria* (control = 1 - 2 cm: 29%, 2 - 3 cm: 26%; FP = 1 - 2 cm: 24%, 2 - 3 cm: 59%; DP = 1 - 2 cm: 22%, 2 - 3 cm: 47%).

In contrast, the nematode community in natural sediment exhibited a different pattern. Here, *Desmoscolex* was the dominant genus in the uppermost sediment layer (16%), while *Amphimonhystera* dominated the two deeper layers (1-2 cm: 16%, 2-3 cm: 13%).

These findings highlighted distinct differences in the vertical distribution and community composition of nematodes between artificial and natural sediments, with a stronger stratification observed in artificial environments compared to the more even distribution found in natural conditions.

The diversity indices indicate the lowest values for J' (evenness), $EG_{(50)}$ (genus richness), and $H'_{(log2)}$ (Shannon-Wiener diversity) in the nematode community from the artificial control sediments (J' = 0.624 ± 0.08, $EG_{(50)}$ = 13 ± 1.48, $H'_{(log2)}$ = 2.968 ± 0.43). The enriched artificial sediments support a more diverse nematode community, with the highest evenness (J' = 0.786 ± 0.03) observed in the community from the artificial DP sediments. However, the diversity patterns of nematode communities in FP and DP sediments show little variation. Whereas, the nematode community from the natural sediment (MUC) exhibited the highest values for $EG_{(50)}$ and $H'_{(log2)}$ ($EG_{(50)}$ = 20 ± 0.44, $H'_{(log2)}$ = 4.464 ± 0.05) (Table 4).

The nMDS plot (Fig. 5) shows that the nematode community from the natural sediment (MUC) is distinctly different from those in the artificial sediments, regardless of treatment (ANOSIM: R = 0.436, p = 0.01%). All MUC samples cluster together and are clearly separated from the experimental approach.

In the artificial sediments, community composition is primarily influenced by sediment depth rather than enrichment treatment. Notably, samples from the uppermost layer (0 – 1 cm) cluster together across all treatments and differ significantly from those in the deeper layers (ANOSIM: 0 – 1 cm vs. 1 – 2 cm, R = 0.401, p = 0.01%; 0 – 1 cm vs. 2 – 3 cm, R = 0.834, p = 0.01%).

Despite this depth effect, nematode communities were still found to differ between artificial control and enriched sediments. The SIMPER analysis indicates that the nematode community from the control sediments has an average internal similarity of 19.01%, whereas the enriched sediments exhibit a higher internal similarity of 30.49%. Additionally, the average dissimilarity between the communities from the control and enriched sediments is 75.49%, highlighting the impact of enrichment on community composition.

Table 4
Diversity of the nematode communities within the artificial sediments (control, FP, DP) and the natural sediment (MUC). Calculated for different diversity indices: G = number of genera, N = number of individuals, J' = Pielou's evenness, $EG_{(50)}$ = rarefaction, $H'_{(log2)}$ = Shannon-Wiener diversity. Data are based on sediment samples from the 0–3 cm depth range.

	G	N	J'	$EG_{(50)}$	$H'_{(log2)}$
control	27	260	0.624	13	2.968
FP	31	448	0.727	15	3.601
DP	30	243	0.786	16	3.858
MUC	54	1120	0.772	20	4.464

The SIMPER analysis also reveals that in the artificial sediments, the nematode genus *Sabatieria* is the primary contributor to the within-group similarity of the enriched sediment communities, accounting for 31% in both the FP and DP sediments. In contrast, *Monhystrella* is the dominant contributor (29%) to the within-group similarity in the community from control sediments.

In the community from natural sediments, no single genus dominates; instead, three genera – *Acantholaimus* (9%), *Desmoscolex* (9%), and *Amphimonhystera* (9%) – together contribute to a 30% within-group similarity of the nematode community.

Regarding dissimilarities, *Desmoscolex*, *Amphimonhystera*, and *Acantholaimus* contributed most to the differences identified by the SIMPER analysis between nematode communities from natural and artificial sediments. When comparing the natural sediment (MUC) to the artificial control sediments, *Amphimonhystera* and *Acantholaimus* each contribute 7% to the dissimilarity. When comparing the MUC community to the artificial enriched sediments, *Desmoscolex* and *Acantholaimus* contribute approximately 7% each in both the FP and DP sediments. These genera are dominant only in MUC (>5% relative abundance) and rare in all artificial sediments (<5%).

Within the artificial sediments, the key contributors to dissimilarity between the control and enriched sediments are *Monhystrella* (~13%) and *Sabatieria* (~12%) (with *Monhystrella* dominant in control at 50% and in enriched sediments at 16%, and *Sabatieria* at 8% in control and 11% in enriched sediments). In contrast, the differences between the enriched FP *vs* DP sediments are mainly due to *Leptolaimus* and *Monhystrella*. According to SIMPER, *Leptolaimus* contributed 11% to the dissimilarity (relative abundance: 29% in FP, 7% in DP), and *Monhystrella* contributed 10% (relative abundance: 13% in FP, 23% in DP).

3.2. Morphometric patterns of nematode communities in natural and artificial sediments

3.2.1. Nematode body length/width relationship

The nematode assemblages exhibited considerable variation in body length and width between artificial and natural sediments, with the lowest mean values for both traits observed in the artificial control sediment (Width: 15.3 ± 9.3 μm, Length: 467.7 ± 388.5 μm) and the natural MUC sediment (Width: 17.9 ± 12.2 μm, Length: 370.7 ± 269.8 μm). In contrast, the highest mean values were found in nematode communities from the artificial FP sediment (Width: 20.1 ± 10.3 μm, Length: 522.8 ± 367.6 μm) and the artificial DP sediment (Width: 21.9 ± 15.4 μm, Length: 615.6 ± 455.3 μm) (Fig. 6). ANOVA revealed a moderate effect of sediment type on body length (f = 0.28) and a small effect on body width (f = 0.15), both of which were highly significant (p ≤ 0.001) (Table 5). This suggests that sediment composition plays a significant role in shaping these traits, with a stronger influence on body length. Given the low p-values, these differences are unlikely to be random.

Bonferroni-corrected pairwise comparisons revealed significant differences in both body width and length between artificial and natural sediments, as well as among the different artificial sediment treatments,

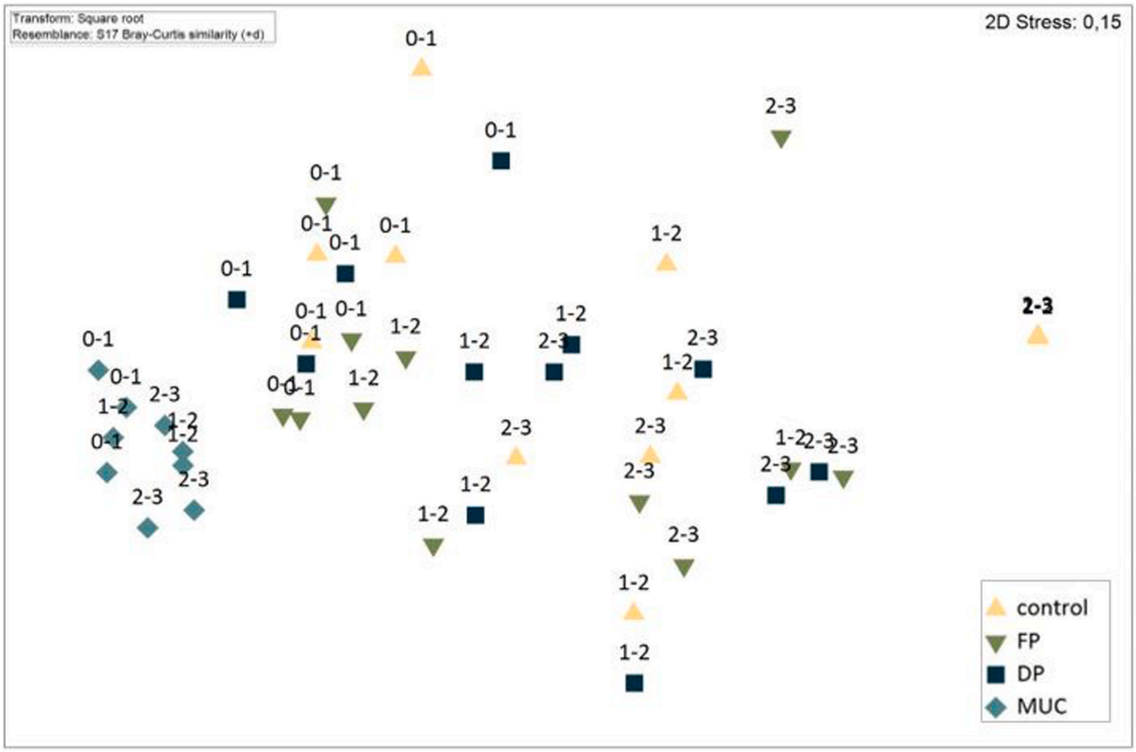

Fig. 5. Non-metric multidimensional scale (nMDS) plot based on Bray-Curtis similarities of square-root transformed nematode abundance data from the top 3 cm (0–1, 1–2, 2–3) within artificial sediments (Control, FP, DP) and natural sediments (MUC).

