**First synthesis of metazoan biodiversity in the world’s largest frontier of mineral exploration**

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# Summary

The predicted global surge in demand for metals such as cobalt and nickel has created unprecedented interest deep-sea habitats with such mineral resources. The largest area of activity is a 6 million km2 region known as the Clarion-Clipperton Zone (CCZ) in the central and eastern Pacific, with 17 contracts for mineral exploration covering 1.2 million km2, regulated by the International Seabed Authority (ISA). Critical to informed policy for the environmental management of potential deep-sea mining activities is baseline biodiversity knowledge of the region, which until recently has been completely lacking. We have conducted the first comprehensive synthesis of CCZ benthic metazoan biodiversity, for all faunal size classes. There has been rapid recent growth in taxonomic outputs and data availability for the region over the last decade. We present here the CCZ Checklist, a biodiversity inventory vital to developing knowledge of the region and future assessments of environmental impacts. For the CCZ, an estimated 92% species are new to science (421 named species from a total of 5301 recorded species). This figure is supported by a meta-analysis of recent taxonomic studies suggesting that 92% of species sampled in the region are undescribed. Species richness estimators place total regional CCZ metazoan benthic diversity over 9000 species, most likely representing a lower bound of diversity in the region. While uncertainty in estimates is high, as comparable datasets accumulate, regional syntheses will become increasingly possible, critical to understanding ecological processes and species extinction risks in the region.

**Keywords:** deep-sea, taxonomy, new species, checklist, polymetallic nodules, Clarion-Clipperton Zone, environmental management, abyss, biodiversity, benthic metazoa

# Results and Discussion

**How many animal species are known to live in the CCZ?**

To determine the current state of knowledge of benthic metazoan biodiversity in this active mineral exploration zone we compiled 106,377 records from six published data sources (literature and databases; Figure 1; S Table 1). There has been remarkable recent growth in taxonomic efforts for the CCZ, particularly over the past five years (Figure 2). To date, 216 taxa have been described from the CCZ; but only seven prior to the year 2000. This clearly illustrates the historic lack of taxonomic work in the region, especially striking given that exploration for seabed mining in the region started in the 1960s (Jones et al., 2017). The large-scale CCZ environmental surveys conducted in the late 1970s to early 1990s produced lists of numerous morphospecies (e.g. Wilson, 2017) but there was almost no alpha-taxonomy done – a few notable exceptions include Pawson (1983) and Pawson & Foell (1986) on sea cucumbers. The need for regional environmental management of the CCZ was recognised in policy-making in the 2000s (Wedding et al., 2013; Glover et al., 2018) has resulted in a resurgence of taxonomic work, including incorporating DNA methods that have allowed for a more robust methodology (Glover et al., 2015).

Critical to the long-term iterative knowledge of CCZ biodiversity, as well as the conservation of the region, is the creation of a curated checklist of known taxa. We present the first CCZ Checklist, which comprises 421 named species (without open nomenclature qualifiers). These include 182 species which have been described from the CCZ (44% of the total). Only six of the CCZ species (including the two redescriptions) have been recorded elsewhere. The total number of undescribed species (including morphospecies) recorded in the CCZ is 4703. These are species that have been differentiated on the basis of morphology and/or molecular approaches, and described as morphospecies/informal names (See Methods). Relative to the named species, this provides an estimate of 92% undescribed species in the CCZ. As another approach to estimating undescribed biodiversity in the CCZ, we conducted a meta-analysis of recent molecular and morphology-based taxonomic studies that provided estimates of the numbers of new taxa. Remarkably, this provides the same figure of 92% undescribed species, although this is limited to ten publications and varies between taxonomic groups, (74-100%; see Table S2).

**What kind of animals live in the CCZ?**

The CCZ Checklist (and morphospecies names) provides a glimpse of the overall composition of the CCZ fauna. The five most diverse groups of animals that inhabit the CCZ are the Annelida (31%); Arthropoda (29%); Nematoda (14%), Echinodermata (10%); Cnidaria (5%), followed by Porifera (4%); Mollusca (3%); Chordata (2%) and Bryozoa (1%) (Figure 2; all size fractions, named and morphospecies combined). While this gives some insight into the relative diversity of CCZ animals, the percentages will be heavily influenced by taxonomic trends, the size-fraction assessed, availability of specialists and sample bias. For example, examining size fraction: meiofauna are generally defined as animals being retained on a 63µm sieve, macrofauna, on a 250-300µm sieve, and megafauna, as 2cm and larger. Most phyla fall into particular size fractions, e.g. Annelida, Arthropoda, Mollusca and Bryozoa, mainly macrofauna, Echinodermata and Cnidaria, megafauna, Nematoda, meiofauna. Most species are macrofauna, 54% (xxx total); with similar proportions for both meiofauna, 24% and megafauna, 22%. Macrofauna however are sampled much more extensively (S File xx). In contrast, megafauna are rarely collected, and there are only three synthetic taxonomic checklist studies that cover multiple megafaunal taxa with archived vouchers (Amon et al 2017a, 2017b; Bribiesca-Contreras et al. 2022). This reflects the challenges of collection of megafauna, either with ROVs (expensive) or trawls (destructive of animals; and these methods can be biased towards certain groups) (add refs, Pawson et al., 1988). The vast majority of megafauna are identified by ROV imagery only (not collection), species-level identification by imagery is generally not feasible, or even desirable given identifications cannot be ascertained with detailed examination of morphology, or molecular data. Meiofauna are often regarded to be the dominant component of deep-sea ecosystems, at least in terms of biomass, if not diversity (Sinniger et al., 2016; Le et al., 2022) and are also likely to have considerable undocumented diversity given significant sampling challenges (Lins et al., 2021).

