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Effects of environmental and climatic drivers on abyssal macrobenthic infaunal communities from the NE Pacific nodule province

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Abstract :

The macrofauna in soft sediments of the deep seafloor is generally diverse and represents a comparatively well-studied faunal group of deep-sea ecosystems. In the abyss of the Clarion Clipperton Fracture Zone (CCFZ) in the NE Pacific, macrofauna are major contributors to benthic biodiversity. Their distribution, composition, and diversity have been frequently investigated to assess the potential impacts of future mining activities on the resident fauna. In this study, patterns of densities and community structure of CCFZ macrobenthic infauna and their relationships with a range of environmental and climatic variables were examined, with a special focus on communities from the eastern German contract area (referred to as BGR CA). However, comparisons were also made with other contractor areas (e.g., IFREMER, IOM, GSR) and one Area of Particular Environmental Interest (APEI3). Material for this study was obtained by means of a box corer during six expeditions to the CCFZ between 2013 and 2018 resulting in 148 samples. Our study uncovered notable spatial and temporal variations in both faunal densities and community composition. While areas within the BGR CA exhibited a similar community composition, slight differences were observed between the various CAs and APEI3. Surprisingly, we found an unexpected negative correlation between food availability and both macrofaunal density and community structure that may be attributed to differences in sampling methodologies and pronounced temporal variation. Furthermore, we explored the impact of climatic fluctuations associated with the El Niño/Southern Oscillation (ENSO) on macrofaunal densities, observing an increase during warm (El Niño) events. Our findings underscore the challenges of accurately assessing spatial and temporal variations in the absence of standardised sampling protocols. Hence, we emphasize the importance of adopting standardised protocols to enhance data comparability, thereby fostering a deeper understanding of the

underlying factors influencing spatial and temporal changes in macrofauna community structure within the CCFZ.

Keywords : Polymetallic nodules, Macrofauna, Distribution, Clarion Clipperton Fracture Zone, Climate-driven changes, Productivity

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Authors' contribution

SK and PB conducted the data analysis; SK wrote the manuscript with the help of all co-authors; AW, TCK and LM helped with data generation; AV and PMA conceived and designed the research. All authors read and approved the manuscript.

Introduction

The deep sea is rich in many ways, harbouring a wide variety of species and habitats, but also, in places, large deposits of mineral resources. Intensive exploration efforts are being made to potentially extract these minerals from the seafloor, in particular polymetallic nodules (PMN), polymetallic sulphides (PMS) and cobalt-rich ferromanganese crusts (CRFC). These activities include resource assessments as well as environmental baseline studies and analyses of the probable impacts that mining activities might have on the resident deep-sea organisms. The International Seabed Authority (ISA), as an autonomous international organisation created under the UN Convention on the Law of the Sea (UNCLOS), is responsible for the management of these non-living resources in areas beyond national jurisdiction (ABNJ or "the Area"), while ensuring the protection of the marine environment there. For PMN, most of the exploration contract areas (CA) are located in the Clarion Clipperton Fracture Zone (CCFZ) in the north-eastern tropical Pacific (granted to 16 entities), whereas one area is also located in the Central Indian Ocean and one in the Western Pacific Ocean (https://www.isa.org.jm/exploration-contracts/polymetallic-nodules, accessed December 2023). In the CCFZ, a network of thirteen "Areas of Particular Environmental Interest" (APEIs) have been designated as part of the ISA's Regional Environmental Management Plan to preserve its biodiversity (Wedding et al. 2013; ISA 2021).

In deep-sea areas, where PMN are found, they lie on or within the top 10 cm of sediments. During mining operations, deep-sea mining vehicles would collect these nodules from the sediment surface and transport them through a pipeline lifting system to a support vessel (Oebius et al. 2011). After onboard crushing, dewatering and ore separation processes, large amounts of waste water as well as fine-grained sediments and solids will likely be returned to the sea (Oebius et al. 2001; Washburn et al. 2019; Christiansen et al. 2020). Numerous sources of risks associated with the collection and processing steps during mining have been identified (e.g., Gollner et al. 2017; Jones et al. 2017; Koschinsky et al. 2018; Washburn et al. 2019), with habitat removal, plume impact (from both mining operations on the seafloor and return water plume) and potentially toxic exposure to the fauna being highlighted as

particularly harmful (Washburn et al. 2019). Most of the fauna lives in the upper five cm of the sediment (Spiess et al. 1987; Smith and Demopoulos 2003) or even uses the nodules themselves as a habitat (Thiel et al. 1993; Veillette et al. 2007; Vanreusel et al. 2016; Drennan et al. 2021; Pape et al. 2021; Sanchez et al. 2022). The latter will be lost for the nodule-obligate biota following PMN extraction (Amon et al. 2016). In addition, sediment plumes of returned mining fines or collector-generated, whirled-up seafloor sediments have been modelled to travel well beyond the actual mining block (e.g. Gillard et al. 2019; Purkiani et al. 2021; Muñoz-Royo et al. 2021; Weaver et al. 2022). Recent tests of hydraulic mining equipment on the seafloor have, however, shown that the benthic plume remains very close to the seafloor in the form of a gravity current and covers distances of several kilometres only due to very fast particle aggregation and redeposition (Muñoz-Royo et al. 2022; Gazis et al. submitted). Such plumes, although much more localized than originally modelled without taking note of fluid dynamics and aggregation processes (e.g. Aleynik et al. 2017), will be detrimental to the sedentary epifauna (Amon et al. 2016; Vanreusel et al. 2016) and the thick layer of redeposition potentially harmful for the infauna.

As deep-sea mining becomes technically feasible and first collector tests have been successfully conducted (Bruyne et al. 2022), there is an urgent need to reliably assess the potential impacts on the deep-sea benthic and pelagic environment. This requires information at least on the nature, scale and strength of the expected mining disturbance, alongside key biological data on ecosystem structure and functions. Although knowledge of environmental baselines, both biotic and abiotic, is better for the CCFZ than for the other PMN regions (Amon et al. 2022), information on natural spatial and temporal variability as well as on associated environmental and ecological drivers is still rudimentary (Smith et al. 2020; Amon et al. 2022). An understanding of the latter is crucial to be able to distinguish between the effects of mining disturbances and the natural dynamics of ecological systems (Jones et al. 2020; Radziejewska et al. 2022).

