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Polymetallic nodules are essential for food-web integrity of a prospective deep-seabed mining area in Pacific abyssal plains

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Polymetallic nodule fields provide hard substrate for sessile organisms on the abyssal seafloor between 3000 and 6000 m water depth. Deep-seabed mining targets these mineral-rich nodules and will likely modify the consumer-resource (trophic) and substrate-providing (non-trophic) interactions within the abyssal food web. However, the importance of nodules and their associated sessile fauna in supporting food-web integrity remains unclear. Here, we use seafloor imagery and published literature to develop highly-resolved trophic and non-trophic interaction webs for the Clarion-Clipperton Fracture Zone (CCZ, central Pacific Ocean) and the Peru Basin (PB, South-East Pacific Ocean) and to assess how nodule removal may modify these networks. The CCZ interaction web included 1028 compartments connected with 59,793 links and the PB interaction web consisted of 342 compartments and 8044 links. We show that knock-down effects of nodule removal resulted in a 17.9% (CCZ) to 20.8% (PB) loss of all taxa and 22.8% (PB) to 30.6% (CCZ) loss of network links. Subsequent analysis identified stalked glass sponges living attached to the nodules as key structural species that supported a high diversity of associated fauna. We conclude that polymetallic nodules are critical for food-web integrity and that their absence will likely result in reduced local benthic biodiversity.

Abyssal plains, the deep seafloor between 3000 and 6000 m water depth, have been relatively untouched by anthropogenic impacts due to their extreme depths and distance from continents¹. This may change in the near future with prospected deep-seabed mining, a commercial activity that will extract polymetallic nodules from the seabed for their metal content². Polymetallic nodules are slow-growing (10s mm My⁻¹³) precipitates of predominantly manganese oxides and iron oxy-hydroxides that contain metals such as nickel, cobalt, and copper². They are found partially buried on the sediment surface with a mean nodule wet weight of 4.5 kg m⁻² (central Indian Ocean Basin) to 15 kg m⁻² (Clarion-Clipperton Fracture Zone, CCZ, North-East Pacific)⁴. Nodules provide the rare commodity of hard substrate in the abyss that is used by sessile fauna, e.g., Porifera, Antipatharia, Alcyonacea, or Ascidiacea, and by mobile fauna, e.g., Cephalopoda⁵⁻⁷. In this way, nodules add a network of non-trophic interactions (i.e., non-consumptive relationships between taxa) among sessile organisms and their associated fauna, the so-called epibiota, to the classical trophic interactions that are known for abyssal food webs.

Abyssal food-web studies traditionally focus on trophic interactions (i.e., consumer-resource relationship; e.g.,⁸⁻¹³), because life at abyssal plains is considered 'food-limited' due to its dependence on fluxes of particulate organic matter (POM) from surface waters¹⁴. The top sediment layer is typically well-oxygenated, reducing the importance of habitat modification by sediment ventilation or bioturbating fauna¹⁵. Deep-seabed mining will remove polymetallic nodules from the seafloor and thereby modify the network of non-trophic interactions that is an essential part of the integrity of a nodule field food web on the abyssal seabed. It is therefore of imminent importance to understand how polymetallic nodules support trophic and non-trophic interactions in the abyss.

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	Number of interaction web compartments <i>S</i>	Number of network links <i>L</i>	Link density <i>D</i>	Connectance <i>C</i>
Clarion–Clipperton Fracture Zone				
With polymetallic nodules	1028*	59,793	58	5.70×10^{-2}
Without polymetallic nodules	844 (– 17.9%)	41,526 (– 30.6%)	49 (– 15.5%)	5.80×10^{-2} (+ 1.75%)
Without the most connected taxon <i>Hymenaster</i> sp.	1027 (– 9.73×10^{-2})	58,774 (– 1.70%)	57 (– 1.72×10^{-2})	5.60×10^{-2} (– 1.75%)
Without the taxon with most non-trophic interactions <i>Abyssarya</i> sp.	1027 (– 9.73×10^{-2})	59,316 (– 0.80%)	58 (0%)	5.60×10^{-2} (– 1.75%)
Without the highest impact taxon <i>Hyalonema</i> sp.	988 (– 3.89%)	53,266 (– 10.9%)	54 (– 6.90%)	5.50×10^{-2} (– 3.51%)
Peru Basin				
With polymetallic nodules	342**	8044	24	6.90×10^{-2}
Without polymetallic nodules	271 (– 20.8%)	6208 (– 22.8%)	23 (– 4.17%)	8.50×10^{-2} (+ 23.2%)
Without the most connected taxon <i>Actinia</i> sp.	341 (– 0.29%)	7795 (– 3.10%)	23 (– 4.17%)	6.70×10^{-2} (– 2.90%)
Without the taxon with most non-trophic interactions <i>Munidopsis</i> sp.	341 (– 0.29%)	8027 (– 0.21%)	24 (0%)	6.90×10^{-2} (0%)
Without the highest impact taxon <i>Caulophacus</i> sp.	319 (– 6.73%)	7387 (– 8.17%)	23 (– 4.17%)	7.30×10^{-2} (+ 5.80%)

Table 1. Changes in network properties dependent on the presence of, or after the removal of, polymetallic nodules. The network properties were calculated for the trophic interaction webs of the Clarion–Clipperton Fracture Zone and the Peru Basin when polymetallic nodules were present and removed, and without the most connected taxon, without the taxon with most non-trophic links, and without the highest impact taxon. The change in percent with respect to the default web is shown in brackets. *1028 interaction web compartments = 1018 faunal compartments + 9 food source compartments + 1 polymetallic nodule compartment. **342 interaction web compartments = 331 faunal compartments + 10 food source compartments + 1 polymetallic nodule compartment.