Another key faunal grouping for the CCZ is animals as sediment-or-nodule dwelling. While several descriptions of nodule megafauna (cnidarians and sponges) have recently been published (Cairns, 2015; Molodtsova & Opresko, 2017; Kersken et al., 2018; 2019; Herzog et al., 2018; Wang et al., 2018), remarkably little is known about the nodule fauna of the region. Excluding studies of microbes and protists there are few studies where nodule fauna has been assessed quantitatively (Veillette et al., 2007; Mullineaux et al., 1987). The majority of CCZ macrofaunal nodule fauna (which includes large numbers of bryozoans and sponges) are almost completely unstudied, a rare exception a recent monograph on Bryozoa describing 16 new species, ten new genera and 3 new families (Grischenko et al., 2018). Overall, 20 Bryozoans have been recorded from the CCZ, of which a remarkable 18 have been described from the region. Preliminary analysis of nodule macrofauna from across the eastern CCZ has recovered 180 new species yet to be described (author GBC). Characteristic sediment-dwelling infauna, including nematodes, isopods and polychaetes are now starting to be discovered living on nodules, illustrating the overlap and interconnectivity of nodule and sediment-dwellers (Drennan et al 2021; Malyutina, 2011; Pape et al., 2021). An estimated 18% of the named species in the CCZ Checklist live on nodules overall, however the relative proportion of nodule fauna is likely to increase with further studies.

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| --- | --- | --- | --- | --- | --- | --- | --- |
| Table 1. Summary of benthic metazoan biodiversity in the Clarion-Clipperton Zone based on published records. \*The new CCZ Checklist contains 421 named species in total; and 644 species including those recorded in open nomenclature (with identification qualifiers, i.e. cf. aff., incertae sedis) or identified solely from imagery. ^Total species from the CCZ: combined total of named species and morphospecies. Species richness estimates range from xx to xx ADD | | | | | | | |
|  |  |  |  |  |  | |
| CCZ Taxonomic Knowledge | | **CCZ Checklist** | | **CCZ Biodiversity Estimators** | |
|  |  |  |  |  |  | |
| New species: | 182 | Phyla: | 29 | Morphospecies: | 4703 | |
| New genera: | 31 | Classes: | 50 | Total species^ | 5124 | |
| New families: | 3 | Orders: | 162 | Chao1 species richness: | 9135 (+/-302 SE) | |
| Total Descriptions from CCZ: | 216 | Families: | 501 | Chao2 species richness: | 6066 (+/-134SE) | |
| Total taxonomic papers: | 164 | Genera: | 1119 | ES(2000): | TBC | |
| Total papers with descriptions | 65 | Species\*: | 421 | ACE Estimator: | 6291 (+/46SE) | |
|  |  | All species\* | 644 | Higher-taxon estimator: | 5274 | |
|  |  |  |  | Non-parametric estimators? |  | |

