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Community structure of deep-sea benthic metazoan meiofauna in the polymetallic nodule fields in the eastern Clarion-Clipperton Fracture Zone, Pacific Ocean

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Abstract :

The abyssal sea floor of the Clarion-Clipperton Fracture Zone (CCFZ) in the Pacific Ocean is expected to become a commercially important nodule mining area in the near future. Hence, it is crucial to understand the community structure of biological communities there, so that nodule harvesting activities can be designed to minimize deleterious impacts on marine life. Meiofauna is an important component of the abyssal infaunal community but relatively little is known on their biodiversity, abundance, and community structure in the CCFZ. We provide here the first quantitative observations of metazoan benthic animals ≥40 µm in a 30 × 30 km area survey stratum in the Ocean Mineral Singapore contract area at the eastern end of the CCFZ. A total of 88 867 individuals, identified to 23 animal groups, were collected from 12 randomly sampled stations using a multiple corer. Even in our small surveyed area, the meiofaunal community structure appeared different at our stations, confirming that the CCFZ deep sea floor is very diverse. From the top 0–5 cm sediment layer, unsurprisingly, the three most abundant animal groups were the Nematoda (87.9 ± 2.9%), the Nauplii (5.0 ± 1.3%) and the Copepoda (4.3 ± 1.1%). The majority of the meiobenthos (76.6%) were in the top 0–2 cm sediment layer. Our results suggested that substratum shear strength was negatively and significantly correlated to meiofaunal abundances among the 12 stations. Nodule cover and nodule volume did not appear to affect the meiofaunal community structure at the major taxon level. The mean meiofaunal abundance (235.7 ± 26.4 ind./10 cm2) was relatively high at our site in comparison with previous studies elsewhere in the CCFZ, further confirming the westward decrease in meiofaunal abundance across the CCFZ.

Highlights

► Provides the first quantitative description of meiofaunal composition in the OMS contract area (eastern CCFZ). ► Community structure was different at 12 stations in a 30 × 30 km area, showing that meiofauna in the CCFZ is very diverse. ► Substratum shear strength was significantly associated with differences

in meiofaunal abundance and community structure. ► Our findings reiterate the decreasing westward trend of meiofaunal abundance in the CCFZ.

Keywords : Meiobenthos, Polymetallic nodule mining, Abyssal benthos, ABYSSLINE 02

1. INTRODUCTION

The Clarion-Clipperton Fracture Zone (CCFZ) refers to an area of about six million square kilometres located in the eastern Pacific Ocean, bounded by the Clarion Fracture Zone to the north and the Clipperton Fracture Zone to the south. The CCFZ is considered as one of the largest reservoirs for high-grade polymetallic nodules, containing commercially valuable metals such as manganese, copper, nickel and cobalt (Hein et al., 2013; Lodge et al., 2014). Compared to a few decades ago, advances in technology now have made deep-sea mining a realistic option to meet the increasing global demand for these metals. Besides, some metals can even be found more abundantly in the CCFZ than in terrestrial reserves (Hein et al., 2013). As a result, mining for nodules from the CCFZ has gained international interest.

Harvesting polymetallic nodules from the sea floor will undoubtedly affect the abyssal marine environment. A key consequence of mining activities is habitat destruction and the loss of animals living on and within nodules, as well as in the sediment. Sediment plumes arising from the mining process will further result in a large-scale smothering of habitats (Rolinski et al., 2001; reviewed in Allsopp et al., 2013). Previous disturbance studies, although conducted on a small spatial scale compared to the foreseeable extent of seabed mining, have demonstrated lasting changes in the abundance and composition of fauna, and exacerbated by long recovery times especially for sessile taxa reliant on hard-substrata (Bluhm et al., 1995; Bluhm, 2001; Miljutin et al., 2011, 2015; Stratmann et al., 2018). Disturbance tracks were also still visible after many years (e.g., after 26 years in Miljutin et al., 2011). To minimise serious environmental harm, it is very important to first study the deep-sea biodiversity of the largely unexplored CCFZ before mining commences, since having baseline data is the first and necessary step to carry out future comparisons, disturbance and recovery studies. These studies will be critical in developing strategic mining plans or techniques having the least impact to the marine environment, towards striking a good balance between conservation and exploitation. Unfortunately, deep-sea baseline data are not extensively available due to the massive expanse of the deep seabed and high costs incurred for deep-sea expeditions, resulting in fewer sampling efforts compared to shallower waters. Hence, relatively little is known about the ecology and biogeography of deep-sea fauna in general (Sinniger et al., 2016).

The International Seabed Authority (ISA) was set up in 1994 under the United Nations Convention on the Law of the Sea (UNCLOS) to manage seabed mining outside the limits of national jurisdiction, including the CCFZ. The first CCFZ exploration contract was granted in 2001, with 19 international contracts to date (ISA, 2022). In January 2015, ISA granted a 15-year seabed exploration contract for polymetallic nodules to Ocean Mineral Singapore, a subsidiary of Keppel Corporation Limited. Under this contract, a 58,280 square kilometre exploratory site in the eastern part of the CCFZ was allocated to Singapore. It is a requirement for every contractor to gather environmental baseline data in order to develop environmental impact assessments as well as implement suitable environmental monitoring and management plans (ISA, 2011, 2013). Previous expeditions to various contract areas have generated new insights on the biology, distribution, connectivity and structure of biological communities (e.g., Janssen et al., 2019; Sánchez et al., 2019; Simon-Lledó et al., 2020; De Smet et al., 2021, Laming et al., 2021, Wear et al., 2021); as well as numerous discoveries of species new to science (e.g., Bonifácio & Menot, 2019; Bai et al., 2020; Gooday et al., 2020; Malyutina et al., 2020), highlighting the importance of carrying out such environmental studies there.

In February 2015, Ocean Mineral Singapore (OMS) and United Kingdom Seabed Resources Limited (UKSRL) set out on a joint research expedition—Abyssal Baseline Project 2015 (ABYSSLINE 02/AB02), which was designed according to ISA's environmental guidelines (ISA, 2013). The aim of ABYSSLINE 02, in terms of improving the biological knowledge in the OMS site, was to conduct a biological baseline by characterising and quantifying the biodiversity in the OMS site. This expedition was very successful and 29 papers which included biological data from this area have been published so far (Table 1 and references therein). These papers covered all benthic size groups (i.e., micro-, meio-, macro- and megafauna) as well as the pelagic larval assemblages, and new species descriptions (a brief description of each study is provided in Table 1).

Table 1.
Brief description of studies that included biological data found in the OMS exploratory area.

Study	Organism group	Sampling device	Brief description
Amon et al., 2017	Animals found at sites of organic falls	AUV, ROV	First record of wood falls and second record of carcass falls in the CCFZ. One wood fall (only observed using AUV) and one cetacean fall (samples also collected using ROV) were found in the OMS area. Three other wood falls were found in the UKSRL and APEI regions. These observations confirm that wood fall can occur far from major land masses. Wood-boring xylophagaid bivalves and other associated fauna colonised these wood falls.
Chim & Tong, 2020	Tanaidacea	Box corer	Description of a new genus and species (*Unispinosus eopacificus*) and a new species in the genus *Portaratrum* (*P. birdi*).
Chuar et al., 2020	Metazoan benthos larger than 250 µm	Box corer	Community structure of abyssal benthos collected using a box corer from 12 stations within the OMS area was presented. A total of 42 families of Polychaeta, 15 families of Copepoda, ten families of Tanaidacea and eight families of Isopoda were reported.
Cordier et al., 2022	Eukaryotic DNA metabarcodes obtained from deep ocean sediments	Multiple corer	This study collected deep ocean sediments collected during various expeditions, including from the OMS area. Eukaryotic DNA metabarcoding datasets were obtained and compared with published datasets from pelagic euphotic and aphotic zones. They found that the eukaryotic taxonomic composition from deep ocean sediment were different from, and at least threefold that of, pelagic realms.
Drennan et al., 2021	Annelida: Nereididae	Box corer, Multiple corer, Epibenthic sledge, ROV	Description of a new species of nereidid annelid, *Neanthes goodayi.* This species was found living in polymetallic nodule crevices, mudballs on nodule surfaces, or burrowing in xenophyophore Foraminifera that were growing on nodules.

Goineau & Gooday, 2019	Foraminifera	Multiple corer	A total of 580 morphospecies were reported from 11 samples. Foraminifera are one of the dominant benthic faunas in CCFZ.
Gooday & Goineau, 2019	Foraminifera	Multiple corer	Examined Foraminifera using finer sieve mesh sizes between 63–150 µm. A total of 462 morphospecies were reported from five samples. Monothalamids (mainly spheres, *Lagenammina* spp., *Nodellum*-like forms and saccamminids), rotaliids, hormosinids, trochamminids and textulariids were identified among the samples.
Gooday et al., 2017a	Foraminifera	Box corer, Multiple corer, Epibenthic sledge	Description of new species of Foraminifera from the genus *Aschemonella*.
Gooday et al., 2017b	Foraminifera	Box corer, Multiple corer, Epibenthic sledge	Abundance, diversity and distribution of xenophyophores were presented. Based on test morphology, 36 morphospecies, including 34 new species, were distinguished among 130 specimens. Molecular genetic data was also used to clarify the phylogenetic relationships of the xenophyophores.
Gooday et al., 2018a	Foraminifera	Box corer, Multiple corer, Epibenthic sledge	Description of new species of Foraminifera from the genus *Psammina*.
Gooday et al., 2018b	Foraminifera	Box corer, Multiple corer	Description of two new species of Foraminifera, *Tendalia reteformis* and *Bizarria bryriformis* using samples collected from OMS.
Gooday et al., 2018c	Foraminifera	Box corer and multiple corer	CT imaging was used to examine the interstructure (granellare, test particles and stercomare) of Foraminifera from the genera *Psammina* and *Galatheammina.*
Gooday et al., 2021	Foraminifera	Multiple corer	The biodiversity and distribution of Foraminifera across the Clarion-Clipperton zone, including data from OMS exploratory area (Goineau & Gooday, 2019; Gooday & Goineau, 2019), was presented.
Guggolz et al., 2020	Annelida: Spionidae	Box corer, Epibenthic sledge	16S and 18S molecular makers were used to study the diversity and distribution patterns of spionid polychaetes from the genera *Prionospio* and *Aurospio*, from the tropical North Atlantic, Puerto Rico Trench and central Pacific (including specimens collected from the OMS area).
Kaiser et al., 2021	Isopoda	Epibenthic sledge	Five *Nannoniscus* species from five licence areas, including the OMS exploratory area, were described. The genetic variation, based on CO1 and 16S mtDNA, of *N. pedro* and *N. menoti* in the Clarion-Clipperton Fracture Zone, was found to be widespread.
Kersten et al., 2017	Larval assemblages	Plankton pump, sediment trap	The first description of the invertebrate meroplankton larval assemblage in the OMS and UKSRL areas was presented. Results from plankton pumps indicated that there was little variation in the meroplankton diversity and abundance but sediment traps samples showed that there was high temporal variability in vertical flux.
Kersten et al., 2019	Larval assemblages	Plankton pump	Pelagic larval assemblages (species richness, diversity, and spatial variability) were examined using tree-of-life (TOL) metabarcoding. They detected a diverse assemblage, including a number of taxa not previously reported at abyssal depths or within the Pacific Ocean. This method also found 2.7–4.3 times higher diversity when compared to morphology-based analyses.
Kristensen et al., 2019	Loricifera	Multiple corer	Undescribed loriciferans from the genera *Rugiloricus* and *Pliciloricus* were found nested in spherical agglutinated structures.
Leitner et al., 2017	Bait-attending animals	Baited camera	A detailed description of the bait-attending community of the CCFZ was documented for the first time. The taxa found were *Bassozetus* sp., *Bathyonus caudali*, *Coryphaenoides* spp., *Histiobranchus bathybius*, *Pachycara nazca*, Zoarcidae sp. 2, *Plesiopenaeus armatus*, *Hymenopenaeus nereus*, and *Ophiomusium* cf. *glabrum*.

