Rock outcrops enhance abyssal benthic biodiversity

Alejandra Mejía-Saenz [a,b,c,*], Erik Simon-Lledó [a], Louis S. Partridge [d], Joana R. Xavier [b,e], Daniel O.B. Jones [a]

[a] National Oceanography Centre, European Way, Southampton, SO14 3ZH, UK
[b] Interdisciplinary Centre of Marine and Environmental Research (CIIMAR), University of Porto, 4450-208, Matosinhos, Portugal
[c] Faculty of Science, University of Porto, Rua do Campo Alegre, 4169-007, Porto, Portugal
[d] Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton Waterfront Campus, Southampton, SO14 3ZH, UK
[e] Department of Biological Sciences, University of Bergen, 5006, Bergen, Norway

ABSTRACT

Abyssal polymetallic nodule fields represent a unique deep-sea habitat. The hard substratum provided by nodules is thought to increase habitat complexity, promoting the occurrence of highly diverse abyssal assemblages. However, hard substratum in these habitats is also available as outcropping rock fragments, but their contribution to habitat heterogeneity has been largely overlooked. Here, we assessed if the type and size of hard substratum can modulate benthic biodiversity at local scales within the Clarion Clipperton Zone (N Pacific abyss). We compared megafauna (animals >10 mm) assemblages in nodule bearing habitats with those in areas containing rocks in addition to nodules. We found a lower faunal density but a clearly higher diversity and more heterogenous composition in the assemblages of rock bearing areas compared to those with only nodules. In addition, hard substratum patch size appeared to positively influence the size of some taxa, like bamboo corals. These results suggest that rocks, in addition to nodules, constitute keystone structures enhancing habitat heterogeneity at local scales within nodule fields. Rock areas appear common in some abyssal plains and may make regionally-important contributions to abyssal biodiversity, suggesting that they may be relevant to include in conservation efforts.

1. Introduction

Hard substratum availability is a fundamental driver of biological change in the seabed, as sessile taxa require an anchor site to settle and feed (Wildish and Kristmanson, 2005). In the deep sea, hard substratum commonly outcrops at seamounts (Rogers, 1994), hydrothermal vents and seeps (Levin et al., 2016), and canyons (Orejas et al., 2009). Abyssal plains also harbour diverse sources of hard substratum, ranging from biological structures (e.g. whale-bones, wood, sponge stalks) to geological formations (e.g. exposed rock, glacial drop-stones and steamship clinker). Polymetallic nodules, potato-size mineral concretions growing on the seabed (Hein et al., 2020), provide one of the largest known resources of hard substratum in the abyss, extending in variable density for vast areas in regions like the Clarion-Clipperton Zone (CCZ) in the N Pacific.

The habitat heterogeneity hypothesis states that an increase in physical environmental complexity results in increased species diversity (MacArthur and MacArthur, 1961). Habitat heterogeneity occurs at a range of scales across the CCZ, but at fine scales (e.g. tens of meters), nodule presence plays a key role in the structuring of benthic communities (Simon-Lledó et al., 2019b), often driving variations of comparable magnitude to those resulting from regionally varying factors (Simon-Lledó et al., 2020). By providing a source of essential hard substrate for sessile species (i.e. dominant CCZ taxa), nodules act as keystone structures supporting more abundant and diverse benthic communities (Simon-Lledó et al., 2020; Goineau and Gooday, 2017), including the conspicuous benthic megafauna (i.e. animals >10 mm). Yet nodules are not the only source of native hard substratum in the CCZ. Hard-rock fragments of basaltic origin (Radziejewska, 2014), often associated with local faults (NM, 2016), can also be found exposed or outcropping within nodule fields (Alevizos et al., 2022; Parianos et al., 2022). Larger and more irregularly-shaped than nodules, rock patches have been predicted to enhance habitat heterogeneity and deep-sea biodiversity (Riehl et al., 2020; Smith, 2020). However, the presence and ecological effects of native rock patches have received little scientific attention, both in the CCZ and generally in the wider abyss.

Here, we use seabed image data to explore the potential role of the typology and size of hard substratum structures, beyond their simple presence, in the regulation of habitat heterogeneity in an abyssal seafloor community. We demonstrate how these factors can modulate local megabenthic community density, size and biodiversity patterns and discuss the ecological implications.

