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Are seamounts refuge areas for fauna from polymetallic nodule fields?

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Running title: Seamounts as refuge areas for nodule fauna

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Abstract

Seamounts are abundant and prominent features on the deep-sea floor and intersperse with the nodule fields of the Clarion-Clipperton Fracture Zone (CCZ). There is a particular interest in characterising the fauna inhabiting seamounts in the CCZ because they are the only other ecosystem in the region to provide hard substrata besides the abundant nodules on the soft sediment abyssal plains. It has been hypothesised that seamounts could provide refuge for organisms during deep-sea mining actions or that they could play a role in the (re-)colonisation of the disturbed nodule fields. This hypothesis is tested by analysing video transects in both ecosystems, assessing megafauna composition and abundance.

Nine video transects (ROV dives) from two different license areas and one Area of Particular Environmental Interest in the eastern CCZ were analysed. Four of these transects were carried out as exploratory dives on four different seamounts in order to gain first insights in megafauna composition. The five other dives were carried out in the neighbouring nodule fields in the same areas. Variation in community composition observed among and along the video transects was high, with little morphospecies overlap on intra-ecosystem transects. Despite these observations of considerable faunal variations within each ecosystem, differences between seamounts and nodule fields prevailed, showing significantly different species associations characterising them, thus questioning their use as a possible refuge area.

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1. Introduction

Seamounts are abundant and prominent features on the deep-sea floor (Wessel et al., 2010). They are common in all the world's oceans, occurring in higher abundances around mid-ocean ridges, island-arc convergent areas, and above upwelling mantle plumes (Kitchingman et al., 2007). Seamounts are generally isolated, typically cone shaped undersea mountains rising relatively steeply at least several hundred meters from the deep-sea floor. Seamounts comprise a unique deep-sea environment, characterised by substantially enhanced currents and a fauna that is dominated by suspension feeders, such as corals (Rogers, 2018). They represent hard substrata in the otherwise soft sediment deep sea and can thus be considered habitat islands (Beaulieu, 2001). Given the growing evidence that seamounts differ substantially across a range of spatial scales, the concept of seamounts as a single, relatively well-defined habitat type is outdated (Clark et al., 2012). Depth and substrate type are key elements in determining the composition and distribution of benthic fauna on seamounts, while location is likely the subsequent most important driver of faunal composition and distribution patterns (e.g. Tittensor et al., 2009). Connectivity varies substantially between seamounts, resulting in the presence of taxa with very localised to very wide distributions (Clark et al., 2010).

The Clarion-Clipperton Fracture Zone (CCZ), in the equatorial eastern Pacific Ocean, is most known for its extensive polymetallic nodule fields that will potentially be mined in the future. In this area, nodules represent the most common hard substrate on the soft-sediment abyssal plains, and many organisms rely on them for survival (Vanreusel et al., 2016). Removal of hard substrate through mining actions will impact all these organisms, which were estimated at about 50% of all megafaunal species in the CCZ (Amon et al., 2016). Nodule fields in the CCZ are interspersed by seamounts (Wedding et al., 2013), the only feature offering hard substrata besides the nodules. Based on this feature/characteristic, it has been hypothesised that seamounts could provide refuge for organisms during deep-sea mining activities or that seamounts could play a role in the (re-)colonisation of the disturbed nodule fields. Whether or not this is true may have important implications for management of the impacts of polymetallic nodule mining in the CCZ. However, knowledge on the biodiversity inhabiting seamounts in this region is currently lacking.

The objectives of the current study were twofold: (i) Provide first insights in seamount megafauna within the CCZ, (ii) Compare the benthic fauna inhabiting seamounts and nodule fields in the eastern CCZ. Since this is the first time the seamounts at the eastern CCZ were visited, a separate section is dedicated to describe these first insights.

2. Material and Methods

2.1. Study site and data

During the SO239 ECORESPONSE cruise (Martinez Arbizu and Haeckel, 2015), four seamounts were visited for the first time within two different license areas and one area of particular environmental interest (APEI) within the Clarion-Clipperton Fracture zone (CCZ) (Table 1). Nodule fields within the same license areas were visited and sampled as well. Video imagery and faunal samples were collected by a Remotely Operated Vehicle (ROV Kiel 6000 (GEOMAR), equipped with a high definition Kongsberg OE14-500 camera).

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Seamount transects were carried out uphill towards the summit resulting in a depth gradient along the transect, whilst nodule transects featured rather stable depth ranges (Table 1). The four seamount transects were characterised by different depth ranges and lengths but were all situated on the north to north-western flanks of the seamounts (Table 1 and Fig. S1). The names of the seamounts used here, Rüppel and Senckenberg (BGR, German License area), Heip (GSR, Belgian License area) and Mann Borgese (APEI3), are the ones agreed upon by the scientist during the ECORESPONSE cruise (Martinez Arbizu and Haeckel, 2015), pending incorporation of these names in the GEBCO gazetteer. The seamounts differed in shape and size with Senckenberg and Heip being a sea-mountain range, while Rüppel and Mann Borgese were more isolated, stand-alone seamounts (Fig. S1). Nodule field dives were carried out on relatively flat surfaces (maximum depth range covered during a dive or transect was 30m difference, Table 1) and were referred to by the dive number and license area. The five nodule transects were all located between 4000-5000m depth and the transects differed in length between dives as well (Table 1). Within the same license area distance between different transects was 16 to 60km, while distance between license areas added up to several hundreds of kilometres (minimum ~700kms BGR – GSR, Fig. 1).

Investigated areas were restricted to the eastern part of the CCZ with APEI3 being the most north- and westward bound area. The optical resolution of the camera enabled reliable identification of organisms larger than 3 cm (Martinez Arbizu and Haeckel, 2015). The combination of exploration and opportunistic sampling restricted a systematic image collection. ROV travelling altitude, speed and camera zoom were kept constant whenever possible, while pan and tilt of the ROV camera were not.

2.2. Video analysis and statistics

All videos were annotated to the lowest taxonomic level possible. The number of morphospecies, defined as morphologically different organisms within the lowest taxonomic group identified, were assessed. Identifications were double checked with scientists working in the same area as well as taxonomic experts and comprise different taxonomic levels (e.g. Genus, Family). Those ID's restricted to higher taxon groups (Family, Class, etc.) and for which it was impossible to attribute a morphospecies, are referred to as taxa and are likely to morphologically differ between transects. Xenophyophores, living on the soft sediment deep-sea floor, were less prominently present at seamounts than at nodule fields and were not quantified. Fish (Actinopterygii), crustaceans (Nematocarcinidae, Aristeidae, Peracarida) and Polychaeta were quantified but left out of the comparing analysis due to their lack of representativity and possible attraction due to ROV lights. The same was done for jellyfish and other doubtful ID's that could not be confidently assigned to a higher taxonomic group (Table A1).

ROV transects on the seamounts were carried out as exploratory dives. Sampling strategy both at seamounts and nodule fields combined video and sampling or specimen collection. Due to varying altitude of the ROV and the use of camera pan, tilt and zoom, it was not possible to use surface coverage as a standardisation measure. We used video transect length instead. Faunal densities were calculated as the number of observations per 100m, in order to compensate for time spent collecting samples and differing transect lengths. Statistical testing was carried out in R (R core team, 2018) and the Non-metric multidimensional scaling analysis (NMDS) was based on Bray-Curtis dissimilarity and used the vegan package (Oksanen et al., 2018).