The CCFZ exhibits spatially and temporally heterogeneous conditions, shaping benthic communities there. At a larger spatial scale, the region is characterised by an increasing depth gradient from east to west, opposite to the decreasing surface productivity gradients from east to west and from south to north, which have been shown to directly affect faunal abundance and diversity (e.g., Smith et al. 2008; Wilson 2017; Bonifácio et al. 2020; Washburn et al. 2021b). Atmospheric-oceanographic phenomena such as El Niño-Southern Oscillations (ENSO) and multidecadal Pacific Decadal Oscillations (PDO) have emerged as an important source of temporal variability in primary productivity in the eastern tropical Pacific, with reduced macronutrient supply during warm (El Niño) phase of the ENSO and similar conditions during the El Viejo phase of PDO (Pennington et al. 2006). Geomorphological features, including seamounts, abyssal hills, and ridges, but also valleys, troughs and channels can divert, intensify or slow down currents and thereby influence the distribution of organisms (Janssen et al. 2019; Simon-Lledo et al. 2019). Nodules are the dominant hard substrate in the abyssal plains of the CCFZ and host distinctly different communities than soft-sediment communities (sedentary vs. mobile in the sediments), in that way increasing

habitat complexity and hence diversity at the regional scale (Vanreusel et al. 2016; Yu et al. 2018).

The objective of this study was to investigate the spatial and temporal variability of soft-sediment macroinfaunal assemblages within the CCFZ and relate these to a set of available environmental factors, notably nodule densities, bottom water current velocity, food availability and water depth. The latter are considered to be key in shaping CCFZ macrobenthic communities (Wilson 2017; De Smet et al. 2017; Bonifácio et al. 2020; Pasotti et al. 2020; Washburn et al. 2021b). Benthic macrofauna, which includes metazoan taxa being retained by a 300 µm mesh (Hessler and Jumars 1974), represents an abundant and diverse group of organisms within the CCFZ (e.g., Wedding et al. 2013) and has often been used to assess the status quo and possible mining impacts (e.g., Janssen et al. 2015, 2019; De Smet et al. 2017; Gollner et al. 2017; Jones et al. 2017; Wilson 2017; Yu et al. 2018; Bonifácio et al. 2020; Chuar et al. 2020; Pasotti et al. 2020; Washburn et al. 2021b). We have analysed quantitative data deriving from box core (BC) samples to assess patterns of macrobenthic infaunal densities and community structure. Parts of our data have already been published elsewhere (Washburn et al. 2021b). Here, however, we have focused in particular on examining macrofaunal spatiotemporal patterns in the eastern German contract area (hereinafter BGR CA) using additional data from the BGR CA and how these relate to other CAs. In particular, we sought to examine: (i) how large is the spatial and temporal variability in density and community composition (at higher taxon levels) between sampling sites and areas, and (ii) what are the main environmental factors and processes that might be responsible for this variability.

Material and methods

Macrofaunal samples were collected from four CAs in the CCFZ (eastern BGR CA [Germany], IFREMER [France], GSR CA [Belgium], IOM CA [jointly Bulgaria, Cuba, Czech Republic, Poland, Russian Federation and Slovakia] and one APEI (#3; hereafter APEI3; Fig. 1) during six expeditions conducted between 2013 and 2018 (Table 1, Rühlemann et al. 2013, 2015, 2017, 2019; Kuhn 2015; Martínez and Haeckel 2015). Samples were taken by means of a box corer (BC) with a surface area of 0.25 m² at 148 stations with depths ranging from 4082 to 4963.7 m (Table S1 in the electronic supplementary material).

Within the BGR CA (Fig. 1), different working areas were designated (i.e., PA1, PA2, PA3, PRZ, WA-1, WA-2, WA-3, WA-4), allowing spatial differences within the BGR CA to be assessed. Furthermore, two of these areas (PA1, PRZ) were revisited between 2013 and 2016, allowing a comparison between years (PRZ: 2013, 2015; PA1: 2013–2016). The PRZ was defined as a potential Preservation Reference Zone within the BGR CA, i.e., a control site, where no mining or mining effects should occur (ISA 2011).

Sample processing protocols differed slightly between expeditions, but unless otherwise noted, sample processing was performed as follows: once the BC was back on board, surface water (SW) above the sediment was removed with a hose and sieved through a 300 µm sieve. Thereafter, a photograph was taken of the BC surface. Individual biota visible to the eye on the surface (either attached to the nodules or lying on top of the sediment) were removed and fixed separately (in DESS [Yoder et al. 2006] or 96% ethanol). Nodules were removed and washed thoroughly to remove surface sediment, then measured and weighed. One sub-core with a surface area of 0.01 m² was taken from each BC for sedimentological analysis (e.g., Rühlemann et al. [2010], not analysed in the present study). The sediment in the BC was cut into three layers: 0–3 cm, 3–5 cm and 5–10 cm. Each layer was transferred to cold, filtered seawater (2–4°C), carefully elutriated, sieved (through a 300 µm sieve) and fixed. During MANGAN 2013 and MANGAN 2014, samples were only divided into two fractions: surface water and 0–10 cm. During SO239, no subsamples were obtained prior to slicing; the surface water was added to the 0–3 cm layer and not separately fixed; the 0–3 cm layer was immediately sorted, and specimens separately fixed (96% undenaturated ethanol). The remaining layers were fixed in 4% formalin and later transferred to 80% denaturated ethanol (Martínez and Haeckel 2015). Sorting of the BC material was partly conducted on board, but mainly back in the home laboratories (IFREMER in Plouzané [France], and Senckenberg am Meer - DZMB in Wilhelmshaven [Germany]) using stereomicroscopes. The systematic classification followed the World Register of Marine Species (WoRMS; Horton et al. 2023) with higher taxonomic levels retained in order to preserve the comparison among different cruises datasets. Arthropods and annelids were only counted if the head was present; echinoderms only if the oral disc was present. For colonial organisms, specifically Porifera and Bryozoa, individual counting was not conducted as fragmentation hindered accurate enumeration of separate individuals. Instead, their occurrence was recorded in the dataset simply as presence (noted as 1 individual) or absence (see also Wilson 2017).