Here, we develop high-resolution trophic and non-trophic interaction webs for two nodule-rich areas in the Pacific Ocean, i.e., the CCZ and the Peru Basin in the South-East Pacific, based on an extensive literature compilation, supplemented with the analysis of high-resolution seafloor images. An important element of these webs is that they include trophic and non-trophic dependencies between taxa and between polymetallic nodules and taxa. Deep-seabed mining impacts are subsequently simulated by assessing the knock-down effects through the food web following the initial removal of only the non-trophic links among nodules and taxa. We focused our analysis on the following questions:

- (1) Can the importance of polymetallic nodules as hard substrate in abyssal plains be quantified?
- (2) Are faunal taxa that provide habitat structure (i.e., structural faunal taxa) more important for food-web integrity than faunal taxa that are highly connected via trophic and non-trophic links?

Results

Food web of the abyssal plains in the Clarion–Clipperton Fracture Zone. Based on the literature survey and image analysis, we identified 1,018 faunal food-web compartments (Table 1) across the size ranges of protozoan and metazoan meiobenthos (36%), macrobenthos (37%), invertebrate megabenthos (25%), and fish (2%). From the literature survey we further identified feeding preferences for all compartments so that we could show that 56% of all faunal compartments were exclusive deposit feeders (265 compartments), filter/suspension feeders (112 compartments), or carnivores (188 compartments) (Fig. 1A). Feeding interactions among nine food-source compartments (bacteria, carrion, dissolved organic matter, fungi, (labile-) sedimentary detritus, phytodetritus, Protozoa, suspended detritus) and all faunal compartments resulted in the highest-resolved trophic interaction deep-sea food web to date of 59,793 links (Fig. 2, Table 1). The non-trophic interaction web contained a total of 386 links (Fig. 2). The megabenthic *Hymenaster* sp. (Echinodermata) was the so-called ‘most connected taxon’, i.e. the taxon with most trophic interactions (sensu van der Zee et al.¹⁶). The macrobenthic *Abyssarya* sp. (Annelida) was the taxon with most non-trophic (commensal) interactions.

In our model, polymetallic nodule removal led to 18% less faunal food-web compartments (Table 1). Food-web compartments that were affected consisted of protozoan and metazoan meiobenthos (4%), macrobenthos (50%), invertebrate megabenthos (45%), and fish (0.5%). The removal of nodules caused the reduction of microphagous feeders by 50%, of suspension feeders and carnivores by 58%, and of suspension feeders by 58% (Fig. 1A). Furthermore, the feeding-type group bacterivore and suspension feeder and the feeding-type group deposit feeder, carnivore, and scavenger disappeared completely (Fig. 1A). The most affected phyla were Bryozoa (81% loss), Cnidaria (52% loss), Platyhelminthes and Porifera (both 50% loss) (Fig. 1B). All compartments that were lost from the food web, except for the fish *Pachycara* sp., were lost due to a loss of non-trophic interactions, i.e., obligatory dependence on nodules as substrate (69%), facultative dependence on nodules (6%), obligatory dependence on other faunal compartments (12%), and the facultative dependence on other organisms (13%) (Table S1). The latter associations between faunal food-web compartments included the commensal relationships with Antipatharia, Alcyonacea, and Pennatulacea (all Cnidaria), Ophiurida (Echinodermata), and Porifera (Table S1).