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3. Results

A total of 252 taxa were observed across the two adjacent ecosystems, of which 207 (or 82%) could be identified to a morphospecies level. At a first view, morphospecies revealed to be quite different between seamounts and nodule fields (Fig. 2). While the number of faunal observations at the seamount transects were within similar ranges (33.1-40.7 ind./100m), those at the nodule transects featured both highest and lowest values (7.59-89.23 ind/100m) (Table 1). The lowest number of faunal observations were done at the two APEI3 nodule transects (ROV13 and 14) and highest at the GSR nodule transect ROV08. What follows is a first description of eastern CCZ seamount megafauna (3.1.) and a detailed comparison with the neighbouring nodule fields (3.2.)

3.1. Insights in CCZ seamount megafauna

The most abundant and diverse (most morphospecies) taxa at the seamount transects comprised Echinodermata (Asteroidea, Crinoidea, Holothuroidea and Ophiuroidea), Anthozoa (Actiniaria, Alcyonacea, Pennatulacea, Scleractinia) and Porifera (Hexactinellida) (Table A1, Fig. 3). Keeping in mind the limitation of the video sampling, differences among the benthic seamount community composition are described here.

The transect at Mann Borgese (APEI3) was characterised by high densities of Antipatharia, more specifically Antipathidae (19.11 ind./100m), and solitary Scleractinia (8.11 ind./100m) (Table A1, Fig. 3). Antipathidae observations were mostly grouped at the end of the video transect, i.e. at the summit. Densities of both Antipatharia and Scleractinia were much lower on the other seamount transects (≤0.2 ind./100m) with Scleractinia being absent from Heip and Senckenberg transects. Alcyonacea corals were observed on all seamount transects. Isididae were found at Senckenberg and Heip transects, and one individual from Chrysogorgiidae was observed at the latter as well. Varying numbers of Primnoidae were observed on all transects (Table A1). High abundances of Pennatulacea were observed at Senckenberg (3.64 ind./100m), representing about 26% of sessile fauna annotations for this transect.

Enteropneusta were only observed on Rüppel and Senckenberg transects in the BGR area, represented by two different morphospecies, namely *Yoda* morphospecies (Torquaratoridae) at Rüppel and *Saxipendium* morphospecies (Harrimaniidae) at Senckenberg.

Highest Polychaeta densities were observed at Heip transect in the GSR area (4.2 ind./100m vs. 0.56 and 0.32 ind./100m in BGR and 0.11 ind./100m in APEI3). Free-swimming Acrocirridae were observed in very high densities as well (Table A1). Aphroditidae polychaetes were only present at the BGR transects (3 ind. at Rüppel and 1 at Senckenberg) (Table A1).

Porifera densities were highest at the Heip transect (3 ind./100m), followed by Rüppel (2.72 ind./100m), Senckenberg (1.92 ind./100m) and lastly Mann Borgese (0.68 ind./100m). Six Porifera families were annotated featuring >7 to >10 morphospecies (Fig. 3, Table A1). Cladorhizidae (two individuals) were only observed on Heip transect, and one *Poliopogon* sp. (Pheronematidae) was observed at Mann Borgese transect. Rossellidae gen. sp. nov. was present on three seamount transects, exception being Mann Borgese.

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Overall Echinodermata densities were highest at Senckenberg seamount (17.64 ind./100m), followed by Rüppel (12.24 ind./100m) (Table A1, Fig. 3), both adding up to 60% of all image annotations for these transects. The number of morphospecies for all echinoderm taxa (Asteroidea, Echinoidea, Holothuroidea and Crinoidea) was also highest at these 2 seamounts in the BGR area (Fig. 3). For comparison, echinoderms at Heip (11.68 ind./100m) and Mann Borgese transects (3.08 ind./100m) were responsible for 49% and 8.8% of observations respectively. Crinoid densities were highest at Senckenberg (4.32 ind./100m), while Holothuroidea were most abundant at Rüppel (5.2 ind./100m). The holothuroid families of Elpidiidae and Laetmogonidae were only observed at Senckenberg and Rüppel (BGR). Psychropotid and synallactid holothuroids were observed on all seamounts, represented by different morphospecies. Deimatid holothuroids were not observed on Mann Borgese, but were present in the three other seamount transects, again with different morphospecies and densities. Velatid Asteroidea were only observed at Senckenberg and Rüppel (BGR), while Brisingida and Paxillosida were observed on all four seamounts. Aspidodiadematid echinoids were absent from the Heip transect and urechinid echinoids were absent from the Mann Borgese transect.

A species accumulation curve (Fig. 4a) confirmed the limitations of the restricted and exploratory nature of the sampling as no asymptote was reached. The rarefaction curves (Fig. 4b) showed that the transects with the most faunal observations, which corresponded here to the longer transects, were more diverse. However, at smaller sample sizes curves did not cross, thus maintaining the differences observed at higher sample sizes with the Senckenberg transect (ROV04) most diverse followed by Rüppel (ROV02) (both BGR). The video transect carried out at Mann Borgese (ROV15, APEI3) was the least diverse.

A comparison of all morphospecies observed along the 4 transects was presented in a Venn diagram (Fig. 5a). Each seamount transect was characterised by a highest number of unique morphospecies, only observed on the transect in question and not elsewhere. Only two morphospecies were present in all seamount transects, namely a small red galatheid crab and a foliose sponge. Highest number of overlapping morphospecies (#14) was observed between Rüppel and Senckenberg, both in the BGR area (Fig. 5a). Mann Borgese showed the smallest degree of overlap with the other transects (Fig. 5a).

Due to the limited sample size, the representativity of the observed biological patterns remains to be corroborated by a more elaborate sampling strategy.

3.2. Comparison of seamount and nodule field faunal composition and variation

The faunal composition and richness (number of morphospecies in higher taxonomic groups) of the nodule transects can be consulted in Fig. 3 and Table A1. In concordance with the seamount transect, the species accumulation curve of the nodule transects did not reach an asymptote either (Fig. 4c). The rarefaction curves showed that the relations among transects were less linear for the nodule transects versus the seamount ones and did cross at smaller sample sizes (Fig. 4d). ROV13 and ROV14 transects (both APEI3) were the longest in distance travelled (Table 1) but featured less faunal observations. At small sample sizes, the richness atROV13 and 14 was highest. ROV08 and ROV10 (both GSR) showed parallel curves with ROV08 being more diverse (Fig. 4d).

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A venn diagram showing the morphospecies overlap among the nodule transects showed a total of 5 species re-occurring on all 5 transects (Fig. 5b). These were: Munnopsidae msp. 1 (Isopoda, Crustacea), Actiniaria msp.7 (Cnidaria), Ophiuroidea msp. 6 (Echinodermata), *Holascus* sp and *Hyalonema* sp. (Hexactinellida, Porifera). There was a high number of unique morphospecies for each transect, though not as high as for the seamount transects (Fig. 5). ROV13 and 14 (both APEI3) showed littlest overlap with the other transects, which is similar to what was observed at the seamounts.