**How many species might live in the CCZ?**

This synthesis of all published biodiversity from the CCZ has allowed the first estimates of both the known and unknown species richness across the region. This is important as it sets a baseline of the current state of knowledge as well as indicating where the CCZ might sit in terms of its importance in a global context. It is useful to first examine diversity at a family level because at a high taxonomic rank the uncertainty is lower, with less likelihood of synonyms and misidentifications than at species level, and it provides an overview of the degree of undersampling in the dataset. The family accumulation curve is approaching asymptote, with an estimated 440 (+/-22SE) families in total (Chao1, *N* = 3257; Figure 3, based on records where abundance and site information are available, a subset of the Checklist). The total families recorded in the CCZ Checklist is 501. As it is unlikely that the family count includes a lot of synonyms (unlike the morphospecies), we can be reasonably confident that the family diversity of the CCZ exceeds 501, suggesting that even at higher taxonomic levels Chao1 here underestimates diversity. Systematic negative bias of these non-parametric species estimators are well known, often ascribed to the difficulty of detecting rare species (Coddington et al., 2010; Cowell et al., 2012; O’Hara, 2005; Ugland and Gray, 2004; Chao & Chiu, 2016- check), but this is particularly problematic for deep-sea environments given the very low densities and high numbers of singletons (Higgs & Atrill, 2015; Brandt et al., 2014). The Chao1 estimator for total species richness in the CCZ is 9135 (+/-302 SE) (Table 1). At a species level, it is clear that sampling of the CCZ is very far from complete, with the numbers of species still accumulating rapidly with increasing sampling, and the accumulation and rarefaction curves far from asymptote (Figure 3). We also estimated species richness based on higher taxonomy (Mora et al., 2011, Balmford et al., 1997) with a species estimate of 5274 (R2 = 0.96; P = 0.003), similar to total species diversity recorded from the CCZ (Table 1). Family and in particular genus-level diversity in the CCZ Checklist is unlikely to be complete at this point in time which may reduce the estimate, and there are inherent limitations of this approach, impacted by sampling effort, implies direct relationship of higher taxonomy (which itself may be taxon specific, and doesn’t account for reassignments (Balmford, 1997, Mora et al., 2011, add). ES(2000) ADD

These estimates of species richness (and the 92% of species undescribed) are subject to many other caveats. For example, the species lists may contain many synonyms, which can inflate the species estimate. While synonyms that could be identified were removed (i.e. 952 from the morphospecies names), it is highly likely further synonyms are present which cannot be ascertained. For example, Spionidae sp. A is assumed to be a different species to Spionidae sp. B while evidence in terms of high resolution morphological or DNA data, is missing. Inflation of informal names will also accrue over time as designations change, and names accumulate. Misidentifications in contrast could either inflate, or reduce the diversity estimates but similarly contribute to overall uncertainty. Potentially many of the species in the CCZ Checklist are misidentified, owing in part to the lack of field guides and keys to the fauna of the region. Similarly many of the morphospecies names may be known species that are yet to be correctly identified. In the meta-analysis, the misidentification of species is removed as groups are examined by their specialists and the same proportion of biodiversity undescribed (92%) but this could be a coincidence more than anything. This lack of field guides can also contribute to the problem of range-inflation of so-called ‘cosmopolitan species’ (add refs). For the key macrofaunal groups in the CCZ Checklist, the polychaetes, tanaids, and isopods, 32 of 157 species have type localities outside the region (including other ocean basins). This is likely to inflate connectivity and underestimate diversity, given the prevalence of cryptic species (Knowlton 1993, add refs), particularly in the deep-sea (Brasier et al., 2016, Brandt xxxx, add refs) (and including the CCZ – see Bonifacio & Menot (2019; 2020), Smith et al., (2019). The only way to overcome this is to obtain genetic data from both the sample and the type locality of the species it most closely resembles. Recent detailed molecular taxonomic studies have shown repeatedly that diversity based solely on morphological assessment under-estimates biodiversity, by potentially 20-25% (Brasier et al., 2016; Smith et al., 2019). Although almost all CCZ species have been described since the advent of DNA taxonomy methods (Figure 2B), over 50% overall are still described solely by morphology (S file xx). For meiofauna 86% are described on morphology alone, likely because of the challenges of subsampling for molecular work from small-sized specimens. Unknown cryptic speciation may be even higher in this size fraction therefore (Sanchez et al., 2019) but this may be quite taxa-specific (Miljutin & Miljutina, 2016).

Another factor that can lead to underestimates of diversity but one that is often not considered is data duplication. Extensive record duplication was identified in the ISA database DeepData; and while removed for analysis, further duplication was suspected but could not be definitively identified owing to underlying limitations in data handling in the database (including lack of unique record identifiers; S file xx; preprint doi). Duplication can reduce estimates of diversity, as relative proportions of rare species including singletons will be affected (Bonifacio et al., 2020; Chao & Chiu, 2016; Cowell et al., 2012; O’Hara, 2005). Indeed, analysis including the duplicate records resulted species richness estimates reduced by >1000. Perhaps most importantly, there are vast regions and habitats of the CCZ that have been barely sampled at all. For example, there are only five published studies of rocky seamounts and outcrops in the CCZ, which appear to host very different communities (Cuvelier et al., 2020; Jones et al., 2021; Leitner et al., 2021; Durden et al., 2021; Bribiesca-Contreras et al., 2021). The CCZ is notable for high habitat heterogeneity, which will in turn sustain high biodiversity (Simon-Lledó et al., 2019; 2020). There are many regions of the CCZ with almost no published data at all, for example between the west and central CCZ (Figure 1). Even within relatively well-sampled areas such as contract areas in the eastern and central CCZ there are vast data and sampling gaps (for example YUZ2 has >420 sample stations (Grishenko et al., 2021) but only data for nodule fauna are available). This observation is supported by the data showing very high proportions of singletons (60% for named species, 70% for all species, named and unnamed, literature records only). These high proportions of singletons will reduce diversity estimates (Coddington et al., 2010). An important overall caveat is that is these estimates were made by pooling disparate studies, with variable sampling methods, sampling effort, size-fraction assessed and taxonomic approach (and even within studies, incomplete analysis by sample as many samples are only partly worked up also/ (Bonifacio et al., 2020).All indicators point to great unsampled diversity in the CCZ, but markedly high uncertainty. With all these factors in mind, we estimate that actual biodiversity exceeds our Chao1 estimate, potentially by several orders of magnitude.