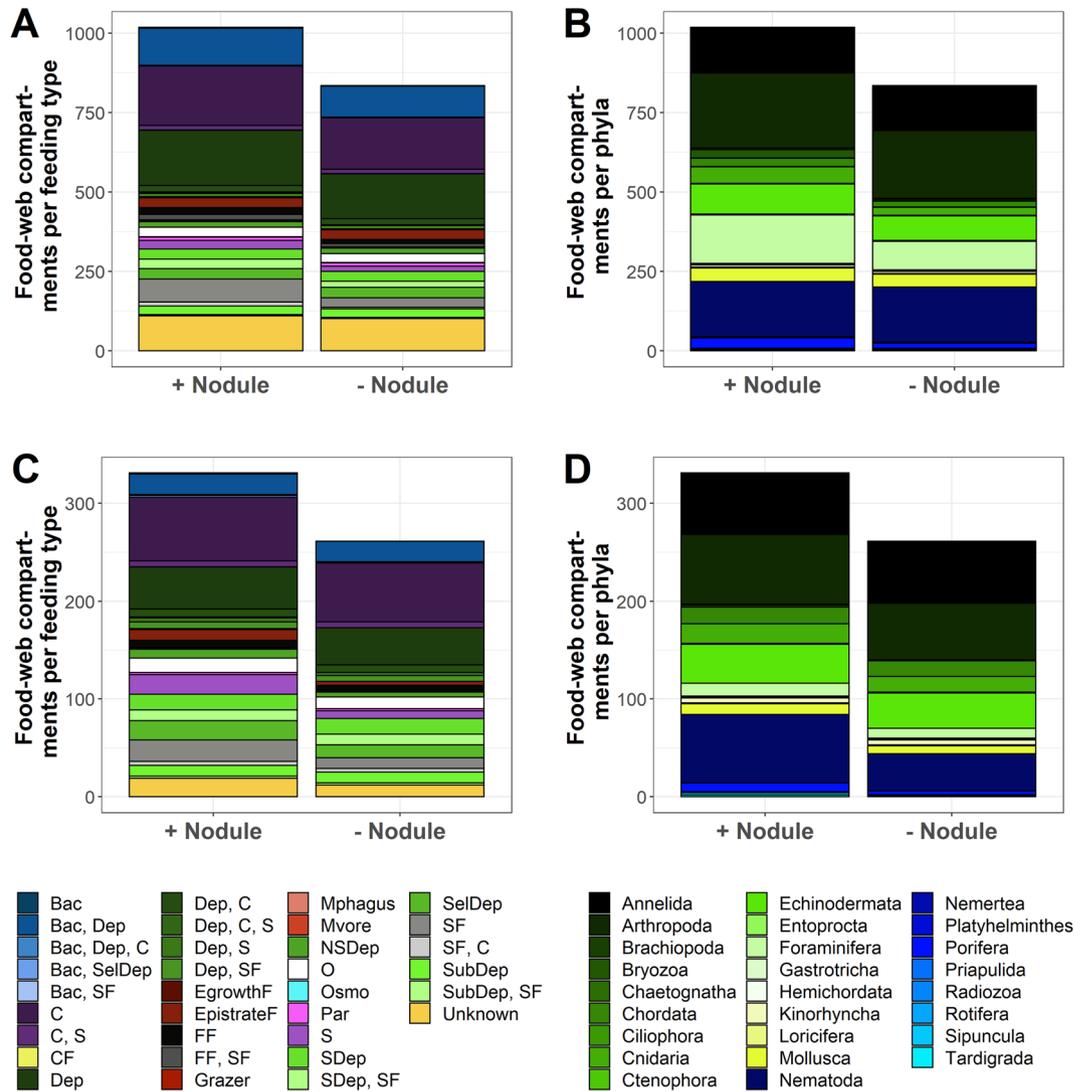


Figure 1. Number of feeding types and phyla present in the Clarion-Clipperton Fracture Zone (CCZ) and the Peru Basin. (A) All compartments that are part of trophic and non-trophic interaction webs of the CCZ are split into feeding types and shown in the presence (+ nodule) and after removal (– nodule) of polymetallic nodules. (B) All compartments from the CCZ interaction webs are divided into phyla and presented in the presence (+ nodule) and after removal (– nodule) of nodules. (C) All compartments of the Peru Basin interaction web shown as feeding types in the presence (+ nodule) and after removal (– nodule) of nodules. (D) All phyla that occur in the Peru Basin in the presence (+ nodule) and after removal (– nodule) of nodules. *Bac* bacterivore, *C* carnivore, *CF* ciliate feeder, *Dep* deposit feeder, *EgrowthF* epigrowth feeder, *EpistrateF* epistrate feeder, *FF* filter feeder, *Mphagus* microphagous, *Mvore* microvore, *NSDep* non-selective deposit feeder, *O* omnivore, *Osmo* osmotroph, *Par* parasitic, *S* scavenger, *SDep* surface deposit feeder, *SelDep* selective deposit feeder, *SF* suspension feeder, *SubDep* subsurface deposit feeder, *Unknown* unknown feeding type.

The taxon with the highest impact, i.e., the faunal compartment whose removal has the largest impact on food-web properties (sensu van der Zee et al.¹⁶), was the megabenthic hexactinellid sponge *Hyalonema* sp. (Fig. 3A), whose removal resulted in the loss of 4% of the food-web compartments (Table 1). In comparison, the removal of the ‘most connected taxon’ *Abyssarya* sp. (Annelida) did not lead to any knock-down of other faunal compartments (Table 1).

Food web of the abyssal plains in the Peru Basin. Our literature and seabed photography analysis yielded 331 faunal food-web compartments (Table 1), of which 34% belonged to metazoan and protozoan meiobenthos, 34% to macrobenthos, 28% to invertebrate megabenthos, and 4% to fish. Our literature survey indicated that 65% of all faunal compartments were carnivores (65 compartments), deposit feeders (99 compartments), filter/ suspension feeders (29 compartments), and bacterivores and deposit feeders (23 compartments) (Fig. 1C). Feeding interactions among ten food-source compartments (bacteria, carrion, dissolved organic matter, fungi, (labile) sedimentary detritus, phytodetritus, suspended detritus, Protozoa, and Rotifera) and all faunal