Observations and quantifications of morphospecies confirmed the high degree of dissimilarity between the two neighbouring ecosystems. Porifera, Ophiuroidea (Echinodermata), Actiniaria and Alcyonacea (Cnidaria) were more abundant at nodule fields (Fig. 3). These taxonomic groups were also most diverse on nodule fields (i.e. highest number of morphospecies), exception being the Alcyonacea which featured more morphospecies on the seamounts (12 to 8 morphospecies for seamounts and nodule fields respectively) (Fig. 3). Of all Porifera, Cladhorizidae were more diverse at nodule fields than at seamounts (7 to 1 morphospecies, respectively).

There were only 21 morphospecies (10%) that were observed both on seamounts and nodule fields (Fig. 6). While this subset of morphospecies occurred in both ecosystems, they did so in very different densities, i.e. very abundant in one ecosystem and very low in abundance in the other, examples are Galatheidae small red msp. (Decapoda, Crustacea), *Synallactes* white msp. (Holothuroidea), Ophiuroidea msp. 5 and 6, Comatulida msp. 1 (Crinoidea), *Hyalonema* sp. and *Hyalostylus* sp. (both Hexactinellida, Porifera) (Fig. 6).

Three Ophiuroid morphospecies were present at both seamounts and nodule fields (Fig. 8). The majority of the very abundant ophiuroids observed at the CCZ seamounts were small and situated on hard substrata (morphospecies 5). While the most abundant morphospecies at nodule fields (morphospecies 6) was mostly observed on the soft sediments of the nodule transects. This morphospecies was only rarely observed on the seamounts (Fig. 3). Another easily recognisable morphospecies was found on Porifera, corals and animal stalks and was more abundant at seamounts than at nodule fields (morphospecies 4) (Fig. 2 and 3).

Crinoidea, Asteroidea (both Echinodermata) and Antipatharia (Cnidaria) were more abundant on the seamounts. This coincided with a higher diversity for Asteroidea and Antipatharia on the seamounts as well. Crinoidea diversity was similar (5 to 4 morphospecies comparing seamounts to nodule fields). Holothuroidea occurred in similar densities in both ecosystems, though they were characterised by different morphospecies (Fig. 3). Overall densities of Echinoidea were highest at nodule fields, though this was mostly due to one very abundant morphospecies, namely Aspidodiadematidae msp 1 (Fig. 3). Besides this one very abundant morphospecies, which was only present at nodule fields, echinoids showed higher densities at seamounts and were more diverse (11 morphospecies vs. 5 at nodule fields).

There was no morphospecies overlap for Tunicata, Antipatharia, and Actiniaria. Alcyonacea, Ceriantharia, Corallimorphidae and Crinoidea only shared 1 morphospecies between seamounts and nodule fields, namely *Callozostron* cf. *bayeri*, Ceriantharia msp. 2, *Corallimorphus* msp. 2 and Comatulida msp. 1 respectively (Fig. 6).

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There were no observations of Enteropneusta, Scleractinia and Zoantharia (Cnidaria), Aphroditidae (Polychaeta) or holothuroid Deimatidae at the nodule fields transects (Table A1). While Actinopterygii were left out of the analysis, it should be noted that fish observations were more abundant and diverse at the seamounts than on the nodule fields (Table A1).

There was quite some faunal variation observed along the video transects carried out in the different license areas, both for seamounts and nodule fields (see fig. 5). The (dis)similarities were analysed by a nMDS analysis, which grouped the 9 different video transects based on their taxonomic composition. Despite the large intra-ecosystem variation, they pooled in two distinct groups separating the nodule fields from the seamounts (Fig. 7a). Within each group, BSR and GSR transects were more similar to one another both for seamounts and nodule fields, whilst APEI3 transects stood out more.

The Kendall's coefficient of concordance (W, Legendre, 2005) corroborated the existence of two significantly different species associations, whose composition corresponded to the fauna characterising the nodule fields ($W=0.20$, $p<0.001$, after 999 permutations) and the seamounts ($W=0.30$, $p<0.001$, after 999 permutations).

Depth was fitted as a vector on top of the nMDS plot (Fig. 7b) and showed that the discrepancy in faunal composition between the two ecosystems also corresponded to a difference in depth, with the nodule transects all being situated below the 4000m isobath and the seamount transects ranging from 1650 to >3500m (Fig. 7b).

4. Discussion

4.1. Intra-ecosystem faunal variation

Community composition varied markedly within seamounts and nodule fields. The limited sampling (n=9 transects), across different localities and for the seamounts different depth gradients, precluded any general conclusions on quantifications of biodiversity *per se*. However, taking this into account, it was also the first time seamounts were visited in the area, thus granting first insights in the fauna inhabiting these seamounts and allowing a first comparison with nodule faunal composition.

The two BGR seamount video transects were geographically closest to each other and were most similar in faunal composition but also in depth. For seamounts, distance separating them might be a less determining factor since adjacent seamounts were shown to be very different in inhabiting fauna (Schlacher et al., 2014; Boschen et al., 2015). Overall, parameters that vary with depth are considered major drivers of species composition on seamounts (Clark et al., 2010; McClain et al., 2010). Depth could be explanatory for the higher degree of similarity of these two BGR seamount transects and, to a lesser extent, the Heip seamount transect (GSR). Similarly, it could explain the higher dissimilarity with Mann Borgese (APEI3) who featured the shallowest transect and summit, which was dominated by Antipatharia. Antipatharians were previously reported to be more dominant towards peaks as compared to mid-slopes at corresponding depths (Genin et al., 1986). Based on their filter-feeding strategy, Porifera (except carnivorous Cladorhizidae), were also thought to benefit from elevated topography (peaks) or exposed substrata in analogy to corals (Genin et al., 1986; Clark et al., 2010), though no such pattern was apparent here. Porifera are notoriously difficult to identify based on imagery. Although the sampled individuals allowed some identifications to genus or species level (Kersken et al., 2018a and b), identifications remained hard to extrapolate

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across the different video transects. Generally, as in our study, seamount summits have been more intensively sampled (Stocks, 2009) although the little work done at seamount bases and deep slopes indicated that these areas support distinct assemblages (Baco, 2007).

Among the nodule transects a considerable amount of variation in faunal composition was observed (this study, Vanreusel et al., 2016). The two APEI3 nodule transects (ROV13 and 14) stood out, both in the low number of faunal observations, faunal composition and diversity. They were also the only two transects situated below the 4500m isobaths. But rather than depth, the nodule coverage was thought to be more of a driving factor, since the density of nodule megafauna was shown to vary with nodule size and density/coverage (Stoyanova, 2012; Vanreusel et al., 2016, Simon-Llédo et al., 2019). Here as well, the APEI3 transects were characterised by a high nodule coverage (~40-88%, Vanreusel et al., 2016), whereas the BGR and GSR nodule transects (ROV3 and ROV 8 + 10, respectively) had a nodule coverage <30% and were more similar in faunal composition (Vanreusel et al., 2016). The more oligotrophic surface waters of the northern CCZ were proposed to be the cause of the overall lower densities at APEI3 nodule fields (Vanreusel et al., 2016).

The species accumulation curves showed that no asymptote was reached not at seamounts, nor at nodule fields. Consequently, longer transect lengths might be necessary to representatively quantify and assess megafauna density and diversity (Simon-Lledó et al., 2019). In addition, for a first in-depth description and assessment of seamount fauna composition, one video transect is insufficient to describe the diversity and shifts in faunal assemblages of the surveyed seamounts. Rather, an ampler imaging strategy should be developed, with a minimum transect length exceeding 1000ms (Simon-Llédo et al., 2019) and replicate transects carried out on different faces of the seamount, on slopes with varying degree of exposure to currents and different substrate types. Wider depth ranges should be taken into account as well. Despite its limitations, this study grants first insights in the seamount inhabiting megafauna of the eastern CCZ and an important first comparison with nodule fauna.