All taxa retained on a 300 µm mesh and thus classified as macrofauna were analysed (i.e., macrofauna *sensu lato*). These also include taxa typically defined as belonging to the meiofauna, i.e., Acari, Copepoda, Kinorhyncha, Nematoda and Ostracoda. For comparability with other studies (e.g., Yu et al. 2018), an additional dataset was created that excludes these meiofaunal taxa (macrofauna *sensu stricto*). Sample processing of BC samples with respect to slicing varies widely between published studies (e.g., Yu et al. 2018; Chuar et al. 2020; Washburn et al. 2021b). Therefore, the top 10 cm, including surface water, have been summarised together for the analyses of densities and community composition in this study. The analysis of the encrusting nodule fauna (individually picked from the nodules) is part of another analysis and is not included here. In addition, the vertical distribution of macrofauna in the bottom sediment was analysed in the sediment layers (SW & 0–3 cm merged, 3–5 cm, 5–10 cm), where these data were available (SO239, SO240, KM16, KM18). The data can be accessed via Pangaea (https://doi.pangaea.de/10.1594/PANGAEA.887207?format=html#lcol16_ds13380747) and the ISA Deep Seabed and Ocean Database (DeepData; http://data.isa.org.jm).

Environmental data

The nodules from each BC sample were weighed on board to calculate nodule density in kg per square meter ($kg.m^{-2}$). Seafloor depth was acquired from shipboard multibeam data. Furthermore, a set of oceanographic variables that were expected to be important for the structuring of CCFZ macrofaunal communities were extracted from the Bio-Oracle 2.1 database (Tyberghein et al. 2012; Assis et al. 2018) using the R-packages 'sdmpredictors' (Bosch 2020) and 'raster' (Hijmans 2016) in R Studio (R Core Team 2023) (Table 2, Table S2 in the electronic supplementary). These variables encompassed nitrate concentration, phosphate concentration, iron concentration, dissolved oxygen levels, seabed temperature, current velocity, and primary productivity (summarized in Table 2). Nitrate, phosphate and iron are considered limiting nutrients that control primary productivity in surface waters of the oceans (Arrigo 2005; Ellwood et al. 2018) and thus are considered here as proxies for food availability. The environmental layers have a spatial resolution of 5 arc minutes (~ 9 × 9 km) and describe monthly mean values for the period 2000-2014 (Assis et al. 2018)

Statistical analyses

Faunal densities were calculated as the number of individuals per square meter of seafloor based on the size of the BC of 0.25 m² (SO239) or 0.24 m² (remaining expeditions). In our study, we encountered a disparity in spatial resolution between the environmental data obtained from BioOracle and the data collected at the BC stations. Specifically, BioOracle provided data at a coarser spatial resolution of 5 arc minutes or ca. 9 km, whereas the BC samples yielded much finer-scale information at 0.25 m² per sample. To investigate the potential influence of environmental variables on faunal density and community composition, we recognized the need to address this spatial resolution discrepancy and circumvent potential issues related to pseudo-replication. At the same time, we aimed to maintain the integrity of our analysis by ensuring valid associations between the response variables (faunal density and community composition) and the explanatory variables (environmental factors). To achieve this, we adopted a clustering approach, where we grouped the BC stations that fell within the same environmental "grid" provided by BioOracle into station clusters. In other words, if multiple BC stations were overlaid by the same environmental layers as provided by BioOracle, we considered them as a single environmental cluster (see Tables S1, S2 in the electronic supplement). For this approach, response variables were averaged where necessary to adjust to the scale of the explanatory variables. That is, values for nodule densities and depth were also averaged, even though *in-situ* data were available, in order to maintain consistency and prevent any biases that could arise from using different data sources for different variables. Yet in addition, we conducted separate analyses for each station to examine the impact of nodule densities and depth on densities and community composition. This approach ensures that we do not overlook any crucial information due to the considerable spatial differences in nodule densities even at small spatial scales (Table S1 in the electronic supplement).

To examine differences in densities between (i) environmental clusters (ii) BGR areas (PA1, PA2, PRZ, WA1-3), (iii) as well as between years within the BGR CA (for PA1 and PRZ) a

non-parametric Kruskal-Wallis rank sum test (Hollander and Wolfe 1973) was employed. In cases where significant differences were found, post-hoc Conover multiple pairs rank comparisons (adjusted p value by Holm) were utilized to identify the specific pairs displaying such differences (Conover and Iman 1979; Holm, 1979). Spearman-rank correlations were calculated to assess the relationships between univariate biotic and abiotic variables. Possible intercorrelations between the individual parameters were first analysed and those with strong (Spearman's rho > 0.9) significant correlations were excluded in order to avoid collinearity.

To test for differences in community composition and their relationships with densities and community structure, Bray-Curtis similarity analyses were computed based on (1) square root-transformed faunal densities (ind.m^{-2}) and (2) (Hellinger transformed) relative abundances (%) (Legendre and Gallagher 2001). Specifically, we were interested in investigating spatial differences between CAs (BGR, IOM, GSR, IFREMER) and APEI3, different working areas within the BGR CA, as well as temporal variation between different years in the areas PA1 (2013–2016) and PRZ (2013, 2015) within the BGR CA. Therefore, the following matrices were produced: 1) a taxa-by-station matrix based on densities and relative abundance including stations from all CAs; 2) a taxa-by-station matrix based on densities and relative abundance including stations from the BGR CA, separated by working area; 3) a taxa-by-station matrix based on densities and relative abundance including stations from PA1 and the PRZ within the BGR CA separated by year. Non-metric multi-dimensional scaling (nMDS) was used to visualise differences between stations and areas. A one-way ANOSIM was employed to test for differences in community composition between different areas, working areas and years. In case of significant ANOSIM results, similarity percentages (SIMPER) analyses were computed to identify those taxa that were most responsible for differences in community structures.

In order to understand the connections between macrofauna and environmental factors and identify the key variables that influenced the distribution patterns of different macrofaunal taxa, Canonical Correspondence Analysis (CCA) was utilized. The statistical significance of the findings was evaluated by employing permutation (999). The *ordisted* function was employed to identify the most suitable set of environmental variables from the options provided in Table S2. To ensure the highest R2adj value with lower value of *vif* (<10), any remaining correlated variables were subsequently eliminated in a sequential manner.

The relationship between the Southern Oscillation (SO, also called ENSO – El Niño/Southern Oscillation) and benthic communities in the studied area was explored by conducting a meta-analysis. Temporal trends in macrofaunal densities (*sensu lato* and *sensu stricto*) from the PA and PRZ areas in the BGR CA were compared with the multivariate ENSO Index (MEI) Version 2 developed by Kobayashi et al. (2015) that is available at https://psl.noaa.gov/enso/mei/. The Southern Oscillation index measures the sea-level pressure difference between the cities of Darwin (Australia) and Tahiti, whereas the multivariate ENSO index version 2 includes more relevant atmospheric and oceanic conditions (i.e., sea level pressure, sea surface temperature, surface zonal winds, surface meridional winds, and Outgoing Longwave Radiation; Kobayashi et al. 2015).

