

## RESEARCH ARTICLE

# A trophic niche-based approach to unravel potential vulnerabilities of soft-sediment infauna from the Clarion-Clipperton Zone to nodule mining impacts

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Current understanding of the potential vulnerabilities of the soft-sediment food web of the Clarion-Clipperton Zone (CCZ) nodule fields to future mining impacts is based largely on benthic stock, taxonomic and modelling assessments, lacking in ground-truthing observations of trophic interactions. Using dual stable isotope analysis and related metrics, we investigated the trophic relationships of meiofauna and macrofauna as a whole and of their key taxa (Nematoda, Copepoda, Polychaeta, Tanaidacea, Isopoda, Amphipoda) across nodule-rich and nodule-free sediments at two sites within the Global Sea Mineral Resources NV (Deme group, Belgium) contract area. Our results suggest higher trophic redundancy (more trophic niche overlap) among the two investigated size classes in nodule-free sediments where the two size classes likely share more of the present basal resources. The nodule-rich sediments represented a more structurally complex habitat, where the taxa belonging to both infaunal size classes may have been using alternative energy pathways, leading to enhanced trophic niche partitioning and a narrowing of their isotopic niches. The metrics highlighted the importance of meiofauna as a foundational trophic link for the re-establishment of the soft-sediment food web following mining. The larger trophic niche partitioning observed between Nematoda and Copepoda hinted at higher sensitivity of the smaller-sized metazoan assemblage to functional cascading, with a potentially crucial role of copepods in bridging between the sediment detrital pool and the next trophic levels. The macrofauna displayed more trophic redundancy between its taxa, known to increase functional resilience to disturbance. Polychaetes displayed smaller trophic niche widths in nodule-free compared to the nodule-rich sediments. This novel dataset and metrics analyses confirm results from a previous modelling study of the sediment food web at this contract area and suggest a need for future research to focus on the links between the meiobenthos and sediment prokaryotes in order to assess potential mining impacts.

**Keywords:** Deep-sea mining, Stable isotopes, Benthos, Deep-sea mining impacts, Food-web ecology, Trophic niche

## Introduction

The Clarion-Clipperton Zone (CCZ) is an area of about 6 million km<sup>2</sup> situated in the equatorial Pacific Ocean where, at about 5 km depth, large quantities of polymetallic nodules cover the vast abyssal plain. Polymetallic nodules (hereafter referred to as 'nodules'; Verlaan and Cronan, 2021) are so-named due to their multi-metal nature. The CCZ nodule field is known to contain large amounts of critical minerals such as nickel, cobalt, manganese, copper, as well as rare-earth elements (Miller et al.,

2018; Hein et al., 2020), all of which have been identified as important to decarbonise the world's energy systems (e.g., International Energy Agency, 2021). As a result, and over the past decade in particular, interest in recovering these minerals on a commercial scale has risen dramatically.

As with any new extractive industry or project, deep-seabed mining comes with a complex set of technological, environmental, geopolitical and ethical challenges. Most marine mineral exploration is currently taking place in the international seabed area (the 'Area'), where activities are regulated and managed by the International Seabed Authority (ISA, 2023), which has 168 Member States in addition to the European Union. To date, the ISA has issued 17 exploration contracts in the CCZ. At the time of writing, no ISA contractor (i.e., any government or company that holds an exploration contract in the Area) had

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applied for an exploitation (mining) contract and exploitation has not yet occurred. Regulations for exploration have been established, and exploitation regulations have been drafted and undergone years of negotiations, which continue (Pickens et al., 2024).

As part of their exploration contract requirements, ISA contractors must gather information and data from their contract area to assess the environmental baseline conditions, including the associated habitats and biota, to be able to monitor the impacts of exploration and potential future exploitation activities. In addition to undertaking these studies, an application for mining will require an environmental impact assessment, culminating in an environmental impact statement, as well as an environmental management and monitoring plan.

Among the direct impacts that mining activities are expected to have on the benthic biota in the CCZ nodule fields, those connected to the nodule collector operation at the seabed have received the most attention (Jones et al., 2020; Lefaible et al., 2023). Benthic biota is primarily comprised of small organisms living within the sediment, with Nematoda, Copepoda, Polychaeta, Amphipoda, Isopoda and Tanaidacea being the most abundant taxa. The extraction of the nodules will result in the removal of those organisms that live on the outer surface of the nodules and/or within the nodule crevices (Vanreusel et al., 2016; Pape et al., 2021; Lefaible et al., 2023; Stratmann, 2023), potentially causing irreversible local biodiversity loss. This loss is expected to negatively impact long distance connectivity across the CCZ for nodule-bound organisms (Paterson et al., 2014; Taboada et al., 2018; Stewart et al., 2023) if appropriate impact mitigation measures are not established (e.g., the designation of 'set aside' areas aimed at ensuring that biodiversity and connectivity are maintained on a regional scale). Furthermore, the disturbance of the very fine sediment that makes up the surface layer of the seafloor caused by the passage and action of the nodule collector is expected to impact the benthic biota in several ways. The relocation of smaller-bodied organisms via sediment resuspension coupled to the damage and/or elimination of larger benthic fauna is expected to influence diversity and abundances of benthic biota (Vanreusel et al., 2016; Lefaible et al., 2024). Finally, the surface blanketing (up to 2–3 cm deposition) resulting from the sediment resuspension and dispersion has been observed to affect sediments in the vicinity of the collector tracks, altering both sedimentary properties and meiofaunal abundances (Lefaible et al., 2024).

As part of their environmental baseline studies, contractors are recommended to study food-web structures in pelagic and benthic habitats in their contract area (ISBA/25/LTC/6/Rev.3; ISA, 2023). Food webs are essentially networks of trophic entities, or nodes, that interact adaptively with fluxes of organic matter and energy within and across ecosystems. The quantification of the responses of ecological networks to environmental change is instrumental to the assessment of potential impacts of human activities on natural communities. In recent decades the development of metrics based on stable isotope analyses and the emergence of the concept of the 'isotopic niche'

(Newsome et al., 2007) have provided a quantitative framework for the study of food-web resilience. The use of natural stable isotopes can help to unravel trophic relationships between (groups of) organisms in marine ecosystems because the ratio of heavy-to-light isotopes, such as  $^{13}\text{C}/^{12}\text{C}$  ( $\delta^{13}\text{C}$ ) and  $^{15}\text{N}/^{14}\text{N}$  ( $\delta^{15}\text{N}$ ), in consumer tissues discloses information on both the food source and the trophic position of the consumers, respectively (Peterson and Fry, 1987).

More recently, a series of stable-isotope-based metrics have been developed to extract additional information from these data and gather insight into the trophic behaviour of organisms within a specific organisational level, such as a species, population, community or size class (Jackson et al., 2011; Abrantes et al., 2014; Pasotti et al., 2015; Jackson, 2023). Calculating standard ellipse areas (SEAs; Jackson et al., 2011) and Layman's community-wide metrics (Layman et al., 2007; Jackson et al., 2011) from the dual-isotope bi-plot space ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) position of individual samples within a community or group sheds light on possible differences in resource pool use, vertical structuring (trophic level organisation) and trophic niche diversification at different organisational levels. The quantification of these metrics provides part of the evidence for environmental baseline conditions and, at the same time, may help in the prediction of potential impacts and effects of the mining-associated pressures.

Nonetheless, stable isotope studies in the deep sea, including the CCZ, have been limited due to the analytical constraints of such analyses in habitats where individual organism densities and biomasses are particularly low, making sample preparation and sufficient replication challenging (Rex et al., 2006; Veit-Köhler et al., 2013; Parzanini et al., 2019). In particular, the soft-sediment benthic communities of the CCZ have been studied mostly in terms of their overall taxonomic composition and abundances for different geographical areas (e.g., Pape et al., 2017; Min et al., 2018; Washburn et al., 2021). Some studies made comparisons between the assemblages of nodule-rich and nodule-free stations (e.g., Vanreusel et al., 2016; De Smet et al., 2017; Pape et al., 2021), whereas little work has been dedicated to their functional roles and importance for ecosystem functioning. Recently, Sweetman et al. (2019) and Cecchetto et al. (2023) have focused on identifying possible energy pathways via the macrobenthic infauna (i.e., organisms living inside the sediment) by means of short-term pulse-chase experiments, hence touching upon the role of this soft-sediment size class in the abyssal carbon flux of the CCZ. Additionally, making use of CCZ benthic standing stock data and potential trophic relationships between different biological units gathered from the scientific literature, Stratmann (2023) modelled the possible food-web architecture in a CCZ exploration contract area. These energy pathway studies provide a window into the overall ecosystem functioning and possible carbon fluxes. Being either experimental (i.e., the pulse-chase experiment by Sweetman et al., 2019) or in a theoretical framework (i.e., the ecological network modelling by Stratmann, 2023), they lack ground-truthing in the unravelling of the

interdependency and/or competitive forces that are at play between different groups of organisms or between different biological levels of organisation.

This investigation is the first to address baseline soft-sediment infaunal food-web structure in the CCZ based on dual ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) natural stable isotope signatures and deduced trophic metrics. The effects of the geographic situation of sites ('Site'; B4S03 versus B6S02), the presence of nodules ('habitat'; by comparing nodule-rich versus nodule-free stations), as well as taxonomic identity ('taxon'; see later for the list of taxa investigated) and size class (meiofauna versus macrofauna) of the present organisms are also evaluated. We focused on two soft-sediment infaunal size classes, that is, meiofauna ( $>32\ \mu\text{m}$ ) and macrofauna ( $>300\ \mu\text{m}$ ) and the most abundant taxa (i.e., Nematoda, Copepoda, Polychaeta, Amphipoda, Isopoda, Tanaidacea), comparing nodule-free with nodule-rich sediments at two different sites within an exploration contract area in the northeastern CCZ. Results from the present analysis are discussed with a threefold goal: (i) unravel possible sensitivities at the different organisational levels investigated (taxon, size class, habitat, site) making use of isotopic niches and related metrics; (ii) consider these results in the context of vulnerabilities of the soft-sediment benthic food web in relation to potential mining impacts; and (iii) formulate recommendations for further research needed prior to mining and for monitoring practices of post-mining activities.