4.2. Faunal (dis)similarities between seamounts and nodule fields

Seamounts were shown to share fauna with surrounding habitats (Clark et al., 2010) and potentially serve as source populations for neighbouring environments (McClain et al., 2009). While generally few species seemed restricted to seamounts only (Clark et al., 2010), in this study, morphospecies revealed to be quite different between seamounts and nodule fields with little overlap between both. Despite the high degree of variation observed among all the video transects, these grouped into two distinctly separate clusters, separating nodule from seamount transects. The few overlapping morphospecies did occur in different densities in each ecosystem, implying a different role or importance in the ecological community and its functioning.

Taxa contributing to the differences between the two ecosystems are discussed here. Ophiuroids were more abundant on the nodule fields. Asteroids and echinoids (with exception of one very abundant morphospecies at the nodule fields) were both more abundant and diverse on the seamounts. Both ophiuroid and echinoids were shown to be present in both nodule-rich and -free areas, though their densities decreased more than 50% comparing the former to the latter (Vanreusel et al., 2016). Despite the abundance of hard substrata at seamounts, this was true for the ophiuroid densities observed here (>50% decrease form nodule fields to seamounts), but not for the echinoids, where differences in overall density between ecosystems were less pronounced.

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Ophiuroids did not show high levels of richness or endemism on seamounts (O'Hara, 2007). Same ophiuroid morphospecies were present at seamounts and nodule fields but in very different abundances and they showed preference for different substrata (at nodule fields on soft sediment (morphospecies 6), at seamounts on hard substrata (morphospecies 5)), which appeared to correspond to different lifestyles, feeding behaviour and corresponding dietary specialisations (Persons and Gage, 1984). Ophiuroids were often observed in association with xenophyophores at nodule fields (Amon et al., 2016) and at east Pacific seamounts (Levin et al., 1986), though no such associations were observed on the seamounts studied.

Holothuroid composition varied distinctly between nodule fields and seamounts with more families being observed at the latter. Many holothurians feed on the upper layers of the soft-bottom sediment (Bluhm and Gebruk, 1999), suggesting that their numbers would decrease when there is less sediment available. However, at the seamounts, many holothurians were observed on top of rocks, possibly reflecting different feeding strategies and explaining the observations of different morphospecies. Geographical variations, different bottom topography, differences in nodule coverages and sizes and/or an uneven distribution of holothurians on the sea floor were thought to play a role in holothuroid community composition (Bluhm and Gebruk, 1999). On the other hand, variability in deep-sea holothuroid abundance was proposed to depend primarily on depth and distance from continents (see Billet, 1991 for a review).

Stalked organisms, such as Crinoidea and Hexactinellida (except for Amphidiscophora) rely on hard substrata for their attachment. Crinoidea were proportionally more abundant on seamounts, possibly because hard substrata were less limiting than in the nodule fields. Porifera proportions (stalked and non-stalked) varied among all analysed transects, revealing no particular trends in abundance. However, the species composition of deep-sea glass sponge communities from seamounts and polymetallic nodule fields was distinctly different. Polymetallic nodule field communities were predominated by widely-distributed genera such as *Caulophacus* and *Hyalonema*, whereas seamount communities seemed to have a rather unique composition represented by genera like *Saccocalyx*. Stalked organisms are considered being among the most vulnerable organisms when mining is concerned.

While alcyonacean and antipatharian corals were virtually absent from nodule-free areas (Vanreusel et al., 2016), this was not the case for the seamounts (although Alcyonacea densities were lower than on nodules). Depth difference added up to more than 3000m between Mann Borgese seamount (APEI3) and the nodule transects, which could explain the difference in Antipatharia which were more abundant at lower depths (Genin et al., 1986). The antipatharian and alcyonacean morphospecies that were abundant on the seamounts did not occur on the nodule fields and vice versa, with exception of *Callozostron* cf. *bayeri* which was present at the nodule fields but in very low densities (1/10 of those observed at seamounts). Additional presence of Pennatulacea, which were virtually absent from the nodule field transects, resulted in a completely distinct coral community for both ecosystems.

Actiniaria were more abundant on nodule fields. It was denominated the second most common group at CCZ, after the xenophyophores (Kamenskaya et al., 2015). Depending on the species and feeding strategy, the ratio hard/soft substrata and their preference for either one could play a role. Since morphospecies were distinct between seamounts and nodule fields, their role in the

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respective communities are likely to differ as well. Combinations of deposit feeding and predatory behaviour in Actiniaria have been observed, as well as burrowing activity, preference for attachment to hard substrata and exposure to currents (Durden et al., 2015a; Lampitt and Paterson, 1987; Riemann-Zürneck, 1998).

Some taxa were only observed on seamounts, while they were also known to occur on nodule fields, be it in low densities. The exception were the Scleractinia, which were absent at nodule fields but quite common on seamounts (e.g. this study, Baco, 2007). Contrastingly, Enteropneusta were observed previously at CCZ nodule fields though observations were rather rare (Tilot, 2006). They appeared more abundant at the nodule fields of the Deep Peru Basin (DISCOL area), though a wide range in abundances was displayed there as well (Bluhm, 2001).

Explanation for the discrepancies observed here in faunal composition and low degree of morphospecies overlap between seamount and nodule fields can be multiple. For one, nodules may not be considered a plain hard substratum, with their metal composition, microbial colonisation and the nodule/sediment interface influencing the epi-and associated megafaunal composition. The possibility of a specific deep-sea faunal community that tolerates or benefits from manganese substrata has been previously proposed (Mullineaux, 1988). The comparison between seamounts and nodule fields as two neighbouring hard-substrata ecosystems also entailed a comparison between depth gradients and possible thresholds (>4000m for nodule fields and 1500>x <4000m for seamounts). Related to this is the steepness of the seamount slope and its current exposure playing a role in the faunal colonisation (Genin et al., 1986; Rappaport et al., 1997). Other studies showed that habitat heterogeneity increased megafaunal diversity at seamounts (Raymore, 1982) and elsewhere, such as abyssal plains (Lapointe and Bourget, 1999; Durden et al., 2015b, Leitner et al., 2017, Simon-Llédo et al., 2019). Within this perspective the ratio hard/soft substrata or amount of hard substrata available could play a role as well.

5. Conclusions

Based on our current knowledge; seamounts appear inadequate as refuge areas to help maintain nodule biodiversity. In order to conclusively exclude seamount habitats as a refuge for nodule fauna, a more comprehensive sampling should be carried out. The sampling strategy wielded in this study lacked replicates, uniformity and was limited in sample size. Seamount bases should be taken into consideration as well as they can be characterised by distinctly different assemblages than the summits and they occur at a depth range more similar to nodule fields.

While their role as refuge area for nodule field fauna is currently debatable, the possible uniqueness of the seamount habitat and its inhabiting fauna implies that seamounts need to be included in management plans for the conservation of the biodiversity and ecosystems of the CCZ.