All analyses were performed using the R language (R Core Team, 2023) with RStudio (Posit team, 2023), and the following specific packages were utilized: dplyr (Wickham et al. 2023), ggplot2 (Wickham 2016), vegan (Oksanen et al., 2015), PMCMRplus (Pohlert 2022), and psych (Revelle 2023).

3. Results

Environmental settings

Spearman's rank correlation analysis revealed that some environmental variables are strongly intercorrelated, notably nitrate, phosphate, and temperature as well as primary productivity and dissolved oxygen (Fig. 2). Excluding those with rho > 0.9 or < -0.9 from the analysis resulted in the following reduced set of six environmental variables: nodule density, current velocity, water depth, as well as sea-surface primary productivity, bottom temperature, and iron.

Macrofaunal densities

In total, 22,222 macrofaunal specimens were retrieved from the 148 BC samples, which could be assigned to nine phyla, 16 classes and at least 11 orders. Considering macrofauna *sensu lato*, copepods were most dominant comprising 26.3% of all specimens, followed by nematodes (23.1%) and polychaetes (21.2%) (Fig. 3). Some taxa occurred frequently, but at low abundances in the samples (e.g., Trombidiformes [marine mites], cumaceans and pycnogonids), while other appeared only with few individuals at few sites (e.g., Priapulida, Plathelminthes and Tunicata). When typical meiofaunal taxa were excluded, polychaetes were the most dominant group at most stations (comprising between 11.1–78.2%), followed by tanaidaceans (0–55.8%), isopods (0–42.1%) and bivalves (0–16.7%).

Macrofaunal densities *sensu lato* (incl. meiofaunal taxa) ranged between 60 and 1948 ind.m^{-2} exhibiting a slight decrease from the eastern stations (BGR) to the western stations (IFREMER), albeit with considerable variation across this longitudinal range (Fig. S1 in the electronic supplementary). Among the environmental clusters, cluster 2 (APEI3) displayed the lowest faunal density (mean±SD 123.2±56.9 ind.m^{-2}). In contrast, cluster 8 (GSR CA) showed the highest faunal density (1292±495.1 ind.m^{-2}) (Fig. 4, Table S2 in the electronic supplementary). When considering contractor areas (CAs), also highest densities were observed in the GSR CA (1168±412.5 ind.m^{-2}) and lowest in APEI3 (123.2±56.9 ind.m^{-2}) (Table S1 in the electronic supplementary).

Significant differences could be identified between clusters (Kruskal-Wallis test; chi-squared = 67.265, df = 41, p-value = 0.006). As revealed by post-hoc Conover's All-Pairs Rank Comparison Test, these significant differences were mainly caused by particularly low densities in APEI3 (cluster 2) showing significant differences ($p<0.05$) when compared to clusters cluster 8 (GSR) and 9 (BGR-PA2) (cf. Table S1 in the electronic supplementary). For

macrofaunal densities *sensu stricto*, the same result was obtained: that is, significant differences in densities between clusters (Kruskal-Wallis test; chi-squared = 63.883, df = 41, p = 0.01258), largely driven by low densities in APEI3 (Cluster 2), being significantly different (post-hoc Conover's, $p<0.05$) to cluster 8 (GSR) and 35 (BGR-WA2) (Fig. 5; for cluster assignment see Fig. 4 or Table S1 in the electronic supplementary).

Within the BGR area, densities of the macrofauna *sensu lato* varied by an order of magnitude between stations (120.8 to 1760.0 ind.m^{-2}), whilst for macrofauna *sensu stricto* densities ranged between 37.5 and 676.0 ind.m^{-2}. Considering only PA1 and PRZ within the BGR CA, we found significant differences between years in both macrofauna *sensu lato* (Kruskal-Wallis test; chi-squared = 35.397, df = 3, $p< 0.001$) and macrofauna *sensu stricto* (Kruskal-Wallis test; chi-squared = 25.413, df = 3, $p <0.001$). The latter was mainly due to much lower densities in 2013 than 2015 and 2016 as revealed by post-hoc Conover's test ($p<0.05$).
In addition, we found significant differences between years in both macrofauna *sensu lato* (Kruskal-Wallis test; chi-squared = 35.397, df = 3, $p < 0.001$) and macrofauna *sensu stricto* (Kruskal-Wallis test; chi-squared = 25.413, df = 3, $p = <0.001$). The latter was mainly due to much lower densities in 2013 than 2015 and 2016 as revealed by post-hoc Conover's test ($p<0.05$).

Considering the entire dataset, macrofaunal densities (*sensu lato*) showed a significant positive correlation with water depth (Spearman's rank correlation, rho=0.44; $p<0.05$), whereas they were negatively correlated with iron concentration as a proxy for food availability (Spearman's rank correlation, rho=-0.40, $p<0.05$; Fig. 2b). Macrofaunal densities (*sensu stricto*) showed comparable patterns with respect to iron and depth (Fig. 2). Additionally, there was a positive correlation with current velocity (Spearman's rank correlation, rho=0.31, $p<0.1$) and oxygen concentration (Spearman's rank correlation, rho=0.48; $p<0.05$), and a negative correlation with surface productivity (Spearman's rank correlation, rho=-0.57, $p<0.001$; Fig. 2b).

We explored the relationship between macrofaunal densities and MEI based on our sampling in the PA1 and PRZ regions of the BGR CA from 2013 to 2016. The low sample size precluded a statistical demonstration of this relationship. Nevertheless, our observations indicated that macrofaunal densities (*sensu lato*) were notably higher during the positive phase in comparison to the preceding negative phase (Fig. 6). Conversely, for macrofauna *sensu stricto* no discernible differences were apparent.

Community structure and composition

Non-metric multidimensional scaling (nMDS) of faunal densities led to a wide spacing of stations in the BGR CA and APEI3, whereas the stations of the other areas (IOM, GSR, IFREMER) clustered more closely Fig. 7). Using ANOSIM we could identify significant differences between contractor areas (BGR, IOM; GSR, IFREMER) and APEI3 (One-way ANOSIM, 9999 permutations, R=0.2714, p=0.0004). Multivariate analysis considering square root transformed abundances yielded similar results (Fig. S2-S4 in the electronic

supplementary). No significant differences were also observed between environmental clusters (cf. Table S2 in the electronic supplementary) (One-way ANOSIM, 9999 permutations, R=0.1118, p=0.051, but with strong overlap between stations as indicated by the low Global R. Overall, SIMPER analyses identified taxa that contributed most to observed dissimilarities between contractor areas and APEI3 (Table S3 in the electronic supplementary). These differences were largely due to differential numbers of nematodes and polychaetes, with densities being particularly low in APEI3 (Fig. 3).