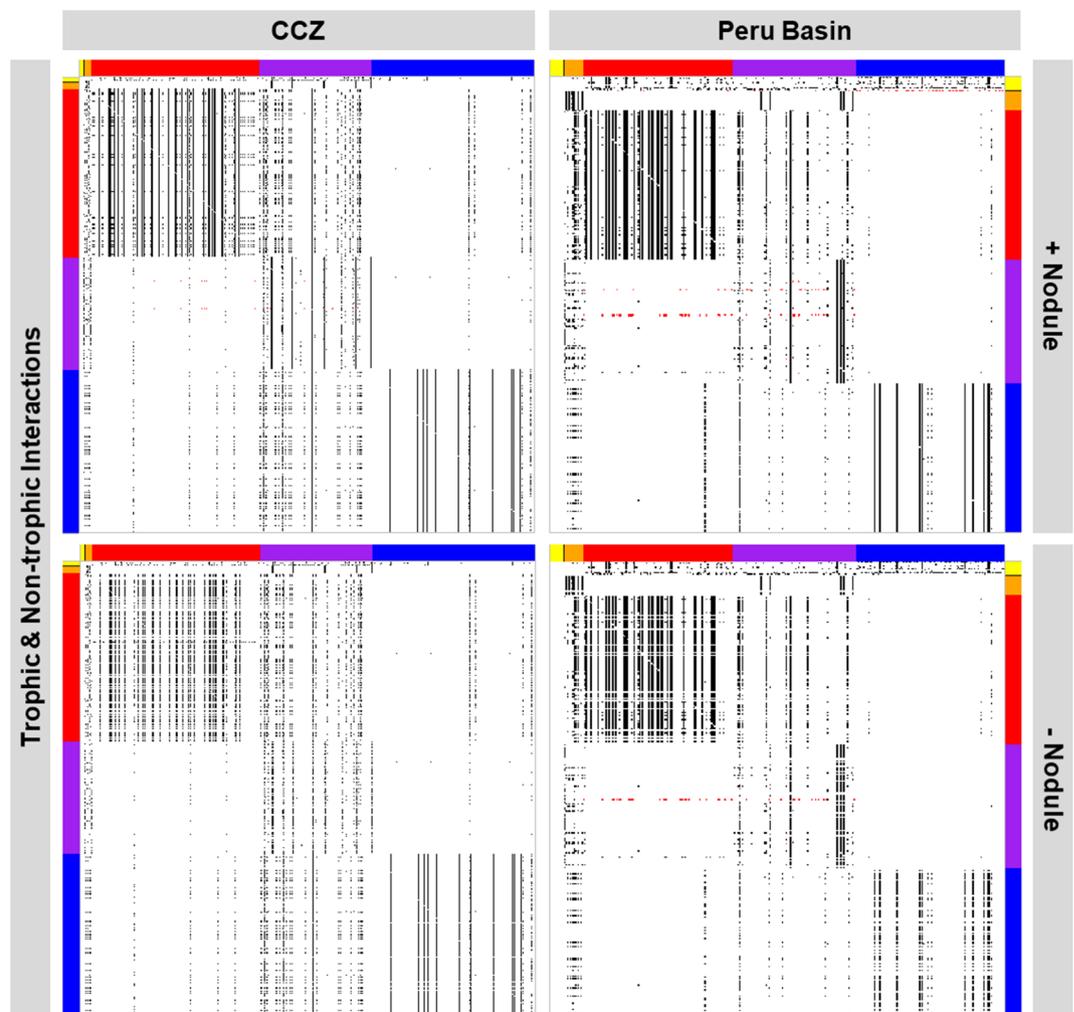


Figure 2. Network links between food-web compartments. Each individual dot represents an interaction between polymetallic nodules (black section) and faunal food-web compartments (orange, red, purple, and blue sections), two faunal food-web compartments, or a faunal food-web compartment and the food-source compartment (yellow section). (Top left) Trophic (black) and non-trophic (red) interactions or links in the Clarion-Clipperton Fracture Zone (CCZ) when polymetallic nodules are present. (Bottom left) All trophic (black) and non-trophic (red) interactions or links that remain in the Clarion-Clipperton Fracture Zone interaction webs after polymetallic nodule removal. (Top right) All trophic (black) and non-trophic (red) interactions or links that exist in the Peru Basin when polymetallic nodules are present. (Bottom right) All trophic (black) and non-trophic (red) interactions or links that remain after polymetallic nodule removals in the Peru Basin interaction webs. Color code of axes: *yellow* food sources, *black* polymetallic nodules, *orange* fish, *red* macrobenthos, *purple* megabenthos, *blue* meiobenthos.

compartments resulted in 8044 links in the trophic interaction web (Fig. 2, Table 1). The non-trophic interaction web included 215 links (Fig. 2). The megabenthic suspension feeding and carnivorous *Actinia* sp. (Cnidaria) was the most connected taxon and had 244 trophic links. The taxon with most non-trophic (commensal) interactions was the megabenthic *Munidopsis* sp. (Arthropoda).

The removal of nodules resulted in the loss of 21% of all faunal compartments (Table 1), of which 49% belonged to meiobenthos, 24% to macrobenthos, 26% to invertebrate megabenthos, and 1% to fish. When nodules were removed, 50% of all suspension feeders, 60% of all scavengers, and 64% of all epistrate feeders (i.e., fauna that tears off protists and swallows them¹⁷) were lost (Fig. 1C). Additionally, all bacterivore, bacterivore and selective deposit feeder, deposit feeder, carnivore, and scavenger, epigrowth feeder (i.e., fauna that scrapes off surfaces of sand grains or bores into single cells¹⁷), and microvore were absent (Fig. 1C). Highest losses occurred in Bryozoa (50% loss), Porifera (56% loss), Brachiopoda and Tardigrada (both 100% loss) (Fig. 1D). Except for the fish *Pachycara* sp. that was lost due to the loss of its food source, all other compartments were removed because non-trophic interactions disappeared. Twenty-nine percent of the lost compartments were removed as they obligatory depended on nodules as substrate and 38% because of their facultative dependence on the nodules (i.e., the compartment was not always found attached to nodules) (Table S1). The remaining 33% were