Author Contributions

DC, PAR, SPR, DK analysed the images. DC analysed the data. PMA, PAR, AC conceptualised and carried out the sampling. All authors contributed to the redaction of the manuscript.

Data Availability

Data sets are made available through OSIS-Kiel data portal, BIIGLE and PANGAEA.

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Competing interest

The authors declare that they have no conflict of interest

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Tables

Table 1: Overview table on details of imagery transects analysed in the Clarion-Clipperton license areas. Video duration includes time spent sampling. Transect lengths do not include parts visualising ancient disturbance tracks.

Station/Dive	License Area	Seamount (SM) or Nodule field (NF)	Depth (m)	Video duration	Transect length	# obs/ dive	# obs /100m
SO239_29_ROV02	BGR	SM: Rüppell	3000-2500	7h47	1250m	414	33.1
S0239_41_ROV03	BGR	NF	4080-4110	6h32	1590m	1023	64.3
SO239_54_ROV04	BGR	SM: Senckenberg	3350-2850	8h45	2500m	853	34.1
S0239_131_ROV08	GSR	NF	4470-4480	7h35	710m	486	68.5
SO239_135_ROV09	GSR	SM: Heip	3900-3550	7h35	1000m	365	36.5
S0239_141_ROV10	GSR	NF	4455-4480	7h35	520m	464	89.2
S0239_189_ROV13	APEI 3	NF	4890-4930	9h01	1790m	136	7.6
S0239_200_ROV14	APEI 3	NF	4650-4670	9h19	1490m	184	12.2
SO239_212_ROV15	APEI 3	Mann Borgese	1850-1650	6h25	900m	366	40.7

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Figures

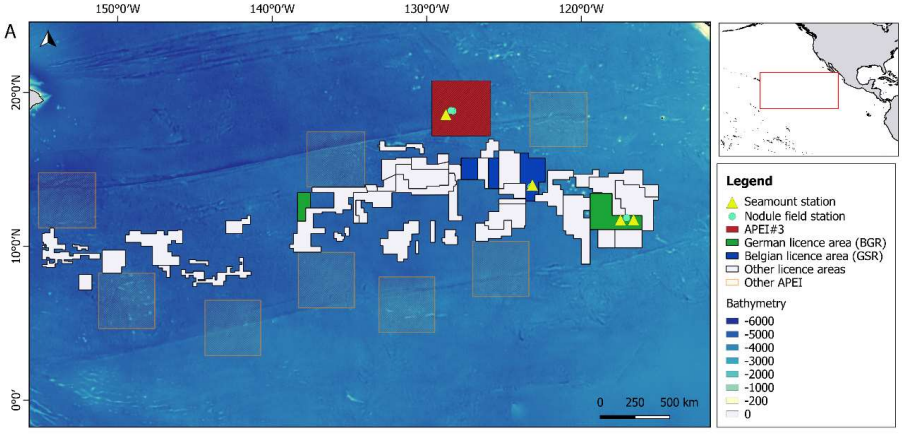

Fig. 1. Location of the Clarion-Clipperton Fracture zone in the equatorial eastern Pacific Ocean featuring the contract areas from the International Seabed Authority (ISA) and the positions of the sampled areas (seamounts and nodule fields). Information on transect length and depth gradients can be found in Table 1.

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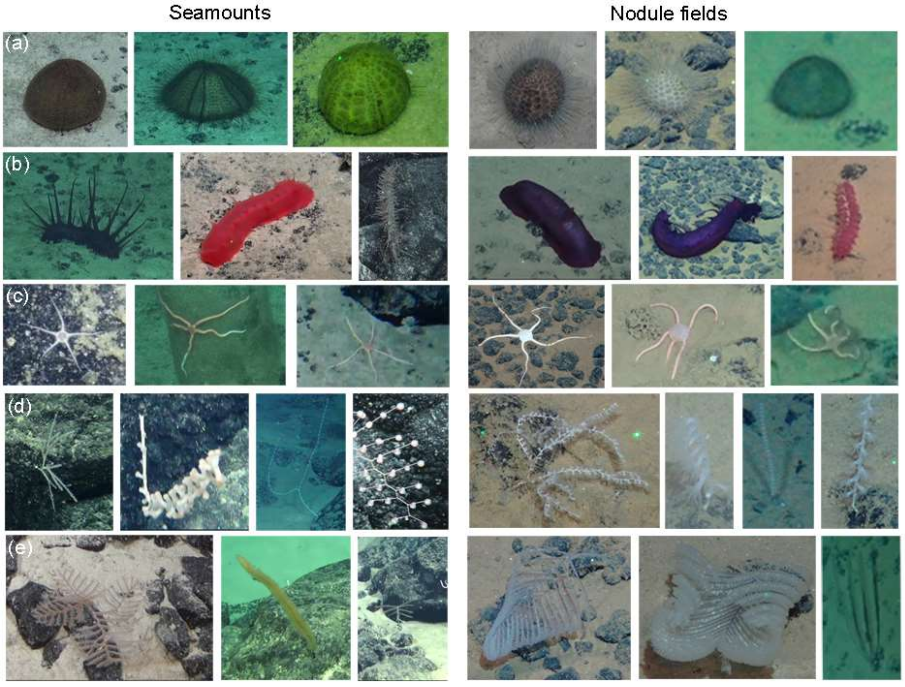

Fig. 2. Some examples of different morphospecies at seamounts and nodule fields in the CCZ. Selected taxa were (a) Echinoidea, (b) Holothuroidea, (c) Ophiuroidea, (d) Alcyonacea, (e) Antipatharia. Copyright: SO239, ROV Kiel 6000, GEOMAR Helmholtz Centre for Ocean Research Kiel