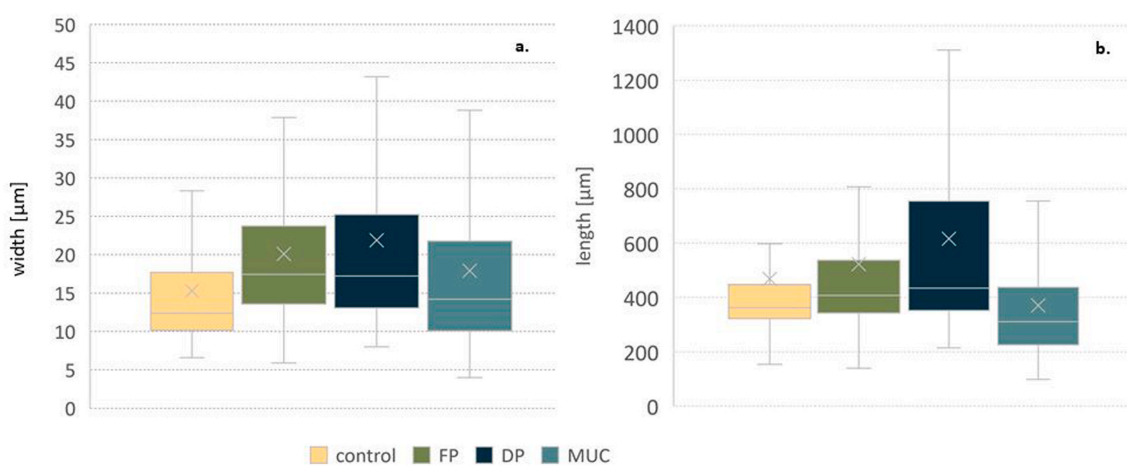

Fig. 6. Box-and-Whisker-Plots for nematode body width **[a.]** and length **[b.]** in the artificial sediments (control, FP, DP) and natural sediment (MUC). Box-and-Whisker-Plots (without outliers) showing the minimum, first quartile (Q1), median (Q2) and third quartile.

with two exceptions: no significant difference in body width between artificial FP and DP sediments and no significant difference in body length between control and FP sediments (Table 5).

Effect size analysis showed moderate to large effects in body width for control *vs*. FP sediments (d = 0.49) and control *vs*. DP sediment (d = 0.51), and in body length for FP *vs.* MUC sediments (d = 0.53) and DP *vs.* MUC sediments (d = 0.82).

Although statistical differences are generally observed, ecological significance is most pronounced for body width within artificial sediments (control *vs* FP and DP sediments) and for body length between artificial and natural sediments (FP and DP *vs* MUC sediments). In all other comparisons, despite showing (highly) statistical significance, the effect sizes remained small, suggesting limited ecological relevance.

In general, two distinct morphological groups of nematodes can be distinguished: Group I— characterized by a body length generally shorter than 280 µm, a width greater than 22 µm, and an L/W ratio <13, and Group II— comprising significantly longer and more slender nematodes with an L/W ratio >13.

The contribution of Group I nematodes (L/W < 13) to the nematode communities differed significantly between natural and artificial sediments. In natural sediments, they accounted for approximately 12% of the community, while they were almost absent in artificial sediments, ranging between 0 and 2% (Fig. 7, Table 6). More than 90% of these nematodes belonged to the Desmoscolecidae family.

In Group II nematodes, distinct differences were observed between the communities in natural and artificial sediments, particularly in the outermost subgroups (short/slender and long/thick). The shortest and most slender (Q1/Q1) nematodes were significantly more abundant in

Table 5
Results of one-way ANOVA and Tukey's pairwise comparisons for nematode body width and length distribution across artificial (control, FP, DP) and natural (MUC) sediments. **bold**: medium or greater effect size *f* (ANOVA) and effect size *d* (Tuckey's pairwise test) (Cohen, 1988) and significance after Bonferroni correction (p-value).

	t-value	df	p-value	Effect size (Cohen's *d*)	F-value	p-value (F-test)	Effect size (*f*)
Width					14.5609	≤0.001	0.15
control *vs* FP	5.6944	628	**≤ 0.001**	**0.49**			
control *vs* DP	5.2992	427	**≤ 0.001**	**0.51**			
control *vs* MUC	2.9098	1299	**0.002**	0.23			
FP *vs* DP	1.5961	675	0.056	0.14			
FP *vs* MUC	3.5447	1527	**≤ 0.001**	0.19			
DP *vs* MUC	3.6948	1346	**≤ 0.001**	0.31			
Length					52.5806	≤0.001	**0.28**
control *vs* FP	1.7917	628	0.034	0.16			
control *vs* DP	3.7848	427	**≤ 0.001**	0.37			
control *vs* MUC	4.7324	1299	**≤ 0.001**	0.37			
FP *vs* DP	2.8706	675	**0.002**	0.23			
FP *vs* MUC	9.3543	1527	**≤ 0.001**	**0.53**			
DP *vs* MUC	11.5452	1346	**≤ 0.001**	**0.82**			

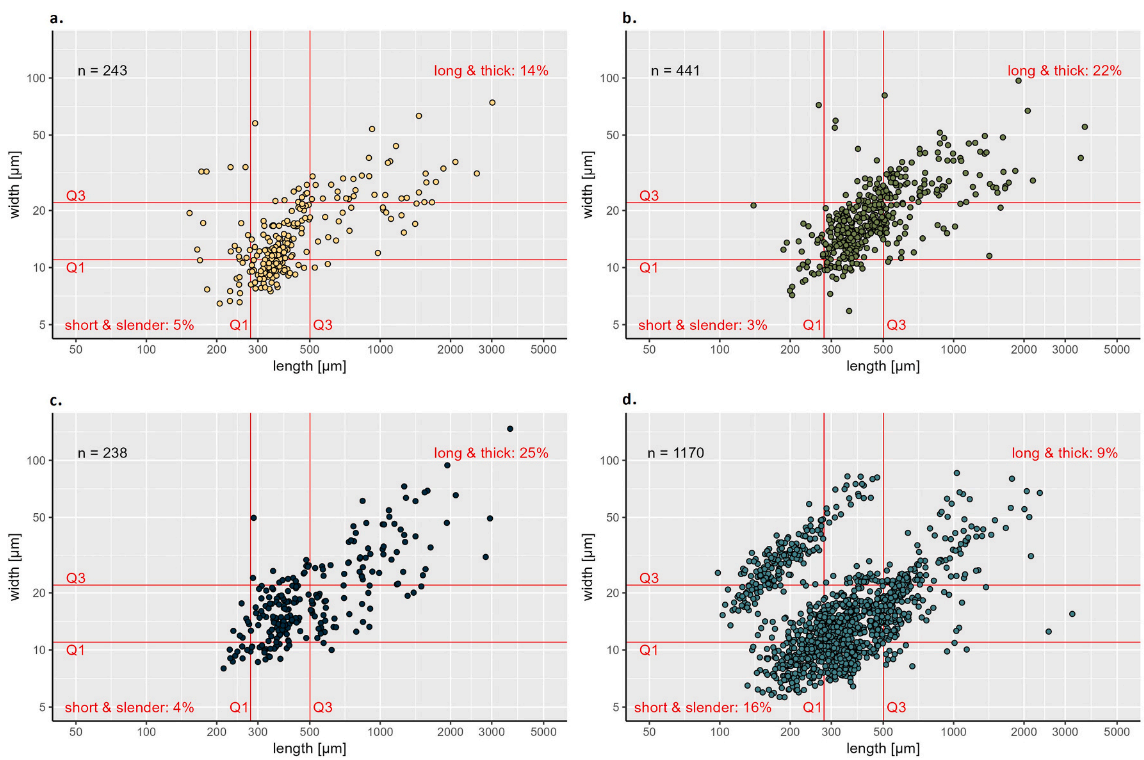

Fig. 7. Length-width relationship plots (log scale) for nematodes within the artificial sediments (**a.:** control, **b.:** FP, **c.:** DP) and natural sediments (**d.:** MUC), with indications for the first and third quartiles (Q1, Q3).

natural sediments (16%) compared to artificial sediments, where their abundance ranged between 3 and 5% (Table 6). Conversely, the longest and thickest (Q3/Q3) nematodes were found in significantly higher proportions in artificial sediments, with relative contributions of 15% in control samples, 22% in FP-enriched sediments, and 25% in DP-enriched sediments, compared to 9% in natural sediments (MUC). The proportion in artificial *Phaeocystis*-enriched sediments was not only similarly high (Table 6) but also significantly different from that in non-enriched control sediments.