Lejzerowicz et al., 2021	Microbial and meiofaunal eukaryotes	Multiple corer	DNA and RNA metabarcoding, targeting microbial and meiofaunal eukaryotes, were conducted on sediment samples from the CCFZ as well as other abyssal regions.
Lim et al., 2017	Porifera	Box corer	Description of a new genus and species of sponge, *Plenaster craigi.*
Lindh et al., 2017	Bacteria	Conductivity, temperature, depth (CTD) rosette equipped with Niskin sampling bottles, Box corer, Multiple corer	Examined bacterial communities in the water column, nodule habitats, and sediment habitats in the OMS and UKSRL areas.
Lindh et al., 2018	Bacterioplanktonic community	16S rRNA amplicons obtained in Lindh et al. (2017)	This study used 16S rRNA amplicons of bacterioplanktonic community composition from the CCFZ, as well as global ocean 16S rRNA gene data, to predict the response of mining impacts on the bacterioplanktonic community. They found that the release of sediment plumes in the epi- and mesopelagic waters could change the microbial community structure.
Mohrbeck et al., 2021	Amphipoda	Baited trap	Ten amphipod species were morphologically identified from four areas (UK-1 Stratum A, UK-1 Stratum B, OMS-1 Stratum A, APEI-6). Mitochondrial COI sequences, however, were grouped into 12–24 MOTUs or putative species. Potential cryptic diversity were found in two species morphologically identified as *Paralicella caperesca* and *Valettietta* cf. *anacantha.*
Sweetman et al., 2019	Bacteria, microbial community, macrofauna	Deep-sea benthic chamber lander	Pulse-chase experiments were used to quantity the cycling of carbon in the CCFZ, which found that benthic macrofauna played a minor role, while benthic bacteria dominated phytodetritus consumption in short-term C-cycling processes.
Taboada et al., 2018	Porifera	Box corer, Multiple corer, Epibenthic sledge, Agassiz trawl, ROV	Investigated the population connectivity of an abyssal demosponge, *Plenaster craigi.* This study suggested that APEI-6 is inadequate on its own as a propagule source for *P. craigi* for the entire eastern CCFZ.
Washburn et al., 2021	Macrofauna	Box corer	Collated macrofaunal biodiversity data sets from eight studies, including data from Chuar et al. (2020). Macrofaunal abundance and diversity across the CCFZ differed substantially; many species were singletons or doubletons; and most species were new to science.
Wear et al., 2021	Bacteria, Archaea	AB02 samples were resequenced from Lindh et al. (2017)	16S ribosomal RNA was used to characterise abyssal bacterial and archaeal communities. In the CCFZ, an east and west distinction in the nodule microbial community composition can be observed, although the magnitude was small.
Wiklund et al., 2019	Annelida: Capitellidae, Opheliidae, Scalibregmatidae, Travisiidae	Box corer, Multiple corer, Epibenthic sledge, ROV	Some 23 species of Annelida were described with specimens collected from the UK-1, OMS-1 and APEI-6 areas.
This study	Meiofauna (metazoan benthos larger than 40 µm)	Multiple corer	First quantitative description of the community structure of abyssal benthos above 40 µm collected using the multiple corer from 12 stations within the OMS area.

Even with these informative papers, the overall picture of the biodiversity at the OMS site is not yet complete and is still missing a crucial component—the metazoan meiofaunal community. The metazoan meiofauna, which we defined as animals retained on a 40 µm sieve in this paper, represent the most abundant and diverse group of benthic metazoan animals in the deep sea. Meiofauna can influence ecosystem processes such as mineralization of organic matter, nutrient recycling, sustaining energy flow between trophic levels—overall maintaining a healthy benthic ecosystem (Nascimento et al., 2012; Bonaglia et al., 2014; Schratzberger & Ingels, 2018). Moreover, their small sizes, high abundance, lack of larval dispersion, high lifecycle turnover, and recolonization rates (Gerlach, 1971; Giere, 2009), allow the meiofauna to potentially serve as biological indicators in the event of any disturbances. As one of the key components of the benthic ecosystem, it is important to include meiofauna while considering deep-sea monitoring (Ingels et al., 2021).

A number of meiofaunal studies have already been done in the CCFZ. Meiofaunal abundance and composition data were collected during various scientific cruises to different contractor areas such as the Federal Institute for Geosciences and Natural Resources (BGR), Germany (Hauquier et al., 2019; Uhlenkott et al., 2020); Global Sea Mineral Resources NV (GSR), Belgium (Hauquier et al., 2019, Pape et al., 2017, 2021); Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER), France (Mahatma, 2009; Hauquier et al., 2019); Interoceanmetal Joint Organization (IOM) (Radziejewska & Modlitba, 1999; Radziejewska et al., 2001; Radziejewska, 2002, 2014); and the Korea Deep Ocean Study area (KODOS) (Kim et al., 2000, 2004; Min et al., 2004, 2018). New meiofaunal species have also been described from these contract areas—Harpacticoida from GSR (Gheerardyn & George, 2019), BGR, IOM and IFREMER (Mercado-Salas et al., 2019) and the Korean contract area (Cho et al., 2016), Tardigrada from the Chinese contract area (Bai et al., 2020), Loricifera (Fujimoto & Murakami, 2020) and Nematoda from Japanese contract area (DORD) (Shimada et al., 2020). Multiple expeditions to the same contract area allow comparison studies of temporal and spatial trends (Pape et al., 2017; Uhlenkott et al., 2020), recovery studies by examining changes before and after disturbances (Radziejewska et al., 2001; Radziejewska, 2002; Fukushima et al., 2022), and the synthesis of meiofauna diversity in the CCFZ by using data across the various contract areas (e.g., Kinorhyncha diversity in Sánchez et al., 2019; Nematoda distribution in Hauquier et al., 2019). As ABYSSLINE 02 was the first cruise to the OMS contract area, there is, naturally, a lack of data on meiofauna from OMS before this expedition. Apart from a description of Loricifera inside spherical agglutinated structures (Kristensen et al., 2019) and sediment DNA and RNA barcodes obtained (Lejzerowicz et al., 2021), all published papers from OMS so far only included metazoan animals of >250 µm (Table 1). A quantitative baseline of the benthic metazoan meiofauna is imperative to obtain a better perspective of the biodiversity in the area. This paper aims to close this knowledge gap.

2. MATERIALS & METHODS

2.1. Study area

All samples were collected during the research cruise ABYSSLINE 02, on board the research vessel Thomas G. Thompson (T-AGOR-23), between 16 February to 22 March 2015 in the eastern CCFZ (Fig. 1). Within a 30 × 30 km area in the southernmost region of OMS contract area (centered at 12˚ 8.2' N, 117˚ 17.7' W), at depths of between 4000–5000 m (Fig. 1), 12 stations were randomly selected for sampling (Fig. 2). Photographs taken from autonomous underwater vehicle (AUV) and box corer deployments showed that the seafloor is covered with polymetallic nodules, often covering more than 30% of the box corer (50 × 50 cm) surface area. Multibeam bathymetry showed that the OMS study area was almost devoid of seamounts, and the 900 square kilometer region sampled in this study was mainly dominated by low relief NNW-SSE lineated ridges and troughs (Chuar et al., 2020).

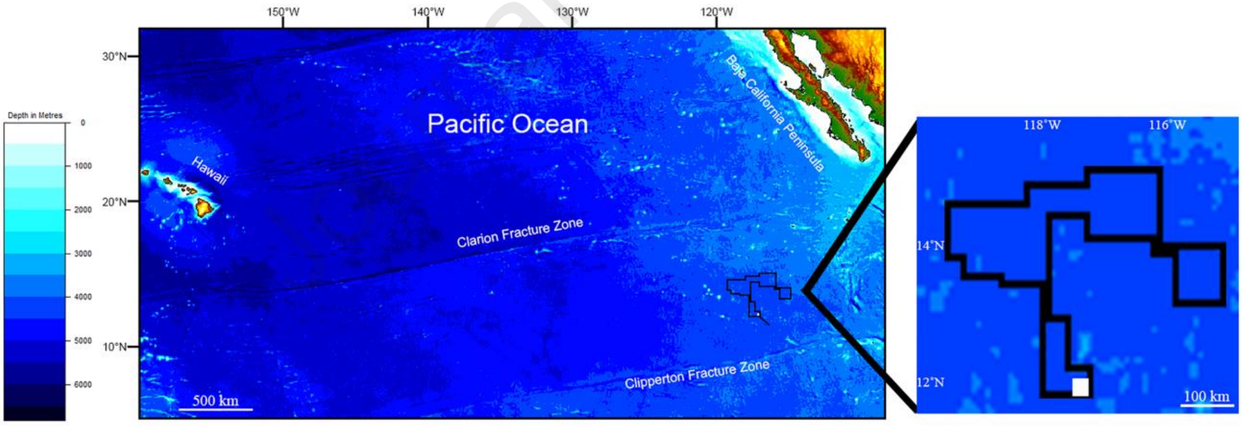

Fig. 1. Map of the Clarion-Clipperton Fracture Zone (CCFZ). Location of Ocean Mineral Singapore (OMS) exploration contract area is outlined in black lines. The 30 × 30 km surveyed area during ABYSSLINE 02 research expedition is indicated by the small white box. Figure reproduced and modified from Chuar et al. (2020).

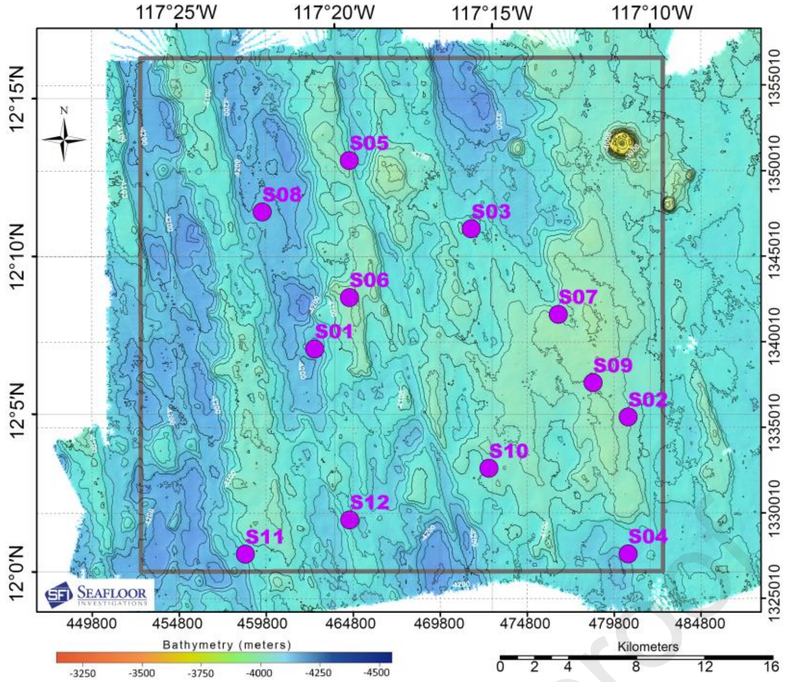

Fig. 2. Twelve randomly assigned stations within the 30 × 30 km surveyed area of the Ocean Mineral Singapore (OMS) exploration contract area. A Mega Multiple Corer was deployed once at each station during the ABYSSLINE 02 research expedition from 24 Feb.–17 Mar. 2015. This figure taken from Chuar et al. (2020) was modified from the map created by Seafloor Investigations LLC for the ABYSSLINE Project using ArcGIS software.