2. Material and methods

Seabed images used in this study were acquired using the *Autosub6000* autonomous vehicle during RRS *James Cook* expedition JC120 (Jones et al., 2021) to the Area of Particular Environmental Interest number 6 (APEI-6; centred: 17°16′N - 122°55′W; water depth: 3950–4250 m), in the eastern CCZ (N Pacific; Fig. 1a; see Jones et al., 2021 for details). We used images collected within a polymetallic nodule field in an abyssal hill area, where rock patches were observed frequently. Seabed cover and typology of hard substratum were quantified in each seabed image. First, we estimated total hard substratum cover (%) using the Compact-Morphology-based polymetallic Nodule Delineation method (CoMoNoD; Schoening et al., 2017) as described in Simon-Lledó et al. (2019b). Then, we visually selected all images containing rock patches in the hill area, and measured each rock (maximum dimension measured in a straight line) using BIIGLE 2.0 software (Langenkämper et al., 2017). Rocks were readily distinguishable from APEI-6 nodules in images owing to their larger size (Fig. 1d) but particularly to their polygonal shape and rugged surface, which makes these clearly different to the flattened, smooth and discoidal shape that characterizes the nodules of this location (e.g. Fig. 1b), which are particularly small compared to other CCZ areas (Jones et al., 2021). With this information, we classified all images in the hill area into three categories: <5% cover (Nodule-free), ≥5% cover without rocks (Nodule areas, Fig. 1b), and ≥5% cover with at least one rock larger than 100 mm in diameter or three rocks larger than 50 mm (Rock areas, Fig. 1c). Note that images classified as Rock areas could also contain small pebbles (i. e. < 50 mm, Fig. 1c) in addition to larger rocks. We excluded Nodule-free areas from analysis as the absence of a hard substratum resource has been widely shown to drive strong variations in benthic assemblages (e.g. Simon-Lledó et al., 2019b, 2020).

We identified invertebrate megafauna (>10 mm) to the lowest taxonomic hierarchy possible (morphotype: typically genus or family level) based on a CCZ-standardised taxonomic catalogue (see (Simon-Lledó et al., 2019a; b, 2020), using BIIGLE 2.0. We identified and measured a total of 1000 megafaunal specimens from both Rock areas (1636 images; area: 3230 m^2) and Nodule areas (1028 images re-annotated from Simon-Lledó et al. (2019a); area: 2270 m^2) for comparative assessment. We resampled the image data randomly, without replacement, into three replicate samples per seabed type, each with c. 333 individuals (Simon-Lledó et al., 2019a) to minimise spatial autocorrelation bias (Legendre, 1993) and the potential effect of varying faunal abundances (e.g. Simon Lledó et al., 2019b) between hard substratum types on diversity metrics. For each resulting sample, we calculated numerical density (ind m^{-2}) and Hill's diversity numbers of order 0, 1 and 2, respectively (all reported as effective number of taxa): taxa richness (S), the exponential form of the Shannon index (exp *H′*), and the inverse form of Simpson's index (1/λ), each expressing an increasingly higher sensitivity to species evenness (Jost, 2006). To assess resemblance in assemblage composition (square-root transformed faunal density data), we used Bray-Curtis similarity and displayed it with non-metric multidimensional scaling (MDS) ordination. We used SIMPER analysis with 719 permutations to determine the taxa
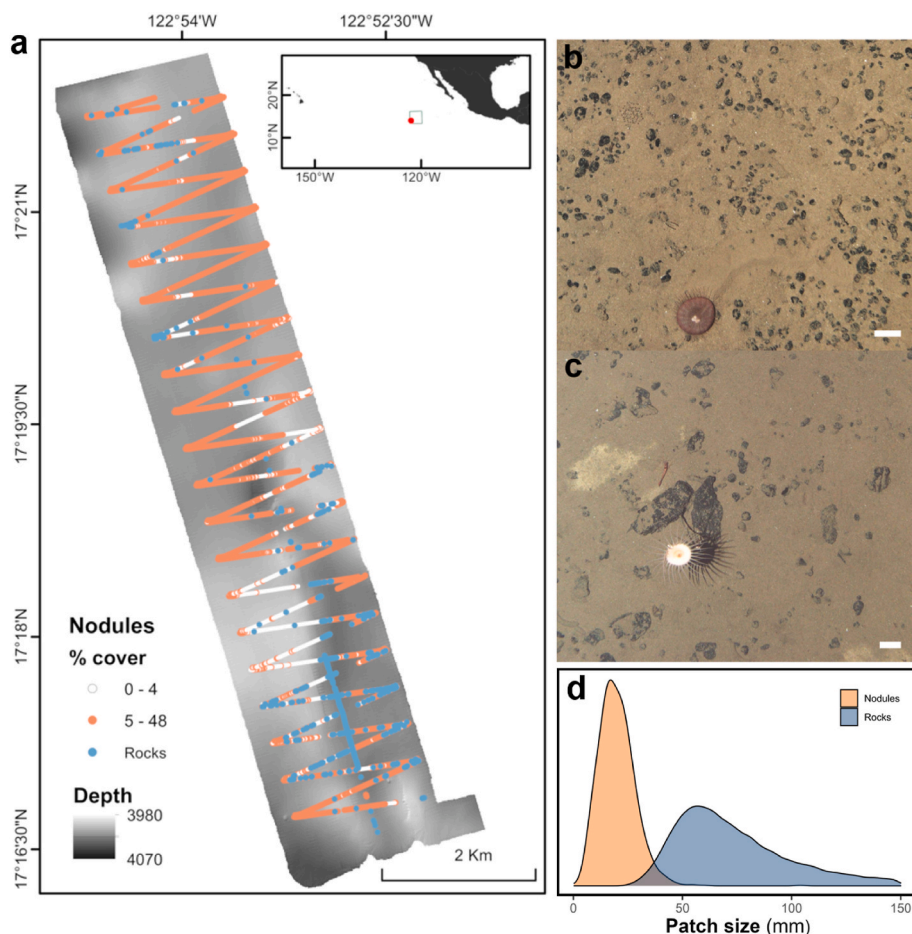