## Materials and methods

### *Study site and sample processing and analysis*

Samples were collected during the GSRNOD17 baseline campaign (May–June 2017) at four stations of the B4S03 and the B6S02 sites of the Global Sea Mineral Resources NV (GRS; Deme group, Belgium) exploration contract area (**Figure 1**). Samples were retrieved from the seafloor at depths ranging from 4480 m to 4649 m below sea level. Average nodule abundance (expressed as  $\text{kg m}^{-2}$ ; De Smet et al., 2017) was observed to be higher at B6S02, although average nodule volume ( $\text{cm}^3$ ) was significantly lower compared to B4S03 (De Smet et al., 2017). Similarly to what has been observed on a larger spatial scale across the CCZ at other sites (Smith et al., 1997; 2008a; 2008b), the more eastern site B6S02 presented higher estimated POC fluxes ( $1.61\ \text{g C}_{\text{org}}\ \text{m}^{-2}\ \text{yr}^{-1}$  at B6S02 versus  $1.56\ \text{g C}_{\text{org}}\ \text{m}^{-2}\ \text{yr}^{-1}$  at B4S03; Pape et al., 2018). Three stations were sampled within the B4S03 site of which two were characterised by a habitat rich in nodules (Nodrich) and one was reported to have sediments free of nodules (Nodfree; for more details on sampling at B4S03, see Pasotti et al., 2021). Another site (B6S02), located about 300 km to the east of B4S03, was sampled at a station rich in nodules. The use of multi-corer samplers (MUCs, comprising a frame mounting eight polycarbonate cores of 70 cm length and 10 cm inner diameter) aimed to target the meiofauna, as well as the bulk sediment. In total, eight MUCs were deployed at B4S03 in nodule-rich sediments (four replicates per station) and three in nodule-free sediments. Three MUCs were deployed at B6S02. From each MUC deployment one

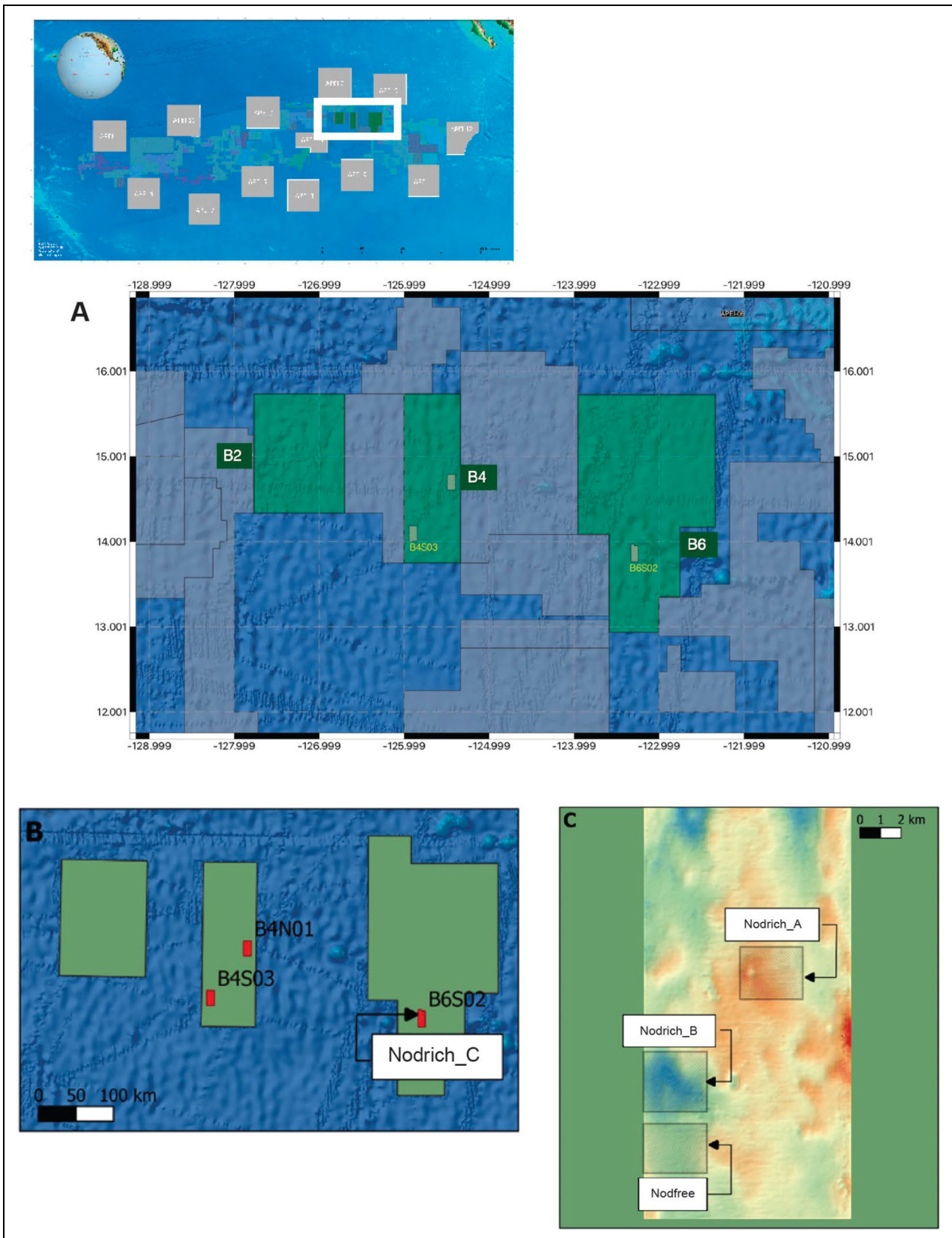
core was sampled and considered as one replicate. Each replicate was sliced in 1 cm layers down to 5 cm depth. Per slice, most of the sample was stored at  $-20^\circ\text{C}$  for meiofauna and bulk sediment stable isotope processing. Two aliquots of sediment ( $2 \times 0.5\ \text{mg}$ ) were freeze-dried and placed in pre-muffled ( $500^\circ\text{C}$ , 4 h) silver capsules for  $\delta^{13}\text{C}$  analysis (acidified with 0.5% HCl) and in pre-muffled ( $500^\circ\text{C}$ , 4 h) aluminium capsules for  $\delta^{15}\text{N}$  (non-acidified) analysis. All samples were left overnight to dry prior to pinch-closing the cups.

The meiofauna ( $\geq 32\ \mu\text{m}$ ) was extracted from the frozen sediment by means of a series of density gradient Ludox solution floatation/centrifugation, pooling all sediment layer depths together per core (0–5 cm bulk). Meiofaunal specimens were hand-picked in sufficient biomass for downstream analyses ( $>200$  nematodes,  $>10$  copepods, 1 or  $>1$  polychaete depending on individual morphotype biomass) by means of sterile needles, washed in milliQ water and placed into pre-muffled silver cups with milliQ water as the medium. The samples were left to dry at  $60^\circ\text{C}$  overnight and then pinched-closed and stored dry. Both meiofauna and bulk sediment samples were sent for dual stable isotope analysis to the Department of Earth and Environmental Sciences of the University of KU Leuven in Belgium. The samples were analysed via combustion using an elemental analyser (Thermo Flash HT/EA or EA 1110) coupled to an isotope ratio mass spectrometer system (Thermo Delta V Advantage) via a ConFlo IV interface. The raw data were calibrated using three standards: IAEA-600, Leucine and Tuna. All sample signatures were blank-corrected.

The larger size class (macrofaunal) organisms were obtained from 3 to 4 box corer deployments at each station ( $0.25\ \text{m}^2$  of surface; for more details, see Pasotti et al., 2021) where the 0–3 cm top layer of sediment was processed on board using the 'cold-chain method' and a  $300\text{-}\mu\text{m}$  mesh size sieve (ISA, 2015; Pape et al., 2018). A portion of the macrofaunal organisms was live-sorted on board, separated by higher taxon (Nematoda, Copepoda and Polychaeta), and stored at  $-20^\circ\text{C}$  until further analysis. The Polychaeta were the only taxon that could be identified to family level, information that was used later to investigate the link between individual sample position within the bi-plot space and feeding habits, according to Jumars et al. (2015). In the laboratory, individuals of the same taxon were pooled to achieve sufficient biomass (a minimum of  $20\ \mu\text{g C}$  per sample) for the dual stable isotope analysis and placed into pre-muffled ( $500^\circ\text{C}$ , 4 h) aluminium capsules, left to dry at  $60^\circ\text{C}$  overnight and pinched-closed and sent for analysis at UC Davis Stable Isotope Facility (University of California, USA).

### *Standard ellipse areas and Layman's metrics*

The present dataset was investigated across various levels of organisation of the trophic web following the ecological questions reported in **Table 1** and the sampling scheme displayed in Figure S1. Different subsets of the data were analysed to minimize the influence of the unbalanced sampling design, while identifying trophic relationships between different 'groups' across different



**Figure 1. Map of the Clarion-Clipperton Zone with details of the Global Sea Mineral Resources contract area.**

Upper map depicts the Clarion-Clipperton Zone (modified from <https://www.isa.org.jm/maps/clarion-clipperton-fracture-zone>), with the Global Sea Mineral Resources (GSR) contract area framed by the white box and the areas of particular ecological interest represented by light grey areas. In panel (A), the three GSR contract sub-areas B2, B4 and B6 are visible in green, with the small grey rectangular plots referring to the sampled sites, B4N01 (the unlabelled plot), B4S03 and B6S02. Panel (B) provides a zoomed map of the GSR contract area, with the sampled sites in red and the B6S02 station Nodrich\_C labelled. Panel (C) provides a zoomed map of B4S03, showing the locations of the three stations Nodrich\_A, Nodrich\_B and Nodfree.

**Table 1. SIBER<sup>a</sup> analysis conceptual scheme, with chosen levels for ‘community’ and ‘group’, research question addressed and outputs (community-wide metrics, group metrics, and Bayesian posterior probability analyses)**

Community	Group	Analysis	Research question	Group		
				Community-wide metrics <sup>b</sup>	Group metrics <sup>c</sup>	Bayes (groups) <sup>d</sup>
Whole dataset	Taxon	$i_a$	How do the higher taxa relate trophically to one another across the whole dataset?	NR, CR, CD, TA, MNND, SDMNND	TA, SEA, SEAc	SEAb comparison; proportional 95% overlap
Size class	Taxon	$i_b$	How do the higher taxa relate trophically within their size class (across the whole dataset)?	NR, CR, CD, TA, MNND, SDMNND	TA, SEA, SEAc	SEAb comparison; proportional 95% overlap
Site	Taxon	$i_c$	How do the higher taxa relate trophically within each site? (nodule-rich samples only)	NR, CR, CD, TA, MNND, SDMNND	Not calculated: $n < 5$	SEAb comparison; proportional 95% overlap
Habitat	Taxon	$i_d$	How do the higher taxa relate trophically within their habitat? (B4S03 site samples only)	NR, CR, CD, TA, MNND, SDMNND	Not calculated: $n < 5$	SEAb comparison; proportional 95% overlap
Site	Size class	$ii$	Does the relative trophic position of the two size classes change between sites? (nodule-rich samples only)	Not calculated because only two groups	TA, SEA, SEAc	SEAb comparison; proportional 95% overlap
Habitat	Size class	$iii$	Does the relative trophic position of the two size classes change at each respective habitat? (B4S03 site samples only)	Not calculated because only two groups	TA, SEA, SEAc	SEAb comparison; proportional 95% overlap

<sup>a</sup>Stable isotope Bayesian ellipses in R (SIBER).

<sup>b</sup>Nitrogen range (NR, y-axis), carbon range (CR, x-axis), mean Euclidean distance to centroid of groups (CD), mean nearest neighbour distance (MNND) and standard deviation of MNND (SDMNND).