**Global biodiversity comparisons**

There are few estimators of biodiversity in other broad-scale regions of the deep sea to compare this with. One study of the Southern Ocean deep-sea reported 674 isopod species of which a high proportion of 87% were new to science (Brandt et al., 2007), which is comparable to our numbers for CCZ isopods with an estimated 93% new (32 named species, 435 unnamed). For the Southern Ocean, over 8000 named species in total are recorded in a regional checklist, RAMS (De Broyer, 2022), of which >5000 are benthic (S table xx); estimators put Southern Ocean diversity at 11,000-17000 (Gutt et al., 2004). Total benthic metazoan species diversity recorded from the CCZ (including unnamed morphospecies) at 5124 is similar to the total of named benthic species for the Southern Ocean (and the overall estimate similar despite much lower sampling effort and data availability for the CCZ). However, this is clearly not a like-for-like comparison, Antarctica having a very specific environment. In the current study we did not assess biodiversity in non-metazoans in the CCZ, but there are indications that diversity is also high in foraminifera for example (Gooday et al., 2017) and where 20 new species and four new genera have been described over the past seven years (Gooday et al., 2017; 2018a, b, c; 2020; Kamenskaya et al., 2015). eDNA surveys have reported considerable undocumented microbial and meiofaunal diversity (Wear et al., 2021; Lejzerowicz et al., 2020), with evidence that the CCZ is in the higher range of diversity globally as well as showing high levels of endemism. Globally, there are at least 28,000 known deep-sea species found at depths >500 m (Glover et al., 2022) hence the current CCZ Checklist represents just 1.5% of these. Including unnamed morphospecies, this would rise to 17%, although this would include synonyms. Total marine species richness reviewed in Appeltans et al (2010) range from 300,000 (Costello et al., 2012) to 10 million (Grassle and Maciolek, 1992), while the latter regarded as a significant underestimate and former, underestimate (add refs). Coral species richness estimates may provide a better comparative measure- one could argue.. estimates of 830,000 for multi-cellular species excl fungi (Fisher et al. 2015) and a separate study, 673,000 for macrofauna only (Reaka &-Kudla et al. 1997) sampling effort.. compare other estimates- proportion wise rather than number, terrestrial systems

# Conclusions and future directions

The proportion of species new to science in the CCZ is commonly reported as being over 80%, but often without citation. Our study has provided the first quantitative support to that figure, being over 90% and clearly shows the large remaining taxonomic impediment to a reasonable understanding of CCZ biodiversity. A robust approach to open nomenclature in the medium term is essential (Horton et al., 2021). There has been a massive and welcome recent effort to increase taxonomic work in the CCZ however. We provide the first CCZ Checklist, which can support future taxonomic efforts including developing field guides for the region. Improved knowledge of CCZ biodiversity will have great value to environmental management, particularly in supporting taxonomic harmonisation of the multiple baseline and monitoring studies across contract exploration areas. This will allow more robust assessments of spatial and temporal patterns, impact and recovery, therefore providing an evidence-base for environmental impact assessments (EIAs), and regional environmental management plans (REMPs; Amon et al., 2022; Durden et al., 2017). Here we also make the first attempt at quantifying undescribed metazoan biodiversity in the CCZ. It is most likely a significant underestimate given systematic bias in non-parametric estimators (especially given the high proportion of singletons), but the scale of the underestimate is unknown. This leaves us with questions- how to estimate diversity with such vast uncertainty? Despite the importance of assessing biodiversity, little progress has been made here over decades now (Caley et al., 2014; Mora et al., 2013; Fisher et al., 2015). This partly reflects the statistical challenges of estimating species richness, particularly pertinent for the deep-sea. We recognise there is very high uncertainty overall in these estimates, but on balance, it is better to provide these figures given they are based on a synthesis of the published data and can be refined as additional data and potentially new statistical approaches become available.