Fig. 1. Map of the study site, different hard substratum, and variations in hard substratum patch size at the Hill area in the APEI-6. **(a)** Hill study area. AUV image transect lines depict areas: with <5% hard substratum cover (white, Nodule-free areas), with ≥5% cover without rocks (orange, Nodule areas), and ≥5% cover with rock patches (blue, Rock areas). **(b, c)** Examples of Nodule and Rock seabed areas, respectively. Scale bars: 5 mm. **(d)** Variation in maximum diameter between nodule and rock patches. Ridge plots depict the frequency of nodules or rocks encountered (i.e. geometric distribution) across different patch sizes (measured as longest dimension). Nodule sizes were measured in a total of 1417 nodules, obtained from 18 randomly allocated boxcore samples collected across the SW sector of the APEI-6 (courtesy of Jones et al., 2021). Rock sizes were measured in a total of 24,106 rocks detected in seabed imagery collected across the Hill seascape of the APEI-6 (this study). Note the end-tail of the rock patch size curve depicted was cut at 150 mm to facilitate visual interpretation (e.g. maximum diameter of rocks encountered in the Hill area ranged between 2.4 cm and 1.53 m).

contributing the most to the dissimilarity between Nodule and Rock areas.

In addition, to explore the possible relation between animal and hard substratum patch sizes, we measured the size of all the nodules and rocks supporting six of the most dominant sessile taxa at the APEI-6: the anemone Hormathiidae gen. indet.; the barnacle Scalpellidae fam. indet.; the soft coral *Bathygorgia* sp. indet.; the bryozoan *Smithsonius* sp. indet.; the primnoid *Abyssoprimnoa gemina* sp. inc.; and the sponge Theneidae fam. inc. (see Supplementary material). Maximum diameter was measured in animals with radial symmetry, while colonies were measured from anchoring point to their longest branch. All analyses were performed in R (R Core Team, 2013), using the *specnumber()*, *metaMDS()*, and *simper()* functions in the "vegan" package (Oksanen et al., 2022). We used Generalised linear models (GLM) in the "car" package (Fox et al., 2022) to assess variations in univariate parameters.

3. Results

Hard substratum cover in the hill area was patchy (seabed coverage range 0–48%; average cover 6.6% ± 4.9% stdev). Total hard substratum cover was slightly higher in Nodule areas (8.6%, stdev 5.8) compared to Rock areas (6.3%, stdev 4.4). Mean density of rocks in Rock areas ranged between 0.3 and 50.5 rocks m^{-2}, with 1–80 rocks image^{-1}. Mean length of rocks in Rock areas was 81.7 mm (stdev ± 48.2), with patch sizes up to 2.1 m (i.e. exposed bedrock patch).