<sup>c</sup>Total convex hull area (TA; requires a minimum of 3 points), standard ellipse area (SEA) and SEA corrected for small ( $n < 30$ ) sample size (SEAc; not calculated for groups with  $n < 5$ ).

<sup>d</sup>SEA accounting for uncertainty due to sampling method (SEAb).

'communities', that is, for the higher taxa groups (analyses  $i_a-i_d$ ):

- $i_a$ ) for all GSR contract area samples (community = infauna across all samples),
- $i_b$ ) within and between size classes (communities = size classes of meio- and macrofauna across all samples),
- $i_c$ ) within and between habitats (communities = infauna at nodule-free or nodule-rich habitats; only B4S03 samples), and
- $i_d$ ) within and between sites (communities = infauna of B4S03 and B6S02 nodule-rich habitats);

or the two size class groups (analyses  $ii-iii$ ):

- $ii$ ) within habitat (infauna at nodule-free or nodule-rich habitats, for B4S03 samples only), and
- $iii$ ) within site (infauna of B4S03 and B6S02 nodule-rich habitats).

To compare the isotopic niches between the various groups, the standard ellipse area (SEA, % $^2$ ; Jackson et al., 2011) of each group was computed by means of the R package SIBER (Jackson et al., 2011; Jackson, 2023) and displayed visually in the bi-plot space by means of the R package ggplot2 (version 3.4.2; Wickham et al., 2020).

Two Bayesian approaches were used to represent graphically the posterior probability of the data distribution of the groups (analyses  $i_a-i_b$  and  $ii-iii$ ; **Table 1**), derived by accounting for the uncertainty due to the sampling process (SEAb) and correcting the data for small sample size (SEAc, when  $n < 30$  within one group; Jackson et al., 2011). The posterior probability that  $SEAb_x$  was smaller than  $SEAb_y$ , where x and y are two different groups within a community, was calculated to compare the overall trophic niche space of two different groups within a community. The estimation of the SEAb overlap between two groups, expressed as a proportion of the sum of the non-overlapping areas of the 95% prediction ellipses (prop.95.over), was calculated to indicate the potential for trophic niche overlap between two given groups (with higher values indicative of greater overlap; ranging from 0 = no overlap to 1 = 100% overlap). Finally, three group metrics were calculated when groups were more than three: the convex hull total area (TA), the SEA, and the SEA corrected for small sample size (SEAc). All these calculations are based on fitting the Bayesian model to the data, as done by the R package RJags (2022, version 4.3.1).

The 'community-wide' Layman's metrics (Layman et al., 2012; 2007) were computed by means of the R package SIBER (Jackson et al., 2011; Jackson, 2023) to compare the trophic characteristics of the communities. These metrics were calculated only when the groups forming the community were more than two (analyses  $i_a-i_d$ ; not possible for analyses  $ii-iii$  as in **Table 1**). The metrics were (as per details in Layman et al., 2007):

- 1) dY-range ( $\delta^{15}N$ -range or NR), indicative of trophic range;
- 2) dX-range ( $\delta^{13}C$ -range or CR), indicative of the resource pool diversity;

- 3) total area (TA; the area encompassed by the polygon drawn by connecting the exterior data points of each group), indicative of total trophic niche area;
- 4) mean Euclidean distance of each group to the centroid (CD), indicative of the average trophic diversity;
- 5) mean near neighbour distance to centroid related to group trophic redundancy and group packing (MNND, where small MNND means high trophic redundancy); and
- 6) standard deviation of MNND (SDNND), indicative of trophic evenness.

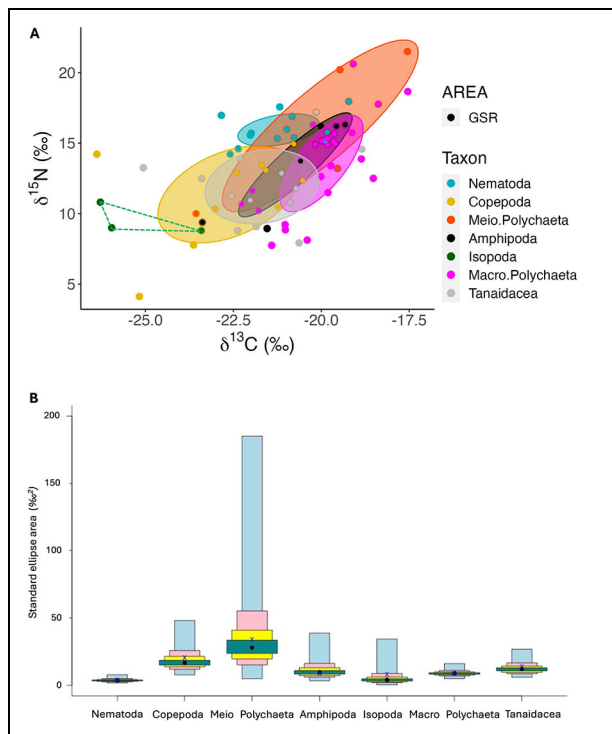
The use of SEA and related metrics to compare distinct (in time and/or space) trophic assemblage characteristics requires that the isotopic signatures of the baseline food source(s) are comparable across the investigated area, either to allow for direct comparability between consumer values or to inform needed corrections of consumer isotopic signatures prior to calculating such metrics (Layman et al., 2007; Hoenighaus and Zeug, 2008). To identify the possibility that the two sites were falling within the same 'isoscape' (same region of isotopic variation; Graham and Bury, 2019; Riccialdelli et al., 2024), we considered the sediment organic pool  $\delta^{13}C$  and  $\delta^{15}N$  signal as a proxy for a time-integrated suspended particulate organic matter isotopic value. We assumed that the phytoplankton bloom in the considered area happened at approximately the same time and that the generated particulate organic matter sank to the seafloor during a comparable amount of time, considering the similar depth of the two studied sites. The sediment organic pool at the two sites (and across stations) did not differ significantly: both  $\delta^{13}C$  and  $\delta^{15}N$  values were nearly identical between the two sites and showed low standard deviation within each site ( $\delta^{13}C = -20.19 \pm 0.51$  and  $\delta^{15}N = 11.97 \pm 0.53$  at B4S03;  $\delta^{13}C = -20.03 \pm 0.49$  and  $\delta^{15}N = 12.33 \pm 0.31$  at B6S02). This close similarity supported the assumption of comparable detrital baseline food sources for the two sites and allowed the use of the SEAs and metrics for the purpose of this investigation.

## Results

### Isotopic niche differences

The results of the SIBER analysis highlight the isotopic niche differences investigated, following the sampling scheme (Figure S1) and research questions (**Table 1**). The SEA (displaying 40% of the posterior probability of the data distribution) for the different analyses are reported in **Figures 2A, 3A** and **4A**, together with the density plot displaying the probability distribution of the SEAb and SEAc data (in **Figures 2B, 3B** and **4B**).

An overview of the results of the group metrics and the community-wide metrics from the Bayesian analysis are presented in **Table 2** and **Table 3**, respectively. The SIBER analysis pair-wise comparison of the group Bayesian posterior probabilities (SEAb; see Table S1 for the probability that one  $SEAb_x > SEAb_y$ , where x and y are two different groups within each analysis level) and the group ellipse overlap, expressed as prop.95.over, are reported in Table



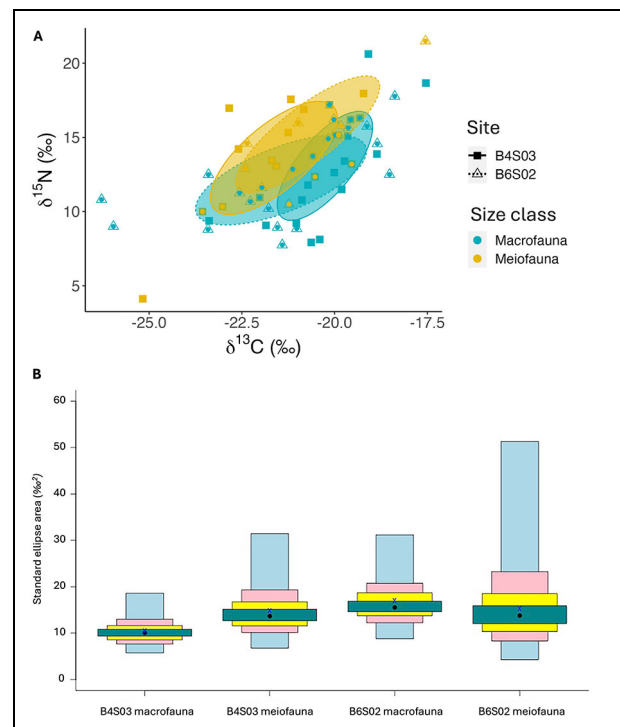
**Figure 2. Higher taxon standard ellipse areas and density plots for the complete GSR dataset.** (A) Standard ellipse areas (SEAs) representing 40% of the  $\delta^{13}\text{C}/\delta^{15}\text{N}$  bi-plot data distribution of the seven higher taxa (Amphipoda, Copepoda, Isopoda, Nematoda, Meiofaunal Polychaeta, Macrofaunal Polychaeta and Tanaidacea) across the Global Sea Mineral Resources (GSR) contract area. For the Isopoda, the SEA could not be calculated given only three data points (a minimum of five is needed); the green dashed polygon allows visualisation of the points. (B) Density plot displaying the standard Bayesian ellipse area (SEAb, dark blue dots) with confidence intervals (coloured boxes) and the SEA value corrected for small sample size (SEAc, purple cross) for the seven higher taxa across the whole GSR area. The colours indicate confidence intervals of 99% (light blue), 75% (pink), 50% (yellow) and 25% (dark green) for distribution of the data.

S2. Information on all the metrics measured is summarised visually, following the ecological research questions of **Table 1**, in **Figures 5–7**.

### Taxonomic analyses

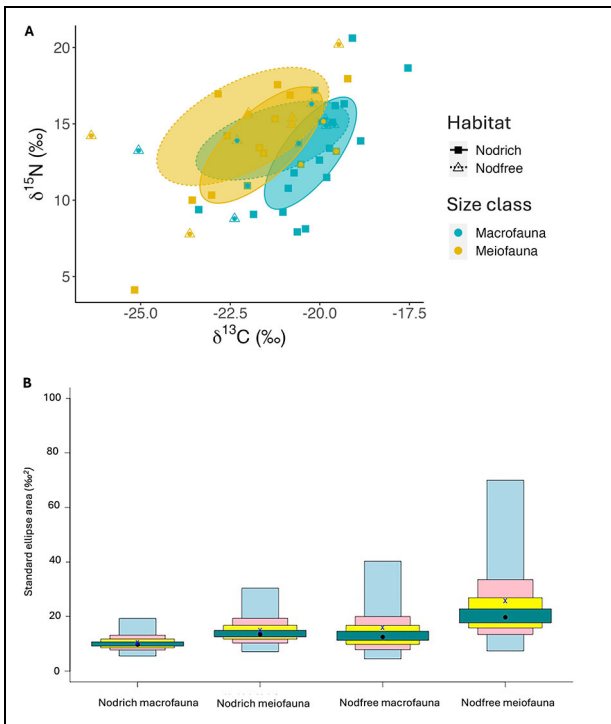
#### *i*<sub>a</sub>) How do the higher taxa relate trophically to one another (complete infaunal dataset)?