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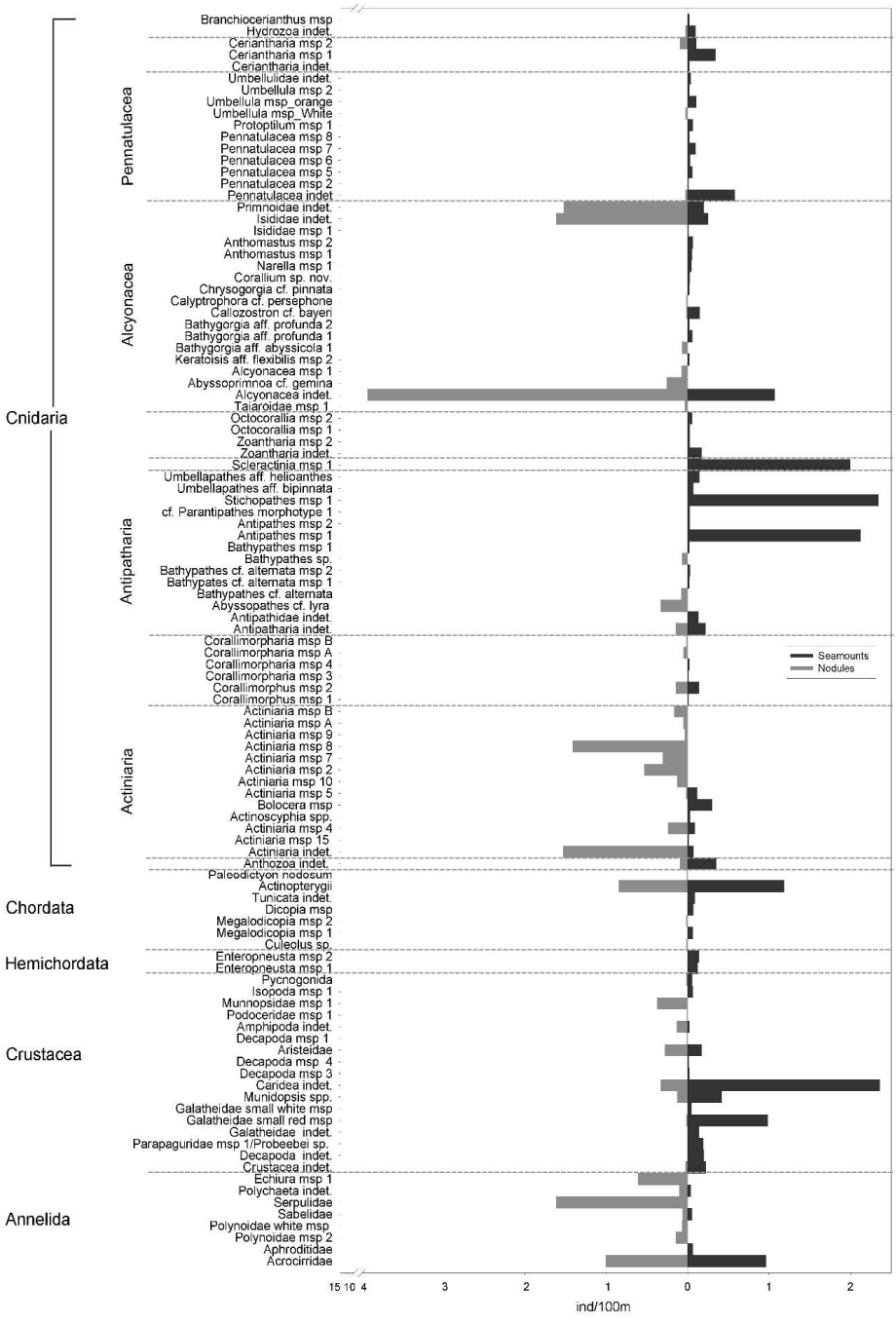

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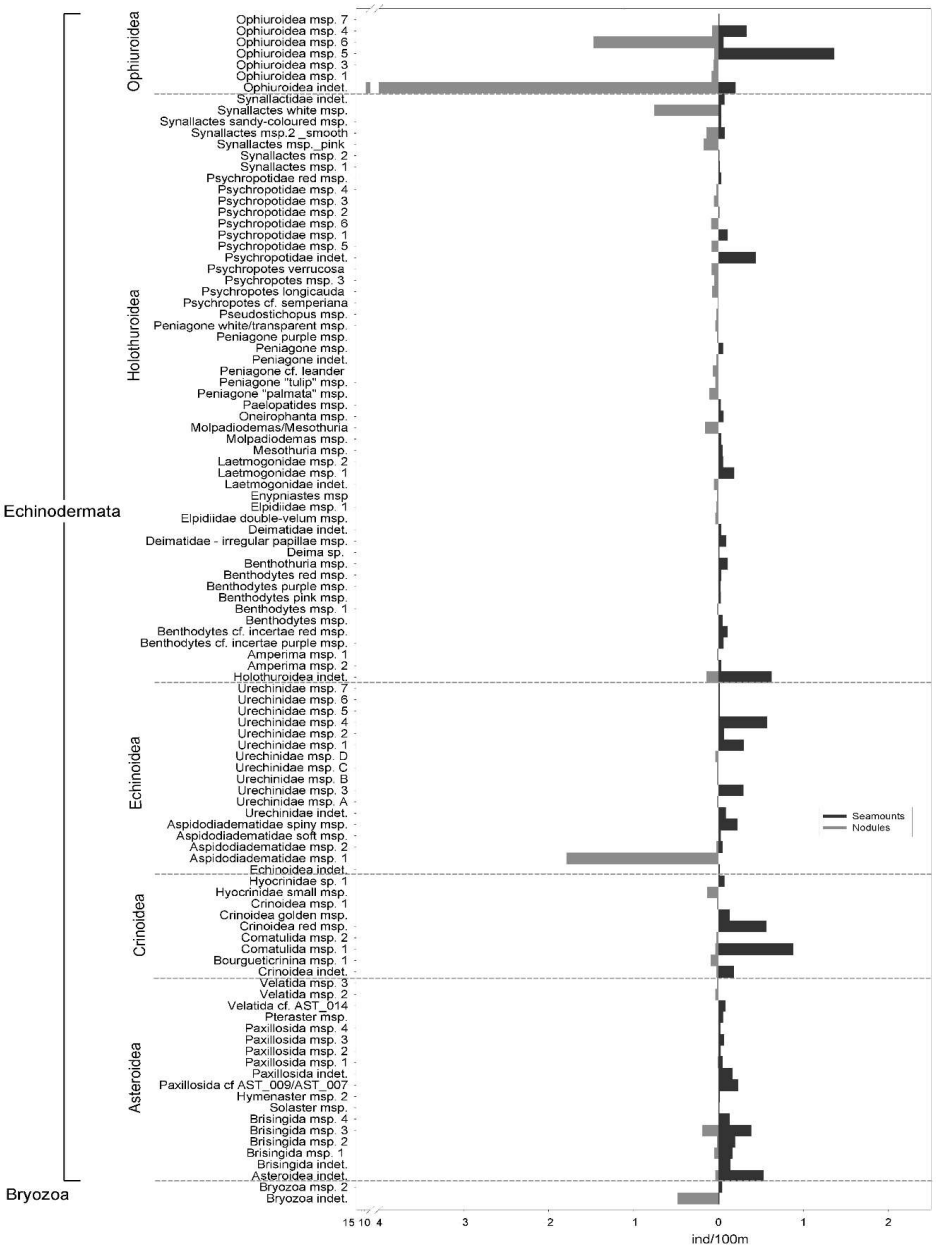

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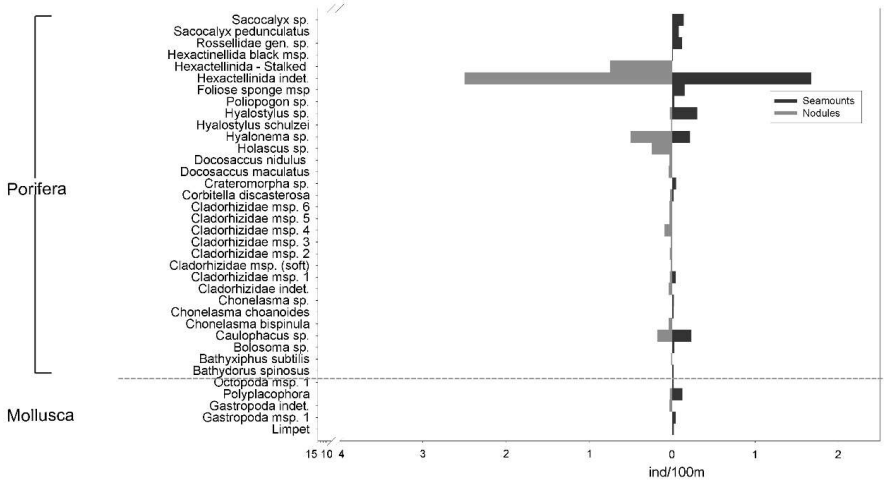

Fig. 3. Back-to-back histogram comparing average densities of morphospecies and taxa (ind/100m) for seamount (#4) and nodule field (#5) video transects.