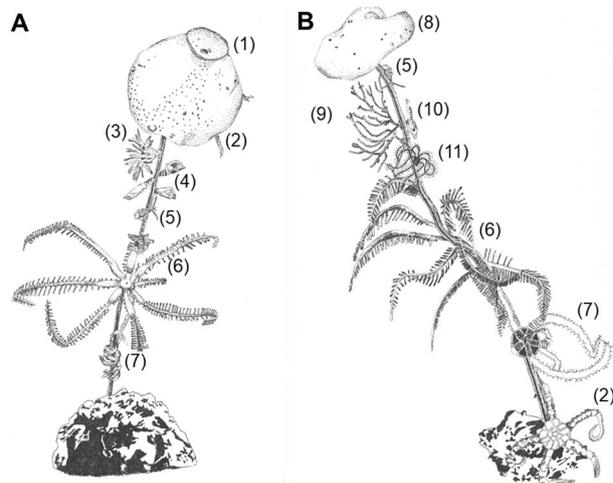


Figure 3. Drawings of highest impact taxa. (A) The highest impact taxon in the Clarion–Clipperton Fracture Zone (CCZ), the hexactinellid sponge *Hyalonema* sp., and (B) the highest impact taxon in the Peru Basin, the hexactinellid sponge *Caulophacus* sp., are shown with their corresponding associated fauna (on Order level) with which they have non-trophic interactions. The taxa presented in the drawings are the following: (1) *Hyalonema* sp., (2) Ophiurida, (3) Actiniaria, (4) Cirripedia, (5) Amphipoda, (6) Brisingida, (7) Ophiacanthida, (8) *Caulophacus* sp., (9) Alcyonacea, (10) Mysida, and (11) Comatulida. Illustrations by Tanja Stratmann.

removed because of their obligatory (29%) and facultative (4%) commensal relationship with the megabenthic hexactinellid sponges *Bathyxiphus* sp., *Caulophacus* sp., *Hyalonema* sp., and *Hyalostylus* sp. (Table S1).

The taxon with highest impact was the megabenthic hexactinellid sponge *Caulophacus* sp. (Fig. 3B) whose removal resulted in the loss of 23 compartments which is 7% of all faunal compartments (Table 1). In contrast, the removal of the taxon with most trophic interactions *Actinia* sp. (Cnidaria) did not result in any knock-down loss of other food-web compartments (Table 1).

Changes in network properties of both abyssal food webs. Removal of polymetallic nodules as hard substrate resulted in a substantial and consistent reduction in the number of network links for both sites (31% in the CCZ and 23% in the Peru Basin; Fig. 2, Table 1). Link density, i.e., the average number of links per interaction web compartment, was decreased by 16% in the CCZ, but by 4% in the Peru Basin, whereas connectance *C*, i.e., the fraction of realized links¹⁸, increased by 2% in the CCZ and by 23% in the Peru Basin (Table 1).

In contrast to nodule removal, the removal of the most connected taxa and the taxa with most non-trophic links decreased the number of network links by only 2% and 0.8%, respectively, in the CCZ and by 3% and 0.2%, respectively, in the Peru Basin (Table 1). In comparison, when the taxa with most non-trophic interactions were removed, the number of network links was 11% (CCZ) and 8% (Peru Basin) lower than the number of links in the corresponding default interaction webs. Link density was not affected by the removal of the taxon with most non-trophic links, but removing the most connected taxon caused a loss in link density of 7% in the CCZ and of 4% in the Peru Basin (Table 1). The connectance decreased slightly when the most connected taxa and the taxa with most non-trophic interactions were removed, but the connectance was unaffected when the taxon with most non-trophic interactions in the CCZ was removed (Table 1). Removing the highest impact taxon resulted in a small loss in connectance (− 4%) in the CCZ, but in an increase in connectance (+ 6%) in the Peru Basin.

Discussion

Model limitations. The highly resolved binary food webs for the CCZ and the Peru Basin are based on systematic meta-analyses and seabed images, but this comes with inevitable limitations: The literature included in this study did not use consistent lower and upper sieve size limits for meio- and macrobenthos. Furthermore, only few studies reported the use of an upper sieve size for meiobenthos (e.g.,¹⁹), whereas the majority of the studies did not report any upper sieve size limit and likely included all infauna that was retained on sieves with the lower size limit. Hence, smaller macrobenthos might be classified as meiobenthos and therefore was erroneously implemented as meiobenthos in the food-web models. In return, many authors used the term ‘meiobenthos’ synonymously to ‘meiofauna’ (e.g.,¹⁷) instead of distinguishing between the statistical entity ‘meiobenthos’ based on body size and the taxonomic category ‘meiofauna’²⁰. Therefore, when authors (e.g.,²¹) stated that specific taxa were excluded from the analysis of a specific size range because the authors used taxonomic categories, we used them in the body-size based size class. Despite these attempts to achieve comparability, the food-web models likely lacked specific meio- and macrobenthic taxa. Hence, phyla rather than size classes should be considered when assessing the importance of polymetallic nodules for the food web.

Additionally, especially for the food web developed for the Peru Basin, data on some phyla were not available. As an example, meiobenthic Foraminifera (see Table S3) did not exist in the literature. This lack of data was likely caused by a lack in specific taxonomic expertise during previous research cruises to the Peru Basin rather than caused by a deliberate omission of specific phyla. In contrast, the CCZ food web was based on a

more balanced dataset for the different taxa due to the extensive baseline studies that were conducted in the CCZ during the last decade.

Authors reported some faunal groups only at higher level taxonomic resolution (see Table S3) which made it difficult to specify diets or feeding preferences. As a result, these compartments had a high number of trophic links which reduces the probability that a compartment is lost due to the loss of trophic interactions. Therefore, this study likely underestimated the importance of polymetallic nodules for food-web integrity, in particular for compartments of coarse taxonomic resolution or for compartments for which information about diet is poor.

The non-trophic interaction matrix only included commensalism and no other types of non-trophic interactions, such as competition²². Interspecific competition for food resources might be one reason for sympatric speciation in abyssal deposit-feeding sea cucumbers: They have a high morphological diversity of tentacles that enabled the sympatric species to develop different feeding strategies and in this way overcome competition for food²³. Hence, on evolutionary time scales, including competition in the food web would likely result in an increase in diversity and therefore an increase in compartments and links. In contrast, on the short term, competition would probably have no effect on the food-web structure and the non-trophic interactions that have been implemented in the model account for most of the secondary extinctions and shifts in food-web structure that can be expected from the absence of nodules.