Comparing the different metrics in detail, the largest TA (group metrics; **Table 2**) was estimated to be for the Copepoda ( $37.2\% \text{‰}^2$ ), followed by the Tanaidacea ( $31.2\% \text{‰}^2$ ), the macrofaunal Polychaeta ( $29.6\% \text{‰}^2$ ) and the meiofaunal Polychaeta ( $20.7\% \text{‰}^2$ ). The SEA was largest for the meiofaunal Polychaeta ( $22.8\% \text{‰}^2$ ) followed by the Copepoda ( $18.4\% \text{‰}^2$ ) and the Tanaidacea ( $12.4\% \text{‰}^2$ ). When SEAs were corrected for small sample size (SEAc), the meiofaunal Polychaeta (SEAc =  $34.2\% \text{‰}^2$ ) displayed the largest SEAc,



**Figure 3. Standard ellipse areas and density plots for the two size classes at only nodule-rich sites.** (A) Standard ellipse areas (SEAs) representing 40% of the  $\delta^{13}\text{C}/\delta^{15}\text{N}$  bi-plot data of the two size class groups (macrofauna in blue, meiofauna in yellow) between the two sites (only nodule-rich sediment samples: B4S03, solid line ellipse; B6S02, dashed line ellipse). (B) Density plot displaying the standard Bayesian ellipse area (SEAb, black dots) with confidence intervals (coloured boxes) and the SEA value corrected for small sample size (SEAc, blue cross) for the two size classes (macrofauna and meiofauna) across all samples from nodule-rich sediments and comparing between sites (B4S03 and B6S02). The colours indicate confidence intervals of 99% (light blue), 75% (pink), 50% (yellow) and 25% (dark green) for distribution of the data.

followed by the Copepoda (SEAc =  $20.6\% \text{‰}^2$ ) and Tanaidacea (SEAc =  $13.6\% \text{‰}^2$ ). The smallest area in the bi-plot space (**Figure 2A** and **B**) was occupied by the group Nematoda (TA =  $8.81\% \text{‰}^2$ ; SEAc =  $3.97\% \text{‰}^2$ ). The probability that SEAb (SEA calculated as the Bayesian posterior probability of the data distribution) of Nematoda would be smaller than that of the other groups ranged from 0.0635 (Nematoda < Amphipoda) to 0.937 (Nematoda < macrofaunal Polychaeta; **Table S1**). Within the meiofaunal size class, Nematoda displayed the smallest SEAb, with  $\text{Nematoda}_{\text{SEAb}} < \text{Copepoda}_{\text{SEAb}} < \text{Polychaeta}_{\text{SEAb}}$  (**Figure 2A**). The SEAc of Polychaeta displayed very different trends for the two size classes, with the meiofaunal Polychaeta displaying a much larger SEAc ( $34.2\% \text{‰}^2$ ) than that of the macrofaunal Polychaeta (SEAc macrofaunal Polychaeta =  $8.92\% \text{‰}^2$ ). In support of this finding, the posterior probability (**Figure 2B**) that the SEAb of meiofaunal Polychaeta was smaller than that of the macrofaunal Polychaeta was null (**Table S1**). Within the macrofaunal size class, the Tanaidacea displayed



**Figure 4. Standard ellipse areas and density plots for the two size classes at the two habitats.** (A) Standard ellipse areas (SEAs) representing 40% of the  $\delta^{13}\text{C}/\delta^{15}\text{N}$  bi-plot data of the two size class groups (macrofauna in blue, meiofauna in yellow) between the two habitats (Nodrich at B4S03 site, solid line ellipse; Nodfree, also at B4S03, dashed line ellipse). (B) Density plot displaying the standard Bayesian ellipse area (SEAb, black dots) with confidence intervals (coloured boxes) and the SEA value corrected for small sample size (SEAc, blue cross) for the two size classes (macrofauna and meiofauna) at site B4S03 between nodule-rich (Nodrich) and nodule-free (Nodfree) habitat types. The colours indicate confidence intervals of 99% (light blue), 75% (pink), 50% (yellow) and 25% (dark green) for distribution of the data.

the largest TA, SEA and SEAc, and the posterior probability of the Tanaidacea to display a smaller SEAb than that of the other macrobenthic groups ranged from zero (Tanaidacea SEAb < Amphipoda SEAb and Tanaidacea SEAb < Polychaeta SEAb) to 0.24 (Tanaidacea SEAb < Isopoda SEAb). The largest overlap was observed between macrofaunal Polychaeta and Amphipoda (prop.95.over = 0.57) and between Copepoda and meiofaunal Polychaeta (prop.95.over = 0.47). The smaller overlap was observed between macrofaunal Isopoda and Polychaeta (prop.95.over = 0.11) and Isopoda and Amphipoda (macrofauna, prop.95.over = 0.14). Within the meiofauna, Nematoda and Polychaeta displayed an overlap of prop.95.over = 0.12 and Nematoda and Copepoda, an overlap of prop.95.over = 0.19 (Table S2).

*i<sub>b</sub>) How do the higher taxa relate trophically within their size class?*

In this analysis, the group metrics of the different taxa were analysed within their size class to estimate the

redundancy and trophic niche extent of the two size classes (Figures 7 and S2). The macrofauna appeared to exploit a larger resource pool, with a carbon range (CR) twice that of the meiofauna. The trophic range (nitrogen range, NR) was about 20% larger for the meiofauna compared to the macrofauna (meiofauna NR = 4.86, macrofauna NR = 4.02; Table 2). The meiofaunal taxa displayed higher trophic niche partitioning, with the Nematoda SEAb posterior probability of niche overlap with the other two taxa being lower than 20% in both cases (Table S1). Within the macrofauna, SEAb for most taxa was estimated to overlap for >20% with the other taxa, except for the Isopoda, which were estimated to overlap only 14% with the Amphipoda and 10% with the Polychaeta (and 26% with the Tanaidacea; Table S2). For the Isopoda, however, these metrics should be treated with caution, as the sample size was lower than the minimum (3 samples instead of 5 minimum replicates). In short, these results show that the macrofaunal community displayed a smaller NR compared to the meiofauna but a much larger resource pool (CR). The MNND was larger for the meiofauna (2.40) compared to the macrofauna (1.89), pointing to a lower trophic redundancy in the former. These results may point to underlying adaptive forces, leading to clearly diverging trophic roles of the Copepoda and Nematoda assemblages within the sediment detrital pool, and to a lower degree of functional redundancy in the smaller size class compared to the larger macrofauna.

*i<sub>d</sub>) How do the higher taxa behave trophically within their habitat (B4S03 samples only)?*

The different taxa were analysed within each habitat (nodule-free versus nodule-rich) at the B4S03 site to estimate the redundancy and trophic niche extent of the two communities. In general, the community at the nodule-rich sediments spanned a larger trophic range (Nodrich<sub>NR</sub> 57.6% larger than Nodfree<sub>NR</sub>), which appeared to be based on a relatively smaller resource pool compared to the assemblage at the nodule-free station (Figure S3; Table 3). The carbon pool of the nodule-free sediments, estimated by the CR metric, was 33% larger than at the nodule-rich stations, with an 11.7% higher trophic diversity (CD; Figure 5). Nonetheless, the Layman’s metrics are known to be affected by small sample size (Jackson et al., 2011), and the number of samples at the nodule-free station was much lower than for the nodule-rich stations; at this organisational level, these metrics should be interpreted with caution. The two habitats showed comparable MNND and SDNND values and thus a comparable degree of trophic redundancy and species packing (Figure 5).

*i<sub>e</sub>) How do the higher taxa relate trophically within each site (nodule-rich samples only)?*

In this analysis, the different taxa were analysed within each site across nodule-rich samples to estimate the redundancy and trophic niche extent of the two infaunal communities. While the trophic range is comparable between sites (difference of only 4.8%; Table 3 and Figure 6), the resource pool at B6S02 was, as calculated by the carbon range metric, 71.7% larger than that of B4S03. Interesting is the SDNND

**Table 2. Group metrics<sup>a</sup> calculated for the different SIBER<sup>b</sup> analyses described in Table 1*****i<sub>a</sub>-i<sub>d</sub>* Taxon analysis: TA, SEA and SEAc for different taxa across all samples (no site or size class effect)**

Community	Group	TA (‰ <sup>2</sup> )	SEA (‰ <sup>2</sup> )	SEAc (‰ <sup>2</sup> )
Size class (complete GSR <sup>c</sup> dataset)	1. Nematoda	8.81	3.64	3.97
	2. Copepoda	37.16	18.35	20.65
	3. Meio.Polychaeta	20.66	22.79	34.18
	4. Amphipoda	9.47	7.33	9.16
	5. Isopoda	2.27	4.13	8.25
	6. Macro.Polychaeta	29.61	8.53	8.92
	7. Tanaidacea	31.23	12.43	13.56

***ii* Size class × site analysis: TA, SEA and SEAc for two size classes within each site (only nodule-rich stations)**

Community	Group	TA (‰ <sup>2</sup> )	SEA (‰ <sup>2</sup> )	SEAc (‰ <sup>2</sup> )
B4S03	Macrofauna	30.86	9.92	10.47
	Meiofauna	34.31	13.72	14.86
B6S02	Macrofauna	40.23	16.01	16.95
	Meiofauna	14.80	12.29	15.36

***iii* Size class × habitat analysis: TA, SEA and SEAc for two size classes within each habitat**

Community	Group	TA (‰ <sup>2</sup> )	SEA (‰ <sup>2</sup> )	SEAc (‰ <sup>2</sup> )
Nodule-rich	Macrofauna	30.86	9.92	10.47
	Meiofauna	34.32	13.72	14.87
Nodule-free	Macrofauna	18.68	13.31	15.97
	Meiofauna	33.31	21.63	25.83

<sup>a</sup>Total convex hull area (TA), standard ellipse area (SEA), SEA accounting for uncertainty due to sampling method (SEAb) and SEA corrected for small sample size (SEAc,  $n < 30$ ).

<sup>b</sup>Stable isotope Bayesian ellipses in R (SIBER).

<sup>c</sup>Global Sea Mineral Resources (GSR).

metric, which indicates the degree of species packing, where lower values are a sign of closer trophic position of the groups (taxa). This metric was more than twice as small at B4S03 compared to B6S02 (122% larger SDNND at B6S02; **Table 3** and Figure S4). In conclusion, B6S02 displayed larger MNND (31.4% larger than at B4S03), hence lower trophic redundancy, with a larger trophic evenness for the different taxa (**Figure 6**).

**Size class analyses (ii –iii)**

In the following analyses, the two size classes were treated as groups (taxa were pooled per size class; **Table 1**) across the two sites (analysis *ii*; only nodule-rich samples) and the two habitats (analysis *iii*; only B4S03 site samples). For these analyses, only group metrics were computed (**Tables 2** and S1).