2.2. Sample collection

At each of the 12 stations a Mega Multiple Corer (OSIL) was deployed once, which collected 12 sediment cores (diameter = 10 cm) simultaneously. Four successful cores were selected from amongst the 12 cores for quantitative analysis of the benthic meiofauna. Nodules collected by a 0.25 m^2 box corer (Ocean Instruments BX-S50 MK-III) at the same stations during the cruise were used to estimate the nodule density of the area (Chuar et al., 2020). From the box core, a Shear Strength Measurement Tool (Humboldt H-4227) was also used to determine the shear strength of the sediment (Chuar et al., 2020), a measure of the stability of sediment (Grabowski, 2014). Shear strength readings were taken for 0–10 cm, 15–25 cm and 25–40 cm depths. The sampling location, date and depth of each station, as well as the shear strength reading for the 0–10 cm depth, and nodule data from 0–5 cm depth obtained from box corer deployments are listed in Table 2.

Table 2.
Stations in the OMS exploratory area during the research cruise ABYSSLINE 02 where the multiple corer was deployed. Shear strength (kPa) value for 0–10 cm sediment layer, surface nodule coverage (%), nodule weight (g) for 0–5 cm sediment layer, and nodule volume (cm^3) for 0–5 cm sediment layer were based on box corer samples from the same location.

Station	Deployment ID	Date	Coordinates	Depth (m)	Shear strength (kPa)	Surface nodule coverage (%)	Nodule weight (g)	Nodule volume (cm^3)
S01	MC07	24 Feb. 2015	12 07.07128 N 117 20.60474 W	4185	2.17	40.5	4219.47	2280
S02	MC10	28 Feb. 2015	12 04.90710 N 117 10.69599 W	4072	2.16	35.8	3228.07	1680
S03	MC08	25 Feb. 2015	12 10.86723 N 117 15.6556 W	4114	1.44	19.1	4527.64	2360
S04	MC09	27 Feb. 2015	12 00.563 N 117 10.690 N	4148	2.09	40.1	3671.63	1910
S05	MC11	1 Mar. 2015	12 13.036 N 117 19.520 W	4106	1.84	30.5	3346.23	1750
S06	MC12	2 Mar. 2015	12 08.695 N 117 19.527 W	4041	4.63	20.4	1759.34	920
S07	MC20	12 Mar. 2015	12 08.163 N 117 12.899 W	4110	1.94	33.2	4431	2210
S08	MC22	14 Mar. 2015	12 11.417 N 117 22.281 W	4179	0.63	0	45.02	15
S09	MC19	11 Mar. 2015	12 05.999 N 117 11.799 W	4082	2.34	35	3390.62	1805

S10	MC21	13 Mar. 2015	12 03.27253 N 117 15.09741 W	4096	2.00	42.8	4158.36	2050
S11	MC23	16 Mar. 2015	12 00.555 N 117 22.818 W	4152	2.25	23.8	3784.49	1975
S12	MC24	17 Mar. 2015	12 01.64107 N 117 19.51164 W	4127	2.81	38.5	6560.21	3680

2.3. Sample processing

On board the vessel, each intact sediment core was sliced into two layers: an upper 0–2 cm layer, and a lower 2–5 cm layer. Overlying water from each core was filtered through a 40 µm mesh sieve and the filtrate added to the 0–2 cm layer. Each layer was then separately preserved in 10% borax-buffered formalin. In the laboratory of Senckenberg am Meer Wilhelmshaven, meiobenthic organisms were separated from the sediments using Levasil®-kaolin medium (McIntyre & Warwick, 1984) followed by three consecutive centrifugations at 4,000 g for 6 minutes each time. The centrifugal supernatant containing the organisms was then filtered through a 40 µm mesh sieve, washed with fresh water, preserved in 10% borax-buffered formalin and stained with Rose Bengal. Sorting of the animals to their animal groups (i.e., major taxa including 'Nauplii') was done under Olympus SZH16 stereomicroscopes, using a Bogorov counting chamber, at the St John's Island National Marine Laboratory, Singapore. The Nematoda was preserved in 10% borax-buffered formalin and the other animal groups were preserved in 70–80% ethanol for storage.

2.4. Data analysis

To examine differences among communities at the 12 stations, the abundance, richness (total number of animal groups) and diversity using Shannon-Wiener diversity indices were calculated. Meiofauna counts from the 0–5 cm sediment layer at each station were pooled from four cores, and then presented as the number of individuals (ind.) per 10 cm^2 prior to further analyses.

Spearman Rank correlation was used to elucidate the existence of possible relationships amongst environmental variables (i.e., shear strength, nodule cover, nodule weight, nodule volume) as determined from box core samples. Nodule weight and volume were not unexpectedly very significantly correlated (p-value < 0.01, rho = 0.99) and thus nodule weight was excluded from further analyses. Overall, only three environmental parameters were used for analyses in this study: shear strength (kPa), nodule cover (%) and nodule volume (cm^3). Spearman Rank correlation between abundance and diversity was also determined to find out their possible relationships with environmental parameters.

Multivariate analyses with abundance data were performed on fourth-root transformed, Bray-Curtis dissimilarity matrix, and environmental variables were untransformed and normalised. Cluster analyses with Type 1 Similarity Profile (SIMPROF) were used to test for any significant clusters. Non-metrical dimensional scaling (nMDS) was used to visualise any patterns in community composition across the 12 stations. BVStep (Spearman Rank correlation) was used to determine which animal groups best explained the differences among stations. BVStep could be considered a generalisation of Similarity Percentages (SIMPER) because the latter routine compares only two groups at a time (Clarke & Gorley, 2015). Marginal and sequential distance-based linear models (DISTLM) tests, visualised using distance-based redundancy analysis (dbRDA), were used to analyse any relationship between communities at the 12 stations in response to environmental variables. Within-group variability was tested using PERMANOVA and PERMDISP.

Spearman Rank correlation tests and Shannon-Wiener diversity indices were calculated using statistical software R version 3.6.1 (R Core Team, 2019). All multivariate tests were conducted in PRIMER v7 (Clarke & Gorley, 2015) with PERMANOVA+ add-on (Anderson et al., 2008). All analyses were carried out at 5% significance level.

3. RESULTS

3.1. Abundance and diversity of metazoan meiofauna

Overall, 88 867 individuals were collected from 23 animal groups (including a group containing undetermined organisms, the 'Unknowns') across 13 phyla (Table 3; see also Appendix).

Table 3.
Abundance (ind./10 cm^2) of metazoan meiofauna (animals retained on a 40 µm sieve) collected at each station in the OMS area of the CCFZ, eastern Pacific Ocean. Meiofauna counts from 0–5 cm sediment layer were pooled from four cores (diameter of each core = 10 cm) and then calculated to individuals/10 cm^2. s.d. = standard deviation.

Animal groups/Station	1	2	3	4	5	6	7	8	9	10	11	12	Mean	s.d.
Phylum Platyhelminthes	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.01
Phylum Nemertea	0.00	0.35	0.10	0.13	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.06	0.10
Phylum Nematoda	207.28	179.94	227.62	199.48	198.94	203.34	208.62	262.54	213.97	212.73	186.24	185.54	207.19	22.06
Phylum Gastrotricha	0.29	0.25	0.16	0.10	0.19	0.00	0.25	0.29	0.25	0.13	0.10	0.19	0.18	0.09
Phylum Rotifera	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.01	0.01
Phylum Loricifera	0.10	1.18	0.57	0.45	0.22	0.13	0.32	0.60	3.28	0.76	0.95	0.06	0.72	0.88
Phylum Kinorhyncha	0.25	0.13	0.38	0.16	0.29	0.03	0.19	0.38	0.00	0.10	0.06	0.10	0.17	0.13
Phylum Annelida														
Polychaeta	2.61	1.81	1.21	1.97	3.12	1.34	2.93	2.48	3.25	2.67	3.41	2.20	2.42	0.72
Phylum Sipuncula	0.00	0.00	0.00	0.00	0.06	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.01	0.02
Phylum Tardigrada	0.16	0.70	0.29	0.25	1.18	0.10	0.10	1.15	0.29	0.76	0.25	0.60	0.49	0.39
Phylum Arthropoda														
Acari	0.19	0.38	0.38	0.25	0.06	0.10	0.06	0.13	0.00	0.03	0.16	0.06	0.15	0.13
Amphipoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.01
Copepoda	11.78	11.49	8.69	7.67	10.19	7.19	14.26	16.33	11.87	10.85	6.72	5.63	10.22	3.19
Cumacea	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Isopoda	0.00	0.22	0.13	0.16	0.13	0.00	0.25	0.10	0.16	0.03	0.03	0.06	0.11	0.08
Ostracoda	1.08	0.57	0.80	0.48	0.45	0.35	1.05	0.86	0.83	0.70	0.67	0.16	0.67	0.28
Tanaidacea	0.22	0.16	0.22	0.22	0.00	0.13	0.19	0.16	0.29	0.38	0.10	0.29	0.20	0.10
Tantulocarida	0.38	0.32	0.13	0.25	0.22	0.19	0.19	0.22	0.41	0.67	0.38	0.06	0.29	0.16
Nauplii	14.45	13.85	9.99	11.27	11.36	5.83	14.45	14.04	13.72	16.04	9.58	5.63	11.68	3.40
Phylum Mollusca														
Bivalvia	0.06	0.10	0.03	0.03	0.03	0.03	0.03	0.19	0.06	0.19	0.06	0.03	0.07	0.06
Gastropoda	0.00	0.00	0.00	0.10	0.00	0.00	0.06	0.00	0.00	0.00	0.06	0.00	0.02	0.03
Phylum Echinodermata														
Asteroidea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.01
Unknown	3.63	0.86	0.22	1.15	0.19	0.48	0.92	0.45	1.66	1.11	1.02	1.24	1.08	0.92
Total abundance (ind./10 cm^2)	242.52	212.34	250.92	224.12	226.67	219.22	243.92	299.94	250.13	247.26	209.80	201.87	235.73	26.39
Richness	15	17	16	17	16	13	17	16	14	18	16	15	15.83	1.40
Shannon-Wiener index	0.63	0.66	0.45	0.52	0.55	0.36	0.61	0.55	0.65	0.61	0.53	0.41	0.54	0.10

The number of individuals ranged from 201.9 ind./10 cm^2 at Station 12 to 299.9 ind./10 cm^2 at Station 8 (Table 3). The average meiofaunal abundance across the 12 stations within the 30 × 30 km sampling area was 235.7 ± 26.4 ind./10 cm^2

(Table 3). Despite the near absence of nodules at Station 8, diversity and abundance of meiofauna were among the highest (Table 3).

Nematoda, Nauplii, Copepoda, Loricifera, Tantulocarida, Tardigrada, Annelida, Bivalvia, Ostracoda and Unknowns were present at all 12 stations (Fig. 3).The Nematoda was the dominant animal group (mean of 87.9 ± 2.9%), followed by the Nauplii (5.0 ± 1.3%) and the Copepoda (4.3 ± 1.1%). Other animal groups comprised the remaining 2.9% (Fig. 3; see Appendix). A few animal groups were only present in just one or two stations. Amphipoda was only present in Station 10; Cumacea in Station 5; Platyhelminthes in Station 8; Asteroidea in Station 10; and Sipuncula in Stations 5 and 7 (Fig. 3).