In addition, within artificial sediments, significant differences were observed between the nematode communities from control and enriched sediments across various other subgroups: short/thick (Q1/Q3) nematodes were nearly absent in enriched sediments (control: 2%, FP: 0.2%, DP: 0%); medium/slender (Q2/Q1) nematodes were significantly more abundant in control sediments compared to enriched sediments (control: 29%, FP: 5%, DP: 8%); and long/slender (Q3/Q1) nematodes had a significantly lower proportion in control sediments compared to enriched sediments (control: 14%, FP: 22%, DP: 25%).

Further significant differences in two subgroups were found within the nematode communities from artificial sediments between the enriched sediments (FP/DP). The medium/medium (Q2/Q2) subgroup showed a significantly higher contribution in FP sediments (FP: 51%, DP: 37%). In contrast, the long/medium (Q3/Q2) subgroup was more abundant in DP sediments (FP: 9%, DP: 16%).

Additional morphological differences between treatments were observed in other nematode subgroups (see Table 6 for details).

3.2.2. Nematode biomass distribution and juvenile-adult composition across size classes

In both natural and artificial sediments, no nematodes exceed biomass size class 1 (dry weight range: 1.4619 – 2.7729 µg), except for a single individual in size class 4 found in the DP sediments. In natural and

Table 6
Nematode morphological subgroups categorised based on length-to-width (L/W) ratios, with the relative contribution of each subgroup to the overall nematode assemblage and statistical significance determined by $\chi 2$ test results, with significant p-values highlighted in **bold**.

	C%	FP%	DP%	MUC%	C *vs* FP		C *vs* DP		C *vs* MUC		FP *vs* DP		FP *vs* MUC		DP *vs* MUC	
					χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Length																
short (Q1 ≤ 279 µm)	11.9	6.3	7.1	38.6	6.40	**0.011**	3.19	0.074	63.88	**< 0.001**	0.16	0.609	159.5	**< 0.001**	88.28	**< 0.001**
medium (Q1-Q3 = 279-501 µm)	65.4	62.8	51.3	41.5	0.47	0.495	9.94	**0.002**	46.64	**< 0.001**	7.22	**0.007**	58.62	**< 0.001**	7.76	**0.005**
long (Q3 ≥ 501 µm)	22.6	30.8	41.6	19.9	5.24	**0.022**	19.86	**< 0.001**	0.92	0.338	14.49	**< 0.001**	21.65	**< 0.001**	51.60	**< 0.001**
Width																
slender (Q1 ≤ 11 µm)	35.4	8.6	13.4	31.2	75.67	**< 0.001**	31.28	**< 0.001**	1.63	0.202	2.23	0.136	87.05	**< 0.001**	30.78	**< 0.001**
medium (Q1-Q3 = 11-22 µm)	44.4	63.0	55.9	44.0	22.03	**< 0.001**	6.29	**0.012**	0.01	0.903	2.71	0.100	46.36	**< 0.001**	11.21	0.001
thick (Q3 ≥ 22 µm)	20.2	28.3	30.7	24.8	5.53	**0.019**	7.01	**0.008**	2.36	0.125	0.82	0.366	2.12	0.100	3.58	0.058
Length & Width																
short & slender	5.3	2.9	4.2	16.2	2.47	0.116	0.35	0.555	19.39	**< 0.001**	0.97	0.324	51.38	**< 0.001**	23.52	**< 0.001**
short & medium	4.9	3.2	2.9	10.5	1.33	0.248	1.26	0.261	7.24	**0.007**	0.31	0.578	22.17	**< 0.001**	13.53	**< 0.001**
short & thick	1.6	0.2	0.0	11.9	4.35	**0.037**	3.95	**0.047**	23.17	**< 0.001**	0.48	0.488	54.81	**< 0.001**	31.37	**< 0.001**
medium & slender	29.2	5.4	8.4	13.9	74.05	**< 0.001**	33.96	**< 0.001**	34.01	**< 0.001**	3.39	0.066	22.50	**< 0.001**	5.35	**0.021**
medium & medium	32.1	50.8	37.0	23.6	22.21	**< 0.001**	1.26	0.261	7.76	**0.005**	9.55	**0.002**	110.7	**< 0.001**	18.48	**< 0.001**
medium & thick	4.1	6.6	5.9	3.9	1.76	0.184	0.79	0.373	0.02	0.894	0.23	0.634	5.05	**0.020**	1.84	0.174
long & slender	0.8	0.2	0.8	1.0	1.28	0.259	0.00	0.983	0.08	0.772	1.40	0.236	2.55	0.100	0.07	0.793
long & medium	7.4	9.1	16.0	9.9	0.56	0.455	8.56	**0.003**	1.47	0.225	9.53	**0.002**	0.26	0.600	7.44	0.006
long & thick	14.4	21.5	24.8	9.0	5.19	**0.023**	8.25	**0.004**	6.64	**0.010**	2.22	0.137	46.52	**< 0.001**	48.07	**< 0.001**

control sediments, nematodes are present in biomass size classes ranging from −10 to 1 (dry weight range: 0.0008 – 2.7729 µg), whereas in FP and DP sediments, they occur between biomass size classes −9 and 1 (dry weight range: 0.0014 – 2.7729 µg) (Fig. 8).

The ANOSIM analysis shows no significant differences in biomass distribution across size classes between natural and artificial sediments in the upper 0 – 2 cm of the sediment. However, in the 2 – 3 cm sediment layer, significant differences are observed (R = 4.49, p = 0.1%). Pairwise comparisons indicate that these differences exist between the natural (MUC) and artificial sediments: MUC vs. control (R = 0.907, p = 2.9%), MUC vs. FP (R = 0.815, p = 4.7%), and MUC vs. DP (R = 0.833, p = 4.7%). These differences in the 2 – 3 cm layer are reflected in distinct size class distributions of nematode communities. Natural sediments in this layer contained nematode communities spanning all $\log_2$ size classes (−10 to 1), with biomass predominantly distributed in intermediate to large size classes (−6 to −1), peaking at −1. In contrast, artificial sediments (control, FP, DP) exhibited several unoccupied size classes and biomass was largely concentrated in the largest size classes (0 and 1), lacking contributions from very small and intermediate size classes. These patterns highlight distinct size class distributions and significant biomass differences between natural and artificial sediments, particularly in deeper layers.

In artificial sediments, adult nematodes dominate the biomass (50 – 75%) across size classes −8 (control, FP) and −7 (DP) to size class −5. The highest proportions of adults are found in size classes −7 (FP, DP) and −6 (control). In all other occupied size classes, juveniles dominate the biomass, appearing exclusively in size classes −10, −9, −1, 0, and 1 in control sediments and in size classes −9 and 1 in DP sediments. In FP sediments, juveniles are particularly abundant in biomass size classes −9 and −1, (≥70%) (Fig. 9).

The biomass distribution pattern in natural sediments differs clearly from that observed in artificial sediments. Juveniles dominate the biomass in smaller size classes (−10 to −8), accounting for 52 – 86%, whereas adults predominate in all larger size classes, representing 59 – 87% of the biomass, with the highest adult proportions observed in size classes −4, −3, and 0 (~86%). Although, the biomass of the nematode community in natural sediments is largely dominated by adults across most size classes, juveniles constitute the majority in terms of abundance, making up 70% of the population. In artificial sediments, their proportion is significantly lower, with juveniles comprising 47% in control sediments, 42% in FP sediments, and 45% in DP sediments.