Considering working areas within the BGR CA only, nMDS revealed WA-1, WA-2 and WA-3 (all located in the north of the BGR CA) to be more distinct, whereas stations of the remaining areas, all in the east of the BGR CA, were widely dispersed and showed large overlap. This was also supported by ANOSIM revealing no overall significant differences between areas (One-way ANOSIM, p=0.1121; Fig. 8). In contrast, significant temporal differences in community composition became evident, as revealed by ANOSIM (one-way ANOSIM, 9999 permutations, R= 0.5562; p=0.0001; Fig. 9).

In the CCA analysis, depth and temperature turned out as key determinants in the distribution of macrofauna across the CAs (BGR, IOM, IFREMER; GSR) and APEI3, with distinct geographic clusters emerging indicative of varied environmental conditions (Fig. 10a). Taxon-level analysis showcased diverse relationships among macrofaunal taxa: certain taxa (Holothuroidea, Platyhelminthes, Fig. 10b) exhibited a strong alignment with increasing depth, while others showed a pronounced response to temperature fluctuations. These patterns emphasize the critical role of depth and temperature in defining both the broader macrofaunal community structure in specific CAs and the nuanced distribution patterns of individual taxa. The axis-specific permutation tests indicate that both CCA1 and CCA2 contribute significantly to the relationship. The adjusted R-squared value indicates that the environmental variables explain 12% of the variation in taxon abundance.

Discussion

Macrofaunal densities in relation to environmental gradients

The CCFZ's abyssal seafloor is characterised by heterogeneous environmental conditions across a multitude of spatial and temporal scales (e.g., Washburn et al. 2021a). We therefore expected this to be reflected in macrofaunal community patterns. In particular, we anticipated a decrease in macrofaunal densities along with the longitudinal surface productivity gradient from the more eastern CAs (BGR, IOM) towards the central areas (IFREMER, APEI3) as already reported by previous studies (Hecker and Paul 1979; Smith et al. 2008; Wilson 2017; Washburn et al. 2021b). To some extent, we did find such a trend, but only because densities were particularly low in APEI3 and particularly high in the GSR CA. Yet, the remaining CAs displayed similar density levels, with considerable variation, and no such pattern was found for macrofaunal densities *sensu stricto* (Fig. S1 in the electronic supplementary).

This inconclusive finding could in part be explained by the fact that potential productivity-related differences in macrofaunal densities were obscured by temporal variation, i.e., samples were taken in different years, even seasons and under different ENSO conditions. For instance, SO239 samples were taken in March/April 2015, while sampling during the remaining expeditions was conducted between April and June of each year. In addition, 2015/2016 was considered to be a particularly strong El Niño phase (Santoso et al. 2017; Fig. 6). In shallow-water systems, numerous studies have evidenced that regional climatic oscillation indexes, reflecting meteorological conditions such as precipitation, wind speed or temperature, can be used as proxies to assess changes in benthic communities (e.g., abundance, species richness, composition; Kröncke et al. 1998; Bonifácio et al. 2019). Also in deep-sea environments, both warm (El Niño) and cool (La Niña) ENSO events have been observed to influence pelagic productivity (Fiedler 2002; Smith et al. 2008) and subsequently affecting faunal communities (Ruhl and Smith 2004; Min et al. 2018). During the La Niña phase, relatively lower sea surface temperature allows the development of diatoms and large zooplankton improving the particulate organic carbon (POC) exported to the seabed (Smith et al. 2008). On the other hand, higher sea surface temperature during warm El Niño events enables the development of picoplankton and microzooplankton reducing POC exported to the seabed. Our research, conducted in the PA1 and PRZ regions of the BGR CA, included data from four distinct sampling periods between 2013 and 2016. Our findings revealed higher macrofaunal densities during the El Niño phase (Fig. 6), which is linked to warmer surface waters, but possibly reduced POC deposition at the seabed. Notably in our study, variations in densities between these phases seemed more pronounced for macrofauna *sensu lato* (Fig. 6), suggesting at least that the strength and timing of responses may differ among different groups. Ruhl and Smith (2004) investigated the impact of climatic variables on megafauna communities at station M in the Pacific. They observed varied responses, with some species showing an increase in abundance while others displayed a decline. These results suggest that differences in food supply quality and quantity, as well as its (species-) specific utilization, may contribute to these divergent patterns, as further discussed below (see also Galeron et al. 2001). However, our data collection occurred primarily at the onset and towards the end of the positive phase. Thus, enhanced temporal resolution throughout the phase would provide deeper insights into the impact of MEI on faunal patterns.

Pasotti et al. (2021) showed that net primary production (NPP) in the CCFZ can vary greatly over the course of the year. In their study, which reported values for the GSR CA between 2015 and 2017, they showed comparatively higher NPP values during boreal winter months as well as early spring and much lower values between May and October of each year. Net Primary Productivity comprises the amount of carbon produced by phytoplankton that is available for consumers. Although NPP and POC fluxes to the deep sea are linked, there are a number of physical, chemical and biotic factors and processes that determine how much POC ultimately arrives at the seafloor (Lutz et al. 2002, 2007; De La Rocha and Passow 2007). Thus, NPP is not necessarily a good proxy for food availability to the deep-sea benthos (Cael et al. 2021). Furthermore, despite some seasonal or annual fluctuations (e.g., due to ENSO events), regional POC flux is relatively stable over decadal timescales (cf. Lutz et al. 2002, 2007; Washburn et al. 2021a, b), which should also be reflected in different levels of

macrofaunal densities across the CCFZ. Nevertheless, comparison with other studies reporting data from the same year (2015) underlines the effects of seasonal changes in surface primary productivity on macrofaunal densities. De Smet et al. (2017) recorded macrofaunal densities (*sensu stricto*) of 199±15 ind.m^{-2} from the B6 site GSR CA, with samples collected in September/October 2015, and thus much lower than for the GSR B6 site collected during SO239 in March 2015 (this study). Similarly, Chuar et al. (2020) reported elevated densities (mean±SE 635±54 ind.m^{-2}) for the OMS (Ocean Minerals Singapore) CA adjacent to the BGR CA, where samples were collected in February/March 2015, i.e., in the same time period as SO239. In fact, densities found by Chuar et al. (2020) are among the highest reported for the CCFZ to date, only exceeded by Wilson (2017) for the PRA in the central CCFZ (mean±SD 774.5 ±254.8 ind.m^{-2}). In comparison, the highest densities of macrofauna *sensu stricto* found in our study were obtained during SO239 in the BGR and GSR CAs (506.2 ± 59.4 ind.m^{-2} and 611.2 ± 45.8 ind.m^{-2}, respectively).

