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RESEARCH ARTICLE

Influence of seabed heterogeneity on benthic megafaunal community patterns in abyssal nodule fields

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Polymetallic nodule fields, at 3000–6000 m depth, harbour some of the most diverse seabed communities in the abyss. In these habitats, nodules are keystone structures for many sessile species that require hard substrate for growth. The combination of exposed nodules and background sediment increases the heterogeneity of these habitats compared to nodule-free fields, and thereby potentially influences the assembly of animal communities across space. Polymetallic nodule patches can vary in size, shape and nodule density; however, the effect of these variations on benthic communities remains largely unclear. Understanding the role of nodule-habitat type (defined by nodule size and density) and seabed heterogeneity on biodiversity is urgently needed to accurately assess the impacts of potential nodule removal in areas like the Clarion-Clipperton Zone, a region targeted for deep-sea mining. Here, we explored variations in benthic invertebrates (megafauna > 10 mm) across space and nodule-habitat types within an abyssal seascape. We quantified changes in megafaunal density, diversity and community structure using quantitative seabed imagery in four study areas. Study areas were separated by distances of 1–110 km and exhibited varying levels of seabed heterogeneity, as defined by the proportions of different nodule-habitat types present in each area. We found that different nodule-habitat types harboured distinct assemblages. Areas with higher nodule coverage supported higher megafaunal densities, while areas with larger, sparsely distributed nodules had higher diversity. Higher species richness and distinct community structure were associated with the most heterogeneous study area, which had multiple nodule-habitat types and nodule-free sediment patches. These results suggest that type of nodule habitat and degree of seabed heterogeneity are important drivers of local benthic megafaunal diversity patterns in abyssal nodule fields. By establishing a baseline prior to human disturbance, our study provides essential insights that should inform future monitoring programmes, mining regulations and biodiversity conservation in this area.

Keywords: Deep-sea ecology, Habitat heterogeneity, Deep-sea mining, Biodiversity, Megafauna

Introduction

Polymetallic nodule fields, between 3000 m and 6000 m depth, represent a unique habitat within the abyssal plain environment that hosts highly diverse biological communities (Glover et al., 2002; Amon et al., 2016; Simon-Lledó et al., 2019b). Nodule fields are characterised by slow bottom currents and low sedimentation rates that allow for the formation of polymetallic nodules, accretions of metallic minerals that precipitate out of pore/bottom water and form over millions of years (Hein et al., 2020). Nodules support specialist fauna (Amon et al., 2016; Simon-Lledó et al., 2019b; Pape et al., 2021) distinct from those found in the background sediment (Mullineaux, 1987) and other hard substrates (Mejía-Saenz et al., 2023). Consequently, they are considered keystone structures in these habitats (Vanreusel et al., 2016). Some of the most extensive nodule fields occur in the Pacific Ocean (Hein et al., 2020). This study focuses on the Clarion-Clipperton Zone (CCZ), a polymetallic nodule field in the eastern Pacific that covers roughly 6 million km^2 of the seabed (Wedding et al., 2013). Given the interest in its mineral resources, understanding how variability within nodule fields influences megafaunal biodiversity pattens and assemblages in the CCZ is important.

Biological communities in the CCZ contain many nodule-reliant species, particularly sessile suspension feeders (Dahlgren et al., 2016; Gooday et al., 2017; Bribiesca-Contreras et al., 2022), whereas the surrounding soft sediment supports burrowing infauna, including

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polychaetes and crustaceans (Glover et al., 2002; Janssen et al., 2019), as well as deposit-feeding megafauna (Bribiesca-Contreras et al., 2022). Therefore, nodule fields are able to support both specialist and more generalist fauna. The combination of soft sediment with hard substrate increases seabed heterogeneity, with dominance by one habitat type leading to greater homogeneity. According to the habitat heterogeneity hypothesis, more heterogeneous areas should support greater biodiversity (Wilson and MacArthur, 1967). Habitat heterogeneity can increase biodiversity by increasing the number of available niches (Cramer and Willig, 2005; Stein et al., 2014). In the CCZ, an increase in different habitat types (i.e., those with varying sizes and densities of nodules vs. nodule-free sediment) in a given area would thus be expected to increase diversity overall.

Nodule fields can vary in their nodule coverage, nodule size and other characteristics, including patchiness. These features vary over different scales and can influence the animal communities inhabiting nodule habitats (e.g., Simon-Lledó et al., 2019b). For example, nodule topography can generate variation in smaller size classes of fauna (Mullineaux, 1987), whereas variability in hard substrate (Mejía-Saenz et al., 2023), nodule coverage (Simon-Lledó et al., 2019b) and seabed geomorphology (Simon-Lledó et al., 2019a) influence megafaunal densities and community structure over intermediate scales (100–1000 km). In this study, three types of nodule habitat are defined by the size and density of the nodules, and thus percentage coverage of the seabed (**Table 1**; AMC Consultants Pty Ltd, 2021). The CCZ contains large stretches of seabed (km^2) that are covered with the same nodule-habitat type as well as areas that show greater patchiness of habitat type that can change within 10–100 m. The effect of nodule-habitat type and patchiness on benthic communities is largely unknown.

In this study, we explored local scale variations (1–100 km) in benthic invertebrates (megafauna > 10 mm) across space and nodule-habitat type in the eastern CCZ. We quantified changes in megafaunal density, diversity and community structure across four study areas, separated by distances of 1 km to 110 km, using seabed image data. The study areas encompassed varying levels of seabed heterogeneity, determined by the observed proportions of available nodule-habitat types in each area. This approach allowed us to test more explicitly the influence of nodule-habitat type and seabed heterogeneity on megafaunal diversity. We tested whether (i) local scale biodiversity patterns and the distribution of megafauna are driven by fine scale (10–100 m) variations in nodule-habitat type and (ii) whether seabed heterogeneity drives differences in megafaunal diversity between study areas. We hypothesised that areas with more variation in nodule-habitat type (and so greater seabed heterogeneity) will have greater megafaunal diversity. An increase in knowledge of what drives deep-sea biodiversity patterns at local scales has implications for future regulation of mining activities, environmental monitoring plans and the design of protected areas in the CCZ.

Methods

Study area

This study was conducted in the NORI-D deep-sea mining exploration contract area located in the southeastern CCZ. NORI-D covers an area of 25,160 km^2 extending from approximately 10–11°N and 116–118°W (**Figure 1**). The area includes abyssal hill, trough and plain areas with a few seamounts (predominantly in the southwestern corner).