3.3. Functional composition of nematode communities in natural and artificial sediments

3.3.1. Trophic structure of the nematode community

In artificial sediments (control, FP, DP), non-selective deposit feeders (1B) dominated, comprising ~70% of the community across all treatments (Fig. 10a). Natural sediments (MUC) showed an equal distribution of selective (1A) and non-selective (1B) deposit feeders, each at 39%. Epistrate feeders (2A) were more prevalent in FP sediments (18%) and natural sediments (20%) compared to other artificial sediments (control and DP 13% each). Predators/omnivores (2B) were the least abundant in both artificial (~2%) and natural sediments (3%). MDS results indicated a distinct trophic structure of the nematode communities in artificial and natural sediments, with pronounced differences in the abundance of non-selective (1B) and selective deposit feeders (1A) in the artificial compared to natural sediments (Fig. 10a).

The Index of Trophic Diversity (ITD) values revealed a clear difference in trophic structure between sediment types. Natural sediments (MUC) showed lower ITD (0.336), reflecting a more even distribution of feeding types. In contrast, artificial sediments had higher ITD values (control: 0.540; FP: 0.518; DP: 0.514), reflecting reduced trophic diversity and a less even distribution, characterized by the dominance of certain feeding types (feeding type 1B, see also Fig. 10a).

Pairwise ANOSIM comparisons revealed significant differences

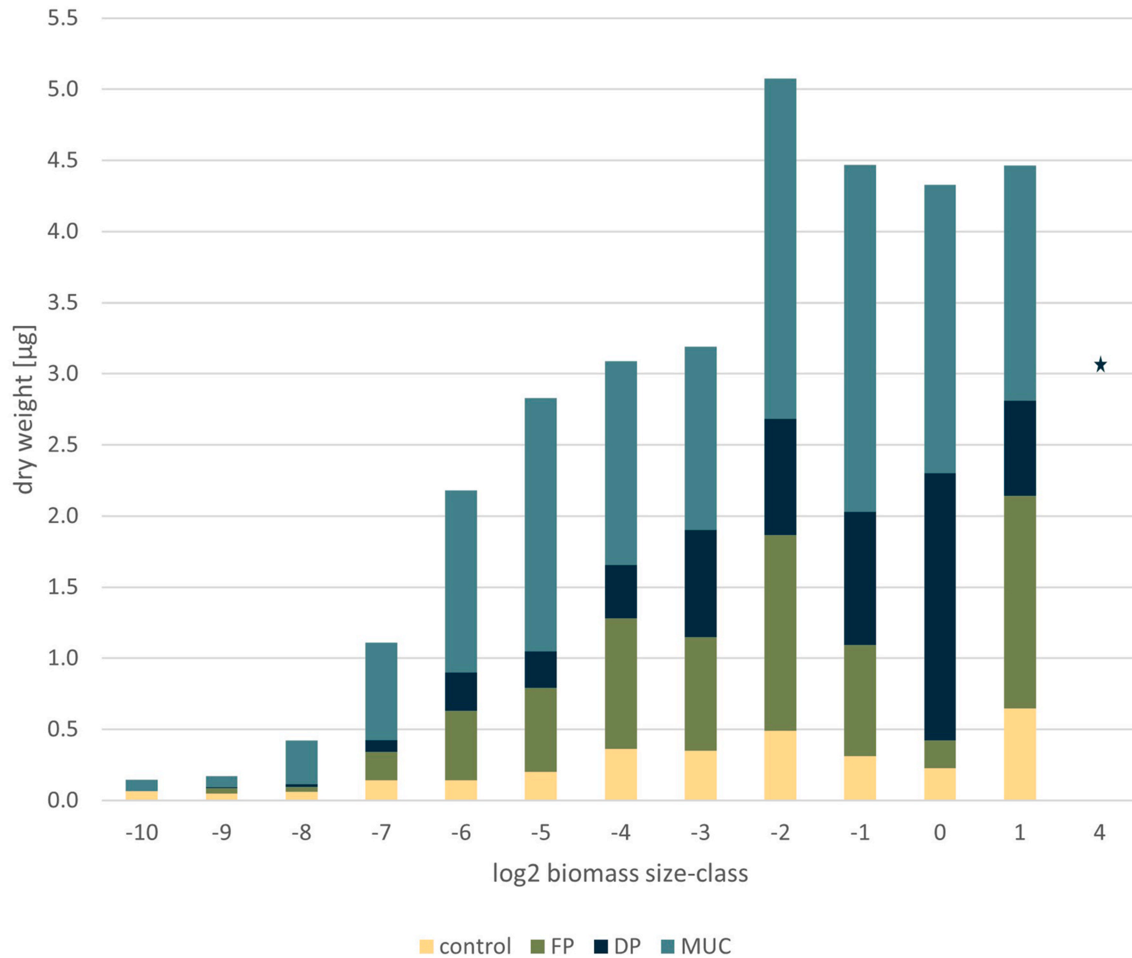

Fig. 8. Dry weights [µg] of nematodes (mean values) within $\log^2$ biomass size-classes in artificial (control, FP, DP) and natural (MUC) sediments. Asterisk: single individual in size class 4 (DP sediments).

between nematode communities in artificial and natural sediments (control *vs.* MUC: R = 0.963, p = 2.9%; FP *vs.* MUC: R = 0.981, p = 2.9%; DP *vs.* MUC: R = 0.63, p = 5.1%), but not among artificial sediment treatments.

3.3.2. Life-history strategy of the nematode communities

Nematode communities in all sediments consisted of genera belonging to c-p classes 2 - 4, with no extreme colonisers (c-p 1) or persisters (c-p 5) present (Fig. 10b). In artificial sediments (control, FP, DP), c-p 2 genera (general opportunists) dominated, accounting for 71 - 77% of the community. They were followed by c-p 3 and c-p 4 genera, which were present in similar proportions in the control (14% each) and FP sediments (12% each), and at 17% (c-p 3) and 11% (c-p 4) in the DP sediments. Natural sediments (MUC) showed a more balanced distribution, with c-p 2 genera at 45%, c-p 4 genera at 35%, and c-p 3 genera at 20%. MDS results showed a clear differentiation between the life-history trait structure of the nematode communities in artificial and natural sediments, and the differences in the abundance of general opportunist (c-p 2) and general K-strategists (c-p 4) were conspicuous between the artificial and natural sediments (Fig. 11b).

Pairwise ANOSIM comparisons revealed significant differences between nematode communities in artificial and natural sediments (control *vs.* MUC: R = 1, p = 2.9%; FP *vs.* MUC: R = 1, p = 2.9%; DP *vs.* MUC: R = 0.704, p = 5.1%), but not among artificial sediment treatments.

4. Discussion

4.1. Environmental drivers of deep-sea nematode community structure: the role of organic enrichment, successional stage, and sediment characteristics

The ongoing transformation of Arctic marine ecosystems due to climate change is altering the composition and dynamics of phytoplankton communities, with *Phaeocystis* blooms becoming increasingly frequent as a result of rising temperatures and enhanced Atlantic water influx (Orkney et al., 2020). These shifts in primary production directly impact the quantity and quality of organic matter exported to the deep-sea floor, with potential consequences for carbon cycling efficiency and trophic energy transfer (Assmy et al., 2017; Sugie et al., 2020; Fadeev et al., 2021).

In polar regions, where sea ice dynamics strongly regulate primary productivity, the transition to open-water conditions may further modify the amount and composition of organic material reaching the benthic environment, influencing meiofaunal communities at various depths (Pantó et al., 2021).