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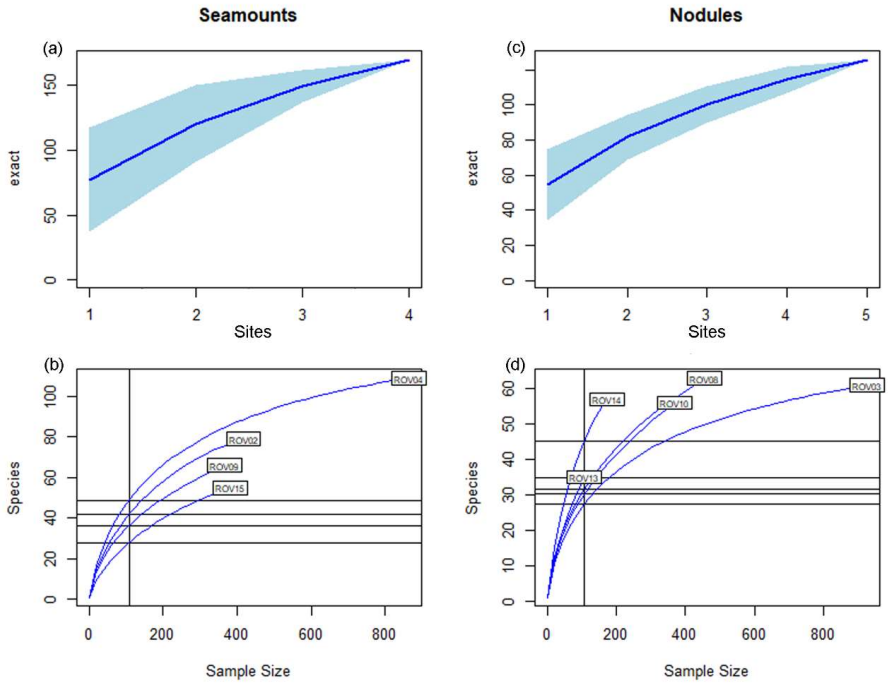

Fig. 4. Species accumulation (upper panel, a and c) and rarefaction curves (lower panel, b and d) for the seamount (#4) and nodule field (#5) transects. Seamount dives: ROV02= Rüppel (BGR), ROV04=Senckenberg (BGR), ROV09=Heip (GSR), ROV15=Mann Borgese (APEI3) in the lower left panel (b). Nodule field dives: ROV03 was carried out in the BGR area, ROV08 and 10 in the GSR area and ROV13 and 14 in the APEI3, presented in the lower right panel (d).

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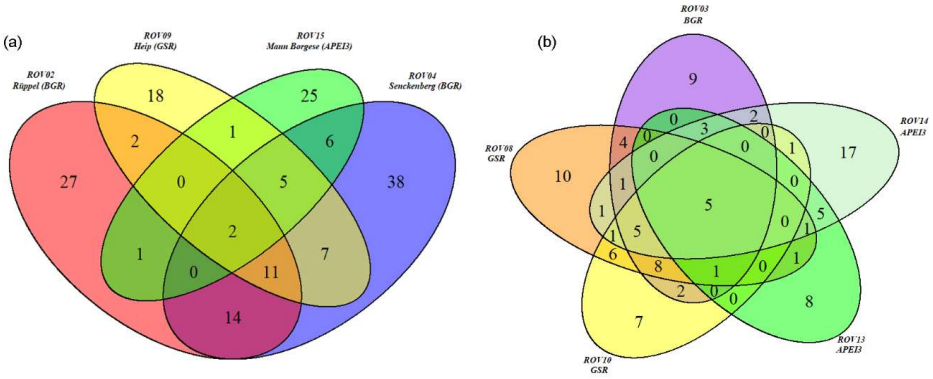

Fig. 5. A Venn diagram showing the unique and shared morphospecies among seamount video transects. Values are relative due to different transect lengths and differences in richness. Left panel (a) features seamount transects and the right panel features the 5 nodule field transects. Colour codes were adapted among panels, with APEI3 nodule transects in green, related to Mann Borgese seamount transect. BGR (ROV03) transect was purple in correspondence to BGR seamount transects (red=Rüppel and blue=Senckenberg). GSR transects (ROV08 and 09) were shades of yellow.

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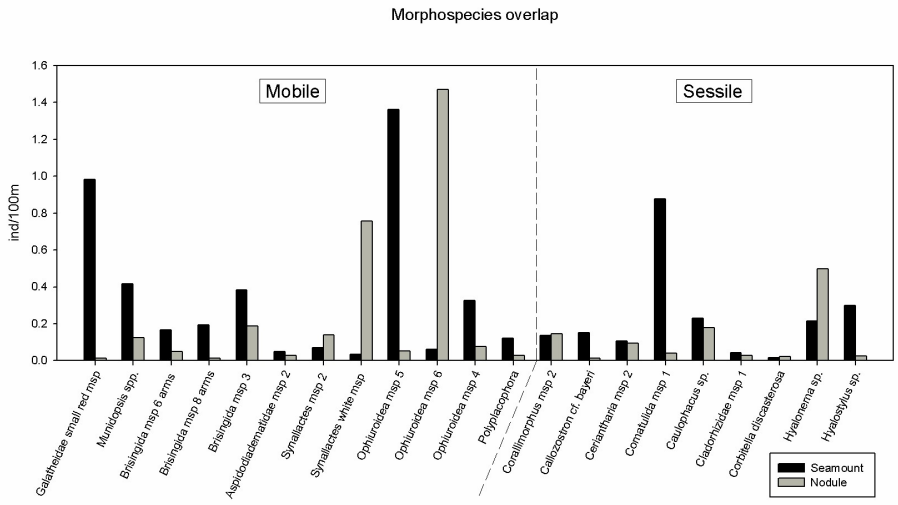

Fig. 6. Morphospecies overlap and average density (ind/100m) between seamounts and nodule fields

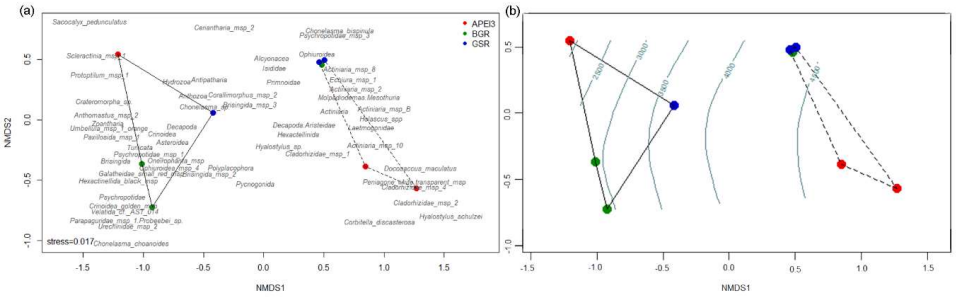

Fig. 7. nMDS-plot with faunal densities and Bray-Curtis distances. Left panel (a) presents the grouping of the video transects based on their faunal composition and right panel (b) features the same plot but with depth as a vector fitting. Dotted lines group the nodule transects while the full line groups the seamount transects.