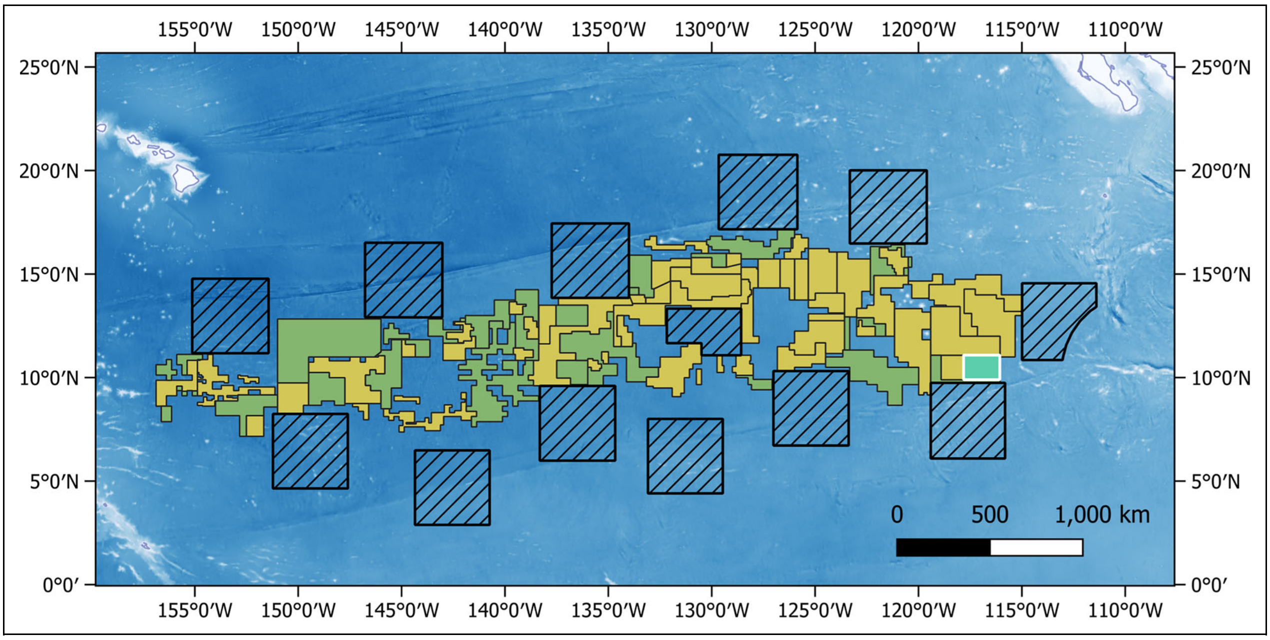

Figure 1. Map of the Clarion-Clipperton Zone (CCZ) and NORI-D study area. Map showing the NORI-D study area (turquoise box bounded in white) in the context of the wider CCZ. Mining contract areas are shown in yellow, 'reserved areas' (areas set aside for access by developing nations; International Seabed Authority, 2019) in green and areas of particular environmental interest with hatched boxes.

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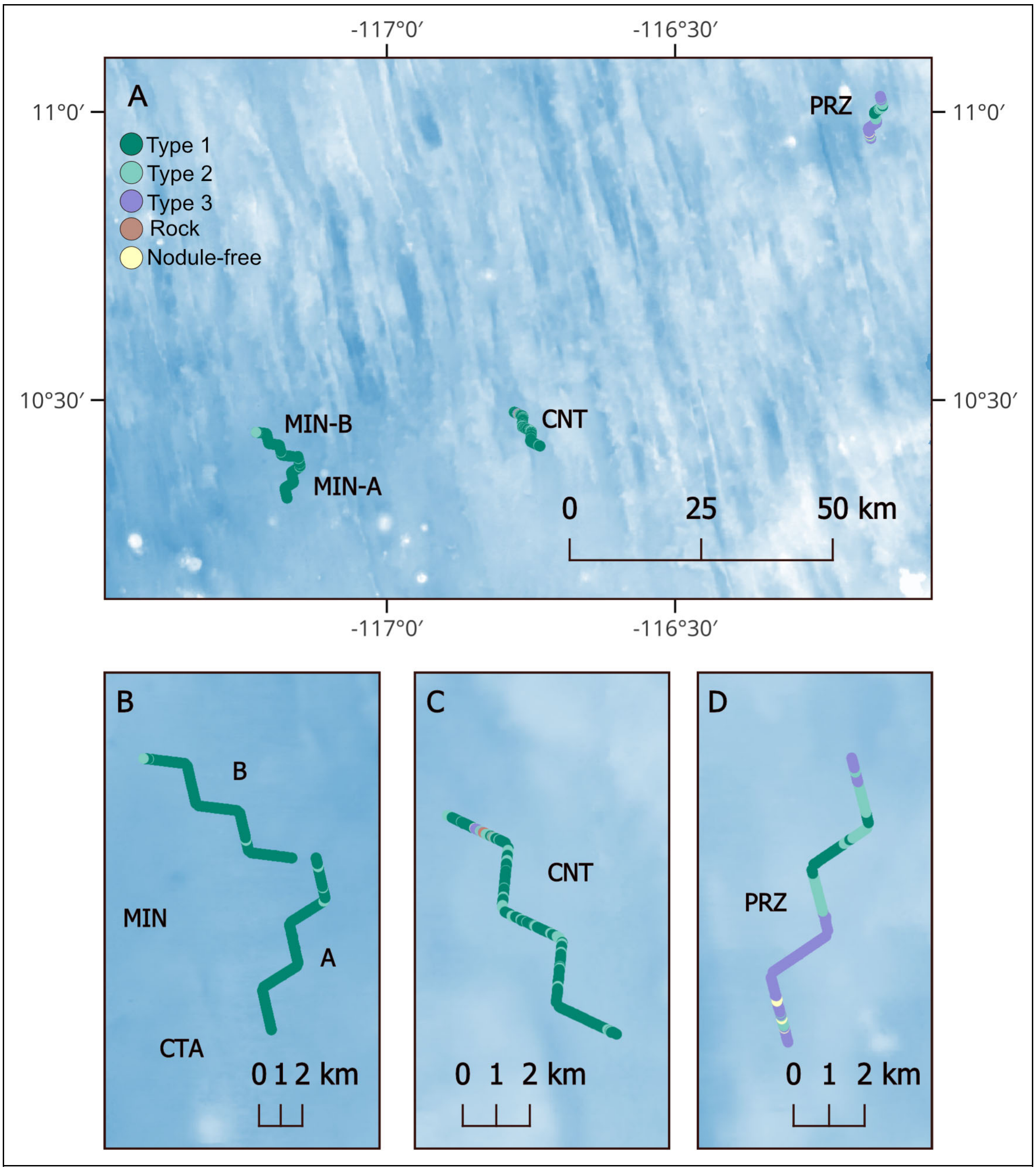