***ii* Does the relative trophic position of the two size classes differ between sites?**

Different patterns in group metrics were observed at the two sites for both size classes (**Table 2**). The differences in TA for both macro- and meiofauna were larger at B4S03

compared to B6S02. The two size classes showed different patterns between sites (**Table 2**), with meiofaunal TA (34.3‰<sup>2</sup>) > macrofaunal TA (30.9‰<sup>2</sup>) at B4S03, and the opposite finding at B6S02, where macrofaunal TA (40‰<sup>2</sup>) > meiofaunal TA (14‰<sup>2</sup>). When the isotopic niche was corrected for small sample size (SEAc;  $n < 30$ ), the meiofauna at the B4S03 site displayed an ellipse 41.9% larger than that of the macrofauna (**Figure 3**), whereas at B6S02 the meiofaunal size class SEAc was 10.3% smaller. The computed Bayesian posterior probability that one SEAb would be larger than the other (Table S1; **Figure 3**) was meiofaunal SEAb at B4S03 < meiofaunal SEAb at B6S02 = 0.57 and macrofaunal SEAb at B4S03 < macrofaunal SEAb at B6S02 = 0.93. The overlap between the two size class SEAb values (Table S2) was 54% at B4S03 and 52% at B6S02, indicating a comparable isotopic niche overlap for these size classes at the two sites. From the SEA results the meiofauna displayed a much larger isotopic niche than the macrofauna at the B4S03 site, whereas at B6S02 the meiofaunal size class displayed a smaller isotopic niche, given a comparable overlap between the two size class isotopic niches at both sites.

**Table 3. Community-wide metrics<sup>a</sup> calculated for the different taxa (group: taxon) across different community levels**

Group	Analysis	Community <sup>b</sup>	NR	CR	TA (‰ <sup>2</sup> )	CD	MNND	SDNND
Taxon	$i_a$	GSR	6.69	5.22	11.14	2.47	1.33	0.83
	$i_b$	Macrofauna	4.02	5.22	2.14	2.17	1.89	1.65
		Meiofauna	4.86	2.61	2.49	2.33	2.41	2.06
	$i_c$	Nodrich	5.64	2.79	7.10	1.97	1.18	0.67
		Nodfree	3.58	3.72	4.14	2.20	1.11	0.72
	$i_d$	B4S03	5.64	2.79	7.10	1.97	1.18	0.67
		B6S02	5.91	4.79	7.87	1.87	1.55	1.49

<sup>a</sup>Trophic range (NR); resource pool or carbon range (CR); total area (TA); average trophic diversity (CD); mean nearest neighbour distance (MNND) and measure of trophic redundancy; and standard deviation of MNND (SDNND) and indication of species packing.

<sup>b</sup>Global Sea Mineral Resources NV (GSR) exploration contract area (**Figure 1**); nodule-rich (Nodrich) and nodule-free (Nodfree).

### iii) Does the relative trophic position of the two size classes differ between habitats?

The two habitat size-class communities were investigated within the B4S03 site. Both the TA and SEA corrected for small sample size (SEAc) of the meiofauna were larger than those of the macrofauna at both habitats, with the difference being larger at the NodFree habitat (**Table 2**). The meiofauna of the nodule-free sediments, displayed a 61.7% larger SEAc than that of the macrofauna, compared to 41% at the nodule-rich stations. The Bayesian posterior probability that the meiofauna SEAb was larger than that of the macrofauna was 84% at the nodule-rich sediments and 83% at the nodule-free sediments (**Table S1**; **Figure 4**). The overlap between the two size classes was 10% larger at the nodule-free habitat and amounted to 56% (**Table S1**; **Figure 4**). The nodule-free meiofaunal samples displayed the highest dispersion within the bi-plot space (**Figure 4B**), encompassing a more variable isotopic niche compared to the other three groups.

## Discussion

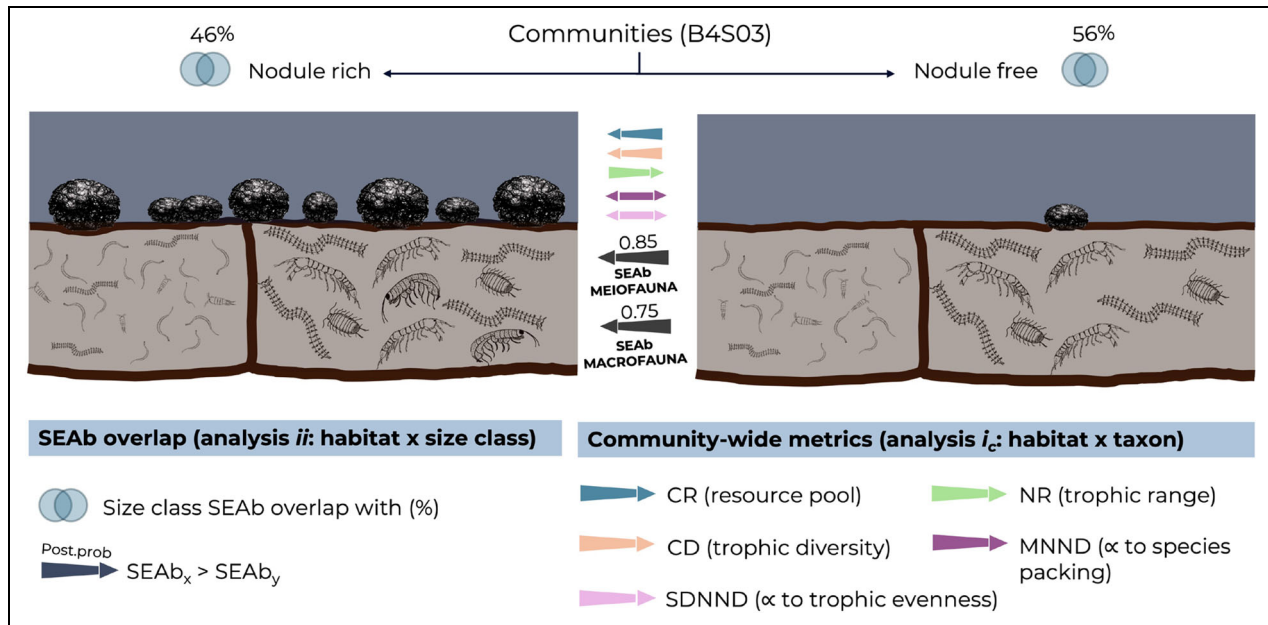
The present analysis deepens our knowledge of the food-web structure of soft-sediment infaunal communities in the GSR exploration contract area in the eastern CCZ. It provides novel data for the region where, to date, natural  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  stable isotopic signatures of meio- and macrofaunal organisms have been reported only within the scope of in situ experiments (C and N uptake of prelabelled detritus), where the preservation method (formaldehyde fixation, appropriate to the experimental goals; Stratmann et al., 2018; Sweetman et al., 2019; Stratmann, 2023) altered the natural signature of the organisms and sediment matrix (Lau et al., 2012). Interpretations of the present analysis have been carried out within this context of limited background knowledge (Tecchio et al., 2013; Sweetman et al., 2019; de Jonge et al., 2020; Stratmann, 2023).

The following discussion is organised in two parts: (1) on the observed trophic niche structure at the various organisational levels in relation to the current available knowledge of the CCZ and the GSR exploration contract

area specifically; and (2) on the potential impacts of the nodule collector activities at the seabed on the investigated taxa, based on the isotopic niche characteristics presented here. The main results are summarised in three infographics: **Figure 5** conceptualises the comparison of metrics between habitats, **Figure 6** depicts the comparison of metrics between sites and **Figure 7** depicts the main metrics for the two size classes and the individual taxa. To interpret and discuss the vulnerability of the different groups (taxa or size classes) and communities (as per **Table 1**), we use the trophic niche ecological theory as extracted from Cachera et al. (2017; and references therein) and Lesser et al. (2020; and references therein).

### Trophic niches of soft-sediment infaunal assemblages in the GSR contract area

Metrics for trophic niche size have been used widely in the assessment of food-web and population responses to habitat fragmentation (Layman et al., 2012; Abrantes et al., 2014; Parzanini et al., 2019; Lesser et al., 2020) and in the spatial analysis of trophic relationships among key benthic taxa along gradients of environmental disturbance and productivity (Tecchio et al., 2013; Abrantes et al., 2014; Pasotti et al., 2015; Alp and Cucherousset, 2022). The use of dual stable isotope natural tracers represents a powerful tool for both comparison of extant conditions and to measure consequences of environmental change over time (Alp and Cucherousset, 2022). Deep-seabed mining activities will significantly change the sediment landscape along the collector tracks and potentially also beyond, and it will affect local biodiversity by removing sessile hard substrate-dependent, hence nodule-dependent fauna (Vanreusel et al., 2016). In a food-web network modelling exercise focusing on the GSR exploration contract area, Stratmann (2023) concluded that nodule-dependent fauna was only responsible for a small fraction of total carbon cycling, whereas her model estimated that, of all carbon flows measured, 69.8% (at B6S02) and 71.2% (at B4S03) flowed through the microbial loop and benthic prokaryotes. The author also reported that the removal of nodules and associated fauna influenced the total local



**Figure 5. Visuals of community-wide metrics and size-class SEAB overlap at the two habitats at site B4S03.**

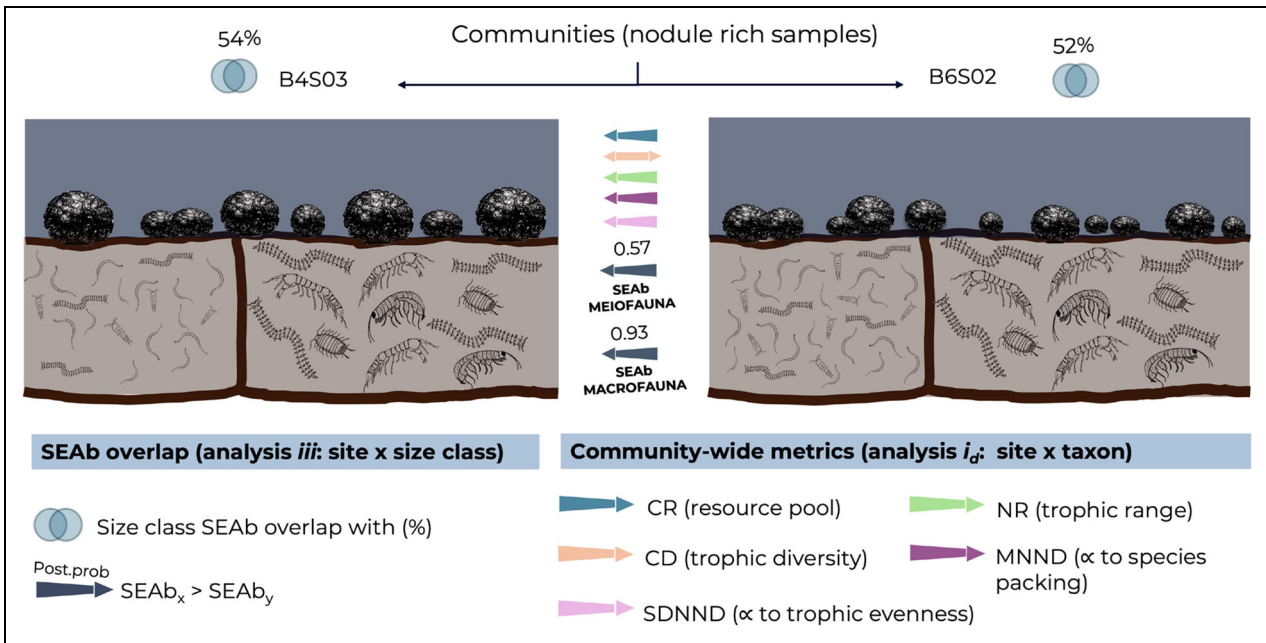
Visual scheme displaying the community-wide metrics (coloured arrows; inset legend) calculated for the two habitats (nodule-rich and nodule-free), considering the various taxa (groups) and analysing for samples only from site B4S03 (analysis  $i_c$  in **Table 1**). The standard ellipse area (SEA) accounting for the uncertainty due to the sampling process (SEAb) of meiofauna and macrofauna (dark grey arrows) is compared between habitats (analysis  $iii$  in **Table 1**). The group SEAb is displayed as  $SEAb_x > SEAb_y$ , with the arrow pointing from larger to smaller SEAb (for details, see **Table S1**). The Bayesian posterior probability is reported above each dark grey arrow as a value ranging from 0 (no overlap) to 1 (complete overlap). The Venn diagram above each habitat schematic represents the proportion of the sum of the non-overlapping areas of the 95% prediction ellipses (overlap) of the two size classes within each habitat (values in %; **Table S2**).

estimated carbon flow, but did not impact the microbial loop, according to the applied model. Contrary to expectations of the model by Straatman (2023) for the GSR area, a disturbance experiment, simulating deep-seabed mining by ploughing of the sediment in the Peru Basin (DISCOL experiment; Vonnahme et al., 2020), showed that microbial activity remained significantly reduced even 26 years from the disturbance. Treating model expectations with caution is therefore important.

In our community niche-based analysis of the higher infaunal taxa inhabiting the sediments at the two habitats (**Figure 5**), the community at the nodule-free station displayed a smaller trophic range (42% lower NR) characterised by a higher trophic diversity (33% higher CD) supported by a relatively larger resource pool (11.8% higher CR) compared to the nodule-rich sediments (**Figure 4**). The meio- and macrofauna displayed a much larger trophic niche width (both SEAb and SEAc) at the nodule-free station, where the two size classes also displayed a 10% larger niche overlap (**Figure 4**) compared to the nodule-rich infaunal assemblage. This difference is indicative of a lower resource partitioning (or niche differentiation), suggesting higher trophic and functional redundancy among the two investigated size classes in nodule-free sediments where they more likely would share the present basal resources. Two competing theories postulate that generalist species (such as omnivores and detritus feeders) would adapt their trophic niche depending on

system productivity. They would adapt either by capitalising on the resources increasing their trophic niche width (by diversifying their food intake and hence the individual trophic niche; Pool et al., 2017) or by focusing on their preferred food source, narrowing the trophic spectrum and diminishing inter-specific competition (as per optimal foraging theory [OFT]; Pyke et al., 1977; example in Lesser et al., 2020). Within the niche variation hypothesis, discussed by Cachera et al. (2017), other mechanisms are identified as the 'ultimate sources' of a species (or population) trophic niche size. These mechanisms are discussed as dependent on individual diet variation, which is the result of the balance between intra- and inter-specific competition for food. Tecchio et al. (2013) observed for deep-sea megabenthic communities of the Mediterranean Sea along a west-to-east productivity gradient that the trophic niche width and the spectrum of the carbon sources (CR) correlated positively with surface productivity. In contrast, Lesser et al. (2020) observed that for two generalist fish species, the trophic niche size and niche overlap decreased with increasing ecosystem productivity of seagrass beds, because the increased productivity would allow each species to focus on a narrower diet, increasing trophic niche partitioning.

In the present study we observed smaller SEAb for both size classes in the nodule-rich sediments compared to the nodule-free assemblages (**Figures 4** and **S3**; **Table 2**) with a reduced overlap between the two size classes. If we

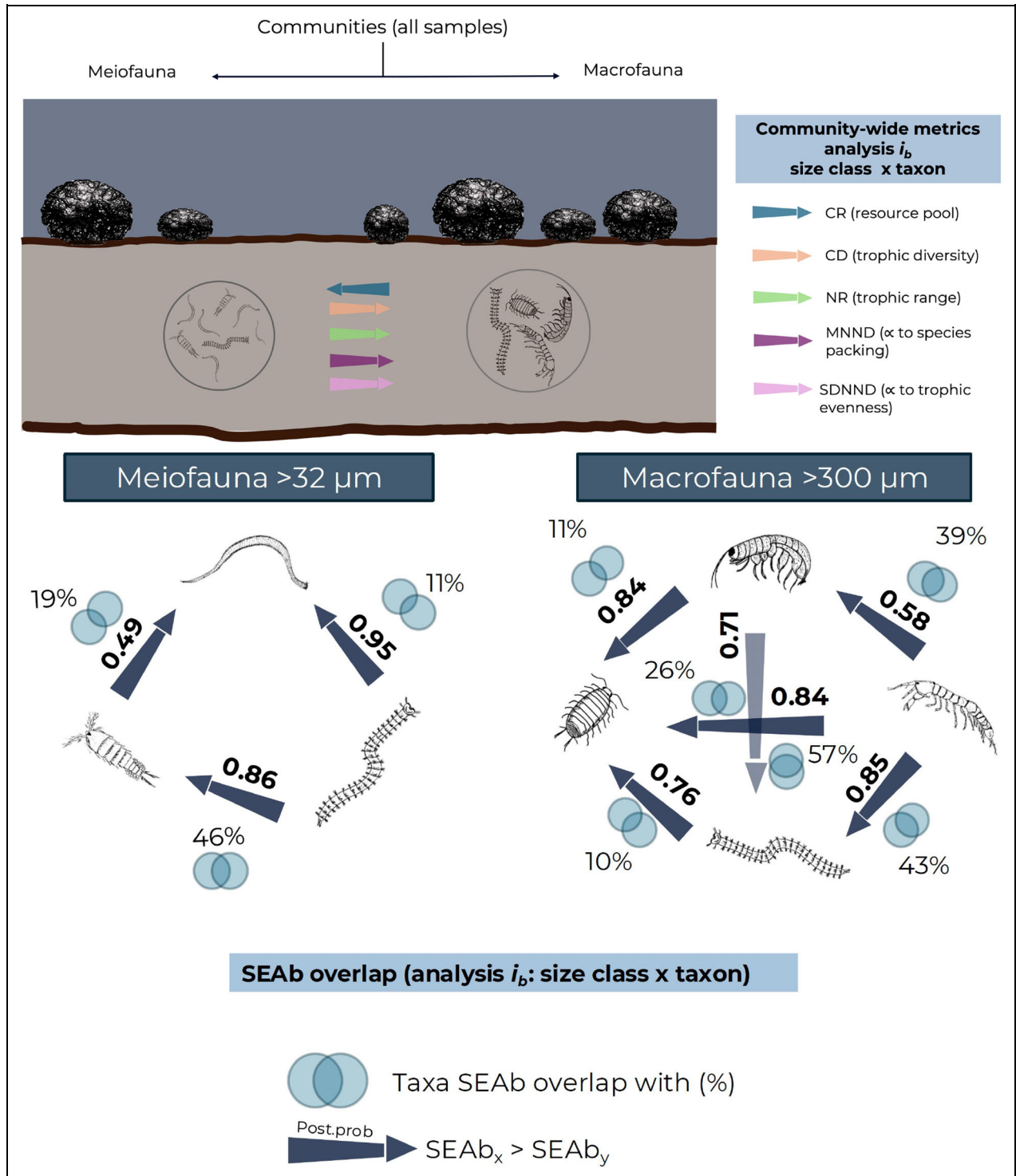


**Figure 6. Visuals of community-wide metrics and size-class SEAb overlap of nodule-rich assemblages at the two sites.** Visual scheme displaying the community-wide metrics (coloured arrows; inset legend) calculated for the two sites (B4S03 and B6S02), considering the various taxa (groups) and analysing only nodule-rich samples (analysis  $i_d$  in Table 1). The group standard ellipse area (SEA) accounting for the uncertainty due to the sampling process (SEAb) of meiofauna and macrofauna (dark grey arrows) is compared between sites (analysis  $ii$  in Table 1). The group SEAb is displayed as  $SEAb_x > SEAb_y$ , with the arrow pointing from larger to smaller SEAb (for details, see Table S1). The Bayesian posterior probability is reported above each dark grey arrow as a value ranging from 0 (no overlap) to 1 (complete overlap). The Venn diagram above each habitat schematic represents the proportion of the sum of the non-overlapping areas of the 95% prediction ellipses (overlap) of the two size classes within each site (values in %; Table S2).

consider the meio- and macrofauna as two competing generalist functional groups (as per optimal foraging theory), the presence of nodules would appear to provide a larger variety of resources, such as nodule-associated microbial organisms (i.e., fungi, protists, prokaryotes), and/or carcasses from sessile organisms associated with the nodules. Meiofaunal organisms are known to be active players in the reworking of detrital organic matter by consuming directly or indirectly the prokaryotes that are the base of the sediment microbial loop (Giere, 2009; Pasotti et al., 2015; Sweetman et al., 2019; Giere and Schratzberger, 2023; Ingels et al., 2023). The taxa belonging to each infaunal size class may possibly use segregated energy pathways as they experience different fractal dimensions within their habitat. This segregation would lead to size-based compartmentalised food webs that would be more pronounced in the nodule-rich habitats, displaying narrower size class isotopic niches with a lower overlap. Nodules are expected to increase seabed structural complexity by providing hard substrate on the abyssal seafloor. Habitat heterogeneity has been linked to the enhancement of trophic niche partitioning across different habitats, where the resulting compartmentalised food webs were linked to higher robustness and persistence (Stouffer and Bascompte 2011; Nonaka and Kuparinen 2021; Nauta et al., 2023). The effect of compartmentalisation on food-web stability is still under debate, as it depends on the definition of stability, the scale at which

food webs are considered and the type of connectance that is expected to exist between the investigated food webs (Mougi, 2018). Nonetheless, the removal of nodules from the seabed is expected to decrease habitat complexity and lead to biodiversity loss in the sites affected by mining (Stratmann et al., 2021). These effects may be reflected in a reorganisation of the soft-sediment food web, with potential effects on overall food-web stability and connectance.

The model of Stratmann (2023) estimated that the removal of nodules and associated fauna would lead to a reduction of the scavenger loop (considered to be formed by the Amphipoda, Mysida and Isopoda) by 56.5% (B6S02) and 71.6% (B4S03). Iken et al. (2001) observed at the Porcupine abyssal plain (NE Atlantic Ocean) that the predator/scavenger role in the deep sea fell under two main groups: those feeding on an exclusively benthic food web of invertebrate deposit-feeder organisms and those highly mobile species functioning as a link between the benthic and pelagic food webs through their feeding on pelagic prey and possibly also settling phytodetritus (Jeffreys et al., 2011). Hence, the reduced scavenging activity predicted by Stratmann (2023) for sediments from which nodules have been removed, coupled with the expected decrease in the benthic-pelagic coupling following the removal of sessile filter- and suspension-feeding nodule-dependent mega-fauna (Vanreusel et al., 2016), might lead to a reduction



**Figure 7. Visuals of community-wide metrics of the two size classes, taxa SEAb overlap and posterior probabilities.** Upper schematic displays the community-wide metrics (coloured arrows; inset legend) calculated for the two size classes (communities), considering the various taxa (groups) and analysing the complete dataset (analysis  $i_b$  in Table 1). Bottom schematic presents Bayesian posterior probabilities for group standard ellipse area (SEA) accounting for the uncertainty due to the sampling process (SEAb; for details, see Table S1), calculated for SEAb<sub>x</sub> > SEAb<sub>y</sub>, with the arrow pointing from larger to smaller SEAb and posterior probability reported above each grey dark arrow as a value ranging from 0 (no overlap) to 1 (complete overlap). The Venn diagrams are not to scale but they indicate by the values reported next to them (in %) the proportion of the sum of the non-overlapping areas of the 95% prediction ellipses of the specific taxa pairs (Table S2).

in the trophic range of the soft-sediment infaunal assemblages following mining. Although such a reduction is only a hypothesis, resulting from reasoning built around

the food-web network model for the GSR exploration contract area by Stratmann (2023) and linking previous observations in other deep-sea habitats (Iken et al., 2001;

Jeffreys et al., 2011), some of our observations (**Figure 5**) appear to be aligned with this hypothesis. In our analysis, amphipods were observed only in nodule-rich samples (Figure S4); their absence might be responsible at least partially for the observed reduction of trophic range in the nodule-free habitat (NR, **Table 3; Figure 5**). Roughly half of the deep-sea amphipod species are known to be scavengers (Havermans and Smetacek, 2018), and even in other taxa, scavenging has often been reported as facultative for predators and omnivores, increasing food-web stability (King et al., 2007; Jeffreys et al., 2011; Wilson and Wolkovich, 2011). Stratmann (2023) reported at B4S03 that 89% of the scavenging took place by amphipods, which were mostly seen in pairs and associated with sponge stalks (Stratmann et al., 2021). Although the amphipods within this study were not identified to family level, hence reducing the *a priori* information available on their feeding habits, the high  $\delta^{15}\text{N}$  values of four out of six amphipod samples (Figure S5) at the nodule-rich stations may hint that these morphospecies belong either to a predator/scavenger feeding type or to deposit-feeding on highly refractory organic matter.

A similar observation was made for the polychaetes (Figure S6). Across the bi-plot space, the polychaete samples from the nodule-rich sediments occupied a larger trophic range compared to the nodule-free samples, which clustered closely together at intermediately high  $\delta^{15}\text{N}$  values. This larger range implies a higher trophic redundancy in nodule-free sediments for the polychaete assemblage compared to the nodule-rich habitat. We can corroborate this implication by linking the feeding habits of the different families (assigned following Jumars et al., 2015; Table S3) to the position of the individual samples within the bi-plot isotopic space. Nereididae, Lumbrineridae and Ophaeliidae occupied the highest trophic positions (Figure S5) and only occurred in the nodule-rich samples. Ophaeliidae are known to be deposit-feeders on highly refractory organic matter, whereas both Nereididae and Lumbrineridae are known to be omnivores and carnivores, respectively, with a facultative scavenging behaviour (Fauchald and Jumars, 1979; Jumars et al., 2015). Nonetheless, the sampling effort was unequal between the two habitats, and these results may be biased due to the overall limited sampling. We strongly recommend future research to focus on more stations free from nodules to be able to make use of such baseline data as proxies for future nodule-deprived sediments assemblages. Furthermore, the importance of scavengers for food-web stability at the CCZ seafloor should be investigated more thoroughly.

The CCZ is known to be characterised, across large spatial scales, by a southeast–northwest gradient of decreasing POC flux to the seabed (Smith and Demopoulos, 2003; Pennington et al., 2006). This gradient has been reported to result in more abundant and diverse benthic communities in the eastern CCZ often coupled to larger sediment prokaryotic biomass compared to the western sites (Smith et al., 1997; Glover et al., 2002; Lamshead et al., 2003; Smith et al., 2008a; 2008b; Washburn et al., 2021). Previously, De Smet et al. (2017) observed higher

diversity and higher estimated total taxonomic richness at B6S02 compared to B4S03 for the macrobenthic polychaete assemblage (family level), an observation that the authors linked to the expected higher POC flux at B6S02 (the more eastern site) and the observed differences in nodule abundance and sediment characteristics between the two sites. Pape et al. (2017) found for the same GSR sites that meiofaunal abundance and nematode genus diversity, as well as sediment bacterial biomass, were on average higher at B6S02, although the differences in these variables were not statistically significant. Of the two investigated sites, B6S02 is situated about 300 km eastward from B4S03 across the GSR contract area. Pape et al. (2018) suggested that the POC flux differences estimated for the two sites ( $1.61 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ yr}^{-1}$  at B6S02 >  $1.56 \text{ g C}_{\text{org}} \text{ m}^{-2} \text{ yr}^{-1}$  at B4S03; for more details, see Pape et al., 2018) were potentially not large enough to drive statistically significant differences in the meiobenthos, although low sampling effort could also explain the lack of statistical significance. These findings would suggest that POC flux differences are not consistently reflected across the two size classes at the GSR sites.

In the work by Stratmann (2023), the ecological network of B6S02 site was modelled across the megafaunal ( $\geq 1 \text{ cm}$ ), macrofaunal ( $>300 \mu\text{m}$ ) and meiofaunal ( $>32 \mu\text{m}$ ) trophic levels down to the sediment detrital pool. The food web was reported to have a lower number of trophic compartments and network links when compared to the network calculated for B4S03. In our study, at B6S02 the community displayed a wider resource pool, a larger trophic range and higher trophic evenness than the assemblage at B4S03 (**Figure 6**). On the other hand, the assemblage at B4S03 was characterised by higher trophic redundancy, with taxa occupying closer trophic positions. Redundant trophic links are thought to reduce vulnerability in extinction cascading (Sanders et al., 2018) because different trophic groups can fulfil the same ecological role in the food web. The community at the B6S02 site was characterised by a larger resource pool for the higher taxon community (**Figure 6; Table 3**) and larger trophic niches for each of the size classes, with a food web likely capable of utilising resources in a more efficient way (slightly higher seafloor POC flux with fewer trophic links; Pape et al., 2017; Stratmann, 2023). The B4S03 site, on the other hand, appeared to have a more resilient trophic assemblage, as suggested by the computed higher trophic redundancy and species packing in this study (**Table 3; Figure 6**) and the modelled higher number of trophic compartments and trophic network links by Stratmann (2023). As previously mentioned, Tecchio et al. (2013) observed a positive correlation between the deep-sea megafaunal trophic niche width (calculated as SEAs) and surface productivity along a west–east gradient in the Mediterranean Sea, suggesting that the deep-sea community in this region adapted to capitalise on the whole range of resources available. In our study, only the macrofauna appeared to follow the trend observed by Tecchio et al. (2013), indicating that meiofauna might follow alternative pathways potentially unlinked to the limited seafloor POC fluxes that characterise the abyssal plains.

These initial observations shed light on possible local vulnerabilities of the soft-sediment food-web assemblages to deep-seabed mining, highlighting the importance of nodules as potential sources of additional energy pathways and suggesting size-dependent roles within the infauna. Such observations may be useful in identifying areas that may require protection during the exploitation phase, thus informing future management practices. Nonetheless, additional sampling with high spatio-temporal resolution is warranted across the different habitats and sites. The biota investigated ideally would include all benthic size classes, including meio-, macro- and megafauna, to obtain a comprehensive picture of the benthic food web. Further, in light of predicted changes to surface primary productivity in the tropical Pacific as consequence of climate change in the region by 2100 (Steinacher et al., 2010; Sweetman et al., 2017), seafloor POC fluxes and related stable isotopic signatures should be monitored, and isotopic niche width of key functional taxa should be investigated with the same spatio-temporal resolution. This comprehensive approach would help to identify cumulative impacts of deep-seabed mining and climate change-mediated impacts on the benthic food-web structure in the CCZ.

#### **Potential impacts of deep-seabed mining: Usage of trophic metrics for monitoring**

The most direct and immediate impacts that deep-seabed mining activities may have on soft-sediment assemblages are those related to the operation of the nodule collector at the seabed. During its passage the collector will pick up nodules, including (nearly) all sessile and less mobile organisms living upon or within them (Muñoz-Royo et al., 2022). The nodules will be lifted into a dedicated compartment. During this process a sediment plume is generated by the ejection of the sediment lifted together with the nodules and the resuspension of sediments by the passage of the nodule collector on the seafloor. During this process (nearly) all the organisms living within the surface sediment matrix could also be resuspended and relocated (Muñoz-Royo et al., 2022; Lefaible et al., 2024). Major concerns have been advanced by both the scientific community and other stakeholders on the impacts of the sediment plume on habitats characterised by one of the lowest sedimentation rates of the global ocean (Muñoz-Royo et al., 2022; Lefaible et al., 2023), and therefore a strong focus has been given to modelling the extent of the plume in time and space (Haalboom et al., 2022; Muñoz-Royo et al., 2022).

The Patania II collector trials that took place in the GSR contract area in 2021 showed how the nodule harvest operations generated a low-lying, laterally spreading turbidity current, which was modelled to resuspend 92%–98% of the sediment mass within 2 m of the seabed, leading to a heavy local deposition in the vicinity of the collector track (Haalboom et al., 2022; Muñoz-Royo et al., 2022; Alhaddad and Helmons, 2023; Peacock, 2023). The proportion of the sediment that was observed to remain in suspension for several hours settled farther away from the collector track, a process that was highly dependent on

the seabed current regime and turbidity current dynamics (Muñoz-Royo et al., 2022). Purkiani et al. (2021) modelled sediment blanketing, resulting from a small-scale seabed disturbance experiment carried out in the German Federal Geological Survey contract area in 2019, and observed up to 9 mm of sediment redeposition within a dredge track and only 0.01 mm sediment at 400 m distance from the track. Interestingly, Lefaible et al. (2023) found the highest nematode abundances and diversity from samples recovered from those sediments that had received the lowest levels of sedimentation (>3 mm), indicating resuspension, followed by dislocation of small-sized organisms from the directly impacted tracks to the nearby sediments, with limited sediment blanketing (Lefaible et al., 2023). For the Patania II trial, Lefaible et al. (2024) reported highest meiofaunal densities immediately after the disturbance in those sediments that received most sediment blanketing, although whether the fauna was alive or dead could not be assessed.

