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Editorial: Biodiversity, Connectivity and Ecosystem Function Across the Clarion-Clipperton Zone: A Regional Synthesis for an Area Targeted for Nodule Mining

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Editorial on the Research Topic

Biodiversity, Connectivity and Ecosystem Function Across the Clarion-Clipperton Zone: A Regional Synthesis for an Area Targeted for Nodule Mining

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The Clarion Clipperton Zone (CCZ) in the equatorial Pacific Ocean is a vast region of abyssal plains and hills, polymetallic nodule fields, and seamounts. Because of the cobalt, nickel and copper content of polymetallic nodules in this region, the CCZ is targeted for deep-seabed mining. In order to safeguard seafloor biodiversity and ecosystem functions across the region in the event of mining, the International Seabed Authority (ISA) in 2012 designated nine 400×400 km no-mining areas, called Areas of Particular Environmental Interest (APEIs) (Wedding et al., 2013). The APEIs were designed based on environmental correlates of biodiversity and ecosystem function to be representative of the full range of seafloor habitats and communities potentially impacted by nodule-mining activities within the licensed mining exploration areas spanning the CCZ (Wedding et al., 2013).

Since APEI establishment in 2012, a substantial number of research expeditions have collected biodiversity and ecosystem-function data within the CCZ. These expeditions mainly focused on individual contract areas or APEIs. To date, there have been limited efforts to synthesize data at the regional level, which is critical for the further development of ISA's CCZ Environmental Management Plan (EMP). The Deep CCZ Biodiversity Synthesis Workshop was conducted in October 2019 with a new focus on the CCZ EMP, specifically to (1) compile recent deep-sea ecosystem data from across the CCZ, (2) synthesize patterns of seafloor biodiversity, ecosystem functions, and potential environmental drivers, and (3) assess the representativity of the APEIs for areas in the CCZ targeted for polymetallic nodule mining (International Seabed Authority, 2020). This Special Research Topic of *Frontiers in Marine Science* draws together scientific papers derived from the workshop, as well as others elucidating environmental variability and deep-sea biodiversity across the region.

Here, we provide a brief synthesis of the results published in this volume, highlighting aspects relevant to environmental heterogeneity, biodiversity, and environmental

management in the CCZ. Six key conclusions are as follows:

1) **The CCZ has substantial environmental heterogeneity at the seafloor and in the water column.** As detailed in Washburn, et al., ecologically important environmental characteristics vary across subregions and exploration contract areas in the CCZ. In particular, seafloor depth and flux of particulate organic carbon (POC) exhibit substantial east-west and north-south gradients, varying, respectively, by factors of 1.4 and 2 across the region. The abundance of polymetallic nodules and seamounts, which provide habitat for specialized biotas (Amon et al., 2016; Laroche et al., 2020; Drazen et al.; Leitner et al., 2021; Leitner et al.), also vary >9-fold across CCZ subregions, with nodules especially abundant in the central and eastern CCZ, and seamounts abundant in the east and west, including in areas rich in nodules and exploration claims (Washburn et al.). The pelagic environment also exhibits substantial regional variability, with an intense midwater oxygen minimum zone (OMZ) along the east-west core of the CCZ overlying most nodule-rich and exploration-contract areas, causing shallower diel vertical migrations of animals in the upper water column (Perelman et al.). However, while these ecologically important variables change considerably across the CCZ, many others, especially in bottom-waters, change little; in particular, suspended particle concentrations above the abyssal seafloor across the CCZ are among the lowest in the global ocean (Washburn, et al.).

2) **Seafloor biodiversity in the CCZ is remarkable, with many 100s to 1000s of molecular/morphological “species” sampled in size classes ranging from microbes to megafauna.** Nonetheless, biodiversity remains incompletely sampled at any given site. For example, Hollingsworth et al. document >30,000 amplicon sequence variants (ASVs) among the bacteria and archaea in sediments and nodules from the eastern CCZ, a result consistent with other molecular studies showing diverse microbial communities in the region (Lindh et al., 2017; Shulse et al., 2017). For seafloor foraminifera, Gooday et al. report >1,000 morphospecies, and >6,000 molecular operational taxonomic units (MOTUs). Limited eDNA seafloor sampling in the CCZ has documented >1,200 MOTUs of metazoan meiofauna (Laroche et al., 2020; Laroche et al.; Lejzerowicz et al.). Within the macrofaunal size class, >600 molecular and morphological species have been sampled (Bribiesca-Contreras et al.; Washburn et al.), while more than 600 morphotypes of invertebrate megafauna have been resolved in seafloor images (International Seabed Authority, 2020; Durden et al.). Based on a global eDNA/eRNA survey of eukaryotic biodiversity in abyssal sediments, Lejzerowicz et al. conclude that the CCZ is a biodiversity hotspot “characterized by a high number of OTUs exclusive to the CCZ” and has “greater beta diversity” than “other abyssal regions.” It should be noted that the vast majority of the many thousands of eukaryotic species detected across all size classes in the CCZ are new to science.