Usually, there is a time lag between peaks of surface primary production and the deposition of phytodetritus on the abyssal seabed, reported to be between 0 and 70 days (Lampitt 1985; Sayles et al. 1994; Smith et al. 2018). Hence, for the SO239 samples, high macrofaunal densities could be a response to increased food input that was formed in the upper surface waters a couple of months earlier (cf. Pasotti et al. 2021), which is further supported by a significant positive correlation with proxies for food availability (i.e., NO_3 and iron). The very low macrofaunal densities found in APEI3 are nevertheless remarkable. The entire study area is characterised by mesotrophic to oligotrophic conditions with POC fluxes ranging between 1 to 2 mg C.m^{-2}.d^{-1}, with particularly low fluxes of 1.1 mg C.m^{-2}.d^{-1} in the APEI3 area (Volz et al. 2018). Overall, Volz et al. (2018) concluded that the biogeochemical conditions in the APEI3 area are not representative of those in the investigated CAs (BGR, IOM, GSR and IFREMER), which may be mirrored by lower macrofaunal and also meiofaunal densities in APEI3 compared to the other areas (cf. Hauquier et al. 2019, Błażewicz et al. 2019; Brix et al. 2020; Bonifácio et al. 2021; Washburn et al. 2021).

In addition to such temporal effects, differences in sampling efficiency between sampling campaigns can be major confounders affecting perceived macrofaunal patterns in the CCFZ, which relates to differences in sampling equipment, sampling protocols as well as sample processing (slicing) and sieving procedures, amongst others (Glover et al. 2015; Washburn et al. 2021b). For example, the unusually high proportion of tanaidaceans collected by Yu et al. (2018) in the Korean CA could be explained by a strong bow wave effect that may have constrained the quantitative collection of less compact specimens (Washburn et al. 2021b). While it is clearly challenging to deduce such sampling effects, different sampling protocols used between different projects and expeditions make comparability of samples and thus of abundance, biodiversity and community structure quite difficult. This has also become very clear in this study and has complicated the comparison between our different data sets, as well as with those already published (e.g., De Smet et al. 2017; Yu et al. 2018; Chuar et al. 2020; Washburn et al. 2021b) because, for example, different mesh sizes (250 vs. 300 µm) or slicing protocols were used. According to the recommendations of the ISA Legal and Technical Commission (LTC) for faunal studies, the top 10 cm of sediment should be collected from the

box core for macrofaunal studies (ISBA/25/LTC/6/Rev.1 2020; ISA 2020). While the ISA initially recommended the use of a 250 µm mesh (ISA 2001), a consensus to retain macrofauna with a 300 µm mesh has now been reached through exchange with the scientific community (ISBA 2020; Lins et al. 2021) and is expected to allow the comparisons of studies in the future. As shown above, errors can occur during sampling and sample processing. For example, the strength of the bow wave effect is related to winch speed, and can be reduced by limiting the speed as the BC approaches the seabed (Hessler and Jumars 1974). Bottom waters and surface sediments, that usually contain most of the fauna, can be washed out or destroyed during gear retrieval and thus may strongly affect faunal densities. Following on from this, there is therefore an urgent need to standardise sampling equipment and protocols, alongside documentation of sampling peculiarities/failure, to ensure the best possible comparability of samples and data (Glover et al. 2015; Lins et al. 2021; Washburn et al. 2021b).

In our study, the relationship between overall macroinfaunal densities and nodule densities was statistically not significant. The presence of nodules may arguably exert a more pronounced effect on epifauna or organisms that encrust the nodules than infaunal communities. However, nodules can influence macroinfauna through changes in sediment variables, including grain size and sorting (Leduc et al. 2015 and citations therein). Additionally, their presence can indirectly affect macroinfauna by providing habitat for mega-epifauna like corals or sponges, which can alter local hydrodynamic conditions (Garcia et al. 2008; Bridge et al. 2011; Leduc et al. 2015). Previous studies in the CCFZ have, however, reported mixed results in the relationship between nodule - and macroinfaunal densities, with increased nodule availability to either an increase or decrease densities (e.g., polychaetes: Bonifácio et al. 2020; isopods, tanaidaceans, polychaetes; Washburn et al. 2021b), or have no effect (e.g., total macrofauna: De Smet et al. 2017; Pasotti et al. 2021, this study; isopods, tanaidaceans, polychaetes: Wilson 2017). Washburn et al. (2021b) argued that the weak or absent relationship between macrofaunal and nodule densities in their study could be due to sampling within a limited range of nodule densities at intermediate levels. Only examining samples with similar nodule densities could therefore lead to a false lack of such a relationship. Furthermore, some studies have derived nodule densities from regional models (cf. Washburn et al. 2021b and citations therein), while others have used direct measurements of nodule densities from the BC (e.g., Bonifácio et al. 2020, this study). Since the distribution of nodules is very heterogeneous in the CCFZ, sometimes in the range of tens of meters (Peukert et al. 2018, Kuhn and Rühlemann, 2021), these changes will not be captured adequately by regional models (cf. Washburn et al. 2021b). To test this, regions across the full range from low to high nodule densities need to be analysed, using direct measurements of nodule densities. However, Pasotti et al. (2021) assessed nodule densities directly from the BC, and found no significant differences in macrofaunal densities between nodule-free and nodule-rich areas in the GSR CA. Furthermore, in this study, over twenty of the analysed BC samples also had low nodule densities of 0-10 kg m^{-2}, yet no significant relationship with densities of the overall macrofaunal communities was found.

Variation in macrofaunal community composition across the CCFZ

Macrofauna (*sensu stricto*) in our study consisted mainly of taxa typically found in deep-sea environments, with polychaetes, tanaidaceans, isopods and bivalves being prevalent (e.g., Hecker and Paul 1979; Cosson et al. 1997; Schriever et al. 1997; Kröncke and Türkay 2003; Fischer and Brandt 2015; Kaiser et al. 2023). We therefore expected that the community composition within the BGR CA in particular would be relatively similar, but also that differences between the CAs and APEI3 would be moderate. Chuar et al. (2020), for example, found that supra-specific taxa (phylum/class/order and families of Polychaeta, Copepoda, Isopoda and Tanaidacea) were distributed fairly homogeneously within the OMS CA. We were able to confirm the same in our study for the BGR CA, where we did not register any major differences between the various working areas. Instead, a significant temporal differences became evident, as shown for PA1 and PRZ within the BGR CA, with contrasting conditions during 2013 versus 2015/2016. This finding lends support to our hypothesis that climate plays a pivotal role in driving shifts within abyssal benthic communities in the CCFZ. Notably, our sampling in 2013 took place during a long La Niña phase of MEI, which extended from 2010 until mid-2013, in opposition to an El Niño phase between 2015 and 2016 (Fig. 6).