A key consideration for the CCZ in particular given the possibility of future mining activities is the application of biodiversity data from an environmental management perspective. UNCLOS states that ‘no serious harm’ should occur from any mining activities, and that necessary measures should be taken to protect the environment from any harmful effects. A key question is what constitutes ‘serious harm’, this is often equated with no biodiversity loss (Niner et al., 2019; add refs). While extinction risk is often assumed to be lower in marine environments, this appears largely an artefact of lower taxonomic knowledge compared to terrestrial ecosystems (Webb & Mindel., 2015). Quantifying species ranges and rarity, key components of extinction risk, is a long while off for most CCZ species, and will require much more extensive sampling. The CCZ in fact represents one of the few remaining areas of the global ocean with high intactness of wilderness (Jones et al., 2016). Here however impact of fisheries and shipping activities were assessed in the region, but deep-sea mining risk was not. Our synthesis showing high diversity and many potentially unique species, alongside markedly high uncertainty, supports the application of the precautionary principle often cited as a guiding principle for environmental policy in the CCZ (add refs). Abyssal plains are a last frontier of discovery on earth and provide endless fascinating areas to ask questions on evolution. These are now beginning to be addressed in the CCZ (Smith et al., 2021) which will shed light both on this unique region and areas beyond.

# Experimental Procedures

(short version – star methods, and long version for online + supplementary)

*Data collection and processing*

All data were analysed and processed in R, version 4.0.2 (2020-06-22) "Taking Off Again" (R Core Team, 2020), and Microsoft Excel 365. All mapping was done in R and in Quantum GIS (QGIS), version 3.10, Coruña (QGIS.org, 2020).

Biological data were downloaded from the DeepData database web portal (<https://data.isa.org.jm/isa/map/>) on the 12th of July, 2021. The data selection was as follows: ‘Layers’ tab: ‘Mineral Type’: ‘Polymetallic Nodules’, ‘Location’: ‘Clarion Clipperton Fracture Zone’, Search tab, ‘Biological data’, ‘Point’, and to export the data, ‘export query’. The same search procedure was then done for ‘Trawl line’. For a full description of subsequent data processing, see S File xx). Data were also collected from the Ocean Biodiversity Information System (OBIS) and the Global Biodiversity Information Facility (GBIF). A search area was created covering the entire CCZ region. All mining exploration contract areas, both active and reserved, and APEI shapefiles were downloaded from the ISA database; combined into one shapefile in QGIS; and coordinates for a polygon covering the entire CCZ including the combined shapefile were established (see S file R script). GBIF occurrence data were downloaded from the web portal on the 12th of July, from all depths, using the polygon search function, with the CCZ polygon coordinates. OBIS occurrence data were downloaded as a Darwin Core file on the 12th of July using the ‘occurrence’ function in the robis package (Provoost & Bosch, 2017), with the same search polygon, for all depths. All records from GBIF and OBIS were mapped together with the CCZ shapefile, using the following R packages: GADMTools, sp, spData, spatialEco, maptools, rgdal and rgeos. All dataset records were then sub-selected by depth, with depths of 3000m and greater included. Some records without depth values were present, those falling within or near the CCZ shapefile were reviewed and included if valid, for example if a benthic species/taxa associated with a publication and a benthic collection method e.g. a box core sample; and/or a relevant reference in ‘datasetName’ or ‘associatedReferences’ column. As an additional check to ensure all relevant benthic records were selected and pelagic records removed, the scientific names recorded were cross-referenced to habitat information recorded in WoRMS (World Register of Marine Species). Following record selection by depth, datasets were remapped. The data selection by depth resulted in a significant reduction in records, with all records at depth falling within contract areas/APEIs or close by. The latter records falling outside the CCZ shapefile were reviewed to check all relevant records were captured. In the final data selection, all non-metazoan and fossil records were excluded from all datasets.