Role of polymetallic nodules and stalked sponges in abyssal plain food webs. Our results consistently show for two polymetallic nodule-rich abyssal plains, the CCZ and the Peru Basin, that nodule removal would have knock-down effects on food-web integrity due to the disturbance of trophic and non-trophic interaction webs. The loss of food-web compartments was almost exclusively the result of cascading effects from existing non-trophic interactions between nodules and sessile organisms and between sessile organisms attached to nodules and their associated fauna. Here, we discuss the importance of hard substrate for soft-sediment communities and we investigate the role of structural species versus highly-connected species in food webs. We also address potential consequences of future deep-seabed mining.

Hard substrate in soft-sediment communities increases habitat heterogeneity and may enhance species diversity and density^{7,24–26}. In abyssal plains, this hard substrate is scarce and consists of clinker, hard-rock patches, polymetallic nodules, and glacial dropstones^{3,27–29}. Dropstones may serve as island habitats³⁰ and host a diverse epifaunal assemblage of mainly Porifera, Chordata (in particular Tunicata), Echinodermata, Cnidaria, and Foraminifera^{29,30}. At the West Antarctic Peninsula margin, for instance, dropstones contribute 20% to the total megabenthic species richness, though they cover less than 1% of the investigated seafloor³⁰. They may also increase epifaunal density, for instance in the Ardencaple Canyon in the Greenland Sea, where epifaunal density is positively correlated with the size of hard substrate³¹. In fact, dropstones can even modify hydrodynamics that lead to increased food supply to parts of the surrounding sediment and affect trophic structure, diversity, and life-history traits of nematodes²⁶.

Polymetallic nodules, in comparison, provide hard substrate for Arthropoda (in particular Crustacea), Bryozoa, Chordata (i.e., Tunicata), Cnidaria, Echinodermata, Foraminifera, Mollusca, Platyhelminthes, and Porifera (this study). Here, we determine that nodules are quantitatively important for filter and suspension feeders because 11% (Peru Basin) to 51% (CCZ) of all fauna are facultatively or obligatorily associated with the nodules. This close association may explain the positive correlation between nodule coverage and increased faunal density in the CCZ³². Furthermore, nodules and in particular the stalks of attached epifauna can trap jelly-falls (Stratmann & van Oevelen, personal observations) and in this way increase the food supply for abyssal scavengers and omnivores. Hence, we conclude, that polymetallic nodules provide an important hard substrate in abyssal plains of the Pacific Ocean. Our highly-resolved interaction food webs allowed to identify the species that have the so-called ‘highest impact’¹⁶. Surprisingly, at both sites, stalked-sponge species (i.e., *Hyalonema* sp. and *Caulophacus* sp.) were identified as ‘highest impact taxa’. Their removal had the largest impact on network properties because these sponges host commensal epibiota, such as filter and suspension feeders (e.g., Bivalvia, Crinoidea, Anthozoa, Cirripedia, and Crustacea), scavengers (e.g., Amphipoda, Mysida, and Isopoda), and predators (e.g., Polychaeta, Anthozoa, Ophiuroidea, and Isopoda). Sponge stalks were identified previously as ‘habitat islands’ for deep-sea fauna^{33,34} as they allow suspension feeders to move higher up into the benthic boundary layer, where higher flow velocities prevail³⁵. Hence, stalked sponges essentially extend the habitat of epifauna from the seafloor into the water column and are therefore considered ‘structural species’ (sensu Huston³⁶). An analysis of photograph transects at the abyssal Station M in the North-East Pacific showed that 87% of the stalks that emerged from the soft sediment were from the hexactinellid *Hyalonema* sp., of which only 14% were alive³⁷. These stalks host a diverse suspension feeding epibiota: The examination of 35 stalk communities showed that they harbored 8580 individuals that could be classified into 139 taxa belonging to 13 different phyla³⁷. In the CCZ (this study) the stalks of *Hyalonema* sp. hosted 41 taxa from 4 different phyla and the stalks of *Caulophacus* sp. in the Peru Basin (this study) harbored 25 taxa belonging to 4 different phyla.

Theoretical food-web studies indicate that removal of highly connected species can lead to a cascade of secondary extinctions^{38,39}. In particular food webs with a low connectance ($C \leq 0.06$) are sensitive to the loss of the most connected species³⁸. Hence, we would expect that the removal of taxa with most trophic and non-trophic interactions in the CCZ (taxon with most trophic interactions: *Hymenaster* sp.; taxon with most non-trophic interactions: *Abysarya* sp.) and the Peru Basin (taxon with most trophic interactions: *Actinia* sp.; taxon with most non-trophic interactions: *Munidopsis* sp.) would lead to a cascade of secondary extinctions, because both webs have a low connectance (CCZ: $C = 0.06$, Peru Basin: $C = 0.07$; Table 1). Surprisingly, the removal of these most connected taxa did not cause any secondary extinctions. In other detritus-based food webs, removing the most connected species similarly had no to very little effect^{16,38,40} on the number of species and connectance, whereas the removal of the basal node, the detritus, resulted in a (rather trivial) immediate food-web collapse³⁸.