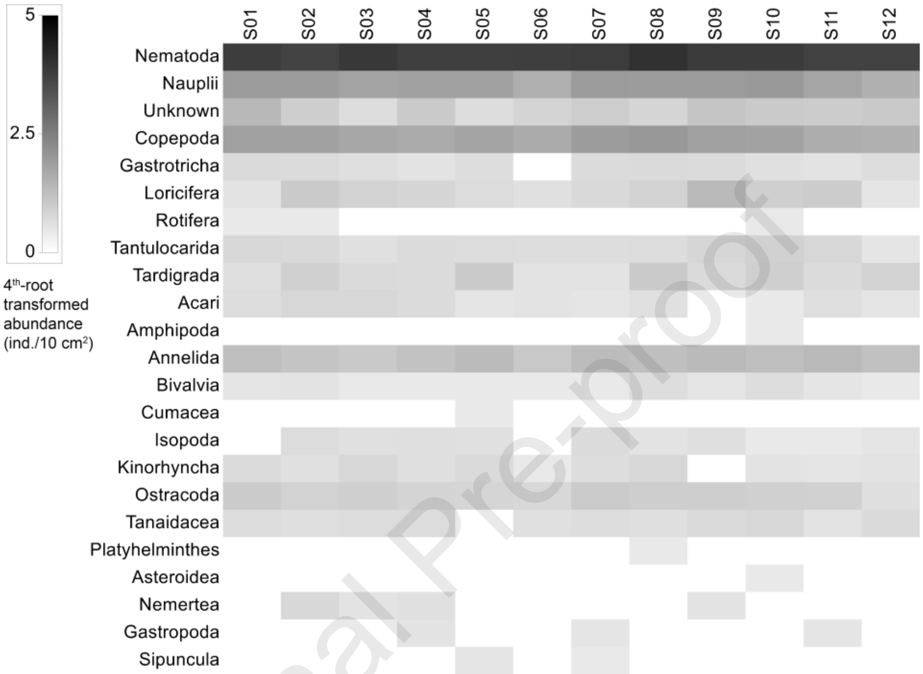

Fig. 3 Shade plot of the 4th-root transformed abundance (ind./10 cm^2) data of each animal group at each of the 12 stations. Darker spaces indicated higher abundances. White spaces indicate a total absence of the animal group.

Significant negative correlations were only found between meiofaunal abundances and shear strength (p-value = 0.02, rho = -0.66) (Table 4). No significant correlations were found between diversity (based on the Shannon-Wiener Index) and environmental parameters (Table 4).

Table 4.
Spearman rank correlations of abundance and Shannon-Wiener diversity indices with environmental variables.

	Shear strength		**Nodule cover**		**Nodule volume**	
	rho	p-value	rho	p-value	rho	p-value
Abundance	-0.66	0.02	-0.26	0.42	-0.09	0.78
Shannon-Wiener diversity index	-0.16	0.62	0.35	0.27	-0.15	0.64

3.2. Multivariate analyses of community structure

Based on the animal group composition and abundance, cluster analyses showed no clusters supported by SIMPROF. Similarly, from the nMDS (Fig. 4), there was also no obvious groupings across the 12 stations. BVStep selected a high number of 13 animal groups—Nauplii, Copepoda, Gastrotricha, Loricifera, Rotifera, Tardigrada, Amphipoda, Bivalvia, Cumacea, Kinorhyncha, Nemertea, Sipuncula and Unknown, that best explain the variability among stations contributing to the overall multivariate pattern. From the BVStep procedure, the differences among stations were driven by the less abundant animal groups. This number was also more than half of the total number of 23 identified animal groups. This might also suggest that OMS area is very diverse since so many animal groups contributed to the multivariate pattern. DISTLM results indicated that both nodule surface coverage and nodule volume (both marginal and sequential p-values < 0.05) did not explain the meiofaunal community variation at the major taxon level, and only results for sediment shear strength was significant (marginal test p-value = 0.03, R^2 = 0.18, Pseudo-F = 2.21; sequential tests mostly significant, or p-values very close to 0.05) (Fig. 5). This could also indicate that there are other factors explaining the variation in meiofaunal community, which should be measured in future expeditions. Within each station, high average similarity of >80 was observed among the four cores for both relative and absolute abundances (Appendix), and PERMDISP did not show any significance (p(perm) = 0.41 and p(perm) = 0.75 respectively). PERMANOVA (Pseudo-F = 2.27, P(perm) = < 0.01) and pair-wise comparisons showed that almost all the stations were different from each other (Appendix).

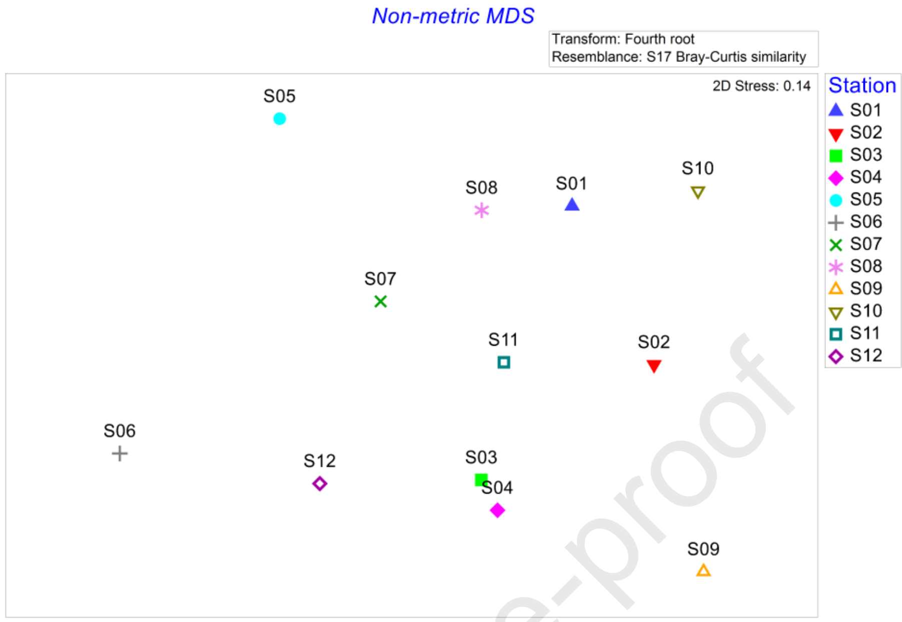

Fig. 4. Non-metrical dimensional scaling (nMDS) visualisation of the 12 stations (0–5 cm sediment layer) in the OMS area of the CCFZ.

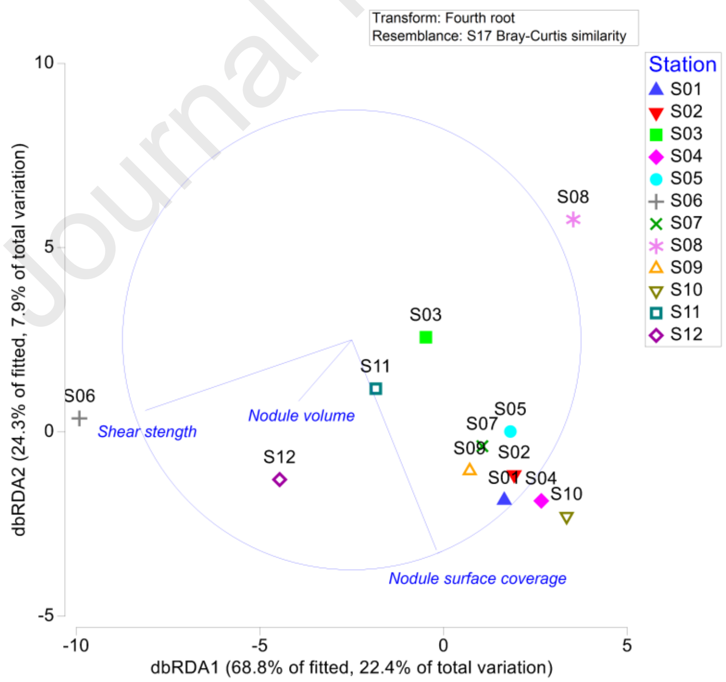

Fig. 5. Distance-based redundancy analysis (dbRDA) illustrating the DISTLM based on meiofaunal community data (0–5 cm sediment layer) and environmental data. The length and direction of vectors represent the strength and direction of the relationship.

3.3. Vertical distribution

Across all animal groups, the majority (76.6%) of the animals were found in the top 0–2 cm sediment layer (Table 5).

Table 5.
Percentage (%) of each animal group in the 0–2 cm and 2–5 cm sediment layers, arranged in descending quantities. s.d. = standard deviation.

Sediment layer							**0–2 cm**							
Station	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**Mean**	**s.d.**
Nematoda	72.86	57.05	60.04	70.59	72.18	69.00	65.29	53.42	69.03	71.37	73.66	61.61	66.34	6.77
Nauplii	5.50	5.70	2.98	4.57	4.72	2.24	5.19	4.01	4.98	5.97	3.99	2.05	4.32	1.31
Copepoda	4.37	4.71	2.65	2.85	3.93	2.58	4.95	4.61	4.12	4.00	2.73	1.94	3.62	1.01
Annelida	1.00	0.72	0.34	0.81	1.32	0.54	1.11	0.65	1.20	1.02	1.38	0.85	0.91	0.32
Ostracoda	0.41	0.25	0.24	0.18	0.20	0.16	0.39	0.23	0.17	0.28	0.30	0.05	0.24	0.10
Loricifera	0.04	0.06	0.05	0.18	0.08	0.03	0.09	0.05	0.81	0.28	0.39	0.03	0.18	0.23
Tardigrada	0.05	0.24	0.05	0.10	0.51	0.04	0.03	0.22	0.11	0.31	0.12	0.24	0.17	0.14
Tantulocarida	0.13	0.13	0.04	0.10	0.10	0.09	0.05	0.07	0.15	0.26	0.15	0.02	0.11	0.06
Gastrotricha	0.09	0.10	0.06	0.04	0.08	0.00	0.10	0.07	0.09	0.05	0.05	0.05	0.07	0.03
Kinorhyncha	0.11	0.06	0.13	0.06	0.13	0.01	0.08	0.11	0.00	0.04	0.03	0.05	0.07	0.04
Tanaidacea	0.09	0.06	0.08	0.07	0.00	0.06	0.07	0.04	0.11	0.15	0.05	0.06	0.07	0.04
Acari	0.05	0.13	0.15	0.10	0.03	0.03	0.01	0.04	0.00	0.01	0.08	0.02	0.05	0.05
Bivalvia	0.03	0.03	0.01	0.01	0.01	0.01	0.01	0.06	0.01	0.06	0.03	0.02	0.03	0.02
Isopoda	0.00	0.04	0.04	0.06	0.06	0.00	0.08	0.02	0.05	0.01	0.00	0.02	0.03	0.03
Nemertea	0.00	0.16	0.04	0.06	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.02	0.05
Gastropoda	0.00	0.00	0.00	0.04	0.00	0.00	0.03	0.00	0.00	0.00	0.03	0.00	0.01	0.02
Amphipoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Asteroidea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Cumacea	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Platyhelminthes	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Rotifera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Sipuncula	0.00	0.00	0.00	0.00	0.03	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Unknown	1.44	0.12	0.05	0.48	0.06	0.20	0.29	0.08	0.55	0.30	0.15	0.50	0.35	0.39
Percentage of meiofauna in the 0–2 cm sediment layer	86.17	69.58	66.95	80.32	83.44	75.00	77.78	63.72	81.42	84.17	83.14	67.49	76.60	7.81
Sediment layer							**2–5 cm**							
Station	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**Mean**	**s.d.**
Nematoda	12.61	27.69	30.67	18.42	15.59	23.75	20.24	34.11	16.52	14.66	15.11	30.31	21.64	7.39
Nauplii	0.46	0.82	1.00	0.45	0.29	0.42	0.73	0.67	0.51	0.51	0.58	0.74	0.60	0.20
Copepoda	0.49	0.70	0.81	0.57	0.56	0.70	0.90	0.84	0.62	0.39	0.47	0.85	0.66	0.17
Annelida	0.08	0.13	0.14	0.07	0.06	0.07	0.09	0.18	0.10	0.06	0.24	0.24	0.12	0.07
Ostracoda	0.04	0.01	0.08	0.03	0.00	0.00	0.04	0.05	0.17	0.00	0.02	0.03	0.04	0.05
Loricifera	0.00	0.49	0.18	0.01	0.01	0.03	0.04	0.15	0.50	0.03	0.06	0.00	0.13	0.18
Tardigrada	0.01	0.09	0.06	0.01	0.01	0.00	0.01	0.16	0.00	0.00	0.00	0.06	0.04	0.05
Tantulocarida	0.03	0.01	0.01	0.01	0.00	0.00	0.03	0.00	0.01	0.01	0.03	0.02	0.01	0.01
Gastrotricha	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.00	0.00	0.05	0.01	0.02
Kinorhyncha	0.00	0.00	0.03	0.01	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.01	0.01
Tanaidacea	0.00	0.01	0.01	0.03	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.08	0.01	0.02
Acari	0.03	0.04	0.00	0.01	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.02	0.01	0.01
Bivalvia	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.01
Isopoda	0.00	0.06	0.01	0.01	0.00	0.00	0.03	0.01	0.01	0.00	0.02	0.02	0.01	0.02
Nemertea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Amphipoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Asteroidea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cumacea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Platyhelminthes	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rotifera	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Sipuncula	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Unknown	0.05	0.28	0.04	0.03	0.03	0.01	0.09	0.06	0.11	0.15	0.33	0.11	0.11	0.10
Percentage of meiofauna in the 2–5 cm sediment layer	13.83	30.42	33.05	19.68	16.56	25.00	22.22	36.28	18.58	15.83	16.86	32.51	23.40	7.81