Despite collections of large numbers of morphospecies, MOTUs and ASVs across the CCZ, biodiversity at any

single site is still under-sampled. For example, Laroche et al. recovered only 40–74% of the estimated meiofaunal ASV richness at any site in the western CCZ. Similarly, macrofauna species accumulation curves and richness estimators indicate that only 25–73% of the total polychaete, 16–85% of tanaid, and 20–80% of isopod morphospecies occurring at any site in the CCZ have been sampled (Washburn, Menot, et al.). Thus, across all size classes, many thousands of species remain to be sampled to achieve a full biodiversity inventory of the CCZ.

3) **Biodiversity and community structure vary substantially across the CCZ, with POC flux, manganese nodule occurrence, and seafloor topography (e.g., seamounts) implicated as key ecological drivers. This variability is a recurring theme across biotic size classes.** For example, the abundance, biodiversity and/or community structure of organisms ranging from microbes to megafauna vary with regional variations in seafloor POC flux (e.g., Bonifácio et al.; Durden et al.; Hollingsworth et al.; Washburn et al.). The occurrence/abundance of nodules also influences seafloor biodiversity, with nodules harboring distinct species and community structure from surrounding sediments for microbes (Hollingsworth et al.; Wear et al.), foraminifera (Gooday et al.), and invertebrate megafauna (Durden et al.). Seamounts also host distinct communities of microbes (Wear et al.), metazoan meiofauna (Laroche et al., 2020; Laroche et al.), invertebrate megafauna (Durden et al.) and mobile scavengers (Leitner et al., 2021; Leitner et al.).

4) **Despite many research expeditions, there are major geographic gaps in biodiversity and other ecological data across the CCZ.** Quantitative sampling of seafloor biodiversity has been heavily concentrated in the eastern CCZ in contractor areas, and in the western CCZ in APEIs. The central CCZ and most APEIs are poorly sampled, resulting in little quantitative biodiversity information for vast areas of the CCZ. These large geographic gaps are clear in quantitative studies of sediment microbes (Wear et al.; Hollingsworth et al.), foraminifera (Gooday et al.), meiofaunal eukaryotes (Lejzerowicz et al.), macrofauna (Washburn, Menot, et al.), as well as for demersal fishes and scavengers (Drazen et al.).

Detailed studies of the ecology and evolution of benthic fauna in the CCZ, which are essential for predicting mining impacts and ecosystem recovery, are even more limited. Laming et al. present the first CCZ study of the reproductive biology of ophiuroids, which are major contributors to megafaunal abundance and biodiversity in the region, with samples available only from the eastern CCZ. Bonifácio et al. hypothesize that a highly diverse CCZ taxon, the scale-worm subfamily Macellicephalinae, may have diversified in response to variations in POC flux, again based on samples restricted to the eastern CCZ.

5) **Only a small proportion of faunal species sampled in the CCZ can be shown to have broad geographic distributions.** The vast majority of recognized foraminiferal and macrofaunal species have been found only at single sites, and often have been collected only as single individuals (Gooday et al.; Washburn et al.). A few common foraminiferal

and macrofaunal species are wide ranging across the CCZ (Gooday et al.; Washburn, Menot, et al.), but this is not true for all abundant species; for example, at least three polychaete species abundant at some stations have been collected over limited ranges of 200–700 km (Washburn et al.). Furthermore, one highly diverse family of annelid worms, the polynoids, exhibits substantial species turnover across the eastern CCZ, with evidence of diversification in more oligotrophic areas (Bonifácio et al.). Thus, even with this new biodiversity synthesis, we cannot determine whether most faunal species in the CCZ have limited geographic ranges, or are simply under sampled.

- 6) **Important habitat variability in the CCZ is not fully captured by the nine original APEIs.** McQuaid et al. conducted a habitat classification of the CCZ based on the key ecological drivers POC flux, nodule abundance, and bottom topography. They identified 24 habitat classes, 18 of which are represented in the original APEIs. However, six nodule-rich habitats are poorly represented in the original APEIs, but are abundant in areas targeted for mining as well as in some areas outside of license areas and APEIs. Inclusion of these nodule-rich areas in new APEIs could improve the habitat representivity of the network, and better safeguard CCZ biodiversity (McQuaid et al.).

Management implications. The Deep CCZ Biodiversity Synthesis Workshop and the papers in this special volume provide an up-to-date evaluation of biodiversity patterns across

the CCZ, and highlight the habitat variability, key environmental drivers, and scales of connectivity that must be considered to assess the efficacy of the current network of APEIs. The workshop and this volume have influenced the ISA Legal and Technical Commission to recommend four new APEIs to capture nodule-rich habitats, reduce the distance between APEIs, and protect core areas of the OMZ (International Seabed Authority, 2021). If implemented, these new APEIs should substantially improve the representivity of the APEI network and further demonstrate the value of state-of-the-art scientific syntheses for enhancing environmental management in the deep sea.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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