We found significant differences in macrofauna community composition between all areas mainly driven by differences in depth and seabed temperature. In particular the composition of APEI3 differed greatly from the other areas, which was also characterised by the lowest POC flux. At larger spatial scales, surface productivity gradients, bottom currents, and depth gradients are considered strong drivers of deep-sea community structure, while at smaller scales, variations are likely attributed to biologically mediated perturbations or localized food patches (e.g. Levin et al. 2001; Kaiser et al. 2007). While a direct relationship between seafloor POC flux and macrofaunal community composition was not explicitly analysed in our study, the deviation observed in APEI3, which is characterised by the lowest seafloor POC flux (see also Volz et al. 2018), supports this hypothesis. An unexpected finding was the positive relationship between macrofaunal densities and seabed temperature, despite minimal temperature variations across the study area that are unlikely to have significant biological impacts. However, there is a strong correlation between bottom temperature and nitrate and phosphate levels, which serve as indicators of food availability (Fig. 2). Although it was not possible to isolate the individual effects of the different variables, the interplay among them could provide an explanation for the significant relationship observed.

The dissimilarities observed among the areas were primarily influenced by the proportion of nematodes and polychaetes in APEI3 compared to other CAs (Fig. 3). While the number of nematodes in our study is likely underestimated, due to the use of a relatively large mesh size (300 µm), Hauquier et al. (2019) also confirmed particularly low densities of nematodes in APEI3. Bonifácio et al. (2020) analysed polychaete communities from BC samples collected during SO239 in more detail. In agreement with our results, they found polychaete assemblages of APEI3 to strongly differ from the remaining CAs. These differences have been attributed to the higher concentration of finer sediments in APEI3, which could have increased the shear strength of the sediments and made it more difficult for fauna to burrow (Bonifácio et al. 2021 and citations therein). Consequently, the reduced density of infaunal

polychaetes and nematodes at APEI 3 may be linked to the combination of smaller sediment grain size and limited food availability (Hauquier et al. 2019; Bonifácio et al. 2020, 2021).

Conclusions

This study aimed to evaluate the spatial and temporal variability in density and community composition of macroinfauna across various sampling sites and areas in the CCFZ, driven by a pronounced productivity and depth gradient. While our initial expectations were to uncover macrofaunal patterns aligning with these gradients, we encountered inconclusive findings, that may be due, at least in part, to significant temporal variation and the coarse taxonomic resolution of our data. Specifically, our findings suggest a possible relationship between macrofaunal densities and atmospheric variability through the ENSO. These climatic fluctuations have the potential to alter the availability and composition of food sources reaching the seafloor, thereby affecting the composition of faunal communities (Ruhl and Smith 2004; Min et al. 2018; Smith et al. 2008). However, a comprehensive evaluation of these effects requires an extended analysis over extended temporal scales, considering that different faunal groups may exhibit distinct response patterns (Ruhl and Smith 2004, this study). Along considerable temporal and spatial variations in densities and community composition, we observed significant differences in both densities and community composition between APEI3 and CAs. Although the temporal comparison was not extensive, this first assay revealed significant differences between years in the PA1 and PRZ areas of the BGR, underscoring the importance of establishing reference points for quantifying natural variability levels. Our study highlighted the lack of standardization in sampling protocols. This inconsistency introduces a degree of uncertainty, making it more challenging to robustly interpret spatial and temporal variations in macrofaunal patterns (also discussed in Washburn et al. 2021b). Therefore, in order to enhance data comparability, it is crucial to conduct sampling using standardized protocols that encompass mesh size, sediment slicing, and equipment usage. This approach is essential for generating reliable and comparable datasets, which are necessary for gaining a better understanding of the spatial and temporal changes in macrofauna community structure and composition within the CCFZ, as well as the driving forces behind them.

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Figure and table legends

Fig. 1 Map of the sampling locations within the different contractor areas and APEI3 across the eastern CCFZ, and within the different working areas in the BGR CA. The average particulate organic carbon (POC) flux at the seafloor during the 2002–2018 period is show in the background (derived from Volz et al. 2018). Figure partially reproduced from Bonifácio et al. (2020) under the Creative Commons license CC BY 4.0.

Fig. 2 Spearman rank correlation (ρ) results between environmental variables and macrofaunal densities, including total macrofauna and excluding meiofaunal taxa. Significance levels are denoted as * ($p < 0.1$), ** ($p < 0.05$), and *** ($p < 0.01$).

Fig. 3 Averaged relative abundances (%) of macrofaunal taxa collected from the different contract areas (CA) across the CCFZ by means of a box corer (BC); a) all contract areas and APEI3; b) working areas within the BGR CA. Individual BC stations are merged per area, number of samples included are indicated above the bars. APEI: Area of Particular Environmental Interest; BGR - eastern German contract area; GSR - Global Sea Mineral Resources NV (Belgium contract area); IFREMER - L'Institut Français de Recherche pour l'Exploitation de la Mer (French contract area); IOM - Interoceanmetal Joint Organization contract area; PA: Prospective Area; PRZ: Preservation Reference Zone; WA: working area (cf. Kuhn 2015). For interpretation of the references to colour in this figure legend, the reader is referred to the online version of this article.

Fig. 4 Comparison of macrofaunal densities (ind./m²) *sensu lato* including all taxa among different environmental clusters (as detailed in Tables S1, S2).

Fig. 5 Comparison of macrofauna densities *sensu stricto* (excluding meiofaunal taxa) among different environmental clusters (as detailed in Tables S1, S2).

Fig. 6. Bimonthly Multivariate ENSO (El Niño Southern Oscillation) values, extracted from the official website (https://psl.noaa.gov/enso/mei/), were correlated with macrofaunal densities in the PA1 and PRZ areas of the BGR contractor area within the Clarion Clipperton fracture zone (CCFZ). Noteworthy patterns include a strong cool/negative (La Niña) phase observed from 2010 to 2013, a strong warm/positive (El Niño) phase during 2015/2016, and a very strong negative phase prevailing since mid 2020. PA: Prospective Area; PRZ: Preservation Reference Zone. Density *ss*: macrofaunal densities *sensu stricto* (excluding meiofauna taxa); Density *sl*: macrofaunal densities *sensu lato (*all taxa included). For interpretation of the references to colour in this figure legend, the reader is referred to the online version of this article.

Fig. 7 Multivariate analyses of macrofaunal community composition across different contractor areas in the Clarion-Clipperton Fracture Zone using box-corer data. The analysis

employed a Hellinger-transformed Bray Curtis resemblance matrix and considered relative macrofaunal abundances (%). The resulting 2D stress value was 0. The plot highlights the dominant and characteristic taxa for each region: BGR CA (shown in red), IFREMER (shown in turquoise), APEI3 (shown in dark blue), GSR (shown in green), and IOM (shown in yellow). Please refer to the online version of this article for further interpretation of colour references in this figure legend. For interpretation of the references to colour in this figure legend, the reader is referred to the online version of this article.

Fig. 8 Multivariate analyses of macrofaunal community composition across different working areas in the BGR contractor area of the Clarion-Clipperton Fracture Zone using box-corer data. The analysis employed a Hellinger-transformed Bray Curtis resemblance matrix and considered relative macrofaunal abundances (%). The resulting 2D stress value was 0. The plot highlights the dominant and characteristic taxa for each area. PA: Prospective Area; PRZ: Preservation Reference Zone; WA: working area.

Fig. 9. Multivariate analyses of macrofaunal community composition in the BGR working areas PA1 and PRZ between years using box-corer data. The analysis employed a Hellinger-transformed Bray Curtis resemblance matrix and considered relative macrofaunal abundances (%). The resulting 2D stress value was 0. The plot highlights the dominant and characteristic taxa for each area. PA: Prospective Area; PRZ: Preservation Reference Zone. Please refer to the online version of this article for further interpretation of colour references in this figure legend. For interpretation of the references to colour in this figure legend, the reader is referred to the online version of this article.

Fig 10. Triplot representation of canonical correspondence analysis (CCA) illustrating the relationships between macrofaunal taxa and environmental factors within various contractor areas located in the Clarion Clipperton Fracture Zone. In this representation, samples are denoted by a hash symbol, with numeric values indicating the environmental cluster they belong to (1-42; see Table S1 in the supplementary electronic materials). The distance between samples reflects their dissimilarity in terms of community composition. Environmental variables are depicted as arrows, where the angle between each arrow indicates the correlation between them. Taxon names are highlighted in red, and the distance between them represents the dissimilarity in the distribution of these taxa across the samples. For interpretation of the references to colour in this figure legend, the reader is referred to the online version of this article.

Table 1 Summary of the CCFZ expeditions during which box corer (BC) material was collected for the present study. APEI: Area of Particular Environmental Interest; BGR - eastern German contract area; GSR - Global Sea Mineral Resources NV (Belgium contract area); IFREMER - L'Institut Français de Recherche pour l'Exploitation de la Mer (French contract area); IOM - Interoceanmetal Joint Organization (joint contract area of Bulgaria, Cuba, Czech Republic, Poland, Russian Federation and Slovakia); PA: Prospective Area; PRZ: Preservation Reference Zone; WA: working area (cf. Kuhn 2015).

Table 2 Sources for abiotic variables used to characterise macrobenthic communities in the CCFZ (see also Table S2). The environmental layers derived from Bio-Oracle v2.0 describe monthly mean values for the period 2000-2014 (Assis et al. 2018).

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Table 1 Summary of the CCFZ expeditions during which box corer (BC) material was collected for the present study.

Expedition	**Vessel**	**Date**	**Area**	**n BCs,** *this study*	**Reference**
KM13	RV Kilo Moana	01/04-13/05/2013	BGR-PRZ, -PA1	40	Rühlemann et al. 2014
KM14	RV Kilo Moana	15/04-03/06/2014	BGR-PA1, -PA2	26	Rühlemann et al. 2015
SO239	RV Sonne	11/03-30/04/2015	BGR- PA1, -PRZ, IOM, GSR, IFREMER, APEI3	34	Martinez and Haeckel 2015
SO240	RV Sonne	03/05-16/06/2015	BGR-WA1, -WA2, -WA3, -WA4	17	Kuhn 2015
KM16	RV Kilo Moana	08/04-20/05/2016	BGR-PA1	24	Rühlemann et al. 2017
KM18/SO262	RV Sonne	06/04-29/05/2018	BGR-PA3	7	Rühlemann et al. 2019

1092 **Table 2** Sources for abiotic variables used to characterise macrobenthic communities in the
1093 CCFZ (see also Table S2). The environmental layers derived from Bio-Oracle v2.0 describe
1094 monthly mean values for the period 2000-2014 (Assis et al. 2018).
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Acronym	Parameter	Layer code (Bio-Oracle)	Unit	Resolution	Source
PP	Mean sea surface net primary productivity	BO2_ppmean_ss	$g/m^3/day$	9x9 km	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu
iron	Mean dissolved iron in sea water at maximum bottom depth	BO2_ironmean_bdmax	$\mu mol/m^3$	9x9 km	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu
velo	Mean sea water current velocity at maximum bottom depth	BO2_curvelmean_bdmax	m/s	9x9 km	Global Ocean Physics Reanalysis ECMWF ORAP5.0 (1979-2013) URL: http://marine.copernicus.eu
nodule	Nodule densities	n.a.	kg/m^2 (wet)	m^2	*in situ* measurement per core
dO_2	Mean mole concentration of dissolved molecular oxygen in sea water at maximum bottom depth	BO2_dissoxmean_bdmax	$\mu mol/m^3$	9x9 km	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu
tmean	Mean sea water temperature at the bottom at maximum bottom depth	BO2_tempmean_bdmax	degrees Celcius	9x9 km	Global Ocean Physics Reanalysis ECMWF ORAP5.0 (1979-2013) URL: http://marine.copernicus.eu
PO_4	Mean mole concentration of phosphate in sea water at maximum bottom depth	BO2_phosphatemean_bdmax	$\mu mol/m^3$	9x9 km	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu
NO_3	Mean mole concentration of nitrate in sea water at maximum bottom depth	BO2_nitratemean_bdmax	$\mu mol/m^3$	9x9 km	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu
depth	Bottom depth	n.a.	m		Ship-based multibeam bathymetry

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