4. DISCUSSION

4.1 Meiofaunal abundance, diversity and community structure across the CCFZ

In this study, our comparatively small sampling area of 30 × 30 km is only ~1.5% of the total allocated OMS area (58,280 square kilometers). Yet, even at the level of major taxonomic groups, our results based on multivariate analyses suggested that the meiofaunal community structure at each of the 12 stations is different, demonstrating that the eastern region of the CCFZ sea floor is very diverse. The average of 235.7 ± 26.4 ind./10 cm^2 across the 12 stations was also relatively higher than previously reported meiofaunal abundances in the other CCFZ areas (Table 6, Fig. 6). There were some exceptions in a few stations across the various studies where more meiobenthos were found (values in bold font in Table 6). At the eastern end, the BGR contract area (483.8 ± 95.2 ind./10 cm^2, 371.8 ± 33.1 ind./10 cm^2 and 306.6 ± 99.0 ind./10 cm^2) (Hauquier et al., 2019; Uhlenkott et al., 2020), the IOM contract area (244.6–394.2 ind./10 cm^2, 552.7 ± 260.3 ind./10 cm^2) (Radziejewska, 2002; Hauquier et al., 2019), and the GSR contract area at B6S02April (242.3 ± 59.2 ind./10 cm^2) (Pape et al., 2017) found higher meiofaunal abundance compared against our 0–5 cm layer results. The NIXO 47 study reported meiofaunal abundance of 187–247 ind./10 cm^2 from some box corer samples (0–2.5 cm sediment depth), which was also comparable to our results from the 0–2 cm layer (Renaud-Mornant & Gourbault, 1990). The KODOS studies utilized sediment layers up to 3 cm depth and found 181 ind./10 cm^2, 229 ind./10 cm^2, 222 ind./10 cm^2 at W135, M03 and M04 respectively (Kim et al., 2004; Min et al., 2018), which were comparable to our 0–2 cm and 0–5 cm findings.

Results from NIXO 47, DOMES, ECHO-1, PRA, IOM-BIE, and JET expeditions, as well as those from survey cruises in GSR, KODOS and COMRA exploration sites (see Fig. 6; Table 6 and references therein) have provided some of the first meiofaunal abundance and composition data from the CCFZ. Differences in collection methods (e.g., multiple corer or subsamples from box corer), lower sieve size limits, and sediment depths sampled make direct comparisons difficult across these studies. However, it is also not possible to exclude all studies using different collection methods or sieve sizes due to the already very limited data from the CCFZ. Hence, to maintain meaningful comparisons, we retained studies using lower sieve size limits of maximum 63 µm, and at similar CCFZ depths of around 4000–5000 m (Table 6). Any comparisons made were as far as possible within the same sediment layer, or across similar sediment layers. The DOMES study (Hecker & Paul, 1979) and PRA sites (Wilson, 1990, 1992) only included meiofaunal groups sized >300 µm and were therefore excluded from comparisons here.

Table 6.
Expedition information and meiofaunal abundances from various studies in the CCFZ. Abundances in bold indicate higher meiofaunal abundances relative to this study. Data from sediment depths of 0–2 cm and 0–5 cm of this study were included to facilitate comparisons. s.d. = standard deviation.

Name of expedition	Contractor/Contract area in CCFZ	Year of expedition	Depth (m)	Sampling method	Lowest sieve size (µm)	Sampling depth (cm)	No. or name of stations	No. or name of replicates	Abundance ± s.d. (ind./10 cm^2)	Remarks	Reference
ABYSSLINE 02	Ocean Mineral Singapore (Singapore)	2015	4000–4200	Multiple corer	40	0–5	12		235.73 ± 26.39		This study
						0–2			180.13 ± 23.09		
Mangan2010,2013,2014,2016,2018, EcoResponse	BGR (Germany)	2010, 2013, 2014, 2015, 2016, 2018	4076–4156	Multiple corer	32	0–5	35 deployments, 106 cores		**306.62 ± 98.95**	converted from 100 cm^2 to 10 cm^2, summed the meiofaunal abundance from each core, and then averaged it by the total number of cores	Uhlenkott et al., 2020
SO239	BGR (Germany)	2015	4342.2	Multiple corer	32	0–5	BGR_PA	5 deployments	**371.84 ± 33.11**	BGR area divided into "Reference area" (BGR_RA; limited future mining) and "Prospective area" (BGR_PA; intensive future mining)	Martínez Arbizu & Haeckel, 2015; Hauquier et al., 2019
			4123.9				BGR_RA	5 deployments	**483.84 ± 95.18**		
	IOM (Interoceanmetal Joint Organization)		4434.5				3	3 deployments	**552.71 ± 260.32**		
	APEI-3		4839.1					4 deployments	53.20 ± 8.86		
	IFREMER (France)		4964.6				1	5 deployments	182.15 ± 62.42		
	DEME-GSR (Belgium)		4511.8				1	5 deployments	211.49 ± 40.36		
IOM-BIE	IOM (Interoceanmetal Joint Organization)	1995	4380–4430	Multiple corer	32	0–6		MC1	100.66		Radziejewska, 2002
								MC2	105.70		
								MC3	**245.14**	control (C1)	
								MC4	86.10		
								MC5	**277.76**		
								MC6	**394.24**		
		1997						MO1	**244.56**	control (C2)	
								MO2	198.94	control (C2)	

								MO3	152.88	control (C2)	
			4380–4410				3 cores		91.56 ± 23.31	nodule bearing area; abundance data taken from Radziejewska (2014)	Radziejewska & Modlitba, 1999; Radziejewska, 2014
		2000	4412–4436					3 (MO2, MO22, MO23)	138.97 ±3.49	control only (C3)	Radziejewska et al., 2001
SO239			4522–4526				B6S02 April	4	**242.3 ± 59.2**		
		2015					B6S02 Oct	3	151.1 ± 54.2		Pape et al., 2017
GSRNOD15A			4470–4526				B4S03	3	106.6 ± 29.3		
							B4N01	3	88.1 ± 55.0		
	GSR (Belgium)			Multiple corer	32	0–5	NodFree (B4S03)	4	126.8 ± 29.0		
GSRNOD17		2017	4480–4649				NodRich_A (B4S03)	4	87.0 ± 21.0		Pape et al., 2021
							NodRich_B (B4S03)	3	45.4 ± 31.5		
							H347		92.98		
							H349		160.53		
							H350		30.53		
ECHO-1		1983	4480–4517	Box corer	63	0–1	H351		98.25	used only the controls at 0–1 cm layer; modified original data to exclude the Foraminifera, Protozoa and Calanoida	Wilson & Hessler, 1987
							H352		8.77		
							H360		118.42		
							H362		31.58		
NOAA-BIE	US-Russian Joint BIE in a test site in Russian contract area	1993	4800	Box corer	45	0–3	Baseline studies from five box cores, two subcores taken from each box core samples		46.2–205.3	total meiobenthos abundance data taken from Radziejewska (2014)	Trueblood & Ozturgut, 1997; Trueblood et al., 1997; Radziejewska, 2014
		1994		Multiple corer			Five control multicorer samples		40.74–91.28		
NODINAUT	IFREMER (France)	2004	5035–5042	Multiple corer		0–5	Five stations sampled, total of eight corers		181.66 ± 35.56	outside nodule area	Mahatma, 2009
			4877–5000				Five stations sampled, total of eight corers		95.97 ± 23.43	nodule area	
							47001	A	**189**		
							47004	A,B	124		
NIXO 47			4905–5140	Box corer	40	0–2.5	47007	A,B	134	modified original data by adding subsamples A,B from the same box corer together	Renaud-Mornant & Gourbault, 1990
							47011	A,B	110		
							47012	A,B	124		

							47014	A,B	**247**		
							47016	A,B	103		
							47018	A,B	156		
							47021	A,B	**187**		
							47024	A,B	120		
							47026	A,B	**203**		
							47029	A,B	**208**		
							47031	A,B	**187**		
							47032	A,B	149		
							47034	A,B	**220**		
							47036	A,B	95		
							47037	A,B	164		
							N05		102.50		
							N06		101.75		
							N07		123.50	averaged; modified original data to exclude the Foraminifera	Kim et al., 2000; Min et al., 2004; Min et al., 2018
							N08		75.00		
							N09		72.75		
							N10		90.75		
							N12		67		
							N13		54		
							N14		4		Min et al., 2004; Min et al., 2018
							N16		6		
							N17		27		
"KODOS"	Korea Deep Ocean Study area (Korea)	1998, 1999, 2001, 2003, 2004, 2005	4090–5091	Multiple corer	37–63	upper 3 cm	W128		84		
							W129		61		
							W130		83	modified original data to exclude the Foraminifera	
							W131		69		
							W131-1		91		
							W131-2		66		Min et al., 2018
							W132		97		
							W133		66		
							W134		50		
							W135		**181**		
							W136		119		
							M01		95		

							M02		38		
							M03		**229**		
							M04		**222**	modified original data to exclude the Foraminifera	Kim et al., 2004; Min et al., 2018
							M05		53		
							M06		71		
							M07		44		
JET1 (Japan Deep-sea Impact Experiment)	Japanese contract area	1994 (prior to disturbance)	~5300	Multiple corer	30	0–3	10	44 subcores	101.0 ± 55.9	meiofauna from 30–300 µm	Kaneko et al., 1997
	China Ocean Mineral Resources Research and Development Association (COMRA) EAST	2005	5100–5400		38	0–1,1–2,2–4,4–6	6		104.40 ± 20.48		Wang et al., 2013
		1998	~5000–5300		32	0–1,1–2,2–4,4–6	10		32.47	average	Gao et al., 2002
"COMRA"	China Ocean Mineral Resources Research and Development Association (COMRA) WEST	2005	5100–5400	Multiple corer	38	0–1,1–2,2–4,4–6	6		40.26 ± 25.84		Wang et al., 2013
		1998	~5000–5300		32	0–1,1–2,2–4,4–6	10		18.05	average	Gao et al., 2002
	Polymetallic Nodule Field	2013	5193	1 random core taken using a perspex tube	31	0–1,1–2,2–4,4–6,6–8	WS1303		45.30		Zhao et al., 2020
			5133				PRZ1302		4.97		