Our analysis revealed strong evidence (GLM: $L\text{-}ratio_{(1)} = 57.77$, $P < 0.001$) of variations in faunal density between hard substrate types, with Nodule areas exhibiting a substantially higher density (mean 42% larger) than Rock areas (Fig. 2a). In contrast, our results showed strong evidence of a higher diversity in Rock areas compared to Nodule areas, in the three metrics assessed: richness (q = 0; GLM: $L\text{-}ratio_{(1)} = 13.04$, $P = 0.001$; Fig. 2b), Shannon's index (q = 1; GLM: $L\text{-}ratio_{(1)} = 17.90$, $P < 0.0001$; Supporting information), and Simpson's index (q = 2; GLM: $L\text{-}

$ratio_{(1)} = 11.83$, $P < 0.0001$; Supporting information). On average, rock patches (mean richness: 53 taxa per c. 333 specimens) harboured ~20 more morphotypes per sample than Nodule areas (mean richness: 33.6 taxa per c. 333 specimens). This was, in part, owing to the higher dominance (i.e. lower evenness) exhibited by few particularly abundant taxa found in Nodule areas, such as the anemone Hormathiidae gen. indet. (ACT_022) and alcyonaceans *Calyptrophora persephone* sp. inc. (ALC_007) and *Callozostron bayeri* sp. inc. (ALC_009), a pattern that was also reflected in assemblage composition patterns (see below).

Differences in assemblage composition between Rock and Nodule areas were evident (Fig. 2d; only 39.5% similarity), with higher variability in communities in Rock areas (75.7% within group similarity) than in Nodule areas (80.7% within group similarity). This pattern was caused by the higher total richness in Rock patches compared to Nodule areas. A total of 96 different invertebrate megafauna taxa were encountered between the Rock (total Richness: 85 taxa) and Nodule areas (total Richness: 53 taxa) assessed. From these, 44 morphotypes were present in both seabed types, 9 taxa were found exclusively in Nodule areas and 42 taxa were found only in Rock patches. Surprisingly, 11 out of the 42 taxa found only in Rock patches (area surveyed: 3230 m^2) were also absent elsewhere in the wider area (i.e. rock-free seafloor: 8326 m^2; total taxa richness: 129) previously investigated within the APEI-6 study site (Simon-Lledó et al., 2019b). All of these morphotypes had low densities (<50 ind ha^{-1}) and seven were singletons. Most (eight of 11) taxa only found on rock patches were sponges.

Variations in density between Rock and Nodule areas were only evident in sessile taxa, with clearly higher densities of anemones, soft corals, and bryozoans in Nodule areas, and higher densities of sponges in Rock patches (Fig. 2c). In contrast, arthropods and echinoderms, both predominantly mobile taxa, exhibited similar densities across seabed types (Fig. 2c). Variations in density were particularly apparent in the abundant morphotypes (Fig. 3). Theneidae fam. inc. (DES_021; Fig. 3a), a small encrusting sponge found typically attached to nodules, was
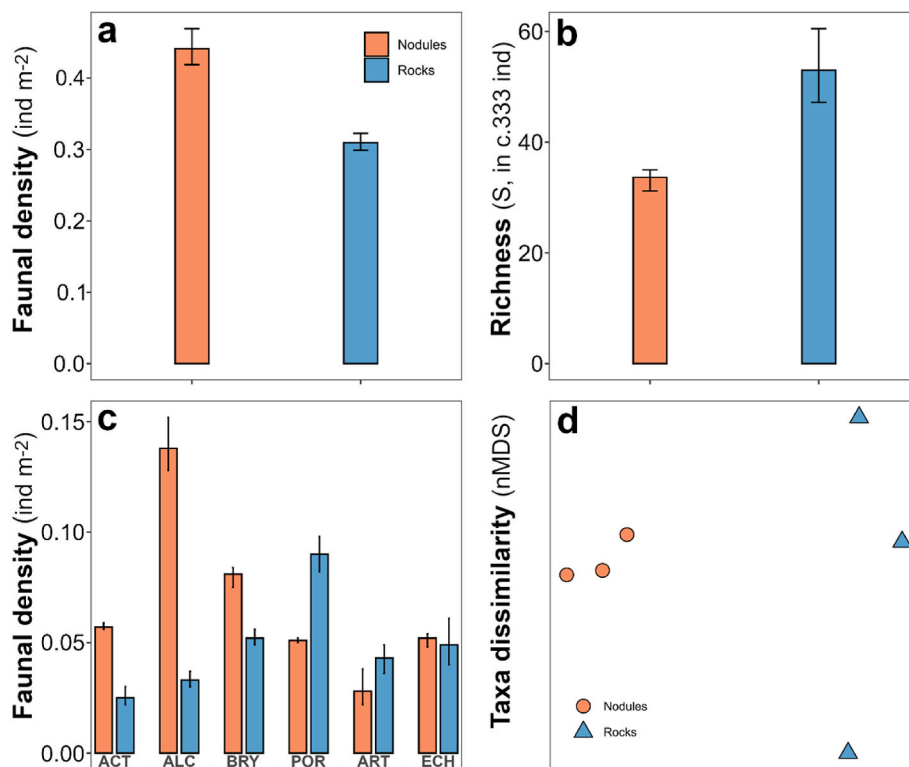