*Published Literature and INSDC*

A systematic review was undertaken according to the guidelines of PRISMA (Moher et al., 2009). The *a priori* research question was as follows: *what taxonomic information is available for benthic metazoans in the CCZ?* Online databases were searched for publications through the Natural History Museum (NHM) London library, including: Google Scholar, Scopus, ScienceDirect, and Web of Science. Citations were checked, and any additional relevant publications identified were included. References of all papers were systematically checked and added if they also had not previously been identified through database searches. The review was carried out primarily from 2nd February to 20th August 2021, with the date of last search the 1st of September, 2022. Search terms included: “Clarion Clipperton (Fracture) Zone”; “Central”/”East”/”Pacific”; new”/“species”/”genera”/”genus”/”family”/description”; “biodiversity”; “megafauna”; “macrofauna”; “meiofauna”; “community”/”composition”; “species”/”assemblages”; “taxonomic studies”; “ecology”; “genetic”; “genomic”; “polymetallic”/”manganese”/”nodule”. Within-journal searches were also conducted for key journals (e.g. Zootaxa) using the same search terms. Criteria for inclusion were publications with records of benthic metazoan taxa. Publications in all languages were included. The search was not confined to lower taxonomic ranks, with all records included regardless of the level of taxonomic resolution. Publications with no taxonomic records were excluded. Any publications solely examining pelagic taxa, microbes, or foraminifera (e.g. xenophyophores) were excluded. Records identified from imagery, e.g. ROV seabed surveys were included, i.e. the selection was not restricted to specimen-based studies. All size classes of metazoans were included. Relevant information was captured, for example faunal size category; taxonomic and sampling information; and compiled into tables (SDF 4; SDF 5). For records held on International Nucleotide Sequence Database Collaboration (INSDC) databases (mainly GenBank) and BOLD, accession numbers were collated from publications, either from tables within papers or supplementary files, and where key information was missing, e.g. marker, the databases themselves were cross-referenced. Taxonomic information was cleaned with the ‘taxon-match’ tool in WoRMS, a QA/QC function on the web portal where scientific names can be validated against the database. Identification qualifiers were standardised as per guidelines in the literature, e.g. n sp. recorded as sp. nov. (Horton et al., 2021; Sigovini et al., 2016).

*CCZ Checklist*

All scientific names were collated from the different data sources to create a checklist of known benthic metazoan species recorded from the region, the ‘CCZ Checklist’. Where names were only present in one data source, the relevant records were reviewed. For morphospecies, scientific name was also added, mapped to the lowest scientific level recorded above species. Names were recorded at their taxonomic level, and post taxon-match to WoRMS, higher taxonomic names were then inferred for the checklist, i.e. for species records present, the genus name was added if it was not already separately recorded. Any unaccepted names were replaced with accepted names, and where names were not found in WoRMS, this was recorded and the original name retained. A taxon match to WoRDSS the deep-sea node of WoRMS, was also done to ascertain if taxa were already logged as deep-sea using the Flanders Marine Institute VLIZ web-services (<https://www.lifewatch.be/data-services/>). Suspected potential pelagic taxa records e.g. Calanoida and Cyclopoida copepods; ostracods; hyperiid amphipods and Tomopteridae polychaetes were present. These groups were assessed by specialists, Geoff Boxhall, Pedro Martinez, (Copepoda); Simone Brandao (Ostracoda); author TH (Amphipoda) and authors AGG and TD (Polychaeta). After these assessments and cross-referencing ‘attribute’ information in WoRMS where available. Any pelagic names identified were removed from the final total, but retained in the main dataset, tagged as ‘pelagic’, and all records of pelagic species/taxa were removed for the diversity analysis (S File xx). Any name with a known degree of taxonomic uncertainty was noted and removed from a version of the CCZ Checklist *sensu stricto*, e.g. a name interpolated from an imagery record, from a morphospecies/temporary name or with any of the following qualifiers: aff.; cf.; indet; incertae sedis; sp. inc. (any records with qualifiers- sp. nov were included at species level or sp.; spp. or gen. nov at genus level) (S File xx). For the two major faunal groups, the arthropods (tanaids and isopods) and the annelids (polychaetes), the names were assessed by authors TH and TD respectively for general data checking and to gauge the general level of potential misidentification in key groups. Here the type locality (including depth) was determined from the original description where available, otherwise the record was checked on WoRMS.

A separate list of ‘open nomenclature’ temporary names was collated for analysis with any duplicates across datasets removed (S file xx). Open nomenclature is a system of signs to describe uncertainty around identifications, or designate morphospecies (Horton et al., 2021; Sigovini et al., 2016). Temporary names are also termed ‘morphospecies’, ‘informal names’, ‘working species’, morphotypes’ or ‘molecular/operational taxonomic units’ (M/OTUs; Horton et al., 2021; Sigovini et al., 2016). These terms differ slightly conceptually, for example morphotype generally refers to a temporary name given to megafauna identified solely from imagery (e.g. ROV footage), and MOTUs to taxa have been discriminated to species level by comparison of genetic sequence data. For consistency, here we use the term ‘morphospecies’ which while less general than temporary names, does specify species level unlike ‘temporary name’, unless specifically referencing names recorded as ‘undescribed new species/genera’. The latter were distinguished as an undescribed species or genus if specifically recorded as such (e.g. ‘*Aurospio* new species A’ or similar). Species recorded with qualifiers, i.e. cf. and aff were included. These records were recorded at genus level only for scientific name and tagged as ‘open nomenclature’, with the verbatim species name recorded in the Darwin Core term ‘taxonConceptID’. ‘new species’ table- subselection of studies. ‘metaanalysis’ – most studied fauna only- major macrofaunal groups, papers where all record identified to species level, group assessed in round as opposed to spp description where only one or 2 spp ADD