Deep-sea nematode communities, as key players in benthic carbon cycling, respond to these environmental changes through shifts in abundance, diversity, and functional composition (Mohammad et al., 2024; Gambi et al., 2003; Rosli et al., 2018; Schnier et al., 2025c). Their community structure is shaped by the interaction between organic enrichment, successional stage, and sediment structure, with long-term environmental conditions playing a critical role in determining species composition and trophic interactions (Liao et al., 2020; Gambi et al.,

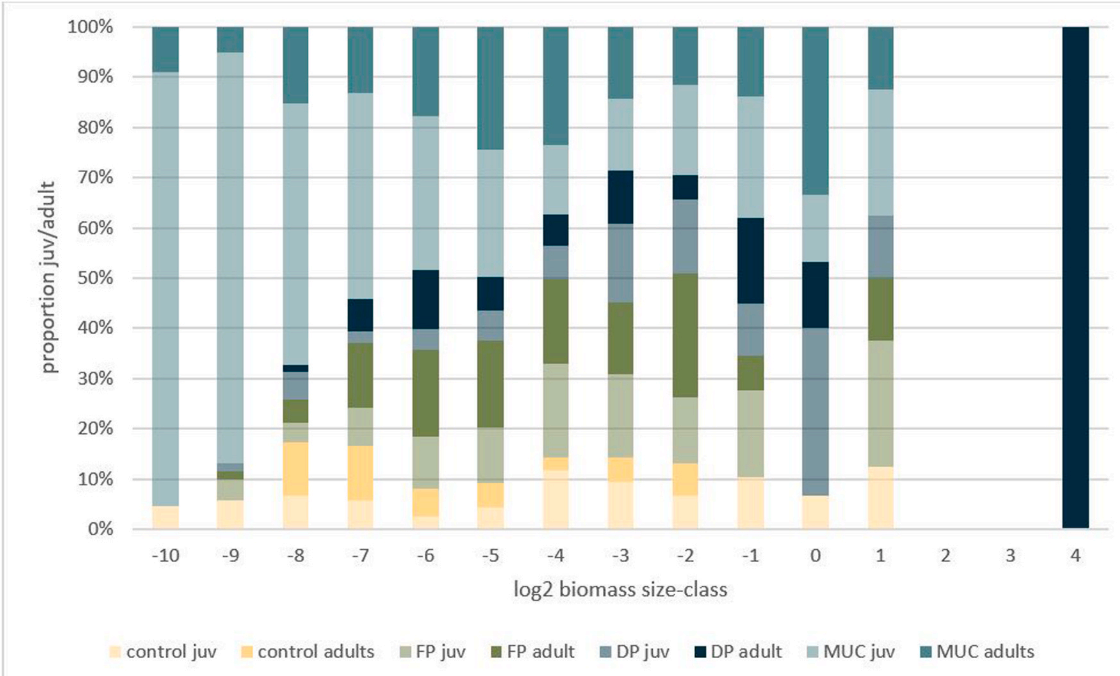

Fig. 9. Percentage distribution of juvenile (juv) and adult (adult) nematodes within $\log^2$ biomass size-classes in artificial (control, FP, DP) and natural (MUC) sediments.

2003; Rosli et al., 2018). However, the extent to which organic matter quality and exposure duration influence deep-sea nematode assemblages remains insufficiently understood (Liao et al., 2020; Gambi et al., 2003; Rosli et al., 2018).

Given the functional importance of nematodes in food web dynamics and biogeochemical cycles (van Gaever et al., 2009; Soetaert et al., 2009; Ingels et al., 2011, Schratzberger and Ingels, 2018; Ingels et al., 2023), understanding these processes is essential for predicting the potential long-term consequences of changing organic matter fluxes and ecosystem stability in response to climate change (Pfannkuche and Thiel, 1988; Braeckman et al., 2018).

4.2. Nematode colonisation patterns in natural and artificial sediments

Nematode abundance and diversity varied significantly between natural and artificial sediments in the upper 0-3 cm layer. Natural sediments (MUC) harboured the highest nematode density (1177 ± 164 individuals per 10 cm^2) and genus richness (54 genera). Artificial sediments displayed markedly lower abundances: fresh *Phaeocystis* (FP) treatment supported 357 ± 180 individuals per 10 cm^2, control sediments 207 ± 152, and decayed *Phaeocystis* (DP) treatment 193 ± 74. Deep-sea nematode colonisation studies show that while nematodes actively migrate into new sediments, their densities remain substantially lower than in natural assemblages (Guilini et al., 2011).

Coastal studies report variable colonisation rates, with nematode densities reaching 4 - 36% of reference levels within days to weeks (Chandler and Fleeger, 1983; Schratzberger et al., 2004; Ullberg and Ólafsson, 2003; Zhou, 2001). In deep-sea settings, Gallucci et al. (2008) observed colonisation rates of 5 - 20% after nine days, with minimal increase after 17 days. Guilini et al. (2011) reported nematode abundance in colonisation cores at just over 2% of reference values after a short period of 10 days. In contrast, our sampling was conducted after a substantially longer period of three months. Therefore, while we cannot determine the pace of initial colonisation, the longer exposure time in our study may have allowed for further progression of community development, even if densities remained lower than in natural sediments. However, the densities we observed after three months are comparable to those reported in other deep-sea studies (Gallucci et al., 2008) and for coastal environments (Chandler and Fleeger, 1983; Schratzberger et al., 2004; Ullberg and Ólafsson, 2003; Zhou, 2001). Our findings challenge the assumption that colonisation in low-energy deep-sea environments is a comparably slow process (Lambshead et al., 2003; Lins et al., 2014; Miljutin et al., 2011, 2015; Miljutina et al., 2010; Pape et al., 2017; Radziejewska, 2014; Singh et al., 2016; Vanreusel et al., 2010a). Although colonisation rates in deep-sea sediments may vary with environmental context, particularly food quality and quantity, in some cases they occur on timescales similar to those observed in coastal environments. It is important to emphasize that these comparisons specifically concern colonisation dynamics in experimentally defaunated sediments and do not reflect natural recovery in undisturbed habitats. The natural MUC sediments analysed here represent fully developed deep-sea assemblages, serving as a reference for mature community structure rather than colonisation potential. This distinction underlines the relevance of our experimental results to succession dynamics, while recognising that natural, undisturbed communities exhibit a different, stable state not characterised by active recolonisation.

In the present study colonising nematode communities exhibited unique composition, with 18 genera (25% of total) found exclusively in artificial sediments. This suggests opportunistic colonisation behaviour among certain nematode genera, contributing to community heterogeneity (Guilini et al., 2011; Liao et al., 2020). Guilini et al. (2011) reported a similar pattern, with rare and previously undetected genera from reference sediments accounting for 35% of the relative abundance in colonising assemblages, underscoring the complexity of colonisation dynamics in disturbed environments. These patterns are partly explained by nematode life-history strategies under the coloniser–persister (c-p) classification, which categorises taxa by traits such as generation time, reproductive rate, and disturbance tolerance. A more detailed analysis of these strategies and their relevance to succession is provided in section 4.6.1.

Monhystrella is a widely distributed deep-sea genus, reported from various habitats, including abyssal plains, cold seeps, and trench environments, highlighting its eurytopic nature and and ecological

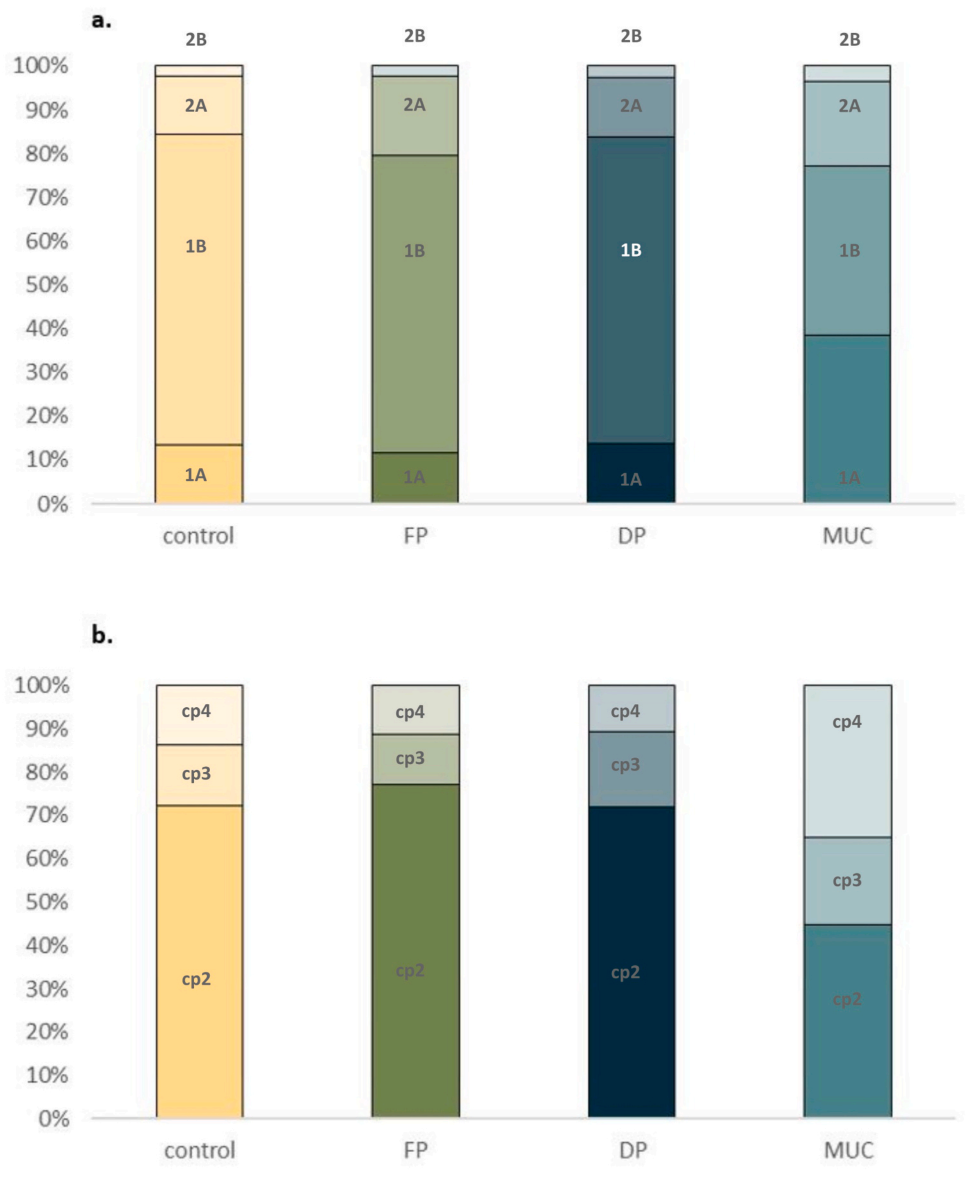

Fig. 10. Relative abundance of **[a.]** feeding types (Wieser, 1953) and **[b.]** c-p classes (Bongers, 1990; Bongers et al., 1995) of nematode communities in artificial (control, FP, DP) and natural (MUC) sediments. Labels for Wieser feeding types (1A, 1B, 2A, 2B) and Bongers c–p classes (c–p 2, c–p 3, c–p 4) are shown directly within the stacked bars. Due to the very low proportion of 2B feeders, this label is placed just above the corresponding bar segment.

versatility adaptability to different conditions (Hauquier et al., 2019; Ingels et al., 2009). This adaptability is also evident in the present study. *Monhystrella* was dominant across all sediment types examined, suggesting its ability to thrive under diverse environmental conditions, consistent with its generalist ecological strategy. Its ubiquitous presence in all sediment types aligns with findings from other studies, which also report the genus' dominance in multiple deep-sea environments (Lambshead et al., 2003; Lins et al., 2014; Miljutin et al., 2011, 2015; Miljutina et al., 2010; Pape et al., 2017; Radziejewska, 2014; Singh et al., 2016; Vanreusel et al., 2010a). However, not all genera exhibit this level of ubiquity. Some genera, in contrast to *Monhystrella*, show clear habitat preferences, indicating that their presence is more restricted to specific environmental conditions rather than being widespread across all sediment types. Certain genera showed clear habitat preferences: *Leptolaimus*, *Molgolaimus*, and *Sabatieria* dominated across artificial sediments. The successful colonisation by specific *Sabatieria* and *Leptolaimus* species observed in this study aligns with previous findings from both shallow and deep-sea environments (Gallucci et al., 2008; Schratzberger et al., 2004; Ullberg and Ólafsson, 2003). These genera are characterized by high motility and opportunistic life strategies, enabling them to rapidly migrate into and colonise defaunated sediments. Their consistent appearance in the early stages of recolonisation across various marine settings suggests that colonisation is not merely a random process, but is shaped by species-specific functional traits.

Vertical distribution patterns differed markedly between natural and artificial sediments. In artificial sediments, 58 - 80% of nematodes concentrated within the top 1 cm (control: 80%, FP: 78%, DP: 58%), while natural sediments showed a more uniform distribution (31 - 35% per layer). This indicates that artificial sediments, especially during early colonisation stages, primarily support surface-dwelling nematodes, whereas natural sediments provide more stable conditions for deeper-burrowing species (Guilini et al., 2011).

Apart from previously described differences in abundance, we also

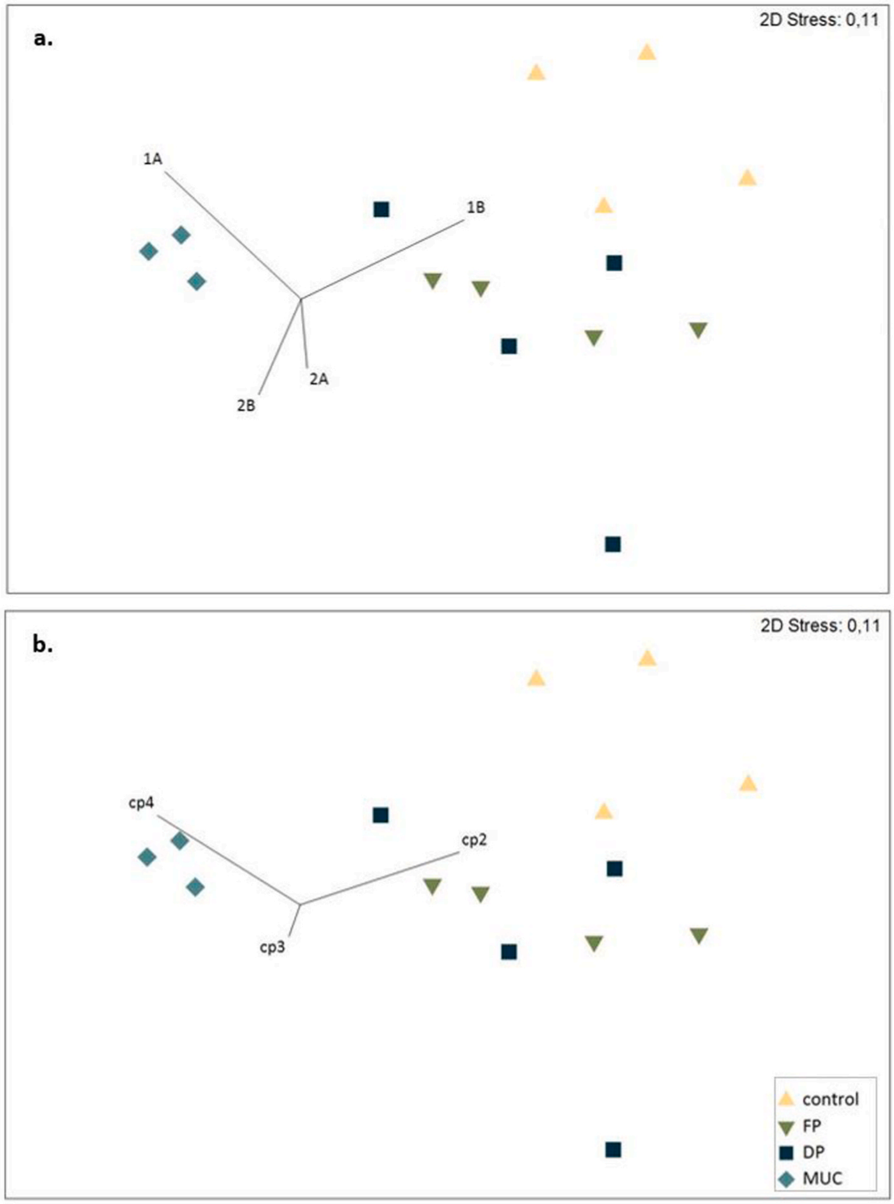

Fig. 11. MDS ordination of nematode communities in artificial (control, FP, DP) and natural (MUC) sediments, based on a Bray-Curtis similarity matrix (square-root transformed data). The vector overlay shows correlations (Spearman rank) with functional traits. **[a]** feeding types (BIOENV: Rho (ρ) = 0.715, p = 0.1 %) and **[b]** cp-classes (BIOENV: Rho (ρ) = 0.651, p = 0.1 %).

observed differences in community diversity patterns among the artificial sediments (unenriched control, enriched with fresh or decayed *Phaeocystis*) and the natural reference sediments.

The unenriched artificial sediments (control) were colonised by a noticeably less diverse nematode community compared to the enriched artificial sediments (FP and DP). Similar patterns of nematode diversity linked to the availability of organic matter have also been observed in other deep-sea studies. For instance, research from the Atacama Trench (southeast Pacific) found that high concentrations of nutritionally rich organic matter supported increased nematode diversity and a broader range of feeding types, particularly in comparison to oligotrophic deep-sea settings (Gambi et al., 2003). Also, at HAUSGARTEN observatory, studies have shown that food availability is a key driver of bathymetric variation in nematode abundance and diversity, with sedimentary organic carbon explaining much of the variation in community structure along depth gradients (Schnier et al., 2023). Experimental additions of organic matter ("food falls") at HAUSGARTEN further demonstrated that both the quantity and quality of food resources can enhance nematode abundance and diversity (Soltwedel et al., 2018). Similarly, in chemosynthetic environments such as cold seeps and hydrothermal vents, locally elevated food availability due to microbial production has been linked to increased nematode densities and variable diversity patterns depending on habitat conditions (Vanreusel et al., 2010b). Pantó et al. (2021) additionally reported increasing nematode diversity in response to the freshness of the food source. In contrast, our study found no significant differences in nematode diversity patterns between artificial sediments enriched with fresh (FP) and decayed *Phaeocystis* (DP). Highest diversity of the nematode communities was found in the reference sediments from the MUC sampling. These findings align with ecological succession models, where reference sediments represent stable "climax communities" with diverse persister species, while enriched conditions favour simplified coloniser assemblages (Ahmed et al., 2024). Natural sediments seem to act as reservoirs for diverse nematode communities due to their stability and organic complexity, the diverse and heterogeneous composition of organic matter from multiple sources and decomposition stages that creates a variety of ecological niches and energy sources. In contrast, artificial sediments reflect early successional patterns driven by environmental constraints and a more homogeneous, simplified organic environment.

4.3. Nematode colonisation dynamics: morphometric patterns

The dominance of longer and thicker nematodes (Group II, particularly Q3/Q3) in artificial sediments suggests that early colonisers were primarily larger-bodied genera, which likely exhibit greater mobility and dispersal capacity over new substrates. This pattern aligns with findings from Gallucci et al. (2008), who observed a similar prevalence of large-bodied nematodes in defaunated deep-sea sediments due to their ability to actively migrate into new habitats. Conversely, the near absence of short/thick nematodes (Group I) in artificial sediments may reflect their limited dispersal abilities or a preference for more structurally complex habitats. Such environments, characterised by a heterogeneous arrangement of particles and organic matter, offer stable microhabitats and protective niches that are largely missing in the uniform and recently deposited artificial sediments. These morphotypes are typically associated with stable and mature deep-sea environments, as reported by Zeppilli et al. (2015), which the artificial sediments have not yet developed. The reduced abundance of short/slender nematodes (Q1/Q1) in artificial sediments further supports the notion that early colonisation is dominated by species with greater mobility and tolerance to unstable sediment conditions (Vanreusel et al., 2010a). Early successional stages in artificial sediments favour motile generalists capable of colonising unstable substrates, whereas smaller, more specialized species require more time and environmental complexity to establish (Levin et al., 2013). Natural deep-sea sediments (MUC) seems to provide a comparable stable environment with well-established biogeochemical conditions that support diverse nematode communities, including a higher proportion of short-bodied species (Group I). In contrast, artificial sediments, recently introduced and colonised over just three months, may lack fine-scale habitat complexity, favouring long/slender nematodes adapted to more homogenous conditions (Guilini et al., 2011; Gallucci et al., 2008).

4.4. Colonisation effects on nematode biomass distribution and juvenile-adult ratio

Juveniles comprised a significantly lower proportion of nematodes in artificial sediments (42–47%) compared to natural sediments (70%), indicating that initial colonisation was largely driven by adults. The dominance of adults in biomass size classes (−7 to −5) in artificial sediments suggests that larger individuals had a competitive advantage in pioneering new habitats. Experimental and field studies have shown that body size plays a key role in colonisation success, with larger individuals being more effective migrants and resource exploiters in newly available sediments (Schratzberger et al., 2002, 2004). This pattern is consistent with observations by Gallucci et al. (2008), who found that early-stage colonisation in defaunated deep-sea sediments was primarily driven by adults, with juvenile recruitment lagging due to environmental variability. Similarly, Vanreusel et al. (1995) reported that disturbed sediments were initially colonised by larger-bodied species, while smaller, less motile individuals became more prominent as conditions stabilized over time. Adult-driven colonisation reflects selective pressures favouring larger individuals capable of pioneering new habitats. Juvenile recruitment depends on sediment stabilization and organic matter accumulation over time, contributing to delayed community maturation. Grzelak et al. (2020) discuss how nematode communities in deep-sea environments exhibit delayed juvenile recruitment due to environmental constraints such as sediment instability. They emphasize that early colonisation is typically driven by adult nematodes, with juveniles only appearing once the habitat stabilizes and microbial activity supports their development. This aligns with our findings, reinforcing the idea that artificial sediments require longer timescales to support a complete age-structured community.

Pronounced differences in nematode biomass distribution between natural and artificial sediments – particularly in deeper layers (2 – 3 cm) – indicate that colonisation in artificial substrates remains incomplete. In natural sediments, well-developed pore structures, established microbial communities, and active bioturbation allow for the settlement of deeper-dwelling and juvenile nematodes (Gallucci et al., 2008; Ingels et al., 2011; Shabdin and Othman, 1999). In contrast, nematodes in artificial sediments remain largely confined to surface layers, reflecting the early developmental stage of these habitats.

This pattern aligns with findings by Zeppilli et al. (2015), who reviewed reduced vertical stratification of nematode communities in disturbed sediments, and by Ingels et al. (2011), who found in a mesocosm experiment using deep-sea sediments from the Nazaré Canyon (~3500 m) that sediment structure and microbial activity support deeper-dwelling taxa. Similarly, Ptatschek and Traunspurger (2020) reviewed nematode dispersal strategies across aquatic systems and highlight how physical and biological sediment features are crucial for vertical nematode distribution, with underdeveloped substrates showing limited colonisation below the surface. Despite different environments and methodologies, these studies report similar trends, suggesting common underlying drivers. The restricted vertical migration and homogeneity of artificial sediments thus underscore the importance of bioturbation and microbial succession for enabling complex vertical community structuring. While initial colonisation occurs relatively quickly, our results suggest that full habitat maturation is a prolonged process. The dominance of larger, mobile nematodes, reduced juvenile presence, and altered biomass patterns further indicate that artificial sediments have yet to develop the structural and functional complexity characteristic of natural deep-sea environments.

These observations are consistent with previous studies showing that early community assembly is shaped by dispersal abilities and environmental constraints, whereas long-term stability and habitat complexity are essential for the establishment of mature and diverse nematode communities (Vanreusel et al., 2010a; Gallucci et al., 2008; Zeppilli et al., 2015).

4.5. Functional traits of the nematode communities in natural and artificial sediments

The trophic structure and life-history strategies of deep-sea nematode communities are shaped by organic enrichment, environmental stability, and successional stage. In this study, artificial sediments – enriched to match the carbon content of natural sediments – were deployed on the deep seafloor for three months. The key distinction between these artificial sediments lies in the type of organic matter provided: fresh *Phaeocystis* (FP sediments), decayed *Phaeocystis* (DP sediments), and unenriched control sediments, compared to naturally established deep-sea sediments (MUC). Despite having comparable carbon content, artificial sediments remained in an early successional state, highlighting the importance of long-term environmental history in shaping deep-sea benthic communities. Long-term environmental history seems to be crucial for shaping deep-sea nematode communities by promoting stability, resource accumulation, and functional diversity over time. Studies such as Schnier et al. (2023), Pape et al. (2013b), Zeppilli et al. (2018, 2016), and Gambi and Danovaro (2016) confirm that sediment stability (via grain size distribution and oxygen dynamics), food availability (organic carbon, nitrogen, POC flux), and bentho-pelagic coupling (phytodetritus deposition) are key drivers of nematode community composition in deep-sea ecosystems.