Figure 2. Map of the photo transects collected in the NORI-D study area. (A) Map of the NORI-D area showing the photo transects in relation to each other, separated by distances of 1–110 km, with two transects in the future proposed mining areas (MIN-A and MIN-B), a third in the control area (CNT) and the fourth in the preservation reference zone (PRZ). (B–D) Close-ups of the transects in each study area: (B) MIN-A and MIN-B, (C) CNT and (D) PRZ. All transects are colour-coded by type of nodule habitat (see **Table 1**).

As part of the mining plans, several areas of NORI-D have been designated for baseline assessment. Two areas in this study are in an area proposed for future seabed mining (MIN-A and MIN-B), one is in a control area (CNT) and another is in a preservation reference zone (PRZ). MIN-A and MIN-B are closest together (separated by roughly 1 km), CNT is approximately 50 km from MIN-A and MIN-B, and PRZ is roughly 100 km further from CNT (**Figure 2**). The seabed is covered by a range of nodule-habitat types, nodule-free areas and rare patches of rock fragments. The area proposed for mining is a flat area of high nodule density (Type 1 nodule-habitat). The control area also has high nodule density, similar to densities found in the MIN areas, but with occasional rock patches. The PRZ contains multiple habitat types including areas with low nodule densities (Type 2/3 nodule-habitats) and nodule-free areas. The area surveyed covered a depth range of 4172–4316 m. The maximum depth range within a study area was roughly 65 m. Total organic carbon in the sediment was similar between mining and PRZ areas (0.77% and 0.72%, respectively; Text S1 and Table S1). General bathymetry and backscatter data for the area were acquired using a Kongsberg EM122 hull-mounted multibeam sonar system. Initial predictions of substrate type in the area were based on backscatter data and confirmed using boxcores. In this study, nodule-habitat type was assigned to individual images visually.

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Survey plan

We used seabed imagery to assess patterns in megafaunal density, diversity and community structure. Seabed imagery, using remotely operated (ROV) underwater vehicles, is an effective way of covering large areas of the seabed quickly while preserving the spatial relationships between observations. Imagery has been successfully applied in several previous megafaunal studies (e.g., Amon et al., 2016; Simon-Lledó et al., 2019a). This survey was designed to sample areas representative of the habitats available across the study areas, while reducing geomorphological variation between transects, which is known to influence megafaunal abundance and community structure (Simon-Lledó et al., 2019a). We targeted 'flat' areas as described in Simon-Lledó et al. (2019a). Photo transects were conducted at four study areas within NORI-D in May–June 2020 (**Figure 1**); in each area, the survey design followed a zigzag pattern made up of five, 2 km-long transects (**Figure 2**, Table S2).

Image collection and processing

Photo transects were collected by the *Kystdesign Supporter 31* ROV deployed from the MPV *Pacific Constructor* operated by Ocean Infinity. Images were collected with a vertically mounted *Imenco Tiger Shark* (Canon IXUS130) camera (resolution: 4320 × 3240 pixels). The camera had vertical and horizontal acceptance angles of 32° and 39°, respectively. Camera angles and field of view were verified in situ using coloured calibration cards that were photographed at known altitudes above the seabed. The camera settings were as follows: shutter speed = 1/60 s, ISO = 100, aperture = F2.8 and focal length = 5 mm. The ROV flew at an altitude of 1.2 m and a speed of 0.1 m s^{-1}, and photos were collected every 15 s (Altimeter: Mesotech Digital Altimeter 675 kHz; navigation: Kongsberg cNode USBL and Nortek DVL 500). This altitude was chosen as it provides the best balance between area coverage per image and detection of individual animals. A total of 26,917 images were collected.

Images taken at an altitude of <0.95 m or >1.99 m were removed to ensure consistent detection between images. Overlap between adjacent images was avoided by removing every second image. Images within 150 m of the start and end of a transect were removed to reduce the effect of spatial autocorrelation on the results (Legendre, 1993) and to ensure that image transects were as independent as possible. Because the illumination was not consistent across the whole image, vignetting was reduced by cropping each image to a central 3600 × 3100 pixel section that was retained for analysis. This approach removed the poorly lit edges of the images where individual animals were less likely to be detected. At the target altitude, each cropped image covered 2.06 m^2 of seabed. For image annotation, 12,282 processed images covering a total area of 24,836 m^2 were uploaded to BIIGLE 2.0 (Langenkämper et al., 2017). Images were annotated in a random order, and all megafauna detected were identified manually with reference to the Abyssal Pacific Seafloor Megafauna Atlas morphospecies catalogue (Simon-Lledó et al., 2023b).

There were five different habitat types found in the images collected over the NORI-D area: Types 1, 2 and 3 for nodule-habitats (see **Table 1** for definitions), nodule-free areas and areas that included rock fragments (**Figure 3**). Images were assigned to a habitat type manually. Because both nodule-free areas and rock fragment areas were relatively rare (34 images and 82 images out of 12,282, respectively), they were not included in analysis. Nodules in Type 1 nodule-habitats are small in size and present in high densities with relatively little exposed sediment (**Table 1**). Type 2 nodule-habitats contain larger nodules found at intermediate densities. In contrast, nodules in Type 3 nodule-habitats are large, more sparsely distributed and surrounded by more exposed sediment.

MIN-A and MIN-B were dominated by high densities of small nodules (Type 1 nodule-habitats) with very little exposed sediment except where burrowing animals had pushed sediment over the nodules in mounds. Neither MIN-A nor MIN-B transects contained nodule-free areas or rock fragments (**Figures 2** and **3**). CNT is the only study area to have rock fragment areas and has a larger proportion of Type 2 nodule-habitats compared to MIN-A and MIN-B, although Type 1 nodule-habitats still cover most of the CNT seabed area. The PRZ was the only area that had Type 3 nodule-habitat areas, which are characterised by larger nodules at lower densities. PRZ showed the greatest variability in habitat type with Type 1 nodule-habitats making up a relatively small proportion and Type 3 being much more common. Overall, the PRZ had much more exposed sediment with some areas being completely free of nodules.

Analyses

A total of 8,348 images were annotated for megafauna. Only individuals with a total length of >10 mm that could

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Table 1. Description of the three main types of nodule habitats found in NORI-D area (as developed earlier for the NORI-D area; see AMC Consultants Pty Ltd, 2021); ranges are approximations

Nodule-Habitat Type	Description	Nodule Coverage (%)	Nodule Size (cm)
Type 1	Small, densely packed nodules	>50	1–10
Type 2	Larger, mostly individual nodules or locally interconnected[a]	20–40	5–20
Type 3	Large, mostly individual nodules, more sparsely distributed	10–20	5–20

[a] Small areas where nodules are touching each other.

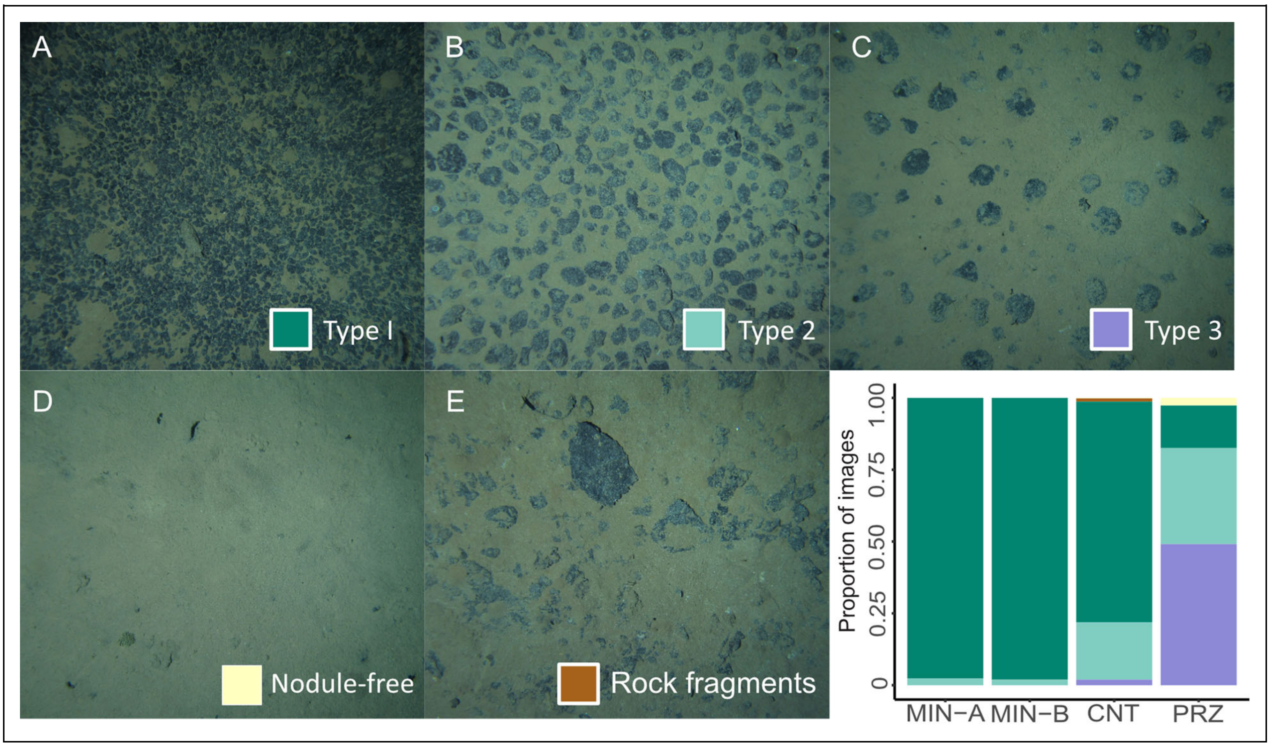

Figure 3. Seabed and nodule-habitat types found in the NORI-D area. Photos of the habitat types found in the NORI-D area: (A) Type 1 nodule, (B) Type 2 nodule, (C) Type 3 nodule, (D) nodule-free and (E) habitats with rock fragments. The inset barplot shows the proportion of images of each colour-coded habitat type in each study area.

be identified down to morphospecies (which also included distinct morphotypes even if they could only be identified to genus or family) were included in the diversity and community structure analyses. An uneven number of images were annotated in each study area. To reduce the impact of differing specimen numbers between transects on the estimate of diversity (Simon-Lledó et al., 2019a) transects were standardised by number of individuals by resampling images without replacement until 300 individuals were reached (the minimum number of individuals annotated in a single transect or nodule type). This approach has been used in other megafaunal studies in this area (e.g., Simon-Lledó et al., 2019a). The standardised samples were used for the calculation of diversity indices and in the community structure analyses.

The role of nodule-habitat type

To explore whether differences in diversity and community structure between areas were related to differences in nodule-habitat type, we compared between types within the PRZ (the only study area to contain all three nodule-habitat types). For analysis of differences between these nodule-habitat types, images containing the same type were pooled together and resampled without replacement to obtain replicate samples of 300 individuals for each nodule-habitat type. There were 3 replicates for Type 1 and 6 replicates for Type 2 and Type 3, owing to the lower proportion of Type 1 nodule-habitats in the PRZ. Nodule-free areas and areas with rock fragments were not included in the analysis because of the limited area covered by these habitat types.

The role of study area/seabed heterogeneity

Study area was used as a proxy for seabed heterogeneity as the study areas differed in the proportions of the nodule-habitat types present. MIN-A and MIN-B were the least heterogeneous, as the seabed was covered primarily with a single nodule-habitat type. The CNT area had slightly more variability in habitat type, while the PRZ was the most heterogeneous, containing multiple nodule-habitat types as well as nodule-free areas (which were excluded from the analysis). For the analysis of differences between study areas, images were sampled without replacement within each transect to generate replicate samples of 300 individuals ($n = 5$ for each study area). We also compared across study areas using only images with Type 1 nodule-habitats (spatial component without habitat variability).

The density of megafauna (individuals m^{-2}), morphospecies richness (S_N; equivalent of Hill numbers of order 0), exponential of the Shannon index (exp H'; Hill numbers of order 1) were calculated for each study area and nodule-habitat type. Increasing order of Hill numbers represents increasing sensitivity to more abundant species (Jost, 2006). Diversity of order 1 favours neither rare nor common species (Jost, 2006). The mean and 95% confidence intervals were calculated for each diversity measure. Generalised linear models (GLMs) were used to test whether density, morphospecies richness and exponential Shannon Index of megafauna were explained by study area and nodule-habitat type (PRZ only). The models for density were fitted with quasi-Poisson errors as the data displayed overdispersion (Gardner et al., 1995). Normal (Gaussian) errors were fitted for all other models.

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To assess differences in community structure, a non-metric multidimensional (NMDS) analysis based on a Bray-Curtis dissimilarity matrix was used (Kruskal, 1964). The Bray-Curtis dissimilarity is commonly used in community ecology studies to assess differences in community structure between areas; it takes into account differences in abundance as well as differences in identity (Bray and Curtis, 1957). The faunal abundance data were square-root-transformed before performing the NMDS analysis, which was done to reduce the influence of dominant morphospecies. Differences in community structure between study areas or nodule-habitat type were tested using pairwise PERMANOVA (Anderson, 2014) with a correction for multiple testing. To give an indication of which faunal groups could be driving differences between nodule-habitat type or study area, we conducted a SIMPER analysis (Clarke, 1993). Analyses was conducted in R version 4.1.2 (R Core Team, 2021), using the 'vegan' package (version 2.5–7; Oksanen et al., 2021) and 'car' package (version 3.1–2; Fox and Weisberg, 2018).

Results

Nodule-habitat type analyses

For comparing between nodule-habitat types, we focused on the PRZ as it was the only study area that contained all three types of nodule habitats. Overall, megafaunal density was higher in Type 1 areas compared to Type 2 ($p < 0.001$) and Type 3 ($p = 0.001$) (**Figure 4A**; GLM: $F_{2,33} = 11.44$, $p < 0.001$, $R^2 = 0.40$). Morphospecies richness and Hill numbers of order 1 were higher in Type 2 and Type 3 areas compared to Type 1 (**Figure 4A**; GLM: $F_{2,12} = 4.19$, $p = 0.04$, $R^2 = 0.31$ for morphospecies richness; GLM: $F_{2,12} = 7.56$, $p = 0.007$, $R^2 = 0.56$ for Hill numbers of order 1). Of the morphospecies found only within one nodule-habitat type area there were four that were found in abundances of ≥3 (CRI_014 Comatulida order inc., CRI_004 Bathycrinidae gen. indet., URC_008 *Echinocrepis* sp. indet.; Table S3; Simon-Lledó et al., 2023b). These morphospecies were found only in Type 3 areas and only in the PRZ. There was some evidence of differences in community structure between nodule-habitat type, as shown in the NMDS, with an apparent gradient of community structure from Type 1 to Type 3 (**Figure 5A**, Table S4c). The main faunal differences between nodule-habitat types were higher abundances of Bryozoa (particularly *Notoplites* sp. indet. BRY_002), Alcyonacea and Polyplacophora MOL_002 (which were also found across the mining and control areas) in Type 1 areas (**Figure 6A**), whereas Type 2 and 3 areas had higher abundances of ophiuroids (e.g., *Ophiosphalma*), Actinaria and *Bathyarca* sp. indet. (MOL_021) (**Figure 6A**). In addition, *Thenea* sp. indet. (DES_021) and echinoids were found in higher densities in Type 3 areas (**Figure 6A**). The high megafaunal densities in Type 1 areas appear to be driven primarily by high densities of sessile Bryozoa and Polyplacophora that were found on top of nodules (**Figure 6A**).

Role of seabed heterogeneity

To assess the influence of seabed heterogeneity, we explored differences in megafaunal diversity and community structure between study areas that differed in the proportion of different types of nodule habitats. Mean density of megafaunal individuals was lower in the CNT and PRZ sites compared to MIN-A and MIN-B (**Figure 4B**; GLM: $F_{3,16} = 11.3$, $p < 0.001$). The differences in morphospecies density between study areas seems largely to reflect differences in nodule density between nodule-habitat types. For example, the high nodule densities in Type 1 areas explain the densities observed in the MIN study areas which are dominated by small Type 1 nodules. The PRZ had significantly lower density than all other study areas, but higher morphospecies richness (65 compared to an average of 56 in other study areas; **Figures 4B** and S1; GLM: $F_{3,16} = 10.26$, $p < 0.001$). Hill numbers of order 1 were generally higher in CNT and PRZ compared to MIN-A and MIN-B, indicating that evenness was higher in the PRZ compared to the other study areas (GLM: $F_{3,16} = 4.67$, $p = 0.01$).

Community structure was similar between MIN-A and MIN-B areas, whereas CNT and PRZ differed in structure from the other areas (**Figure 5B**; Table S4a). Differences between study areas were driven by high densities of Bryozoa and Alcyonacea in the mining areas (**Figure 6**) and higher densities of mobile echinoderms in the PRZ (specifically ophiuroids and echinoids). The PRZ had 30 unique morphospecies (those found only within one study area) and therefore twice as many as CNT (15) and MIN-A and MIN-B grouped (14), while MIN-A had 9 and MIN-B had 2. However, most morphospecies found only in one area were rare (singletons). Morphospecies found only in one study area that had ≥3 individuals were all found in the PRZ (4 morphospecies in total); the majority were from the phylum Echinodermata (AST_054 *Hymenaster* sp. indet., CRI_004 Bathycrinidae gen. indet., CRI_014 Comatulida order inc. and HOL_004 *Molpadiodemas* sp. indet.; Table S3; Simon-Lledó et al., 2023b). The individuals from these morphospecies were all found in areas that had larger nodules and more exposed sediment (Type 3 areas). Crinoids were only found in the PRZ although in low numbers (Table S3).

Comparing animal communities in Type 1 nodule-habitats across all study areas (spatial component without variability in type of nodule habitat) indicated no differences in megafaunal densities (**Figure 4C**; GLM: $F_{3,14} = 1.25$, $p = 0.33$). There was also no evidence of differences in morphospecies richness between study areas (**Figure 4C**; GLM: $F_{3,14} = 0.4$, $p > 0.05$), although there was some evidence for differences in evenness between study areas. CNT had higher Hill numbers of order 1 than MIN-A and MIN-B, while PRZ had lower values than MIN-A and MIN-B (GLM: $F_{3,14} = 9.15$, $p = 0.001$). These results show that the higher evenness found overall in the PRZ was not being driven by Type 1 areas. There was no statistical support for differences in community structure between Type 1 areas across study areas (Figure S2, Table S4b).

Discussion

Spatial variation in megafaunal communities over local scales (1–100 km) in the eastern CCZ appears to be influenced by differences in seabed heterogeneity (characterised

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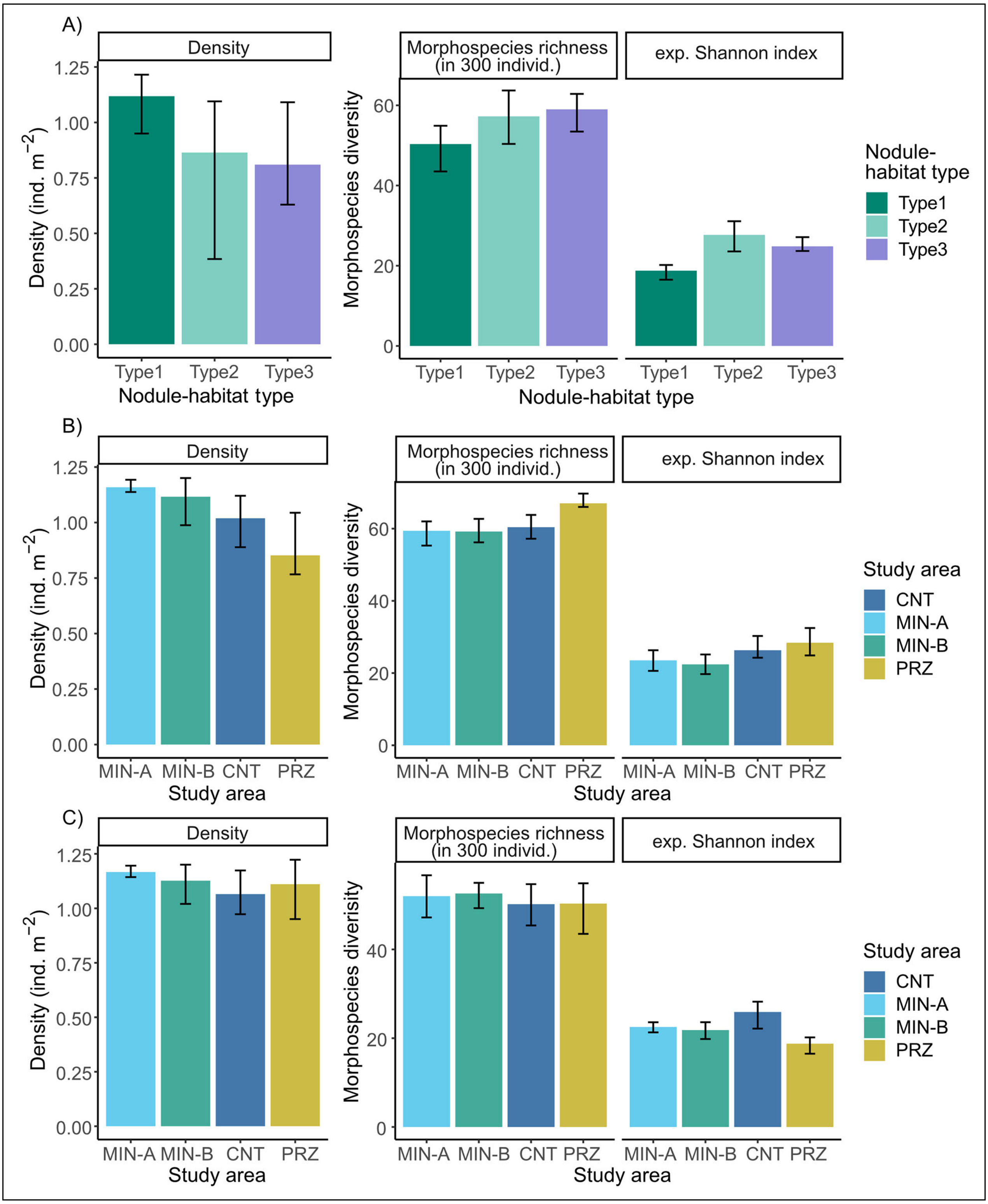

Figure 4. Density and diversity of megafaunal communities in each nodule-habitat type and each study area. Density of megafauna (individuals m^{-2}), morphospecies richness and Hill numbers of order 1 (exponential of Shannon index) in (A) the three types of nodule habitats within the PRZ; (B) each of the four study areas; and (C) only Type 1 areas in each study area. Values were calculated using randomly generated samples containing 300 individuals identified to morphospecies. Error bars show 95% confidence intervals.

by differences in the proportion of different nodule-habitat types), as demonstrated by the distinct differences in diversity and community structure between study areas (1–100 km apart). This finding is particularly evident as faunal communities found in the same type of nodule habitat (Type 1) were largely similar across the study areas, indicating that geographic distance is not the main driver of spatial variation. Diversity and community structure patterns also

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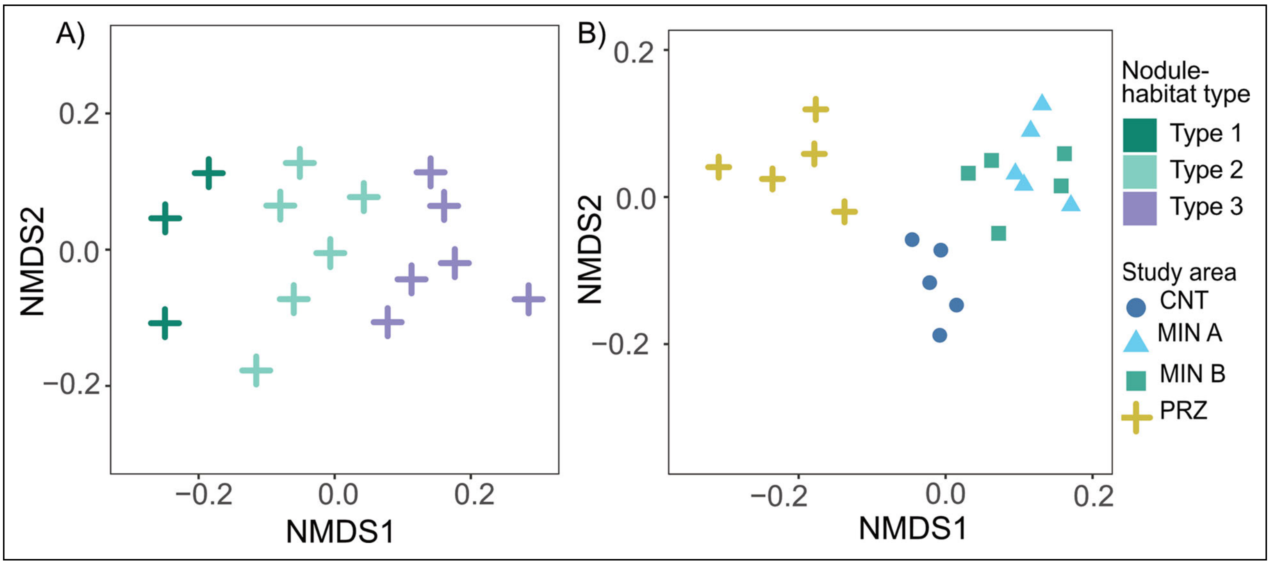

Figure 5. Ordination of megafaunal community structure living in different nodule-habitat types and study areas. NMDS plots show colour-coded differences between (A) types of nodule habitats within the PRZ (stress = 0.18) and (B) study areas (stress = 0.15). The analysis was performed on a Bray-Curtis dissimilarity matrix calculated using square-root-transformed abundance data.

differed between nodule-habitat types suggesting that having multiple types in the same area increases diversity and supports a distinct megafaunal community. These findings suggest that at the spatial scales involved in this study (1–100 km) habitat heterogeneity is an important driver of biodiversity patterns and differences in similarity in abyssal megafauna communities.

We have shown that type of nodule habitat, not just nodule presence, has an important influence on megafaunal communities. Nodule-habitat types differ in a number of features, including the size of the nodules and the amount of exposed sediment (i.e., nodule coverage of the seabed) as considered here. The apparent preference of certain morphospecies for areas with specific nodule-habitat types likely represents a balance of the varying needs of differing functional groups, that is, availability of hard substrate versus exposed sediment (Mullineaux, 1987; Gage and Tyler, 1991). Sessile organisms, which require hard substrate to settle (Dahlgren et al., 2016; Grischenko et al., 2024), are likely to favour high nodule density areas where hard substrate is more readily available (Mullineaux, 1987; Amon et al., 2016; Simon-Lledó et al., 2019b). We found that higher-coverage Type 1 nodule-habitats supported higher densities of sessile, suspension-feeding organisms, such as Bryozoa and Alcyonacea (e.g., *Abyssoprimnoa gemina* sp. inc.) as well as the Polyplacophora, which appear to prefer to remain on top of nodules (Wiklund et al., 2017), whereas larger, sparsely spaced nodules had greater densities of mobile deposit feeders, such as the ophiuroid *Ophiosphalma*, urchins (particularly *Plesiodiadema globulosum* sp. inc., URC_003) and semi-burrowing bivalves (*Bathyarca* sp. indet., MOL_021), which rely on grazing on sediment (Iken et al., 2001). The increased sediment exposure associated with Type 2/3 nodule-habitats means that areas with these habitat types are more heterogeneous, which also likely contributes to the higher diversities found in these areas. Patchiness in food supply can be an important control in benthic communities (Billett et al., 1983; Snelgrove et al., 1992; Lauerman et al., 1996). Patches of higher chlorophyll-a and phaeophytin have been measured in sediments around Type 2/3 nodule-habitats in the NORI-D area (Iannotta et al., n.d.), indicating that there is more organic material available in areas with more exposed sediment (Stephens et al., 1997). Flows over the nodules accumulate particles at the base of nodules (Mullineaux, 1989); the larger nodules in Type 2/3 habitats may act to trap more organic material than nodules that are small and densely packed. The influence of nodule-habitat type on other size classes has not been studied extensively. The presence of nodules did not result in a consistent change in meiofauna diversity (Pape et al., 2021), nor have sediment macrofaunal diversities shown a clear pattern with nodule abundance (Washburn et al., 2021).

Our findings add to the growing number of deep-sea studies that support habitat heterogeneity as an important control of deep-sea biodiversity (Thistle, 1983). The most heterogeneous area (PRZ) had the highest morphospecies richness, a higher proportion of morphospecies that were found only in this area and a different community structure compared to the other areas. Habitat heterogeneity can influence community structure through different habitat patches supporting distinct communities or by the mosaic of habitats changing the quality of the overall matrix (Cramer and Willig, 2005). Differences in community structure between nodule-habitat types was driven primarily by differences in the abundance of particular morphospecies, suggesting that seabed heterogeneity increases the overall quality of the environment (Cramer and Willig, 2005). Differences in fauna between hard substrate and surrounding soft sediment habitats have been documented for nodules (Mullineaux, 1987), dropstones (Meyer et al., 2016) and seamounts (Meyer et al., 2023). The combination of high-density nodule areas that can support sessile, nodule-

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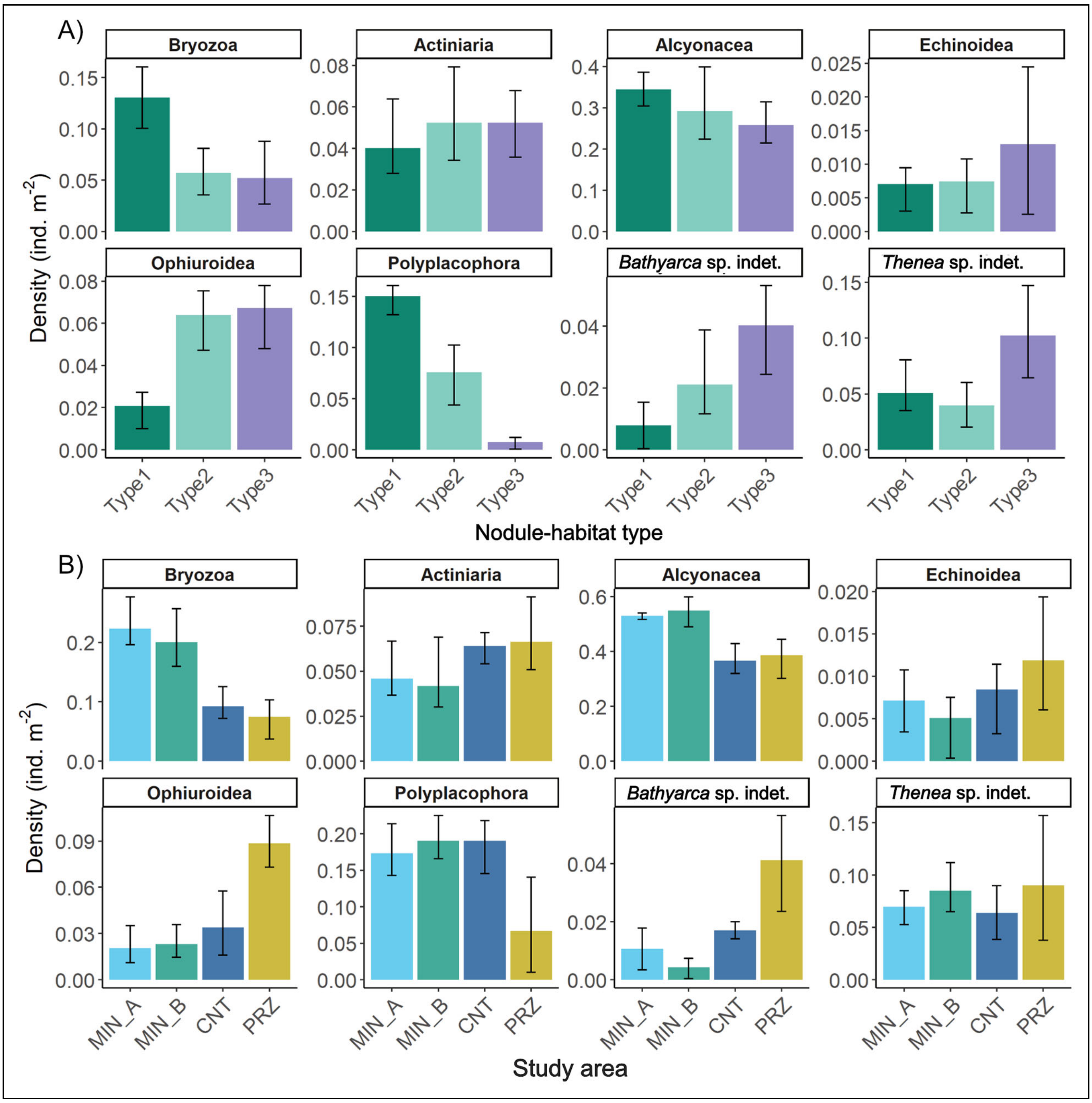

Figure 6. Densities of key faunal groups that differed across nodule-habitat types and study areas. Density (individuals m^{-2}) of the faunal groups or morphospecies that accounted for the most variation between communities on different (A) types of nodule habitats and (B) study areas (see Figures S3 and S4 for summary of SIMPER output). Error bars show 95% confidence intervals.

dwelling organisms and areas of lower nodule coverage more suitable for deposit feeders (and nodule-free patches not found in the other study areas) likely allows the PRZ to support species with different ecological requirements and a more diverse community overall. We have focused on physical habitat heterogeneity over the scale of 0–100 km. On a regional scale (>1000 km), other environmental variables related to depth influence megafaunal species turnover (Simon-Lledó et al., 2023a). In addition, while heterogeneity generated by patches of different nodule-habitat types is relevant to megafaunal size classes, micro-heterogeneity on the scale of individual nodules is likely more important for smaller size classes of fauna (Mullineaux, 1989; Veillette et al., 2007).

Management implications

Our results have implications for the management of deep-sea mining. One of the key challenges of environmental management of mining disturbance is to ensure that the impacts can be clearly resolved against control conditions. The approach currently suggested is to compare impact reference zones, where mining activities take place, to representative control or preservation reference zones (Jones et al., 2020). Preservation reference zones are intended as reference areas for future mining impacts (Jones et al., 2020) and potentially may incorporate principles from marine protected areas (Wedding et al., 2013). The PRZ is required to be representative of the areas that will be mined ("ecologically similar"; International Seabed Authority,

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2011). Our results show that the PRZ of this study had a distinctly different community structure than the areas proposed for nodule mining, although on the spatial scales examined we did not find any evidence of taxonomic endemicity. Monitoring programmes should target nodule-habitat types similar to those found in mining areas to ensure that sufficient sample sizes are reached to compare to impacted areas. Type 1 nodule-habitat areas appear to support megafaunal communities that are similar across all study areas; therefore, Type 1 habitats in the PRZ (or in a more similar control area) could be considered as a target for monitoring future mining impacts. Another priority for conservation is preserving the "full range of habitat types found within each subregion" (Wedding et al., 2013). This PRZ does preserve a wider range of habitat types, which as shown in this study will serve to protect a greater diversity of megafaunal morphospecies. However, noting the presence of morphospecies that, while low in abundance, are only found in the mining areas will also be important.

Conclusions

We have extended knowledge of the role of nodule-habitat type and seabed heterogeneity in controlling megafaunal communities, building on previous studies that demonstrated the influence of substrate type and nodule coverage. We have shown that the varying proportion between nodules and exposed sediment between nodule-habitat types favours different functional groups. In addition, the mosaic of different nodule-habitat patches supporting subtly different communities likely means that more heterogeneous areas are able to support more species overall. This study sets an important baseline for the community structure of megafauna prior to deep-sea mining, providing critical data for evaluating the impacts of future mining activities. As different types of nodule habitats are likely to experience different mining pressure (i.e., small, abundant nodules are the primary target of mining operations), future monitoring will need to account for differences in animal communities between nodule-habitat types.

Data accessibility statement

Datasets associated with this submission are uploaded as Supplemental material.

Supplemental files

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

Tables S1–S4. Figures S1–S4. Text S1. Docx
Density nodtype (csv file)
Density per transect (csv file)
Fauna per sample nodtype (csv file)
Fauna per sample type1 (csv file)
Fauna per transect study area (csv file)

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Competing interests

The authors declare that there are no competing interests.

Author contributions

Contributed to conception and design: ESL, DOBJ.
Contributed to acquisition of data: ESL, DOBJ, BOM.
Contributed to analysis and interpretation of data: BFMF, ESL, NB.
Drafted and/or revised the article: BFMF, ESL, NB, BOM, DOBJ.
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