*Diversity estimates / Diversity and distribution / community composition*

Firstly, simple metrics of biodiversity such as total number of new species were estimated, for example by station, contract area, and size class, from each data source. Species accumulation curves were plotted for species accumulation over sampling effort (defined as number of sampling events), with 1000 randomisations for all; with the following R packages: vegan (Oksanen et al., 2018), picante (Kembel et al., 2010) and knitr (Chao, 2014, 1987, Cowell & Coddington, 1994). Rarefaction curves- no indiv vs no spp add Curves were plotted separately for named species only, and all species- formal names and morphospecies combined), for all DeepData records pooled and literature records, with abundance data (Chao1). Chao1, Chao2, ES(2000) total species richness estimates (and associated standard error) were estimated in vegan (Chao, 1987, 2014). Presence/absence species matrix tables were generated with the R package FuzzySim (Barbosa, 2015). Upset plots (UpSetR) were used to visualise patterns in species common or distinct by region and contract area, these plots allow visualisation of multiple sets in the data, such as species richness intersections with region (Gehlenborg et al., 2019; Conway et al., 2010).

Species level diversity by region- DD and lit data combined- summary

Quantification of sampling gaps/ taxon approaches and impact of duplication on diversity metrics. Assess separately by dataset?

Sampling effort (and comparions of diversity to other regions).

Singletons- occurrence data, abundance where recorded

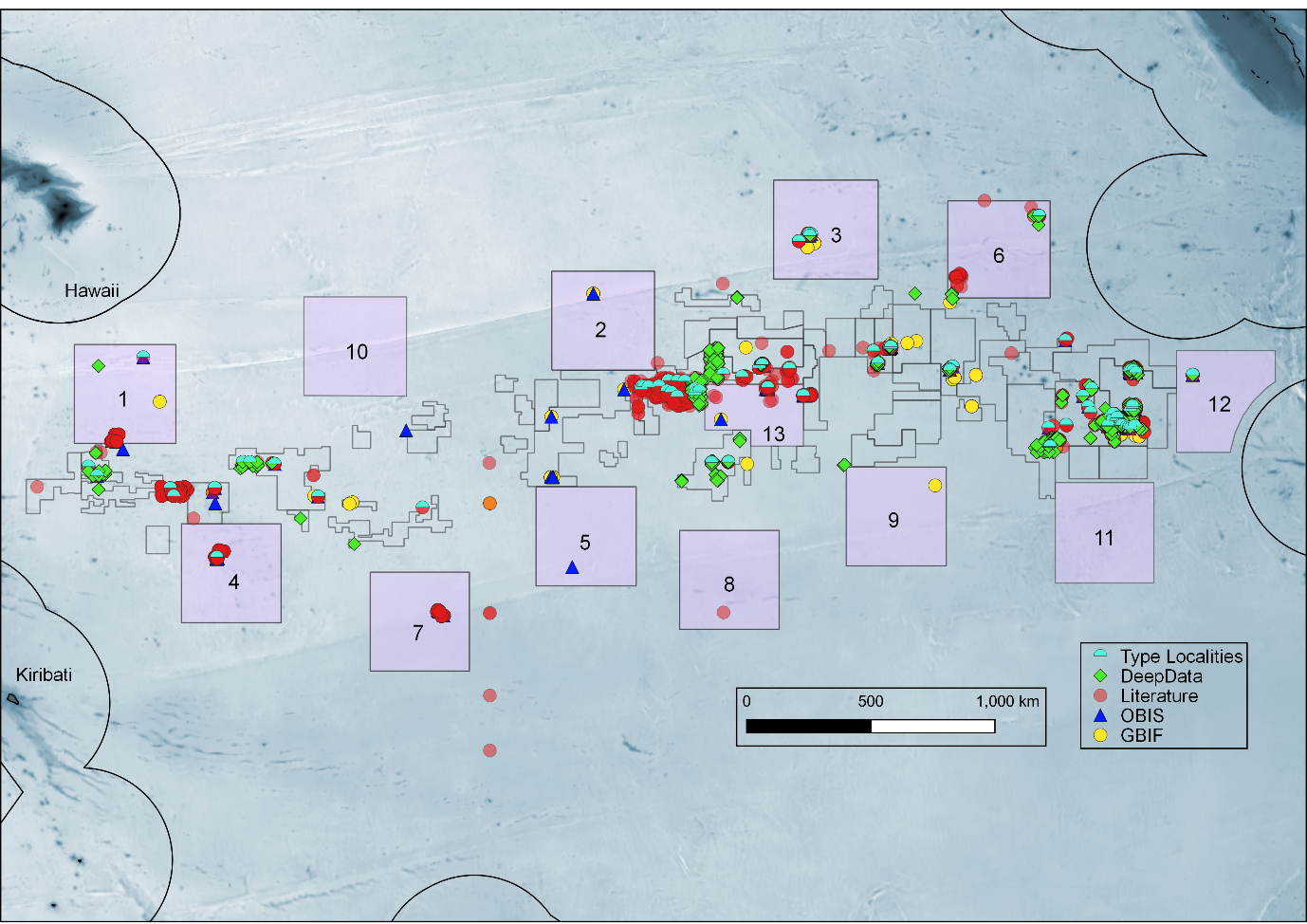
inflation of informal names over time, underestimate- cryptic diversity- but latter somewhat group specific