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Appendix

Table A1. Overview of all taxa densities (ind./100m) and number of morphospecies (msp.) observed within each video transect. Msp. numbers represent often minimum numbers and are indicative. Higher taxa are in bold. * indicates taxa left out of the statistical analyses due to lack of representativity. Indets were organisms impossible to attribute to a lower taxonomic group. ROV02=Rüppel, ROV04=Senkcenberg, ROV09=Heip, ROV15=Mann Borgese

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	SEAMOUNTS								NODULE FIELDS									
	ROV02 (BGR)		ROV04 (BGR)		ROV09 (GSR)		ROV15 (APEI3)		ROV03 (BGR)		ROV08 (GSR)		ROV10 (GSR)		ROV13 (APEI3)		ROV14	
	ind/100m	# msp	ind/100m	# msp	ind/100m	# msp	ind/100m	# msp	ind/100m	# msp	ind/100m	# msp	ind/100m	# msp	ind/100m	# msp	ind/100m	# msp
Cnidaria			0.04	1	0.1	1	0.22	>1										
Actiniaria	0.32	3	0.32	3			0.44	2	4.40	8	6.90	6	9.42	8	0.22	3	1.14	6
Actinoscyphiidae			0.12	1														
Actiniidae/*Bolocera* msp.	1.20	1	0.20	1														
Alcyonacea			0.16	>1	1.7	>1	2.78	>2	9.06	>2	6.62	>1	4.04	>1	0.11	1	0.20	>2
Alcyoniidae	0.24	1	0.04	1			0.11	1										
Chrysogorgiidae					0.1	1												
Isididae			0.20	2	1.2	>4			0.13	>1	5.77	>2	2.50	>2				
Taiaroidea													0.19	1				
Primnoidae	0.80	2	0.64	2	0.2	1	0.11	1	2.83	>3	4.08	>2	2.12	>2				
Coralliidae							0.11	1										
Ceriantharia	0.40	1	0.04	1	0.5	2	1.11	2			0.28	1	0.19	1				
Corallimorpharia/Corallimorphidae			0.64	4					0.38	3	0.28	1	0.38	2				
Antipatharia			0.08	1	0.2	1	0.67	>1	0.25	>1	0.28	>1	0.19	>1				
Antipathidae							19.11	2										
Schizopathidae			0.92	3	0.2	2	0.11	1	0.69	2	0.85	3	0.77	2			0.07	1
Pennatulacea	0.16	>1	3.04	>6			0.11	1										
Umbellulidae			0.56	>2			0.11	1									0.13	1
Protoptilidae			0.04	1			0.22	1										
Scleractinia	0.16	1					8.11	1										
Zoantharia			0.48	1			0.44	1										
Anthozoa	0.16	2	0.08	2	0.60	2	0.67	1	0.13	>1	0.14	>1	0.19	>1				
Bryozoa			0.04	1	0.2	1			0.44	>1	1.55	>1	0.19	>1	0.11	>1	0.13	>1
Echinodermata	0.16		0.16															
Asteroidea	0.32	>1	0.28	>1	1.3	>1	0.11	1	0.19	1.00								
Brisingida	0.64	5	1.44	7	2.0	4	0.44	2	0.44	2	0.42	1	0.19	1			0.20	2
Paxillosida	0.16	2	1.56	8	0.8	3	0.11	1							0.06	1		

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Velatida	0.64	3	0.24	2									0.19	1			0.07	1
Crinoidea	2.80	4	4.32	6	0.2	2	0.56	≥2	0.69	2	0.42	2	0.19	1			0.34	3
Echinoidea																		
Aspidodiadematidae	0.16	1	0.20	1			0.89	2	3.96	1	2.82	2	2.31	1				
Urechinidae	1.76	5	2.40	5	2.0	4			0.06	1					0.06	1	0.27	3
Holothuroidea	1.60		0.84		0.3		0.22		0.38	2	0.56	3	0.58	2			0.13	1
Deimatidae	0.08	1	0.36	3	0.4	3												
Elpidiidae	0.32	2	0.08	1														
Laetmogonidae	0.56	2	0.48	1									0.19	1			0.07	1
Mesothuriidae			0.12	1														
Molpadiodemidae			0.12	1														
Psychropotidae	1.60	>3	1.64	>6	0.4	4	0.22	2	0.50	4	0.99	5	0.77	3	0.06	1	0.07	1
Synallactidae	1.04	3	0.16	3			0.44	1	2.45	2	1.69	3	1.15	2			0.07	1
Ophiuroidea	0.48	2	3.40	5	4.4	3	0.44	1	20.44	4	18.45	4	25.96	3	0.39	2	1.34	3
Crustacea*	0.07		0.31		0.51												0.13	
Decapoda	4.42	4	3.15	5	4.41	3	0.75	2	0.25	2	0.99	2	1.73	2	0.28	3	0.47	3
Galatheidae	4.48	3	1.28	5	1.0	2	0.56	1	0.06	1								
Parapaguridae	0.64	>1	0.24	2														
Peracarida			0.08	1	0.25	2			0.63	2	0.70	2	0.19	1	0.28	3	0.81	2
Enteropneusta																		
Yoda msp.	0.64	1																
Saxipendum msp.			0.52	1														
Mollusca																		
Gastropoda			0.08	2	0.3	2					0.14	1						
Polyplacophora	0.32	1	0.52	1			0.22	1									0.13	1
Cephalopoda	0.08	1																
Pisces*	2.96	9	1.44	10	0.6	5	0.33	3	1.57	4	0.42	2	1.54	3	0.34	3	0.34	2
Annelida/Polychaeta *	0.16	1	0.12	>2			0.11	1	0.13				0.38					
Acrocirridae	0.16	1	0.16	1	4.2	1			0.57	1	0.14	1	0.58	1	1.79	1	1.95	1
Aphroditidae	0.24	1	0.04	1														

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Echiura									0.57	1	1.13	1	1.15	1			0.20	1
Polynoidea											0.28	2	0.58	1	0.06	1	0.13	1
Porifera	0.08	1	0.04	1	0.6	>1												
Hexactellinida	1.76	>2	1.16	>3	3.7	>2	1.00	>2	5.79	>2	5.21	>2	8.27	>2	1.68	>1	2.08	>1
Euplectellidae	0.47	3	0.20	2	1.4	2	0.44	2	1	1	1	3	0	1	0.34	5	0.13	2
Euretidae	0.08	1			0.1	1							0.19	1	0.06	1		
Hyalonematidae			0.08	>1	0.8	>2	0.11	1	0.38	>1	0.70	>1	0.77	>1	0.17	>1	0.47	>1
Rosselidae	0.32	1	0.44	3	0.7	2	0.22	2	0.57	1	0.14	1	0.19	1	0.00	0	0.00	0
Pheronematidae							0.11	1										
Cladorhizidae					0.2	1			0	1	0	2			0	3	1	>6
Pycnogonida	0.16	1			0.1	1											0.07	1
Tunicata	0.08	1			0.1	1												
Megalodicopia msp.	0.16	1	0.04	1	0.1	1											0.07	1
Culeolus msp.																	0.07	1
Dicopia msp.	0.4	1																
*Paleodictyon nodosum**															0.06	1		
Indets	0.88	>1	0.28	>1			0.22	>1										