4.6. Feeding strategies and trophic structure of the nematode communities in natural and artificial sediments

The composition of nematode feeding strategies revealed clear differences between artificial and natural sediments. Artificial sediments (FP, DP, and control) were strongly dominated by non-selective deposit feeders (~70%), whereas natural sediments (MUC) exhibited a more balanced trophic structure, with selective and non-selective deposit feeders present in equal proportions (39% each). This suggests that deposit-feeding nematodes – particularly non-selective deposit feeders – are well adapted to the exploitation of freshly introduced organic matter, allowing them to rapidly colonise artificial sediments (Mohammad et al., 2024). These findings are in line with Schnier et al. (2023), Pape et al. (2013b) and Gallucci et al. (2008), who demonstrated that organic enrichment in deep-sea environments shifts nematode trophic structure towards deposit feeders, favouring species capable of utilizing abundant detrital material.

Interestingly, epistrate feeders were slightly more abundant in FP (18%) and MUC sediments (20%), whereas their proportion was lower in DP and control sediments. This suggests that epistrate feeders benefit from labile organic matter inputs, such as fresh *Phaeocystis* in FP sediments or natural detritus and biofilms in MUC sediments. The findings are consistent with Vanaverbeke et al. (2011), who reported that epistrate feeders thrive in environments with high-quality organic inputs and microbial biofilms. In contrast, their lower abundance in DP sediments suggests that degraded *Phaeocystis* offers less readily available organic material, requiring microbial breakdown before becoming bioavailable to nematodes.

Predators and omnivores comprised only 2 – 3% of nematode assemblages across all sediment types. In natural MUC sediments, this proportion is characteristic of mature, stable communities adapted to local conditions. In contrast, in artificial sediments, it is associated with early successional stages, limited prey availability, and a trophic structure that has not yet fully established. Predator abundance alone may not be a reliable indicator of community maturity. However, the well-documented presence of predator-rich nematode communities in mature deep-sea ecosystems (Zeppilli et al., 2015) supports the interpretation that the low predator values observed in artificial sediments are not unexpected, but instead reflect their early successional stage and relatively short deployment period of only three months.

These results suggest that artificial sediments remain in an early successional state, where opportunistic deposit feeders dominate, and trophic complexity is low, as indicated by higher ITD values (~0.51–0.54). In contrast, natural sediments, shaped by long-term environmental processes, support a more functionally diverse nematode community, with balanced feeding strategies and a lower ITD (0.336), reflecting greater ecosystem stability and complexity.

4.6.1. Life-history traits and successional stage of the nematode communities in natural and artificial sediments

To interpret the nematode community structure and succession patterns observed, we applied the c-p classification system (Bongers and Bongers, 1998). Although developed for terrestrial and shallow-water nematodes, the c–p classification has been widely applied to deep-sea nematodes as a functional framework to interpret their life-history strategies. Its use in the deep sea is supported by numerous studies demonstrating similar successional patterns and community responses (Gallucci et al., 2008; Ingels et al., 2009; Guilini et al., 2011; Leduc et al., 2012; Vanreusel et al., 2010a). Although it cannot be fully guaranteed that the classification is perfectly transferable, it remains a valuable tool for deep-sea nematode ecology.

In the present study, patterns in life-history traits further reinforce the early successional nature of artificial sediments. The artificial treatments were overwhelmingly dominated by opportunistic c-p 2 genera (71 – 77%), while natural sediments hosted a more balanced assemblage, with c-p 2 genera (45%), c-p 3 (20%), and c-p 4 (35%). The dominance of c-p 2 genera in artificial sediments is characteristic of early-stage colonisation, where rapidly reproducing species thrive in unstable environments with high resource availability. This aligns well with the c-p classification, which describes c-p 2 nematodes as opportunists that dominate disturbed environments but decline as ecosystems mature.

The slight differences observed between FP and DP sediments reflect the impact of organic matter quality on nematode community composition. In FP sediments, enriched with fresh *Phaeocystis*, there was a slight increase in epistrate feeders, likely benefiting from the availability of labile organic material and microbial biofilms. In contrast, DP sediments, enriched with degraded *Phaeocystis*, supported a marginally higher proportion of c-p 3 genera, which are more resilient to resource fluctuations and better adapted to environments where organic matter requires microbial decomposition before becoming bioavailable. Different studies (Hoste et al., 2007; Lahajnar, 2005; Moreno, 2017; Zhu et al., 2024) emphasize the pivotal role of microbial activity in transforming refractory detritus into accessible nutrients, enhancing nutrient availability and supporting meiofaunal communities. This collective evidence reinforces the idea that decomposed organic matter sustains later-successional taxa by gradually converting detritus into essential nutrients.

In the present study, no nematode genera characterised as extreme colonisers (c-p value 1) or extreme persisters (c-p value 5) were found in either artificial or natural sediments. This finding aligns with broader observations in deep-sea environments, where extreme colonisers are rare (Heip et al., 1985; Moens et al., 2013) and extreme persisters occur only in very low proportions ($\leq$1.0 %) or are entirely absent (Armenteros et al., 2024; Liao et al., 2020; Schnier et al., 2023; Soltwedel et al., 2018). Instead, most nematode communities are dominated by taxa with intermediate c-p values (c-p 2–4), reflecting their adaptations to the unpredictable and resource-limited conditions of deep-sea habitats (Liao et al., 2020; Schnier et al., 2023; Soltwedel et al., 2018; Vanreusel et al., 2010a).

Altogether, these results highlight the early successional state of the nematode community from artificial sediments compared to natural sediments, where opportunistic genera dominate and functional diversity remains limited. Overall, the community compositional structure found in artificial sediments remains less complex compared to natural sediments.

5. Conclusion

Deep-sea nematode communities are shaped by environmental stability, resource availability, and successional dynamics. This study investigated the influence of organic enrichment on nematode communities by deploying a bottom lander equipped with pre-enriched artificial sediments on the Arctic deep seafloor and assessing colonisation after a three-month in situ incubation period. Despite comparable organic carbon content to natural sediments, artificial substrates supported lower nematode abundance and diversity, reflecting their early successional state. These findings are consistent with earlier research showing that the long-term stability of natural deep-sea sediments facilitates the accumulation of organic matter and the development of complex, resilient trophic structures (Gallucci et al., 2008; Vanreusel et al., 2010a; Danovaro et al., 2014).

Artificial sediments, by contrast, lack essential legacy effects – such as microbial priming, bioturbation history, and established microbial communities – which are critical for supporting diverse and functionally complex assemblages (Zeppilli et al., 2015; Schnier et al., 2023). In our experiment, artificial sediments remained in an early successional stage dominated by opportunistic taxa (e.g., c–p 2 genera), with only subtle differences among treatments: fresh *Phaeocystis* favoured epistrate feeders, while decayed *Phaeocystis* supported slightly more advanced colonisers. However, trophic complexity and functional diversity remained limited compared to natural sediments, which exhibited a broader range of life-history strategies and more stable, mature community structures (Zeppilli et al., 2015; Gallucci et al., 2008; Schratzberger et al., 2004; Miljutin et al., 2015).

Although our experiment was limited to a single sampling event, it nonetheless provides valuable insights into early colonisation dynamics in a logistically demanding deep-sea setting. The patterns observed align with early successional stages described in colonisation studies (Chandler and Fleeger, 1983; Gallucci et al., 2008), and suggest that deep-sea nematode communities can respond rapidly to organic inputs. Yet, achieving full community development likely requires much longer exposure times and environmental stability.

In the context of a changing Arctic, where climate-driven shifts in productivity and organic matter delivery are expected, these findings emphasize the role of organic matter quality and seafloor conditions in shaping benthic ecosystem structure. While long-term, multi-interval studies would be needed to fully resolve successional trajectories (Vanreusel et al., 2010a; Miljutin et al., 2015), our study offers a rare and important baseline for understanding how deep-sea communities initiate and develop under experimental enrichment scenarios.

CRediT authorship contribution statement

Christiane Hasemann: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jannik Schnier:** Writing – review & editing, Visualization, Investigation, Data curation. **Normen Lochthofen:** Writing – review & editing, Methodology, Investigation, Conceptualization.

Data availability statement

Raw data from the colonisation experiment – including genera-abundance, morphometric, and trait data of deep-sea nematodes from both artificial and natural sediments – are available via Mendeley Data (Hasemann and Schnier, 2025). Nematode count, abundance, and biomass data from the same natural sediment samples (used as experimental reference) are archived at PANGAEA (Schnier et al., 2025a, 2025b), with harmonised versions accessible via CRITTERBASE (Teschke et al., 2022).

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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.dsr2.2026.105622.

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