Describe type locality

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# Figures

**Figure 1** All geolocated published records of benthic metazoa from the literature and databases (DeepData, OBIS and GBIF). The type localities of all species described from the CCZ to date are also shown (182 species in total). APEIs – Areas of Particular Environmental interest shown (add into legend), 10-13 are post nov 2021 [update without EQPAC, add inset map, move Hawaii text, add Mexico]

Chart

Description automatically generated

**Fig. 2a** proportion of recorded diversity that is undescribed: known/named benthic metazoan species from CCZ Checklist in blue, morphospecies names in pink. 2b, rates of species descriptions/taxonomic work in the CCZ. Cumulative totals of new taxa described and taxonomic publications per year, over the period 1980-2022, ’all descriptions’ includes descriptions of new species, genera and families combined. (remove grey background, increase font size, redo with updated data)

Chart

Description automatically generated

**Figure 3** Family and Species diversity in the Clarion-Clipperton Zone. (A) family accumulation rates with sampling effort, Chao2 estimator 440 (+/-22 SE); N = 3257; (B) species accumulation rates

with sampling effort (both named and morphospecies); Chao2 estimator 9135 (+/-302 SE); N = 1356. (C) taxon rank/order versus log of total per taxon order – 1- phylum, 2- class, 3- order, 4- family, 5- genus. (D) rarefaction, all sites as CCZ.

Fint size

Chart

Description automatically generated

S Fig xx all species records- depth vs phyla (how to disentangle from taxon approach- no of records) – ask Erik

Other supp figs?

# Tables

Table SX: subset of studies with high certainty described- unknown but new

(incl Wilson, 2017? Other papers? Add column – method of description- which are DNA only)

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Publication | Taxonomic Group | Described by | Total spp. | Total new spp. | Prop new spp. |
| Brix et al., 2020 | Arthropoda (Isopoda) | Mol + morph | 152 | 143\* | 94 |
| Blazewicz et al., 2019b | Arthropoda (Tanaidacea) |  | 96 | 95 | 99 |
| Bonifacio et al., 2020 | Polychaeta |  | 391 | 288 | 74 |
| Glover et al., 2002 | Polychaeta |  | 382 | 374\* | 98 |
| Smith et al., 2008 | Polychaeta |  | 48 | 44 | 92 |
| Bonifacio & Menot, 2019 | Polychaeta (Polynoidae) |  | 25 | 24 | 96 |
| Bonifacio et al., 2021 | Polychaeta (Polynoidae) |  | 95 | 78 | 82 |
| Wiklund et al., 2019 | Polychaeta (Scolecida) |  | 23 | 23 | 100 |
| Guggolz et al., 2020 | Polychaeta (Spioniformia) |  | 12 | 11 | 92 |
| Neal et al., 2022a | Polychaeta (Spioniformia) |  | 25 | 23 | 92 |
|  |  |  | **1249** | **1103** | **92** |

\*Uncertainty in whether species are new (Brix et al., 2020- uncertainty in overall totals)

S Table 1. Summary of available published data, utilised in the current study/compiled and synthesised Summary of data availability in all data sources searched, including literature (include? Inc notes column?

|  |  |  |  |
| --- | --- | --- | --- |
| Data Source | Total Records | Publications | Notes |
| Deep Data | 40518 |  | Total of 52,222 including non-metazoa/records without taxonomy |
| Literature | 7283 | 163 | 27,400 geolocated records (figure 1) |
| OBIS | 2185 |  |  |
| OBIS (ISA node) | 48554 |  | DeepData records published on OBIS via the ISA node in June 2021 |
| GBIF | 2405 |  |  |
| GenBank | 4738 |  | 5 NCBI databases also identified containing genomic datasets |
| BOLD | 1674 |  | 3 BOLD databases also containing multiple sequences |
| TOTAL | **106377** |  |  |

# Supplementary data files

All data files

Checklist- includes pelagic taxa- non-comprehensive though as these were filtered at multiple steps..

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Coddington et al., 2009

Coddington et al., 2010

Costello et al., 2012, Costello & Chaudary, 2017

Cowell et al., 2012

DeBroyer et al., 2022?

Durden

Fisher et al., 2015

Grassle and Maciolek, 199x

Griffiths, 2010

Horton et al., 2021

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