Fig. 2. Variations between the communities in Rock and Nodule dominated areas. **(a)** Faunal density. **(b)** Taxa richness. **(c)** Faunal density of dominant taxonomic groups (ACT: Actiniaria; ALC: Alcyonacea; BRY: Bryozoa; POR: Porifera; ART: Arthropoda; ECH: Echinodermata). Bars indicate mean values across replicate samples surveyed in each study area. Error bars represent 95% confidence intervals. **(d)** MDS ordination (two-dimensional) of megafaunal composition by density.
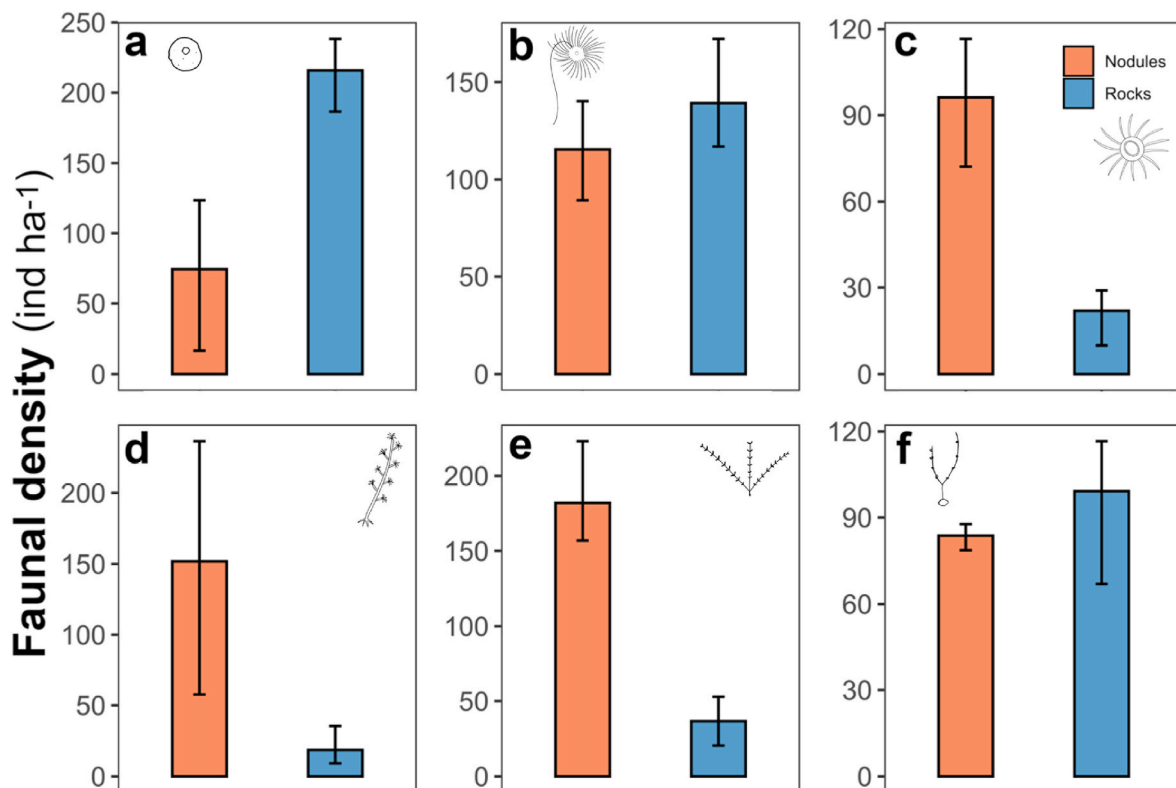
Fig. 3. Key morphotype density variations between Nodule and Rock areas. Mean density between replicate samples, error bars = 95% confidence intervals. **(a)** Demosponge Theneidae fam. inc. (DES_021), **(b)** Demosponge *Axoniderma mexicana* sp. inc. (DES_002), **(c)** Actiniarian Hormathiidae gen. indet. (ACT_022), **(d)** Alcyonacean *Calyptrophora persephone* sp. inc. (ALC_007), **(e)** Alcyonacean *Callozostron bayeri* sp. inc. (ALC_009), **(f)** Alcyonacean *Bathygorgia* sp. indet. (ALC_004).