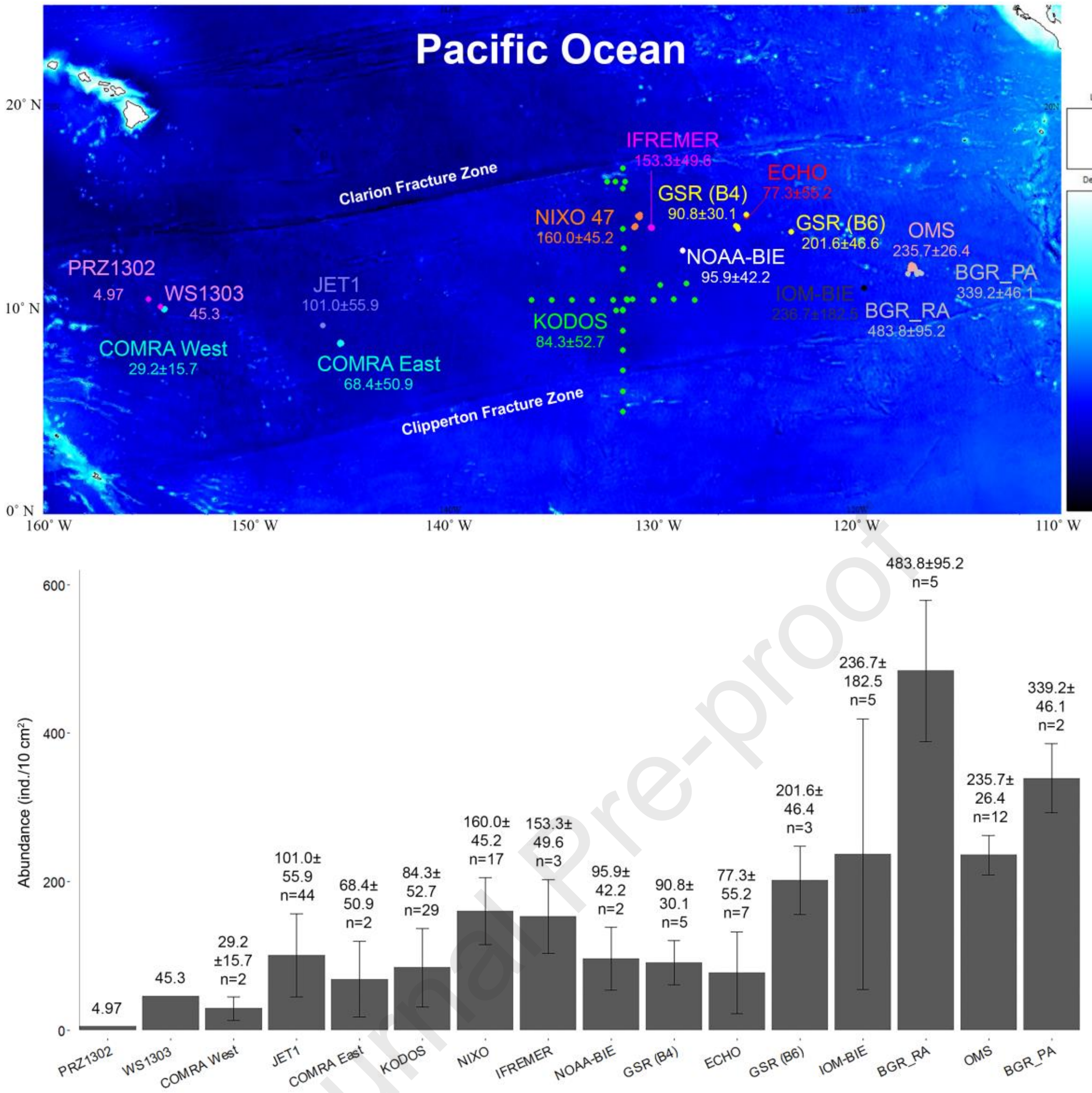

Fig. 6. Mean meiofaunal abundances (ind./10 cm^2) ± s.d. in the CCFZ obtained from various expeditions (see Table 6 for details). The coloured points represent locations of sampling stations. Stations PRZ1302 and WS1303 (closer to COMRA West) were from Zhao et al. (2020). For the GSR contract area, GSR (B4) is further to the west and GSR (B6) is further to the east. The BGR contract area was divided into BGR_RA and BGR_PA (east of OMS sampling locations in this study). Sampling locations from Uhlenkott et al. (2020) were east of OMS, and were therefore combined with data from BGR_PA. The means for COMRA West, COMRA East, IFREMER, GSR (B4), GSR (B6) and BGR_PA were calculated from the means obtained from the various studies (refer to Table 6). The IOM-BIE value was calculated using data from Hauquier et al. (2019), Radziejewska (2014), and the means obtained from C1, C2 and C3 (Radziejewska et al., 2001; Radziejewska, 2002, 2014). The value for NOAA-BIE was obtained by averaging the means of the min and max values reported in Radziejewska (2014). Breakdown of the calculations used in the bar chart can also be found in the Appendix. Map based on GEBCO (General Bathymetric Chart of the Oceans) Digital Atlas published by the British Oceanographic Data Centre on behalf of IOC and IHO, 2003. s.d. = standard deviation.

Regardless, similar to the macrofauna (Veillette et al., 2007b; Wilson, 2017; Chuar et al., 2020), a trend of decreasing meiofaunal abundance from east to west across the CCFZ can be observed (Fig. 6 and Table 6). The upwelling of nutrient rich waters along the equator, as well as the presence of eddies and easterly trade winds contribute to more intense sea surface productivity in the eastern end of the CCFZ, which gradually decreases westwards (Smith & Demopoulous, 2003; Hannides & Smith, 2003). Faunal abundance and diversity could be influenced by this westward reduction of sea surface productivity and therefore a decrease of particulate organic carbon (POC) flux across the CCFZ (Smith & Demopoulous, 2003; Hannides & Smith, 2003; De Smet et al., 2017; Christodoulou et al., 2020; Laroche et al., 2020; Nomaki et al., 2021; Washburn et al., 2021). As deep-sea environments are usually food limited, POC flux, on a regional scale, plays a significant role in determining biological community structure on the sea floor (Smith et al., 1997, 2008; Bonifácio et al., 2020).

Similar to other studies in the CCFZ (Wilson & Hessler, 1987; Kaneko et al., 1997; Radziejewska & Modlitba, 1999; Kim et al., 2000; Gao et al., 2002; Min et al., 2004; Kim et al., 2004; Wang et al., 2013; Min et al., 2018), elsewhere in the Pacific Ocean (e.g., Snider et al., 1984; Shirayama, 1984) and other oceans worldwide (e.g., Ansari & Parulekar, 1981; Woods & Tietjen, 1985; Shirayama & Kojima, 1994; Zeng et al., 2018), the majority of meiobenthos are concentrated in the top sediment layers. Meiofaunal higher taxon composition (including “Nauplii”) was also similar, in that the Nematoda was the most prevalent, or Foraminifera if the study included the protozoans, followed by the Nauplii and Copepoda (Wilson & Hessler, 1987; Kaneko et al., 1997; Radziejewska et al., 2001; Kim et al., 2000; Gao et al., 2002; Kim et al., 2004; Min et al., 2004; Wang et al., 2013; Pape et al., 2017; Min et al., 2018; Hauquier et al., 2019).

4.2 Sediment shear strength contributed to differences in meiofaunal communities and is negatively and significantly correlated to meiofaunal abundance

A significant negative correlation was apparent between sediment shear strength and meiofaunal abundance (i.e., meiofaunal abundance increase with decreasing shear strength), similar to the findings by Radziejewska & Modlitba (1999). Sediment shear strength was also the only significant factor out of the three environmental parameters in this study that contributed to the difference in meiofaunal community structure. The sediment shear strength may be influenced by the size and gradation of individual particles (Langfelder & Nivargikar, 1967). It is commonly known that coarser sediment and a larger grain size will result in an overall looser and less compact sediment (i.e., lower shear strength value) (Trask & Rolston, 1950). Such conditions might provide habitat heterogeneity by increasing the number of available microhabitats, which in turn result in higher diversity and abundance. Some studies did not find any significant relationships between the meiofaunal community and granulometry (Hauquier et al., 2019; Pape et al., 2021). Besides the intrinsic nature of the sediment, movements that occur naturally (e.g., by organisms, currents) could affect shear strength as well (Richards & Parks, 1976). In a stable environment like the deep sea floor, bioturbation caused by the movement of benthic animals could be one such biological process (Richards & Parks, 1976). The differences in shear strength have previously been attributed to bioturbation because burrowing activities loosen sediment and create chambers in the sediment, resulting in a lower shear strength value (Meadows et al., 1994; Richardson et al., 1985). At the same time, more oxygen is made available to deeper layers, which could influence benthic community structure (Aller & Aller, 1992; Löhr & Kennedy, 2015; Schratzberger & Ingels, 2018). These factors might contribute to the differences in the meiofaunal abundance and community structure across the 12 stations.

4.3 Nodule parameters did not affect meiofaunal community structure at the major taxon level

Based on the meiofaunal community at the major taxon level, there appeared to be no significant relationship with nodules, suggesting that the meiofaunal community is not structured by these hard substratum habitats. Although the crevices of the nodules can serve as microhabitats for the smaller metazoans (Thiel et al., 1993; Veillette et al., 2007b; Pape et al., 2021), their abundances were much lower when compared to those found in the surrounding sediment (Thiel et al., 1993). Some nematode genera or species were more abundant inside the nodules, indicating that metazoan crevice fauna might be distinct from the adjacent sediment fauna (Thiel et al., 1993; Pape et al., 2021). However, while Vanreusel et al. (2010) found that dominant Nematoda groups differed between areas with and without nodules in terms of their locomotory behaviour, Pape et al. (2021) found that at least at the genus-level, no genera were endemic to the nodule crevices.

Even so, we cannot discount the importance of these nodules for deep-sea fauna. In the CCFZ, 51% of all fauna are facultatively or obligatorily associated with the nodules (Stratmann et al., 2021). A variety of organisms live on the surface of the nodules, most of which are sessile taxa such as the Porifera, xenophyophores and other Foraminifera (Dugolinsky et al., 1977; Veillette et al., 2007a, b; Vanreusel et al., 2016; Gooday et al., 2015, 2017a, b, 2018a, b; Lim et al., 2017). These hard-substrate taxa would likely be distinct in their abundance and diversity from the sediment-dwelling taxa (Dugolinsky et al., 1977; Mullineaux, 1987; Veillette et al., 2007a, b). Furthermore, these polymetallic nodules are essential to maintain trophic and non-trophic interactions in the abyssal food-web and their removal will result in knock-down effects on food-web integrity (Stratmann et al., 2021). Naturally, it is expected that the presence or absence, and quantity of nodules will change the overall species composition of the benthic fauna. We also emphasize here that our findings do not suggest that nodule removal during mining is not harmful towards the meiofauna. Removal of surface sediment associated with the mining process directly kills the sediment fauna, and the release of sediment and their redeposition will likely smother the seafloor community (Thiel et al., 2001).