The CCZ- and the Peru Basin-food webs are likewise detritus-based, dominated by invertebrates, and the most connected species are generalist-feeding invertebrate predators (i.e., *Hymenaster* sp., *Actinia* sp.). Removing polymetallic nodules as primary habitat modifiers resulted in an increase in connectance by 2% (CCZ) to 23% (Peru Basin). This stresses the importance of non-trophic interactions in these nodule-rich abyssal plain food webs, where the most connected species seem to be less important for overall food-web integrity because most can be considered generalist invertebrates. Therefore, we conclude, that in polymetallic nodule-rich abyssal areas in the Pacific, structural taxa contribute more to food-web integrity and species richness than highly connected taxa.

Our comprehensive analysis evidently and quantitatively shows the importance of polymetallic nodules and attached stalked sponges for the abyssal food web. It is therefore clear that the removal of polymetallic nodules due to deep-seabed mining would lead to a loss of food-web integrity and a significant depreciation of faunal biodiversity. It is not clear, whether this would affect the mined areas only or would result in regional (i.e., the CCZ) or even global loss of biodiversity^{41–43}. Ophiuroidea, for instance, have an unexpectedly high biodiversity in the CCZ^{44,45}, and further discoveries of faunal biodiversity hubs in the poorly-studied deep sea⁴⁶ can be expected. In fact, we even neglected two very diverse taxonomic kingdoms, i.e., Bacteria and Archaea, in our study because we were not able to incorporate them adequately due to a poor understanding of their metabolic pathways. Hence, the polymetallic nodule-mining induced loss of biodiversity may be even higher than shown in this study.

Our model was developed for the entire CCZ, excluding Areas of Particular Environmental Interest (APEIs), and not for specific mining claims or areas with particular geological seabed characteristics, such as specific slope and/or polymetallic nodule abundance. Therefore, we cannot predict whether our results would change when the model would be resolved on a higher spatial resolution. We can also only speculate how the establishment of preservation reference zones (PRZ), i.e., areas that will not be mined and should serve as reference areas to assess deep-seabed mining related changes of the environment⁴⁷, would influence the outcome of our model. However, these zones might potentially help to maintain food-web integrity or at least reduce the expected changes in network properties when nodules will be removed.

Previous modelling studies about the impact of deep-seabed mining on the benthic ecosystem focused on carbon flows^{13,48}. These food-web models, however, group individual taxa in feeding types^{49,50} which can mask biodiversity loss. Furthermore, the models concentrated on trophic interactions. However, for coastal ecosystems it is known that non-trophic interactions are important structuring factors in food webs¹⁶. Therefore, we developed binary interaction webs including both trophic and non-trophic interactions. These webs show that non-trophic interactions are important for food-web integrity: the absence of polymetallic nodules will result in a reduced food-web complexity and a loss in biodiversity. Additionally, we identified stalked sponges as 'structural species' that host a high diversity of commensal fauna.

Materials and methods

Study sites. The CCZ (0°N, 160°W to 23.5°N, 115°W⁵¹) is bound by the Clarion Fracture Zone in the north and the Clipperton Fracture Zone in the south. Water depth ranges from 3900 m in the east⁶ to 5300 m in the west⁵² with an average water depth of 4794 m⁵³. The CCZ is part of the 'mesotrophic' abyss⁵⁴ and experiences a gradient in particulate organic carbon (POC) input from north (1.3 mg organic C m⁻² d⁻¹) to south (1.8 mg organic C m⁻² d⁻¹). The sediment is largely siliceous, silty clay⁵⁵ and contains nodules at a density between 0 and ~30 kg m⁻² with a mean density of 15 kg m⁻²⁴ and a mean diameter of 3.6 cm⁵⁶. Because of this high nodule density, the CCZ is an important area for future nodule mining operations and (until September 2020) the International Seabed Authority has granted 18 15-year contracts for the exploration of polymetallic nodules in the CCZ.

The Peru Basin, ~6000 km away from the CCZ⁵⁷, is located in the southern Pacific (5°S to 24°S) and extends from the Atacama Trench west of Peru westwards (to 110°W) into the Pacific^{58,59}. The water depth ranges from 3900 to 4300 m⁶⁰ and sedimentation rates are between 0.4 and 2.0 cm kyr⁻¹⁶¹. Surface sediments have an organic carbon content of 0.5 to 1.0 wt% and the oxygen concentration decreases from 132 μmol L⁻¹ at the sediment–water interface to 0 μmol L⁻¹ at 6 to 15 cm sediment depth⁶¹. Mean nodule density in the Peru Basin is > 10 kg m⁻²⁶⁰ and mean nodule diameter is 7.8 cm⁵⁶; industrial polymetallic nodule extraction, however, is not anticipated.

Data compilation. Detailed food webs were developed for the size classes protozoan and metazoan meiobenthos, macrobenthos, invertebrate megabenthos, and fish, while explicitly taking into account whether each taxon lives in the sediment, is associated with other taxa, or is attached to polymetallic nodules. For this purpose, a systematic literature review was conducted to identify all taxa (if possible on genus level) of the study areas following the PRISMA guidelines for systematic reviews and meta-analyses⁶². The key words 'polymetallic nodules', 'manganese nodule fauna', 'manganese nodule', 'Clarion-Clipperton Fracture Zone', 'Peru Basin', 'DISCOL' identified 913 publications in the database 'Web of Knowledge' (Fig. S1). An additional 113 records were identified through other sources, 121 publications were listed on the 'DISCOL' homepage (<https://www.discol.de/literatur>), and 66 articles were published in three special issues in *Deep-Sea Research Part II: Topical Studies in Oceanography*⁶³, *Frontiers in Marine Sciences*⁶⁴, and *Biogeosciences*⁶⁵. After duplicates were removed, title and abstract of 854 records were screened for relevancy and 671 records were excluded because they did not report benthos from the CCZ or the Peru Basin. Subsequently, a total of 183 full-text records were assessed for eligibility. The full text was unavailable for three records that were therefore left out. Another 24 publications were excluded as they did not report benthic taxa from the CCZ or the Peru Basin and eight studies were omitted because they presented meta-studies or reviews and not primary research. In the end, 148 studies or datasets were used to develop the trophic and non-trophic interaction matrices. All references can be found in Table S2.