During the 'DISCOL' experiment (at 4150 m depth in the Peru Basin), a simulated sediment displacement disturbance showed that, after 26 years, food-web functioning and the sediment microbial loop cycle was not yet restored to pre-disturbance levels, with estimations that the microbially mediated biogeochemical process rates would need over 50 years to recover to pre-disturbance levels (Thiel and Schriever, 1989; Thiel and Tiefsee-Umweltschutz, 2001; Stratmann et al., 2018; de Jonge et al., 2020; Vonnahme et al., 2020). The same experiment showed a temporally different recovery response of the infaunal macrofaunal assemblage, with relatively comparable pre-disturbance densities achieved 3 years after the disturbance (Borowski and Thiel, 1998; Borowski, 2001). In a literature review, Gollner et al. (2017) considered taxon-specific responses to disturbances comparable to mining (e.g., volcanic eruptions observed at vent sites rich in polymetallic sulphides, fishing impact on seamounts where polymetallic crusts are found). They observed a large variability in faunal recovery rates depending on taxonomic identity, size and mobility. These observations confirm the importance of investigating different benthic size classes across different spatial and temporal scales to evaluate the potential effects of deep-seabed mining activities on the nodule-associated biological communities. In fact, body size has been correlated to several functional traits that are of crucial ecological importance, such as population abundance, productivity and growth rate, as well as the spatial niche that organisms occupy and their competitive/facilitative relationships within their ecological networks (Woodward et al., 2005).

Body size distributions are known to compartmentalise food webs along a multimodal size-spectrum continuum (e.g., microbes, meiofauna, macrofauna, megafauna), leading non-adjacent food webs to have relatively few and weak direct connections between them (Woodward et al., 2005). Depending on their body size, different organisms have different degrees of access to potential food resources, considering their fractal niche space (as an expression of the trophic niche size in relation to its body size) and their actual niche range (Woodward et al.,

2005). The work of Stratmann (2023) makes apparent how phytodetritus, as the main food source for the CCZ benthos, is directly consumed only by a few key taxa. The meiofauna, with its deposit-feeding and grazing strategies (Giere and Schratzberger, 2023), is a crucial link for the transfer and turnover of this allochthonous carbon within the CCZ benthic food web. Meiofaunal organisms are known to represent a highly nutritional food source for benthivore fishes, as they may synthesise *de novo* essential poly-unsaturated fatty acids (PUFAs), as observed in freshwater habitats (Giere and Schratzberger, 2023, and references therein). In the deep sea, nematodes have been suggested to synthesise necessary PUFAs from available saturated and monoenoic acids, enhancing the PUFA pool within the sediment by extracting the PUFAs present in settling detrital phyto- and zooplankton, performing a second stage upgrading for megafaunal invertebrates (Svetašev, 2021; Giere and Schratzberger, 2023). In the Arctic deep sea, a pulse-chase experiment revealed that nematodes derived 99% of their carbon requirement from refractory organic matter (settling phytoplankton) and acted as a link to the deep-sea subsurface deposit-feeding polychaetes for which they represented 35% of their energy requirements (Gontikaki et al., 2011). In this experiment, bacteria were responsible for 98% of the assimilation and respiration of the labile component of the labelled phytodetritus (Gontikaki et al., 2011), representing 70% of total benthic respiration. Pape et al. (2013) observed deep-sea nematodes in the northwestern Iberian margin to feed potentially on dissolved organic matter. Considering these observations and the bacterivorous nature of many nematode genera, based on their buccal morphology, this phylum represents a crucial trophic node between different components of the small food web by creating a bridge between dissolved organic matter, bacterial biomass, refractory organic matter and nematode predators, likely along different time frames.

The meiofaunal size class in the deep sea is largely dominated, numerically and in biomass, by the seemingly trophically diverse phylum of the Nematoda (e.g., Zeppilli et al., 2018; Ingels et al., 2020). In our study, nematodes were processed in bulk to obtain sufficient biomass for the stable isotope analysis. Hence, individual samples were considered to show the average feeding strategy of the assemblage within the sediment core, therefore not reflecting possible differences between the different trophic groups present in deep-sea nematode assemblages (Pape et al., 2021; 2013). Overall, nematodes occupied a relatively narrow trophic niche space, with a high trophic position and relatively high trophic redundancy (**Figure 2**). Within the meiofauna, they showed some degree of trophic niche partitioning (**Figure 7**) with the copepods, which seemed to occupy an overall lower trophic level, likely hinting at a larger and more direct dependency on the detrital pool and some specific bacteria-feeding (very depleted  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values). The meiofauna occupies a high trophic position within the detrital food web, with nematodes only surpassed by the meiofauna-sized polychaetes (higher  $\delta^{15}\text{N}$  values; **Figure 2**). Meiofaunal polychaetes were characterised by

low trophic redundancy and occupied a large trophic range, hence displaying the largest SEAc value of all taxa. These findings are to be expected, as polychaetes can have many different feeding strategies; depending on the family, they can be either deposit feeders or predators (Fau-chald and Jumars, 1979; Bonifácio and Menot, 2019; Bonifácio et al., 2020). Further, as the meiofauna-sized polychaetes (likely juveniles; Vanreusel et al., 2001) are obviously smaller than their macrofaunal mainly adult life stages, they may feed much lower within the food web, as well feed directly and selectively on nematodes, as suggested by their relative position within the bi-plot space. In our analysis, different individual samples of polychaetes within their size class grouped together within the isotopic bi-plot space. These individual samples were composed of few individuals of the same family or morphotype (**Figure S6**). Their relative position within the isotopic bi-plot space may indicate resource partitioning between different families or morphotypes and that polychaetes, as a single taxonomic unit, display a good degree of trophic niche differentiation, as they spanned a relatively large trophic level range (NR = 7.75–21.50).

In general, considering the analysed taxa across the two size classes, the metazoan meiofauna displayed as directly connected to the detrital resource pool, confirming its position within the sediment food-web structure, as previously modelled by Stratmann et al. (2023) for this area. When considering the direct impact of nodule removal on the soft-sediment assemblages mentioned earlier, the potential increase in densities of nematodes (and copepods) in the thick blanketed sediment (Lefaille et al., 2024) may generate competition for resources, as it may concentrate this trophically highly diverse node within the limited trophic fractal space. Moreover, the observed isotopic niche partitioning between copepods and nematodes suggests that, if copepods were affected negatively by resuspension and relocation caused by the sediment plume, the meiobenthic size class may lose a crucial link to the detrital food source.

Aside from the direct effects of the sediment plume (organism relocation and surface blanketing), the potential release of heavy metals on the seabed is of high concern (Hauton et al., 2017). Copepods and nematodes may have different vulnerabilities to the toxicity of these minerals, leading to unpredictable trophic cascading within the small food web. Nematoda are known to suffer behavioural and physiological modifications upon exposure *in vitro* to heavy metals (Monteiro et al., 2014), and different trophic guilds bioaccumulate and biomagnify heavy metals in different measures, becoming a toxic link to higher trophic levels within the sediments of polluted habitats (Danovaro et al., 2023). Harpacticoid copepods have been shown to be sensitive to heavy metal exposure, with different families displaying various levels of sensitivity during recovery following the Deepwater Horizon oil spill (Baguley et al., 2024). Simulated physical disturbance (DISCOL experiment) displayed long-term effects on deep-sea harpacticoids, with the potential for certain families to be indicator taxa for monitoring disturbance (Ahnert and Schriever, 2001). Due to their close association with the

sediment microbial loop and their potential vulnerability to heavy metal toxicity and sediment plume-related disturbances, key meiofaunal taxa should be monitored closely. We suggest that family-level diversity in copepods and trophic guild composition in nematodes should be tracked alongside changes in their realised isotopic niches following mining activities.

### Conclusions and main insights for future research and monitoring

This study is the first trophic niche-based investigation carried out for soft-sediment assemblages of the CCZ, comparing food-web properties across a large spatial scale and habitat type and focusing on the most abundant key taxa belonging to the two size classes of sediment infauna, namely the meio- and the macrofauna. Despite the time-integrating nature of the stable isotope metrics used here, this investigation must be considered as a snapshot in time and be interpreted as a medium-scale (300 km) analysis, with a principal focus on soft-sediment assemblages in the GSR exploration contract area. Moreover, the metrics utilised in this work suffer from small sample size biases, and some of the metrics must be interpreted cautiously given the lack of a thorough baseline resource analysis (Jackson et al., 2011; Brind'Amour and Dubois, 2013), although these effects were considered and minimised within this study, as described in the Materials and Methods section. Nonetheless, our observations have confirmed previously modelled results for the present sediment assemblages (Stratmann, 2023) and can be considered as a reliable baseline for future research on the responses of CCZ sediment communities to deep-seabed mining. Future investigations should be characterised by a higher degree of replication in collecting and analysing samples across different target levels (e.g., trophic unit: taxon, family, size spectrum; organisational level: site, habitat type), with at least a minimum of five replicates for each trophic unit (e.g., taxon) and ideally a minimum of 30 individual samples for higher organisational level grouping (e.g., size class; Jackson et al., 2011; Brind'Amour and Dubois, 2013). Finally, future research should aim at repeating such sampling, increasing the temporal resolution to cover natural changes in food-web structure over time (Woodward et al., 2005; Brind'Amour and Dubois, 2013).

Due to the high importance of the meiobenthic size class in terms of biomass and abundance in the deep sea (Ingels et al., 2020; Pape et al., 2021) and considering the crucial link that its taxa represent between the microbial loop and the larger body-sized predators and deposit feeders living within the shared trophic fractal space, the importance of meiofauna as a foundational trophic link for the re-establishment of a food web following mining activities may be considered high. Future research should thus focus on monitoring meiobenthic responses to mining-related impacts, while linking these impacts to sediment prokaryote recovery and macrofaunal recolonisation. Finally, of paramount importance is to understand the effects of heavy metal release and sediment blanketing on meiobenthic copepods and nematodes, as these

effects may alter their diversity and survival rates, generating potential trophic cascading and a significant increase in the recovery time of the small food web.

### Data accessibility statement

All data used to calculate the metrics of this work are available at the Integrated Marine Information System of the Flanders Marine Institute (VLIZ, [www.vliz.be](http://www.vliz.be)) with the following DOI: <https://doi.org/10.14284/763>.

### Supplemental files

The supplemental files for this article can be found as follows:

Supplemental Material.docx

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### Competing interests

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.

### Author contributions

Contributed to conception and design: FP, EP, AV, BDS.  
Contributed to acquisition of data: FP, EP, BDS.  
Contributed to analysis and interpretation of data: FP.  
Drafted and/or revised the article: FP, EP, AV, BDS.  
Approved the submitted version for publication: FP, EP, AV, BDS.

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