5. CONCLUSIONS

Quantitative baseline data on the meiofaunal abundance and composition of the OMS contract area in the eastern region of the CCFZ are provided for the first time. The CCFZ deep sea floor is very diverse, and community structure was different between the stations, driven by the less abundant animal groups and sediment shear strength. Nodule surface cover and nodule volume have no clear relationship with the meiofaunal community structure. The results of this study also confirmed the westward decrease in meiofaunal abundance across the CCFZ. Although this current study focused more on the sediment shear strength and the amount of nodules, additional environmental data (e.g., organic content, bioturbation tests, sediment granulometry) could provide further insights in explaining differences in community structure.

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DECLARATION OF COMPETING INTERESTS

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

SUBMISSION DECLARATION

This article has not been published previously and is not currently under consideration for publication elsewhere.

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Appendix: Supplementary data

Table S1.
Spearman rank correlations and corresponding p-values between environmental variables.

	Nodule cover		Nodule weight		Nodule volume	
	rho	p-value	rho	p-value	rho	p-value
Shear strength	0.29	0.35	0.04	0.90	0.07	0.83
Nodule cover	-	-	0.36	0.25	0.40	0.20
Nodule weight	-	-	-	-	0.99	< 0.01

Table S2.
Raw data.

Station	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3
Sample	C03-SGN051-B	C03-SGN051-C	C05-SGN052-B	C05-SGN052-C	C07-SGN053-B	C07-SGN053-C	C12-SGN054-B	C12-SGN054-C	C02-SGN077-B	C02-SGN077-C	C07-SGN078-B	C07-SGN078-C	C11-SGN079-B	C11-SGN079-C	C12-SGN080-B	C12-SGN080-C	C01-SGN058-A	C01-SGN058-B	C03-SGN059-A	C03-SGN059-B	C06-SGN060-B	C06-SGN060-C	C07-SGN061-B	C07-SGN061-C
Fraction	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-7cm	0-2cm	2-5cm
Nematoda	1663	152	1149	154	1071	268	1668	387	1369	543	843	280	763	463	831	561	1102	774	1031	446	1059	812	1541	386
Nauplii	88	6	108	2	102	10	121	17	164	8	71	7	86	22	59	18	28	6	23	14	96	49	88	10
Unknown	3	1	9	3	26		72				4	4	1	13	3	2					2		2	3
Copepoda	119	3	70	6	60	15	84	13	108	12	77	4	75	18	54	13	40	23	26	9	60	25	83	7
Gastrotricha			1	1	4		2	1	1		2		2	1	2		2				1		2	
Loricifera	1		2						2			4		19	2	10			1	2		11	3	1
Rotifera								1				1												
Tantulocarida	5		4	1			1	1	4		1		3	1	1						2	1	1	
Tardigrada	3		1					1	6		6		1		3	6					1	5	3	
Acari	2				1	1	1	1			1	2	7		1	1	1		5		2		4	
Amphipoda																								
Annelida	30	1	12	3	18	2	16	0	10	2	17	0	9	3	12	4	1	5	6		12	5	8	1
Bivalvia	1		1							1					2				1					
Cumacea																								
Isopoda										1	1	1	1		1	2			1		1	1	1	
Kinorhyncha	3		4				1				2				2		2	1	2	1	3		3	
Ostracoda	7		3	1	5	2	16		6		5		4		2	1	7	3	1		4	3	7	
Tanaidacea	1		3				3		2	1	1				1		1				2		3	1
Platyhelminthes																								
Asteroidea																								
Nemertea															11						1		2	
Gastropoda																								
Sipuncula																								

Table S2. (continued)
Raw data.

Station	**4**	**4**	**4**	**4**	**4**	**4**	**4**	**4**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**
Sample	C01-SGN071-B	C01-SGN071-C	C03-SGN072-B	C03-SGN072-C	C07-SGN073-B	C07-SGN073-C	C12-SGN074-B	C12-SGN074-C	C04-SGN086-B	C04-SGN086-C	C05-SGN087-B	C05-SGN087-C	C06-SGN088-B	C06-SGN088-C	C12-SGN089-B	C12-SGN089-C	C04-SGN093-B	C04-SGN093-C	C08-SGN094-B	C08-SGN094-C	C09-SGN095-B	C09-SGN095-C	C12-SGN096-B	C12-SGN096-C
Fraction	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm
Nematoda	1177	464	1506	320	1319	168	968	345	1393	445	1449	241	1236	295	1062	129	1084	431	1459	361	1158	289	1051	555
Nauplii	43	6	88	11	94	8	97	7	73	7	126	10	61	3	76	1	53	7	49	8	20	3	32	11
Unknown			7	1	23		4	1			2	1		1	2		7		4		2		1	1
Copepoda	37	11	71	14	46	5	47	10	51	14	68	17	75	4	86	5	37	13	45	10	50	7	46	18
Gastrotricha	1				1		1				3		2		1									
Loricifera	2		2	1	5		4		2		4	1								2	1		1	
Rotifera																								
Tantulocarida		1	2		2		3		2		2		1		2		3		3					
Tardigrada	5					1	2		8		10		4		14	1			3					
Acari		1			5		2						2						1	1	1			
Amphipoda																								
Annelida	9	2	19		14	0	15	3	13	0	38	3	15	1	28		8	1	11	1	6	0	12	3
Bivalvia			1								1								1					
Cumacea															1									
Isopoda	2		1		1			1					2		2									
Kinorhyncha			2		2			1	1		3		2		3				1					
Ostracoda	1		6	2	3		3		7		4		1		2		5		3		2		1	
Tanaidacea			3	1	1	1	1										1		1		1		1	
Platyhelminthes																								
Asteroidea																								
Nemertea					4																			
Gastropoda	1		2																					
Sipuncula													2											

Table S2. (continued)
Raw data.

Station Sample Fraction	**7** C02-SGN153-B 0-2cm	**7** C02-SGN153-C 2-5cm	**7** C05-SGN154-B 0-2cm	**7** C05-SGN154-C 2-5cm	**7** C09-SGN155-B 0-2cm	**7** C09-SGN155-C 2-5cm	**7** C11-SGN156-B 0-2cm	**7** C11-SGN156-C 2-5cm	**8** C01-SGN169-A 0-2cm	**8** C01-SGN169-B 2-5cm	**8** C02-SGN170-A 0-2cm	**8** C02-SGN170-B 2-5cm	**8** C04-SGN171-A 0-2cm	**8** C04-SGN171-B 2-5cm	**8** C05-SGN172-A 0-2cm	**8** C05-SGN172-B 2-5cm	**9** C03-SGN143-B 0-2cm	**9** C03-SGN143-C 2-5cm	**9** C04-SGN144-B 0-2cm	**9** C04-SGN144-C 2-5cm	**9** C08-SGN145-B 0-2cm	**9** C08-SGN145-C 2-5cm	**9** C09-SGN146-B 0-2cm	**9** C09-SGN146-C 2-5cm
Nematoda	1545	809	682	241	1862	196	914	305	1316	857	1193	734	761	779	1764	844	1397	666	1341	184	1412	272	1274	176
Nauplii	48	21	77	17	175	14	98	4	62	13	111	14	70	15	135	21	53	8	130	15	97	8	111	9
Unknown	1		6	6	5	1	10				1	2	5	4	2				16	3	18	1	9	5
Copepoda	62	14	73	23	135	20	109	12	135	17	102	24	80	22	117	16	85	17	80	15	66	10	93	7
Gastrotricha	2				2		4				1		4	2	2		1	1	1		3		2	
Loricifera			3	1	3		1	2		1		9	1	2	4	2	1		32	15	13	17	18	7
Rotifera																								
Tantulocarida	2	1	1		1	1					3				4		1		3		4	1	4	
Tardigrada					1		1	1	3		2		7	1	9	14	2		5		1		1	
Acari							1	1			3		1											
Amphipoda																								
Annelida	7	2	7	2	33	0	38	3	20	4	12	2	10	6	19	5	22	5	25	0	20		27	3
Bivalvia							1				1		3		2			1					1	
Cumacea																								
Isopoda		1	1	1	4		1				1				1	1			1	1			3	
Kinorhyncha	2		3		1				2	1	2	1	2		4									
Ostracoda	3		5	2	8	1	14		4	3	5	1	3	1	10		3	2	2	11	4		4	
Tanaidacea		1					5		1		1		1	1	1		1		5		2		1	
Platyhelminthes											1													
Asteroidea																								
Nemertea																					3			
Gastropoda					2																			
Sipuncula					1																			

Table S2. (continued)
Raw data.

Station	**10**	**10**	**10**	**10**	**10**	**10**	**10**	**10**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**11**	**12**	**12**	**12**	**12**	**12**	**12**	**12**	**12**
Sample	C03-SGN159-B	C03-SGN159-C	C10-SGN160-B	C10-SGN160-C	C11-SGN161-B	C11-SGN161-C	C12-SGN162-B	C12-SGN162-C	C01-SGN178-B	C01-SGN178-C	C02-SGN179-B	C02-SGN179-C	C06-SGN180-B	C06-SGN180-C	C07-SGN181-B	C07-SGN181-C	C05-SGN184-B	C05-SGN184-C	C07-SGN185-B	C07-SGN185-C	C10-SGN186-B	C10-SGN186-C	C11-SGN187-B	C11-SGN187-C
Fraction	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm	0-2cm	2-5cm
Nematoda	1603	287	1639	200	1145	333	1157	319	1532	85	1028	248	975	539	1320	124	736	585	1124	347	1148	735	899	255
Nauplii	62	10	225	7	112	8	65	15	30	2	60	13	84	22	89	1	14	9	38	7	42	25	36	6
Unknown	1		9	4	9	5	4	3			9		1	19		3			26	6	4	1	2	
Copepoda	70	9	138	6	64	6	39	9	47	2	33	9	54	17	46	3	28	12	35	16	28	20	32	6
Gastrotricha			2		1		1						3					1	3			2		
Loricifera	1		6	1	5		10	1	3		4		8	4	11				1				1	
Rotifera			1																					
Tantulocarida	3		8	1	6		3				1	1	6		3	1						1	1	
Tardigrada	3		2		4		15		2				2		4		3	1	9		2	3	1	
Acari					1										5		1					1		
Amphipoda	1																							
Annelida	18	1	47	2	6		8	2	41	0	11	5	28	11	11		8	2	26	5	11	7	9	1
Bivalvia			2		3			1							2		1							
Cumacea																								
Isopoda							1							1			1					1		
Kinorhyncha			3										1		1				3					
Ostracoda	4		8		4		6		4		3	1	6		7				1	1		1	2	
Tanaidacea	4		3		3		2		1		1				1			1	1	3	1		2	1
Platyhelminthes																								
Asteroidea			1																					
Nemertea																								
Gastropoda									1				1											
Sipuncula																								

Table S3.
Mean percentage of meiobenthos across the 12 stations from the 0–5 cm sediment layer.