The extensive literature survey was supplemented by two novel datasets of high-resolution seafloor images (Fig. S1). During RV *Sonne* cruise SO239 to the CCZ⁶⁶ and during RV *Sonne* cruise SO242-2 to the Peru Basin⁶⁷, 1544 seafloor images were taken with the remotely operated vehicle ‘ROV Kiel 6000’ (Geomar Kiel, Germany) and Porifera and its associated fauna were identified.

All metazoan and protozoan specimens that were discovered in the qualitative synthesis and the picture analysis, were compiled in a database. For each specimen, the taxonomic ranks phylum, class, order, family, and genus were determined using the database ‘World Register of Marine Species: WoRMS’⁶⁸ and the genus level of all taxa was selected as food-web compartment. However, when a specimen could not be classified at this taxonomic rank, the lowest taxonomic rank above genus level, to which it could be identified, was chosen as food-web compartment (Table S3). Recorded specimens were furthermore classified as meiobenthos (> 32 µm^{69,70}), macrobenthos (> 250 µm/ > 500 µm^{21,71}), invertebrate megabenthos (> 1 cm), and fish based on information from original publications or based on information published in ‘WoRMS’⁶⁸. It was also noted whether organisms were reported or observed attached to a polymetallic nodule, sitting on or living in sediment, or were associated with an organism attached to a nodule.

Trophic interaction matrix. Feeding preferences/ prey types of each specimen in the dataset were identified by inquiries of published literature and the database ‘WoRMS’⁶⁸ (Data file S1 and S2). One binary trophic interaction matrix per location was developed by connecting all food-web compartments via all reported trophic links to its prey/ food source. Hence, when a specific fish genus preferably feeds on crustaceans, this fish genus compartment was connected via trophic links to all compartments in the food web that include crustaceans. However, it was assumed that predatory megabenthos would not feed on meiobenthos unless they are known to catch their prey by digging in the seafloor.

Bacteria, carrion, dissolved organic matter (DOM), fungi, (labile) sedimentary detritus, phytodetritus, Protozoa, Rotifera, and POM suspended in the water column were reported in the literature as food sources for abyssal food webs and were consequently included (Data file S1 and S2).

Non-trophic interaction matrix. The binary non-trophic interaction matrix contained all non-trophic links between food-web compartments and the additional compartment ‘polymetallic nodules’. Commensal relations among faunal compartments that were reported in the database (“Data compilation” section) were implemented in the matrix as present or absent. All faunal compartments, for which the literature or the image analysis indicated that they would use nodules as substrate, were linked to the nodule compartment. Whenever the taxon of a faunal compartment was observed attached to a nodule and living on/ in the sediment or associated with a faunal compartment and freely, the present non-trophic relation was defined as ‘facultative’. In contrast, when the taxon occurred exclusively attached to nodules or only in association with specific faunal compartments, the present non-trophic relation was defined as ‘obligatory’.

Network indices. The trophic interaction matrix was used to calculate the well-established network indices: ‘number of interaction web compartments’ S , ‘number of network links’ L , ‘link density’ D ($D=L/S$), and ‘connectance’ C ($C=L/S^2$), i.e., the fraction of realized links compared to all possible links⁷².

Assessment of the absence of nodules and the absence of specific faunal compartments. The effect of polymetallic nodules on the food-web structure was investigated by removing the nodule compartment from the non-trophic interaction matrix and assessing the resulting knock-down on other compartments (i.e., the secondary extinction of other compartments because of the loss of the nodule compartment). Hence, all compartments directly depending on the nodules were removed first. In a subsequent iteration, all compartments depending on a removed compartment through a non-trophic or exclusively trophic (i.e., when preying only on the removed compartment) interaction were removed, and so on. After all lost compartments were identified, the previously collected information about the type of non-trophic interaction (facultative vs. obligatory) was used to identify whether the loss was a result of facultative or obligatory dependence.

To compare the loss of non-trophic links through nodule absence against the removal of trophic links, a comparable knock-down analysis of the ‘most connected taxa’ and the ‘taxa with most non-trophic interactions’ was also carried out. The most connected taxon is defined as the food-web compartment with most trophic links, sensu van der Zee et al.¹⁶. The ‘highest impact taxon’¹⁶ was identified by removing each faunal compartment individually and calculating the food-web properties. The compartment whose individual removal resulted in the largest absolute difference in food-web properties between the default food web and the modified food web was defined as said ‘highest impact taxon’.

Data availability

The datasets underlying the trophic and non-trophic interaction webs and the model code are attached as supporting information (Datasets S1 and S2, Programming file S1 and S2).

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Author contributions

T.S. conceived the idea, searched the literature, compiled the datasets, developed the models, analyzed the results, and wrote the manuscript. D.v.O. acquired funding, conceived the idea, developed the models, analyzed the results, and wrote the manuscript. D.K. identified sponges and its associated community on seafloor images, revised and edited the manuscript. K.S. acquired funding, revised and edited the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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