almost three times more abundant in Rock patches. In contrast, densities of *Axoniderma mexicana* sp inc. (DES_002; Fig. 3b), a stalked carnivorous sponge sometimes attached to nodules, were similar. Densities of Hormathiidae gen. indet. (ACT_022; Fig. 3c), a small anemone typically attached to nodules, were four times higher in Nodule areas. Densities of *Calyptrophora persephone* sp. inc. (ALC_007; Fig. 3d) and *Callozostron bayeri* sp. inc. (ALC_009; Fig. 3e), two small primnoids very commonly encountered on nodules in the eastern CCZ (see e.g. Amon et al., 2016; Simon-Lledó et al., 2020), were respectively eight and five times higher in Nodule areas (see Supplementary material for results of SIMPER analysis). Most, but not all, taxa were larger on larger substratum patches (Supplementary material). The 'large' bamboo coral *Bathygorgia* sp. indet. (ALC_004) exhibited the strongest positive association between colony size and hard substratum patch size (Adj R^2 = 0.45, P = 5.324e^{-10}, Supplementary material) although densities were similar between seabed types (Fig. 3f). Colonies of this morphotype in Rock patches (mean length: 86 mm; median length: 68 mm) were almost twice the size of those found in Nodule areas (mean length: 46 mm; median length: 32 mm).

4. Discussion

The results of this study reveal that abyssal polymetallic nodule fields are more complex mosaic habitats than previously thought. Our analyses show that rock patches in nodule fields exhibit lower megafaunal density but a higher taxa richness and diversity than adjacent areas where the only available source of a hard substratum were polymetallic nodules (Fig. 2a and b, Supplementary material). These patches also harboured a more heterogeneous faunal assemblage than those observed in nodule-only areas, despite a similar overall coverage of hard substratum (Fig. 2d). There is some evidence that patch size positively influences faunal size. Our results demonstrate clear biodiversity patterns in line with the habitat heterogeneity hypothesis (MacArthur and

MacArthur, 1961), although these effects were unequal between taxonomic groups and particularly obvious in sessile taxa (Figs. 2c and 3) that require hard substrata for attachment (Atauri and De Lucio, 2001). There are a number of potential explanations for these patterns, including: i) a higher fine-scale habitat heterogeneity on rock areas, with a more complex three-dimensional structure and a higher surface roughness than the smooth nodules (Jones et al., 2021), ii) enhanced feeding opportunities on rocks that extend into increased flow regimes above the seabed (Butman, 1987; Mullineaux, 1988); iii) an increased particle trapping in the wake of the rocks increasing larval or organic matter retention (Mullineaux, 1989); iv) an increased stability of larger rocks, which are less likely to turn over with a large organism attached than smaller nodules; and likely other factors.

In the CCZ, polymetallic nodules had been the only keystone structure considered in both local and regional megabenthic studies. The occurrence of nodules is linked to that of several megabenthic species and different cover percentages hold distinct biological communities (Simon-Lledó et al., 2019b). Here, we show that rocks, present commonly on the abyssal seafloor, constitute an additional keystone structure in the CCZ that increases habitat heterogeneity and controls fine-scale community variations. This contribution of small rock patches has been largely overlooked (although see Cuvelier et al., 2020 for seamounts in the CCZ) potentially as effects are more clearly visible at less-commonly-assessed intermediate scales (meters to several km). To understand their contribution to local biodiversity, future studies should assess the distribution and physicochemical characteristics of rock areas as well as the role of hard substrata in the life histories of the organisms of the CCZ. Given the huge areas of abyssal environments in the world's ocean basins (Harris et al., 2014), the increasing awareness of the presence (Riehl et al., 2020; Smith, 2020) and importance of rocky areas suggests that the contribution of remote abyssal habitats to global biodiversity in the marine realm should be reassessed and conservation strategies adjusted accordingly.

Data accessibility

Primary data used to conduct this study is provided in the supplementary materials. The R scripts used for this study only contain standard functions and analysis methods detailed in the methods section.

Authors' contributions

A.M.S.: Data curation, Formal analysis, Investigation, Software, Visualization, Writing – original draft, Writing – review & editing. E.S. L.: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – review & editing. L.P.: Data curation, Formal analysis, Investigation. J.X.: Writing – review & editing. D.J.: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Writing – review & editing.

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Declaration of competing interest

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

Data availability

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2023.103999.

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