	Station													
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**mean**	**s.d.**
Nematoda	85.36	84.61	91.01	88.93	87.56	92.78	84.24	87.43	85.21	86.37	88.81	91.96	87.86	2.90
Nauplii	6.11	6.39	3.83	5.11	5.00	2.63	6.31	4.68	5.65	6.33	4.60	2.75	4.95	1.33
Unknown	1.40	0.46	0.08	0.52	0.09	0.22	0.50	0.18	0.69	0.46	0.48	0.59	0.47	0.35
Copepoda	4.89	5.46	3.37	3.40	4.64	3.31	6.39	5.52	4.78	4.25	3.18	2.83	4.34	1.13
Gastrotricha	0.13	0.13	0.06	0.05	0.08	0.00	0.11	0.11	0.10	0.05	0.04	0.09	0.08	0.04
Loricifera	0.04	0.60	0.22	0.20	0.09	0.06	0.17	0.20	1.37	0.33	0.45	0.04	0.31	0.38
Rotifera	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01
Tantulocarida	0.16	0.15	0.05	0.12	0.10	0.08	0.07	0.07	0.17	0.27	0.18	0.03	0.12	0.07
Tardigrada	0.06	0.34	0.10	0.12	0.55	0.04	0.04	0.36	0.12	0.34	0.12	0.29	0.21	0.16
Acari	0.08	0.20	0.16	0.12	0.03	0.04	0.03	0.05	0.00	0.01	0.08	0.03	0.07	0.06
Amphipoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Annelida	1.10	0.90	0.47	0.89	1.41	0.60	1.29	0.83	1.31	1.00	1.58	1.07	1.04	0.33
Bivalvia	0.03	0.04	0.02	0.01	0.01	0.01	0.02	0.07	0.03	0.08	0.03	0.02	0.03	0.02
Cumacea	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Isopoda	0.00	0.11	0.05	0.07	0.06	0.00	0.11	0.03	0.07	0.02	0.01	0.03	0.05	0.04
Kinorhyncha	0.11	0.07	0.15	0.07	0.13	0.01	0.10	0.13	0.00	0.03	0.03	0.05	0.07	0.05
Ostracoda	0.43	0.27	0.30	0.20	0.19	0.16	0.50	0.28	0.34	0.28	0.32	0.08	0.28	0.11
Tanaidacea	0.09	0.07	0.08	0.09	0.00	0.06	0.09	0.06	0.12	0.15	0.05	0.15	0.08	0.04
Platyhelminthes	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Asteroidea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Nemertea	0.00	0.17	0.03	0.06	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.03	0.05
Gastropoda	0.00	0.00	0.00	0.04	0.00	0.00	0.02	0.00	0.00	0.00	0.03	0.00	0.01	0.01
Sipuncula	0.00	0.00	0.00	0.00	0.03	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01

Table S4.
Average within-group similarity based on relative abundances (4^{th}-root transformed) and absolute abundances (log x+1 transformed).

	Relative abundance	Absolute abundance
S01	83.46	84.70
S02	84.81	83.23
S03	81.02	80.75
S04	83.94	83.10
S05	84.54	85.15
S06	87.01	87.54
S07	80.55	81.48
S08	85.23	84.52
S09	88.05	86.10
S10	84.85	84.18
S11	81.38	82.46
S12	80.69	81.97

Table S5.
Calculations for bar chart. PRZ1302, WS1303, JET, KODOS, NIXO, ECHO, BGR_RA and OMS were taken or calculated from their reference papers. The means for COMRA West, COMRA East, IFREMER, GSR (B4), GSR (B6) and BGR_PA were calculated from the means obtained from their relevant studies. The IOM-BIE value was calculated using data from Hauquier et al. (2019), Radziejewska (2014), and the means obtained from C1, C2 and C3 in (Radziejewska et al., 2001; Radziejewska, 2002, 2014). The value for NOAA-BIE was obtained by averaging the means of the min and max values reported in Radziejewska (2014). Abundance presented as the number of individuals (ind.) per 10 cm^2. s.d. = standard deviation.

	References	Data in references		Remarks	**Used in Figure 6**	
		Abundance ± s.d.	n		**Abundance ± s.d.**	**n**
PRZ1302	Zhao et al., 2020	4.97	1		4.97	1
WS1303	Zhao et al., 2020	45.3	1		45.3	1
JET1	Kaneko et al., 1997	101.0 ± 55.9	44 subcores		101.0 ± 55.9	44
KODOS	Kim et al., 2000; Kim et al., 2004; Min et al., 2004; Min et al., 2018	84.25 ± 52.72	29	modified original data to exclude the Foraminifera	84.25 ± 52.72	29
NIXO	Renaud-Mornant & Gourbault, 1990	160 ± 45.15	17	modified original data by adding subsamples A,B from the same box corer together	160 ± 45.15	17
ECHO	Wilson & Hessler, 1987	77.29 ± 55.19	7	used only the controls at 0–1 cm layer; modified original data to exclude the Foraminifera, Protozoa and Calanoida	77.29 ± 55.19	7
BGR_RA	Martínez Arbizu & Haeckel, 2015; Hauquier et al., 2019	483.84 ± 95.18	5	abundance and s.d. obtained from Hauquier et al., 2019; number of deployments obtained from Martínez Arbizu & Haeckel, 2015	483.84 ± 95.18	5
OMS	This study	235.73 ± 26.39	12		235.73 ± 26.39	12
COMRA West	Gao et al., 2002	18.05	10	used 18.05 for calculations	29.16 ± 15.7	2
	Wang et al., 2013	40.26 ± 25.84	6	used the average: 40.26		
COMRA East	Gao et al., 2002	32.47	10	used 32.47 for calculations	68.44 ± 50.86	2
	Wang et al., 2013	104.40 ± 20.48	6	used the average: 104.40		
IFREMER	Mahatma, 2009	181.66 ± 35.56	Five stations sampled, total of eight corers	outside nodule area; used the average: 181.66 for calculations	153.26 ± 49.62	3
	Mahatma, 2009	95.97 ± 23.43	Five stations sampled, total of eight corers	nodule area; used the average: 95.97 for calculations		
	Martínez Arbizu & Haeckel, 2015; Hauquier et al., 2019	182.15 ± 62.42	5 deployments	used the average: 182.15 for calculations		

		46.2–205.3	Baseline studies from five box cores, two subcores taken from each box core samples	took the average of min (46.2) and max (205.3) to get: 125.75		
NOAA-BIE	Radziejewska, 2014				95.88 ± 42.24	2
		40.74–91.28	Five control multicorer samples	took the average of min (40.74) and max (91.28) to get: 66.01		
	Pape et al., 2017	106.6 ± 29.3	3	used the average: 106.6		
	Pape et al., 2017	88.1 ± 55.0	3	used the average: 88.1		
GSR (B4)	Pape et al., 2021	126.8 ± 29.0	4	used the average: 126.8	90.78 ± 30.12	5
	Pape et al., 2021	87.0 ± 21.0	4	used the average: 87.0		
	Pape et al., 2021	45.4 ± 31.5	3	used the average: 45.4		
	Martínez Arbizu & Haeckel, 2015; Hauquier et al., 2019	211.49 ± 40.36	5 deployments	used the average: 211.49		
GSR (B6)	Pape et al., 2017	**242.3 ± 59.2**	4	used the average: 242.3	201.63 ± 46.39	3
	Pape et al., 2017	151.1 ± 54.2	3	used the average: 151.1		
	Radziejewska, 2002	100.66				
	Radziejewska, 2002	105.7				
	Radziejewska, 2002	245.14	6	averaged this (C1) to become 201.6		
	Radziejewska, 2002	86.1				
	Radziejewska, 2002	277.76				
	Radziejewska, 2002	394.24				
	Radziejewska, 2002	244.56				
IOM-BIE	Radziejewska, 2002	198.94	3	averaged this (C2) to become 198.79	236.73 ± 182.45	5
	Radziejewska, 2002	152.88				
	Radziejewska & Modlitba, 1999; Radziejewska, 2014	91.56 ± 23.31	3	nodule bearing area; abundance data taken from Radziejewska (2014). Used the average: 91.56		
	Radziejewska et al., 2001	138.97 ±3.49	3	control only (C3); used the average: 138.97		
	Martínez Arbizu & Haeckel, 2015; Hauquier et al., 2019	552.71 ± 260.32	3 stations, 3 deployments	used the average: 552.71		
	Martínez Arbizu & Haeckel, 2015; Hauquier et al., 2019	371.84 ± 33.11	5	used the average: 371.84		
BGR_PA	Uhlenkott et al., 2020	306.62 ± 98.95	106	calculated average from supplementary data in Uhlenkott et al. (2020); used the average: 306.62	339.23 ± 46.12	2

Table S6.
PERMANOVA main test results and significant pair-wise comparisons (P(MC) ≤ 0.05) among the 12 stations (0–5 cm sediment layer) in the OMS area of the CCFZ using relative abundances, when analysing the four cores taken from each deployment at each station separately.

PERMANOVA main test

Source of variation	df	SS	MS	Pseudo-*F*	*P*(perm)	perms	*P*(MC)
Station	11	3534.40	321.31	2.27	< 0.01	9863	< 0.01
Residual	36	5106.10	141.84				
Total	47	8640.60					

Pair-wise comparisons

Groups	*t*	*P*(MC)	Unique perms
1, 6	1.89	0.05	35
2, 6	2.56	0.01	35
3, 9	2.18	0.03	35
3, 10	1.85	0.04	35
4, 6	1.99	0.03	35
5, 6	2.61	0.01	35
5, 9	2.16	0.02	35
5, 10	1.85	0.04	35
6, 7	1.97	0.03	35
6, 8	2.42	0.02	35
6, 9	2.65	0.01	35
6, 10	2.10	0.03	35

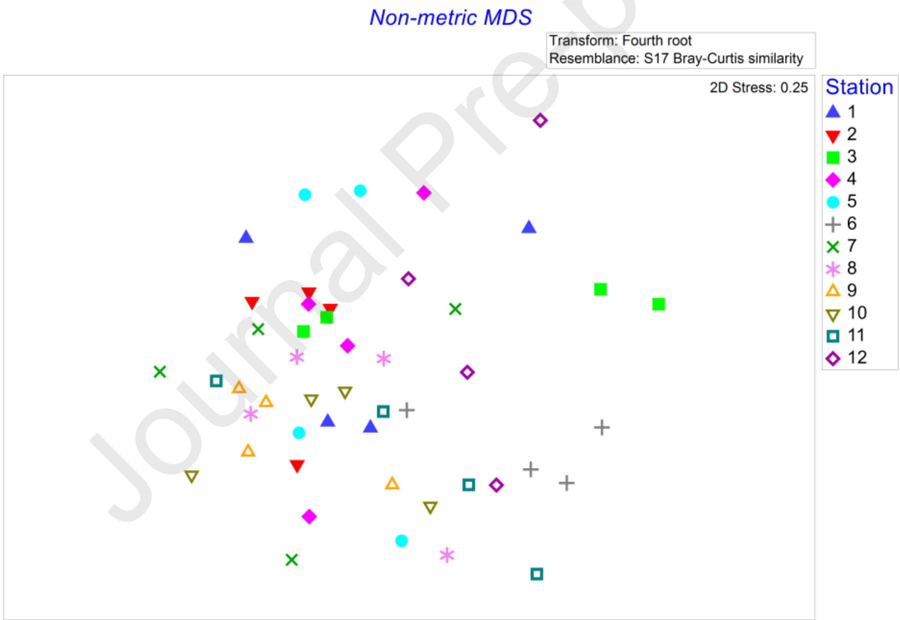

Fig. S1. Non-metrical dimensional scaling (nMDS) of 12 stations (0–5 cm sediment layer) in the OMS area of the CCFZ, including four cores taken from each deployment at each station. Symbols and numbers represent the 12 stations and replicates.

Community structure of deep-sea benthic metazoan meiofauna in the polymetallic nodule fields in the eastern Clarion-Clipperton Fracture Zone, Pacific Ocean

HIGHLIGHTS

- Provides the first quantitative description of meiofaunal composition in the OMS contract area (eastern CCFZ)
- Community structure was different at 12 randomly sampled stations within a 30 × 30 km area, confirming that the meiofauna residing in the CCFZ deep sea floor is very diverse
- Substratum shear strength was significantly associated with differences in meiofaunal abundance and community structure
- Our findings reiterate the decreasing westward trend of meiofaunal abundance in the CCFZ

Declaration of interests

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

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: