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How many metazoan species live in the world's largest mineral exploration region?

Highlights

- We provide the first checklist for the Clarion Clipperton Zone (CCZ) metazoan fauna

- 5,142 unnamed species (informal names) are recorded from the CCZ

- Total estimates of species richness range from >6,000–>8,000

- An estimated 88%–92% of species in the CCZ region in total are undescribed

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In brief

Species-level biodiversity information is key to understanding ecosystems and tracking environmental impacts. Rabone et al. provide the first checklist (436 species) and total species estimates (>6,000–>8,000) for the world's largest mineral exploration region, the CCZ. Estimates provide a baseline to build biodiversity knowledge at a regional scale.

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How many metazoan species live in the world's largest mineral exploration region?

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SUMMARY

The global surge in demand for metals such as cobalt and nickel has created unprecedented interest in deep-sea habitats with mineral resources. The largest area of activity is a 6 million km^2 region known as the Clarion-Clipperton Zone (CCZ) in the central and eastern Pacific, regulated by the International Seabed Authority (ISA). Baseline biodiversity knowledge of the region is crucial to effective management of environmental impact from potential deep-sea mining activities, but until recently this has been almost completely lacking. The rapid growth in taxonomic outputs and data availability for the region over the last decade has allowed us to conduct the first comprehensive synthesis of CCZ benthic metazoan biodiversity for all faunal size classes. Here we present the CCZ Checklist, a biodiversity inventory of benthic metazoa vital to future assessments of environmental impacts. An estimated 92% of species identified from the CCZ are new to science (436 named species from a total of 5,578 recorded). This is likely to be an overestimate owing to synonyms in the data but is supported by analysis of recent taxonomic studies suggesting that 88% of species sampled in the region are undescribed. Species richness estimators place total CCZ metazoan benthic diversity at 6,233 (+/−82 SE) species for Chao1, and 7,620 (+/−132 SE) species for Chao2, most likely representing lower bounds of diversity in the region. Although uncertainty in estimates is high, regional syntheses become increasingly possible as comparable datasets accumulate. These will be vital to understanding ecological processes and risks of biodiversity loss.

INTRODUCTION

The Clarion-Clipperton Zone (CCZ) is an area of seabed roughly twice the size of India (approx. 6 million km^2), spanning 5°–20° North between the Clarion and Clipperton oceanic fracture zones, and 115°–160° West. This vast region, between Hawaii, Kiribati, and Mexico, lies entirely within areas beyond national jurisdiction (ABNJ), legally designated under the United Nations Convention on the Law of the Sea (UNCLOS). The region is composed of abyssal seafloor at depths of 4,000–6,000 m, characterized by muddy sediments overlain by potato-sized polymetallic nodules, rich in minerals. Despite the darkness and low food availability, nodule field habitats contain diverse communities of benthic invertebrate fauna, albeit at low densities compared with coastal and shelf ecosystems.[1]

Mineral exploration began in the CCZ in the 1960s, later formalized under the International Seabed Authority (ISA).[2] Currently, there are 17 contracts for mineral exploration covering 1.2 million km^2. Despite decades of intensive exploration, there

has been a historical lack of taxonomic work in the region. Large-scale CCZ environmental surveys conducted in the late 1970s to early 1990s produced lists of informal species names,[3] but few species were formally described. Informal names refer to species differentiated by morphology and/or molecular data and recorded with temporary names before formal description[4,5] (hereafter "unnamed species"). These names present challenges to taxonomic standardization and regional-scale synthesis of biological data. Molecular work provides an arbiter for compatibility across identifications,[6–8] but is not without challenges. Adding to this complexity, cryptic species, or those with similar or identical morphology but separate molecular lineages are numerous in deep-sea environments,[9,10] including the CCZ.[11,12]

Other factors contributing to the lack of comparability across datasets are variable sampling methods,[13] and more fundamentally, a lack of data.[14] As a result, CCZ synthetic works are rare and primarily focus on particular taxa, size classes, and/or regions.[15–19] Information gaps span all size classes, from
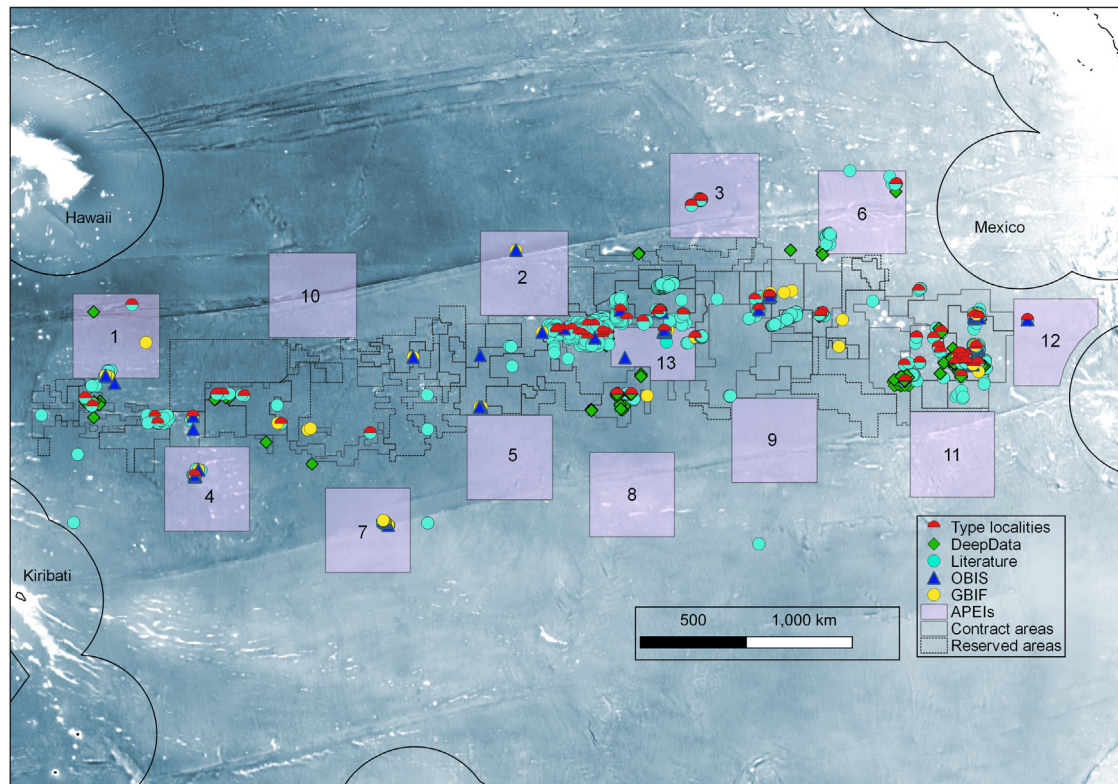
Figure 1. All geolocated published records of benthic metazoa from the literature and databases
Areas of Particular Environmental Interest (APEIs) and exploration mining contract areas, both active and reserved, are shown in outline. The type localities of all species described from the CCZ to date are also shown (185 in total). Background layer: the GEBCO Grid, 2022.
See also Figures S4–S6, the key resources table, and supplemental information.

small meiofauna (typically >150 μm) and macrofauna (> 300 μm), to large megafauna (typically >10 mm).[20] The data deficiency is particularly notable for the network of Areas of Particular Environmental Interest (APEIs), regions protected from mining[21] (but see Bonifácio et al.,[15] Brix et al.,[17] Błażewicz et al.,[22] and Hauquier et al.[23]). This has hampered assessment of their representativeness, with clear implications for environmental management.[20] Biodiversity knowledge is essential to robust assessments of species ranges and rarity over time and space, and therefore to evidence-based Regional Environmental Management Plans (REMPs) and future environmental impact assessments (EIAs) in the event of mining operations.[24,25] The need for regional-scale environmental management has been increasingly recognized by policymakers and the ISA,[21] supporting a recent resurgence of comparative taxonomic work, including incorporation of DNA methods that allow for a more comparable methodology.[13,26] Critical to the development of CCZ biodiversity knowledge is the creation of a curated checklist of known taxa and estimates of total undescribed species. Building on recent regional syntheses,[20] we present the first comprehensive synthesis of benthic metazoan biodiversity and checklist for this vast region on the eve of possible large-scale mining operations. We make these data and interpretations open to all stakeholders to inform the ongoing debate on deep-sea mineral extraction and to grow our knowledge of the largest ecosystem on our planet.

RESULTS

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

The synthesis produced >100,000 records compiled from seven data sources (Figure 1, key resources table). Recent growth in taxonomic efforts for the CCZ is evident, particularly over the past 5 years (Figure 2A). To date, 219 taxa new to science (families, genera, and species) have been described from the CCZ. Most of these new taxa have been described in recent years, with only seven descriptions prior to the year 2000. The CCZ Checklist presented here comprises 436 named benthic metazoan species of all size classes (Table 1; Data S1). These include 185 species, three families, and 31 genera described from the CCZ (see Figures 2 and 3). Only six of the 185 CCZ new species have also been recorded elsewhere, namely the sea cucumbers *Psychronaetes hanseni* (Pawson, 1983)[41] and *Psychropotes dyscrita* (Clark, 1920)[32]; the nematode, *Erebussau tenebricosus* (Bussau, 1993) Bezerra, Pape, Hauquier & Vanreusel, 2021[36]; the carnivorous sponge, *Axoniderma longipinna* (Ridley & Dendy, 1886)[42]; the crinoid *Hyocrinus foelli* Roux & Pawson, 1999[43]; and the antipatharian coral, *Abyssopathes anomala* Molodtsova & Opresko, 2017[31] (latter in Figure 3).

The CCZ Checklist records 27 phyla, 49 classes, 163 orders, 501 families, and 1,119 genera in total (Table 1). For all species-level identifications in the Checklist, 42% are based on morphology and molecular data (185/436), 50%, morphology only (217/436),

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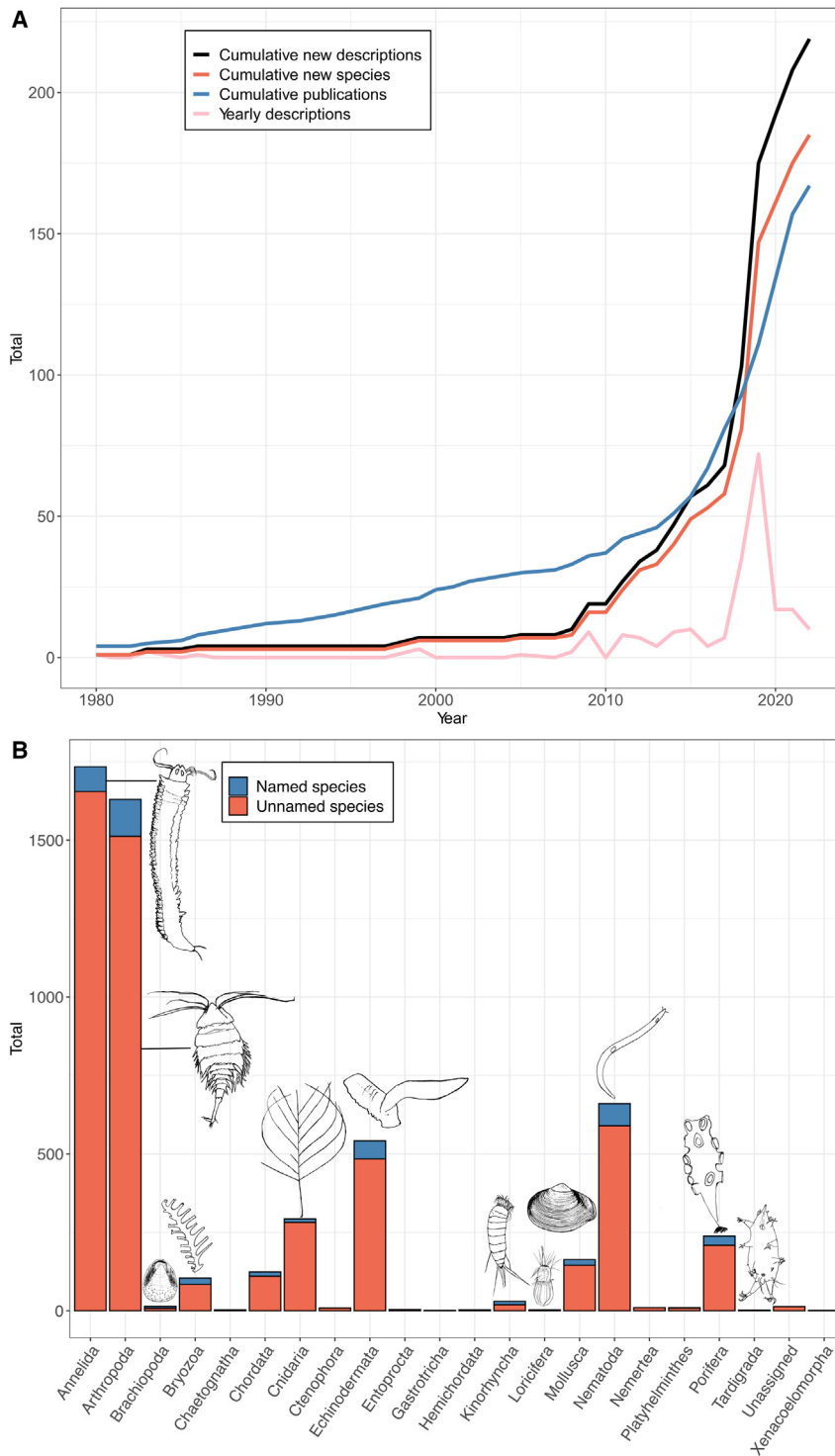
Figure 2. Rates of species descriptions in the CCZ; proportion of species diversity in the CCZ that is undescribed

(A) Rates of new descriptions and publications in the CCZ. Cumulative totals of new taxa (families, genera, and species combined) and new species described from the CCZ and taxonomic publications per year, over the period 1980–2022. Yearly totals of new descriptions also shown.

(B) Proportion of recorded benthic metazoan diversity from the CCZ that is undescribed: named species recorded in red (both those described from the CCZ and elsewhere), unnamed species shown in blue ("unassigned" are records not identified to phyla). Depictions of some of the new CCZ species by phyla: Annelida, *Neanthes goodayi* Drennan, Wiklund, Rabone, Georgieva, Dahlgren & Glover, 2021[27]; Arthropoda, *Siphonis aurreus* Mercado-Salas, Khodami & Martínez Arbizu, 2019[28]; Brachiopoda, *Oceanithyris juveniformis* Bitner & Zezina, 2013[29]; Bryozoa, *Pandanipora helix* Grischenko, Gordon & Melnik, 2018[30]; Cnidaria, *Abyssopathes anomala* Molodtsova & Opresko, 2017[31]; Echinodermata, *Psychropotes dyscrita* (Clark, 1920)[32]; Kinorhyncha, *Meristoderes taro* Sánchez, Pardos & Martínez Arbizu, 2019[33]; Loricifera, *Fafnirloricus polymetallicus* Fujimoto, 2020[34]; Mollusca, *Ledella knudseni* J. D. Taylor & Wiklund, 2017[35]; Nematoda, *Odetenema gesarae* Bezerra, Pape, Hauquier & Vanreusel, 2021[36]; Porifera, *Chaunoplectella megapora* Wang, Zhang, Lu & Wang, 2018[37]; and Tardigrada, *Moebjergarctus clarionclippertonensis* Bai, Wang, Zhou, Lin, Meng & Fontoura, 2020.[38]

See also Data S1 and S2 and Table S1.

species, different names for the same species), resulting in a corrected total of 5,142 (Table 1; Data S2).

What types of animals live in the CCZ?

The CCZ Checklist illustrates the overall composition of the CCZ fauna identified to date. The five most speciose phyla are the Arthropoda (27%), Annelida (18%), Nematoda (16%), Echinodermata (13%), and Porifera (7%) (Figures 2B and 4; all size fractions, named species only). Proportions for unnamed species are similar, apart from a predominance of Annelida (class Polychaeta, Figures 2B and 4). In the World Register of Deep-Sea Species (WoRDSS, 2023),[44] a thematic node of the World Register of Marine Species

the remainder, data not available (Data S1). 51% of the new species are described solely by morphology, and for meiofauna, 86% are described on morphology alone. For the key macrofaunal groups (tanaids, isopods, and polychaetes), 23% of species in the Checklist have type localities outside the CCZ, including other ocean basins (33/145). In total, 5,367 unnamed species are recorded, an estimated 3.9% of which are synonyms (sensu named

(WoRMS, 2023),[45] there are currently 36,579 named metazoan deep-sea species found globally at depths >500 m. Within WoRDSS, the most speciose phyla are Arthropoda, 31%, Mollusca, 17%, Chordata, 15%, and Annelida and Echinodermata, 10%. Key differences include relatively more annelids, nematodes, and echinoderms in the CCZ (and to a lesser degree, sponges and bryozoans), and conversely more molluscs (class

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Table 1. Summary of benthic metazoan biodiversity in the Clarion-Clipperton Zone based on CCZ Taxonomic Knowledge (published taxonomic and ecological works); the CCZ Checklist (summary of all named benthic metazoans from all published data sources) and CCZ Biodiversity Estimators (based on the analysis in this study)

CCZ Taxonomic knowledge		CCZ Checklist		CCZ Biodiversity Estimators	
New species:	185	Phyla:	27	Unnamed species:	5,142
New genera:	31	Classes:	49	Total species:[a]	5,578
New families:	3	Orders:	163	Chao1 species richness:	6,233 (+/−82 SE)
Total CCZ Descriptions:	219	Families:	501	Chao2 species richness:	7,620 (+/−132 SE)
Taxonomy/ecology papers:	168	Genera:	1,119	ACE estimator:	6,109 (+/45 SE)
Papers with descriptions:	64	Species:	436	Jacknife2 estimator:	8,514 (+/−438 SE)
N/A		Species inc. qualifiers:[b]	654	N/A	

[a]Total species from the CCZ: combined total of named species and unnamed species. The overall proportion of unnamed species diversity in the CCZ is estimated at 92% (5,142/5,578). Sample sizes for CCZ species Biodiversity Estimators: Chao1 and ACE, N = 112,428 ind., S(obs) = 4716; Chao 2 and 2nd order Jacknife, N = 1,668 samples, S(obs) = 4,779. Extrapolation max. N: Chao1: 224,858 ind.; Chao2: 3,336 samples. See also Table S1, Data S1–S5.

[b]The CCZ Checklist contains 436 named species in total without identification qualifiers (i.e., cf. aff.) and 654 species including those recorded with identification qualifiers e.g. c.f. of aff (i.e., in open nomenclature) or identified solely from imagery.

Gastropoda) and chordates (class Teleostei) in WoRDSS (Figure 4). Another notable difference at class level is that Holothuroidea (named and unnamed) are relatively more specious in the CCZ than other key echinoderm classes (Asteroidea, Ophiuroidea) compared to WoRDSS. Though many faunal gaps are evident in the CCZ Checklist across phyla (e.g., no Pycnogonida in Arthropoda), these groups are recorded from the CCZ in the unnamed species list (Data S2).

Examining common faunal groupings, 50% of the species in the Checklist are macrofauna (220), with similar proportions for megafauna, 28% (122), and meiofauna, 22% (96). Similarly, most studies primarily assess macrofauna (46%), followed by megafauna (30%) and meiofauna (22%). Descriptions by size class (families, genera, and species combined) are 153 for macrofauna, 24 for megafauna, and 42 for meiofauna. A dominant feature of the CCZ is the unusual combination of mud and hard substrate/nodule fauna. Overall, 14% of named species and 13% of unnamed species in the CCZ are estimated to be primarily nodule dwellers (Data S1 and S2). Several nodule megafauna descriptions (cnidarians and sponges) have recently been published[37,39,40,46,47]; but only two quantitative studies for metazoan nodule fauna.[48,49] The majority of CCZ macrofaunal nodule dwellers (primarily bryozoans and sponges) are undescribed (Figure 2, Data S2), a rare exception being a recent monograph on Bryozoa describing 16 species, nine genera, and two families new to science.[30]

How many species might live in the CCZ?

The Chao1 estimator (abundance-based) for total species richness in the CCZ is 6233 (+/− 82 SE, N = 112,429 ind., S(obs) = 4,716) and Chao2 (sample-based), 7,620 (+/−132 SE; N = 1,668 samples, S(obs) = 4,779; Table 1). Species rarefaction and accumulation curves are far from reaching an asymptote (Figures 5 and S1). Other species estimates range from 6,109 (+/42 SE), ACE to 8,514 (+/−438 SE), Jacknife2 (Table 1). At lower taxonomic levels, the family accumulation curve approaches asymptote, with an estimated total family richness of 469 total (+/−18 SE, N = 70,597 ind., F(obs) = 406) for Chao1 and 544 total (+/−24 SE; N = 2,179 samples, F(obs) = 423) for Chao2 (Figures 5 and S1). These estimates are based on a

subset of the data where abundance and site information are available. In comparison, the CCZ Checklist incorporating all records includes 501 families in total. Estimates of total genera range from 947 (+/−26 SE) for Chao1 to 1,034 (+/−32 SE) for Chao2, with relatively more flattening of rarefaction curves than for species but still far from asymptote (Figures 5 and S2). This compares to 1,119 genera in the Checklist (Table 1). Sampling completeness curves show higher completeness for family-level estimates than species, and higher completeness for Chao1 than Chao2 estimates (Figure S3).

The proportion of undescribed species in the CCZ overall is estimated at 92% (5,142 unnamed species/5,578 named and unnamed species combined; Table 1). The subset-analysis of 18 publications provides an average figure of 88% undescribed species (Table S1). Proportions undescribed within the major macrofaunal groups range from 99.4% for tanaids[3,22] to 96.8% for isopods[3,17] and 87% for polychaetes[11,15,50–56] (Table S1). The figure of 92% undescribed CCZ species is similar to the proportion of known global marine (eukaryotic) species currently in WoRMS[45] versus the global estimate of Mora et al.[57] at 89% (241,129 described versus 2,200,000 estimated). It is notably higher than the ranges of Appeltans et al.,[58] from 59%–70% (241,129 described compared to 704,000–972,000 estimated).

Distribution of sampling effort

Sampling effort, as density of unique sampling sites, shows a highly uneven distribution across the region. Samples are concentrated in central and eastern CCZ contract areas, and large regions with very few samples are evident (Figure S4). APEIs have very low density of sampling or no samples at all. Large regions, particularly between the west and central CCZ, are close to unsampled (Figures 1 and S4). The density of sampling is highest at certain depths (e.g., ~4,200m, ~5,000m; Figure S5). These densities correlate with depths of the contract areas in the eastern and central CCZ (Figure S6). Where abundance data are available, 37% of species occur as singletons, i.e., represented by a single specimen across all sampling deployments (1,586/4,409), indicating extensive under-sampling. Of these singletons, 91% are in mining/reserved areas/the vicinity (1,441), the remainder (145) are found only in

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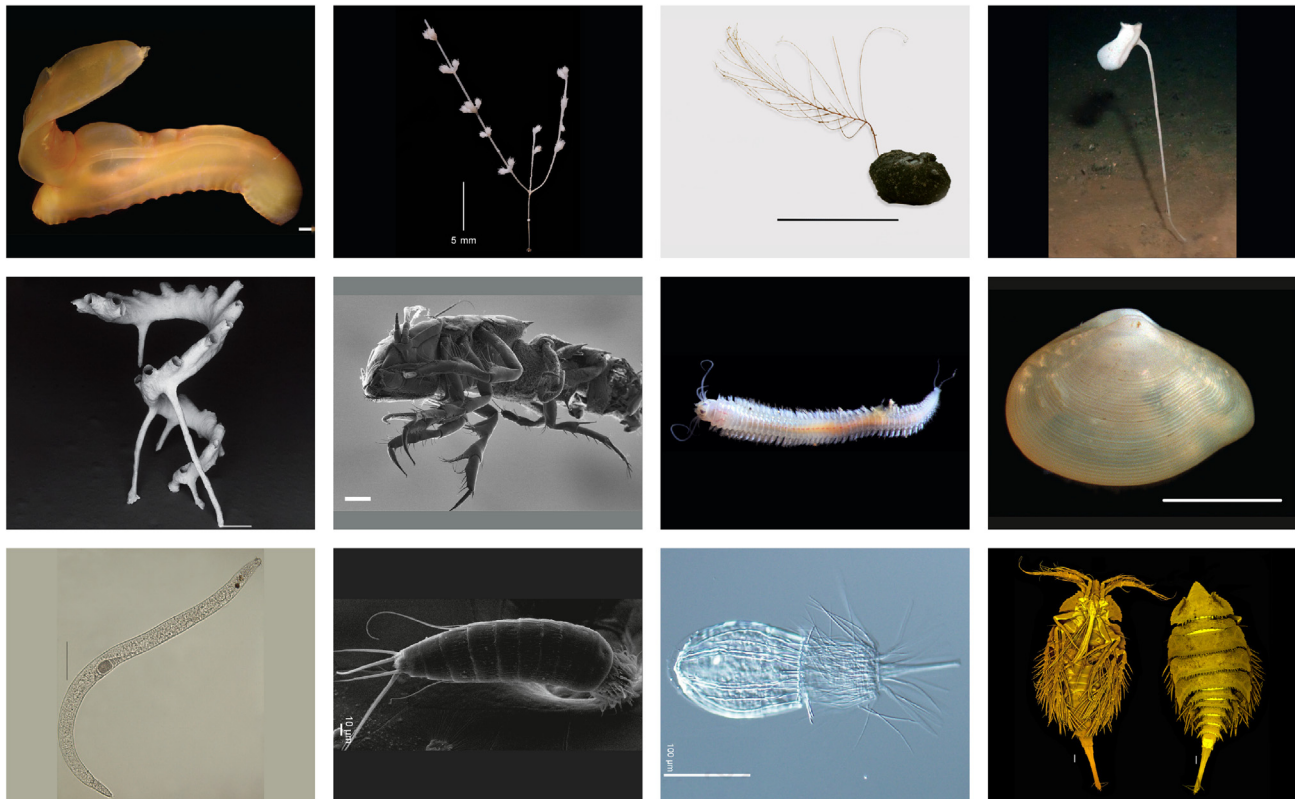
Figure 3. Fauna from the CCZ

(A–J) All fauna are species described from the region and illustrating a range of phyla and size classes, (A) the sea cucumber, *Psychropotes dyscrita* (Clark, 1920),[32] commonly known as the "gummy squirrel" (scale bar: 5 cm); (B) the primnoid coral *Abyssoprimnoa gemina* Cairns, 2015[39] (scale bar: 5 mm, note the rights to this image are owned by Springer Nature who have granted permission for reuse); (C) the antipatharian coral, *Abyssopathes anomala* Molodtsova & Opresko, 2017[31] (scale bar: 2 cm); and (D) the hexactinellid sponge, *Sympagella clippertonae* Herzog, Amon, Smith & Janussen, 2018.[40] (scale bar: 1 cm).

Row 2, (E) the cyclostomatid bryozoan, *Pandanipora helix* Grischenko, Gordon & Melnik, 2018[30] (scale bar: 500 μm); (F) the isopod, *Macrostylis metallicola* Riehl & De Smet, 2020[7] (scale bar: 0.2 mm); (G) the polychaete, *Neanthes goodayi* Drennan, Wiklund, Rabone, Georgieva, Dahlgren & Glover, 2021[27]; and (H) the mollusc, *Ledella knudseni* J. D. Taylor & Wiklund, 2017[35] (scale bar: 0.5 mm).

Row 3, (I) the nematode, *Odetenema gesarae* Bezerra, Pape, Hauquier & Vanreusel, 2021[36] (scale bar: 100 μm); (J) the kinorhynch, *Meristoderes taro* Sánchez, Pardos & Martínez Arbizu, 2019[33] (scale bar: 10 μm); the loriciferan, *Fafnirloricus polymetallicus* Fujimoto, 2020[34] (scale bar: 100 μm), and the copepod, *Siphonis aurreus* Mercado-Salas, Khodami & Martínez Arbizu, 2019[28] (scale bar: 100 μm).

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APEIs (Data S3 and S4). Most species are recorded in the eastern CCZ, closely followed by the central CCZ, with few in the west (Figure 6). The majority of all species are recorded from contract or reserved areas, with few in APEIs. Overall, 95% of named/unnamed species have not been recorded in the APEIs.

DISCUSSION

Species richness estimates are likely to increase as the data improve

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 for the current state of knowledge while placing the CCZ in a global context.

At species level, it is clear that sampling of the CCZ is very far from complete. Species are accumulating rapidly with increasing samples, with rarefaction and accumulation curves far from asymptote (Figures 5 and S1). Estimates at family level may be more robust given the lower likelihood of synonyms and misidentifications than for species.[59] The Chao1 total family estimate of 469 (+/18 SE) falls short of the current total in the Checklist at 501, but Chao2 at 544 (+/−24 SE) exceeds it. Family-level diversity is expected to be higher than is currently recorded in the Checklist given evidence of extensive under-sampling and the observation that curves have not reached asymptote (Figures 5, S1, and S2). Chao2 (sample-based) estimates exceeding the Checklist appear more robust, which may partly stem from Chao2 accounting more for missed data in surveys. However, few species records in the dataset represent whole-sample analyses (i.e., only select taxa are identified), likely contributing to underestimation of diversity in these estimates also.[60,61]

Data duplication can contribute to underestimates of diversity, as relative proportions of rare species, including singletons, will be affected.[15,62–66] Extensive record duplication is evident in the ISA database DeepData, estimated to be at least a quarter of the total. Although removed for final analysis, further duplication is suspected but cannot be definitively identified owing to
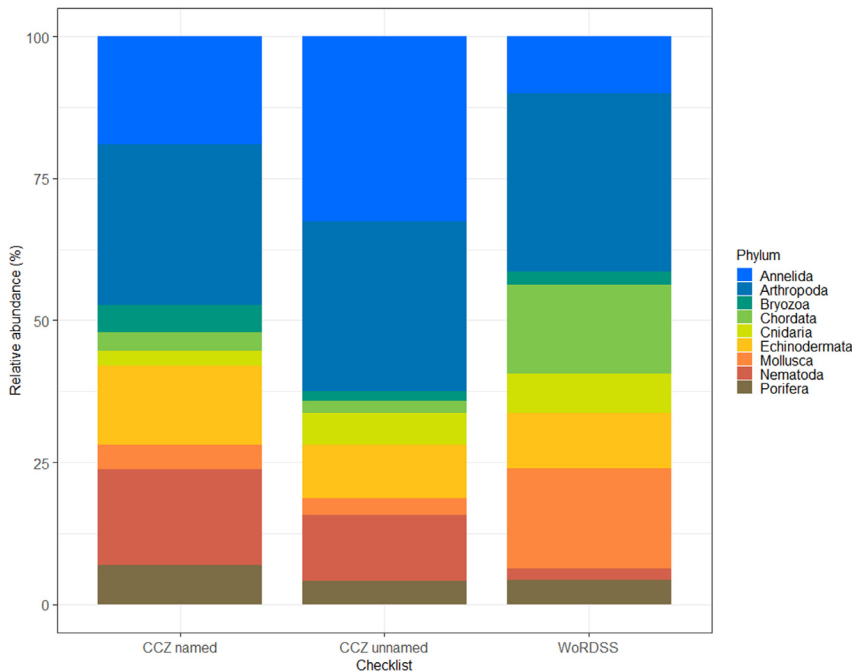
Figure 4. Phylum-level composition of CCZ and global benthic metazoan checklists
Relative abundance of phyla in the CCZ Checklist—named/known species (Data S1); the CCZ unnamed species list (Data S2); and all global deep-sea metazoan species recorded in WoRDSS (World Register of Deep-Sea Species)[44] on 1st January, 2023.

prevalent in the deep sea[9,10,82,83] and previously recorded from the CCZ.[11,12] Resolving these identifications requires genetic data both from the CCZ specimen and the type locality of the species it most closely resembles. Diversity based solely on morphological assessment can underestimate biodiversity by 20%–25%.[82,84] Although most of the CCZ new species have been described since the advent of DNA taxonomy methods (Figure 2A), 51% are described by morphology only. This figure rises to 86% for meiofauna, partly reflecting challenges of molecular sub-sampling from small-sized specimens.[85] Unknown cryptic speciation may be high in this size fraction for the CCZ[33] but this may be quite taxon-specific.[86] The figure of 92% of species undescribed is likely to be overestimating undescribed species owing to synonyms, but underestimating given known levels of cryptic species[11] and under-sampling in the CCZ (Figure S4). In the subset-analysis of taxonomic studies, the potential for misidentification is greatly reduced as groups are examined by their specialists (Table S1). This provides an additional line of evidence to support ~90% of CCZ species being undescribed.

underlying limitations of the database.[67] Including the known duplicates, species estimates are >1,000 lower.

Perhaps most importantly for these estimates, some regions and habitats of the CCZ have barely been sampled at all. For example, there are only six published studies of rocky seamounts and outcrops, which appear to host very different communities.[68–73] The CCZ, with abundant nodules and rocky outcrops, exhibits high habitat heterogeneity[16,74] compared with sedimented abyssal plains[75,76] (although a recent study suggests rocky outcrops may be more common than widely assumed[77]). This unusual "mosaic" habitat of nodule and sediment at local scales supports relatively higher benthic biodiversity.[16,74,78,79] Overall, many regions of the CCZ are almost unsampled (Figures 1 and S4) and this data deficiency will contribute to underestimation of diversity for the region.

Estimates of species richness are subject to other biases which can either inflate or reduce projections. Synonyms for unnamed species appear rare at 4%, but additional synonyms yet to be identified are inevitable, which would inflate the species estimate. Inflation of informal names can also accrue over time as designations change, and names proliferate. Misidentifications could increase or reduce the diversity estimates, but similarly contribute to overall uncertainty. An unknown proportion of the named species in the CCZ Checklist will be misidentified, owing in part to the lack of regional field guides. Conversely some of the unnamed species may be known species yet to be correctly identified. The lack of field guides can also contribute to range-inflation of cosmopolitan species.[80,81]

For the key macrofaunal groups in the CCZ Checklist (polychaetes, tanaids, and isopods), 23% of species have type localities outside the region, including other ocean basins (33/145). Although wide-ranging benthic species have been confirmed,[80,81] including in the CCZ[26], the 23% may be undescribed cryptic species (or species complexes), particularly

Where does CCZ biodiversity fit in a global context?
Species composition of the CCZ Checklist differs from WoRDSS, even at phylum level (Figure 4). Though some trends (such as relatively high diversity of holothurians) may be real, they will be heavily influenced by taxonomic trends, size fractions assessed, sampling bias, and availability of specialists. The majority of species (named and unnamed) are macrofauna, reflecting numerous studies on this size class. Megafauna, comprising the largest and thereby least abundant species[87] are rarely collected, compromising species-level identification. Aside from descriptions, there are only two synthetic taxonomic checklist studies with archived vouchers that cover multiple megafaunal taxa,[88,89] and three covering specific taxa.[90–92] This reflects the challenges of collecting larger animals, typically involving remotely operated vehicles (ROVs)—which are expensive and require specialists to operate—or trawls, which are inherently destructive of animals.[93] Meiofauna, often regarded as the dominant component of deep-sea ecosystems, at least in terms of biomass if not diversity,[94,95] are also likely to have considerable undocumented species richness given significant sampling challenges.[96] Biases may also be present in WoRDSS (Figure 4) given chronic under-sampling in the deep sea[97,98] and taxon-specific factors, e.g., Nematoda being highly speciose but notoriously difficult to identify to species level.[36,96]

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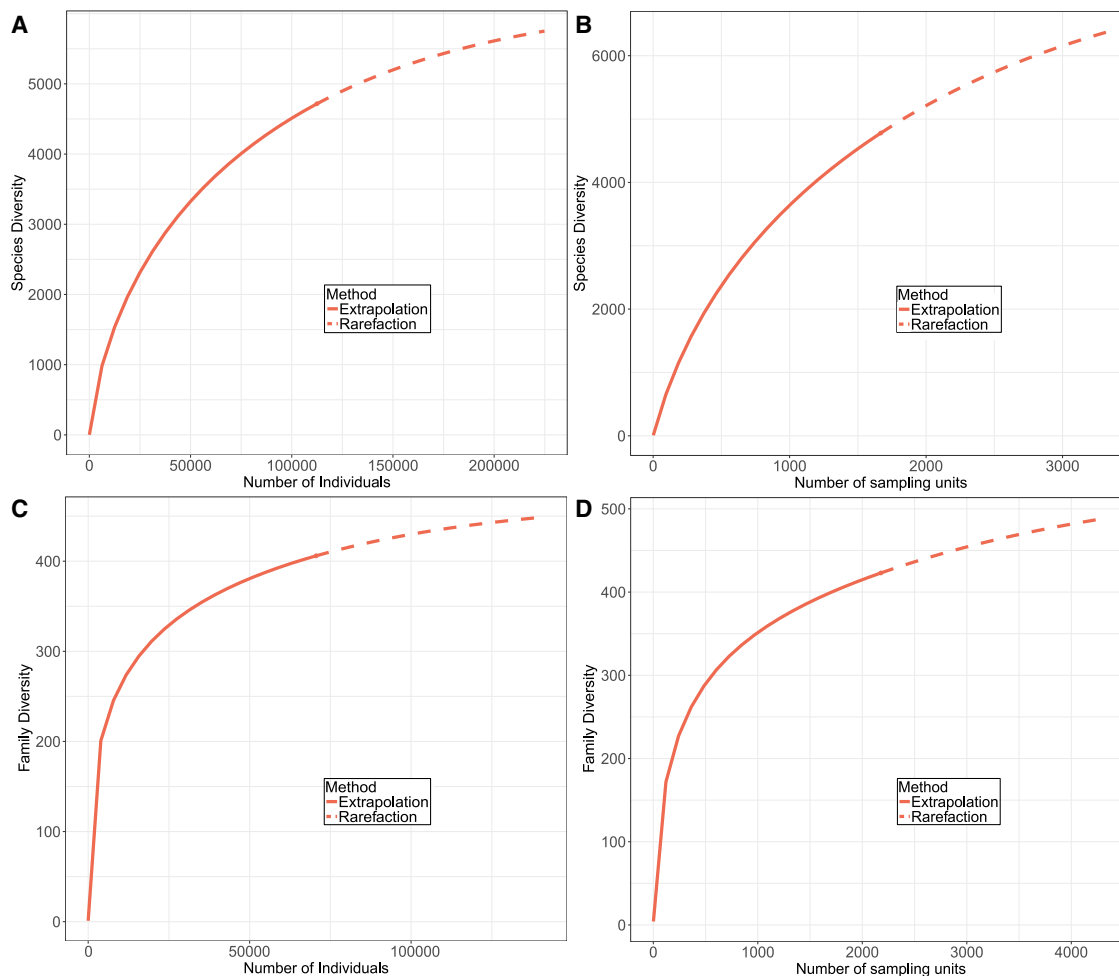
Figure 5. Species and family diversity in the Clarion-Clipperton

(A–D) Diversity estimators (solid line, rarefaction; dashed line, extrapolation): (A) Chao1 species diversity 6,233 (+/−82 SE); N = 112,428 ind., S(obs) = 4,716; extrapolation maximum sample size: 224,858 ind; (B) Chao2 species diversity 7,620 (+/−132 SE); N = 1,668 samples; S(obs) = 4,779, extrapolation maximum sample size, 3,336 samples. Family diversity estimators: (C) Chao1 family diversity 469 (+/−18 SE); N = 70,597 ind., F(obs) = 406; extrapolation maximum. N: 141,194 ind.; (D) Chao2 family diversity 544 (+/−24 SE); N = 2,179 samples; F(obs) = 423; extrapolation maximum N: 4,358 samples.
See also Table 1, Figures S1–S3, and Data S3 and S4.

There are few comparable estimators of biodiversity in other broad-scale regions of the deep sea. One study of the Southern Ocean deep sea reported 674 isopod species of which a high proportion (87%) were new to science.[83] Undescribed CCZ isopods are higher with an estimated 96% being new species[3,17] (23 named species, 474 unnamed). Total marine species richness estimates reviewed in Appeltans et al.[58] range from 300,000[99] to 10 million,[100] the latter regarded as a significant overestimate, and the former a significant underestimate.[97,101] Our figure of 92% is similar to the proportion of currently known marine species in WoRMS (241,129)[45] to the Mora et al.[57] global estimate at 89%. The current CCZ Checklist represents just 1% of currently recorded deep-sea species in WoRDSS (36,579).[44] Including unnamed species, this would rise to 15%, or species estimators, 17%–24%.

Clearly the CCZ represents significant undescribed biodiversity. With 31 new genera and three new families, (and several additional new genera and at least one additional new family known to the authors), the Checklist illustrates the novelty of the region at deep taxonomic levels. Evolutionary novelty has been previously recorded in the CCZ for echinoderms,[12] but it is noteworthy that this extends across further taxa. Diversity of life-history strategies are beginning to be recorded in the CCZ[102] as elsewhere in the deep sea, such as association with sponge stalks.[89,103] Characteristic sediment-dwelling infauna such as nematodes, isopods, and polychaetes are now being found living in and on nodules, illustrating the interconnectivity of nodule-sediment dwelling lifestyles.[27,104,105] Beyond nodule-dwellers, many suspension-feeding forms depend on nodules. Spatial ecology studies report 60%–80% of the megafauna (largely dominated by suspension feeders in the CCZ) to be found growing attached to nodules.[78,79] Pertinent questions remain on the relative vulnerability of nodule and sediment fauna to mining impacts.[106] Remarkably little is known of life-history traits of these species and answering these questions is an immense challenge in a region where most species are rare and a third appear to have been found only once.
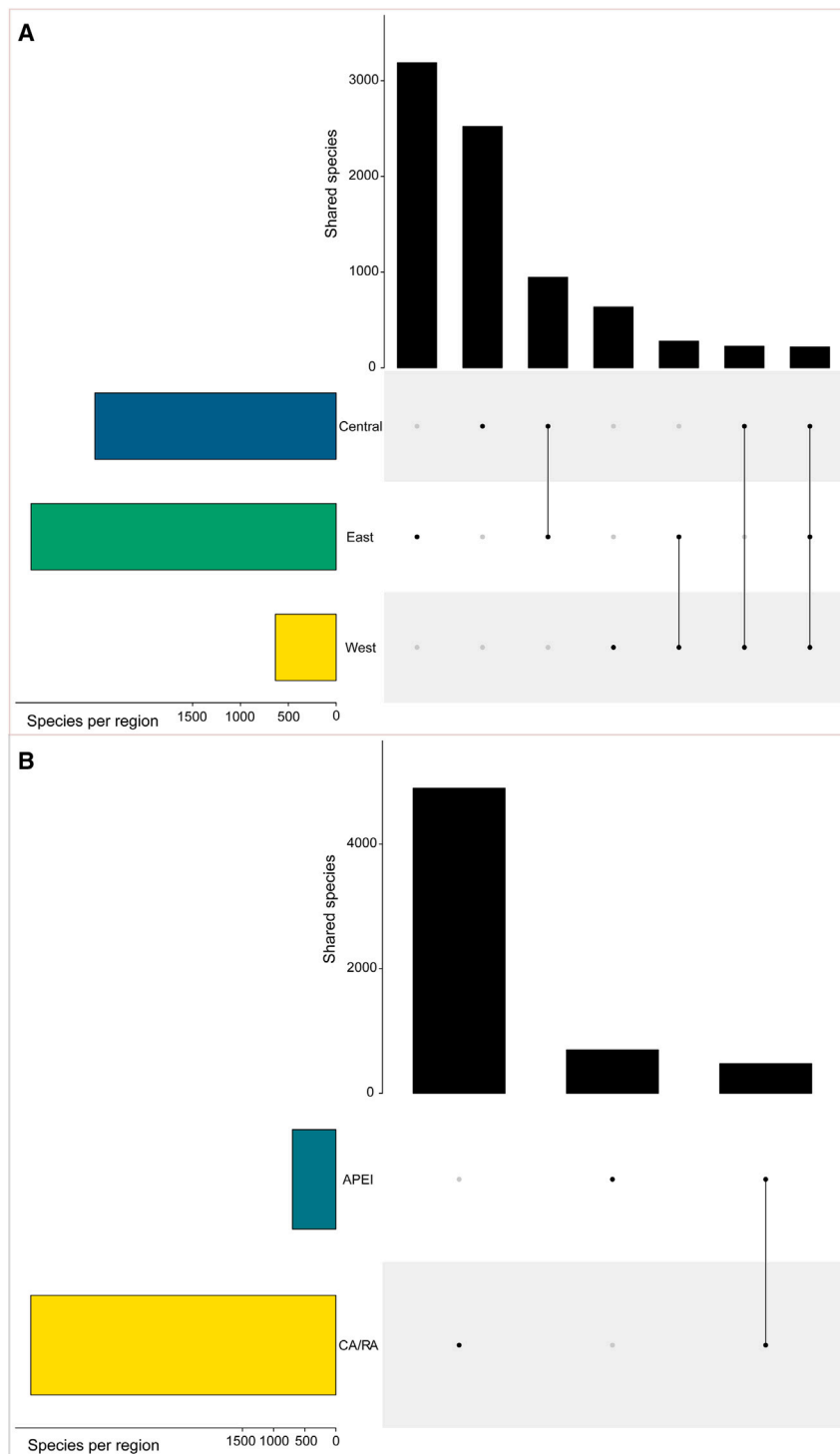
Figure 6. UpSet plot of all CCZ species (named and unnamed species combined) at regional scales

(A and B) Top bars show total species shared or independent, intersecting with region in the lower panel (species independent per region correlate to a "dot" or shared between region to a "dash" connecting the regions). Side bars show total species per region. (A): all species by region, (B), all species in contract areas and reserved areas pooled versus those in APEIs pooled.

See also Data S3 and S4.

CCZ taxonomy will require extensive collaboration between stakeholders supported by regulatory bodies/governments and appropriate and sustained funding.[17,67,85,107,108] Programs such as the new ISA Sustainable Seabed Knowledge Initiative (SsKI)[109] recognized under the UN Ocean Decade should be leveraged to fund descriptions in all taxonomic groups. As the new species will take years to be formally described, a robust approach to open nomenclature in the medium term is also important to ensure that species-level taxa can be referenced and that datasets are comparable and linked to open data and specimen vouchers.[5,85,90,91] The CCZ Checklist is a key step forward in an iterative process towards field guides for the region, which will dramatically improve identifications and reduce uncertainty. Our study provides the first regional estimates of species diversity for all size classes. Although uncertainty is high, these estimates provide a starting point to be developed as additional data and approaches become available. Development in statistical methods for estimating species richness will be critical to future assessments of diversity in such poorly sampled environments.[110,111] Given mining operations may be imminent, a key consideration for the CCZ is the application of biodiversity data for environmental management, in particular assessing species extinction risk. Often assumed to be lower in marine environments, this appears largely an artefact of lower taxonomic knowledge compared to terrestrial ecosystems.[112] The UNCLOS states that "no serious harm" can occur from any mining activities and that necessary measures must be taken to protect the environment from any harmful effects. Although sometimes equated with no loss of biodiversity, the definition of the term "serious harm" (and that of "lower environmental thresholds") remains to be clarified.[24,113] Accurately quantifying species ranges and rarity, key components of extinction risk, requires a comprehensive

Conclusions

The proportion of undescribed species in the CCZ has been reported as being over 80% within taxa.[11,17,22] Our study provides the first quantitative support for that figure across multiple taxonomic groups, with two estimators (88% and 92%) clearly illustrating the remaining taxonomic impediment to an understanding of CCZ biodiversity. Addressing the "lost decades" of

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approach to taxonomy,[114] extensive molecular studies,[115] and standardized quantitative methods[20] enabling regional analyses. This is particularly important given that the CCZ remains one of the few remaining areas of the global ocean with high intactness of wilderness.[116] Sound data and understanding are essential to shed light on this unique region and secure its future protection from human impacts.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2023.04.052.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw and Processed data compiled from secondary sources (see 'Other'); analysis script	This paper	https://github.com/howlerMoonkey/CCZ_BIODIVERSITY/; Data S5
CCZ Checklist	This paper	https://www.marinespecies.org/deepsea/ccz_checklist.php/; Data S1
Software and algorithms		
WoRMS (World Register of Deep-Sea Species)	WoRMS[7]	https://www.marinespecies.org/; https://github.com/howlerMoonkey/CCZ_BIODIVERSITY/tree/main/Data-fin
R version 4.0.2 (2020-06-22) "Taking Off Again"	R Development Core Team[117]	https://www.r-project.org/
QGIS (Quantum GIS) version 3.10, Coruña (QGIS.org, 2020).	QGIS Development Team[118]	https://www.qgis.org/
Other		
DeepData (database of the International Seabed Authority)	N/A	https://data.isa.org.jm/isa/map/
OBIS (Ocean Biodiversity Information System)	OBIS[140]	http://www.obis.org/
GBIF (Global Biodiversity Information Facility)	GBIF[141]	https://www.gbif.org/
Published literature	N/A	https://github.com/howlerMoonkey/CCZ_BIODIVERSITY/tree/main/Data-fin
GenBank	GenBank[142]	https://www.ncbi.nlm.nih.gov/genbank/
BOLD (Barcode of Life)	N/A	https://ibol.org/
PANGAEA	N/A	https://www.pangaea.de/

RESOURCE AVAILABILITY

Lead contact
Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Muriel Rabone (m.rabone@nhm.ac.uk).

Materials availability
This study did not generate new reagents, sequences or eventuate in the archiving of specimens.

Data and code availability

- This paper primarily analyses existing, publicly available data. The sources are listed in the key resources table and the datasets are also available in this paper's supplemental information (Data S1–S4). All data generated/utilised in this study are also deposited at GitHub and publicly available as of the date of publication. DOIs are listed in the key resources table.
- All code has been deposited at GitHub and is publicly available as of the date of publication. DOIs are listed in the key resources table. All code is also available in this paper's supplemental information (Data S5).
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

METHOD DETAILS

Data collection, processing and exploratory analysis: Databases
All data were analyzed and processed in R, version 4.0.2 (2020-06-22) "Taking Off Again", R Core Team,[117] and Microsoft Excel 365. The R script is included in supplementary (Data S5 and in GitHub (https://github.com/howlerMoonkey/CCZ_BIODIVERSITY/tree/main/R). All mapping was done in R and in Quantum GIS (QGIS), version 3.10, Coruña (QGIS.org, 2020).[118]

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 run for 'Trawl

line'. The separate 'Point' and 'Trawl Line' data downloads were combined into the same dataset. Data and column headings varied between the two datasets, e.g. 'actual latitude' in the 'Point' data, and 'start latitude' and 'end latitude' in the 'Trawl Line' data. Data were harmonized, e.g. for coordinates and depth the end-point was used and additional columns added to the 'Point' data to allow the datasets to be combined. Initial data exploration found that the database export did not contain a record identifier. To examine the data, first it was necessary to establish a unique key or record identifier for every individual record (or row of data) in the dataset. A composite key was created to ensure a unique key or identifier for every record by combining the following DeepData identifier fields: 'ContractorID' + 'StationID' + 'SampleID'. The composite key was checked for any duplicates, and none were found. Data columns were checked and edited where necessary, e.g. for depth, missing values were listed as −9, these were replaced with 'NA'. Where possible this was scripted in R, but where multiple entries for character variables were present, this was done in Microsoft Excel 365. Any data point needing cleaning or editing was copied so the original data column and the processed data column were in the same dataset, with the latter renamed with a suffix '_ed'.

Initial examination of taxonomic information found variable recording of data. 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. As above, data columns were copied and edits made on the copied column, with spelling and formatting mistakes removed. Taxonomy was mapped to the correct column, e.g. class names in the order column were moved to the class column. No column for scientific name was present, i.e. the actual identification of the specimen referenced in a given record, here a column was added, populated with the lowest taxonomic level reported (i.e. species name if recorded rather than genus name only). If a name was noted with question mark, recorded with a qualifier indicating uncertainty in identification (e.g. *Incerta*) or written as two names, then the next highest taxonomic level was recorded, e.g. if two family names were recorded, the order name was recorded instead. For informal names or open nomenclature designations, scientific name was also recorded, mapped to the lowest scientific level recorded above species level. If a species name was present, e.g. *Paralicella* cf. *caperesca* no 5, the genus name was recorded for the scientific name. This resulted in a final dataset of 40,518 records for DeepData (https://github.com/howlerMoonkey/CCZ_BIODIVERSITY/blob/main/Data-fin/Data_S6_DeepData.csv).

For contextual spatial data, all mining exploration contract areas, both active and reserved, and Areas of Particular Environmental Interest (APEI) shapefiles were downloaded from the ISA website (https://www.isa.org.jm/exploration-contracts/maps/); combined into one shapefile in QGIS version 3.10, Coruña (QGIS.org, 2020). Bathymetric data were sourced from GEBCO (General Bathymetric Chart of the Oceans; https://www.gebco.net/). A search area was created covering the entire CCZ region. Coordinates for a polygon covering the CCZ including the combined CCZ shapefile were established with the following coordinates (in decimal degrees): northwest −164.01462, 15.70629; southwest −155.04998–5.51238; southeast −101.9181 6.05623; northeast −117.66088 23.72549 (see R script, Data S5).

Data were collected from the Ocean Biodiversity Information System (OBIS) and the Global Biodiversity Information Facility (GBIF). OBIS occurrence data were downloaded as a Darwin Core file also on the 12th of July, 2021 using the 'occurrence' function in the robis package,[119] with the CCZ polygon as delineated above, for all depths. DeepData records have been harvested by OBIS since June 2021 and published on the OBIS ISA node.[120] These records were analyzed separately in the parallel study, Rabone et al.[67] to examine ISA data mapping procedures. To avoid duplication of DeepData records across the databases, they were not included in the dataset for analysis (identified as records tagged as owned by the ISA in the Darwin Core 'accessRights' field). GBIF occurrence data were downloaded from the web portal also on the 12th of July, 2021; from all depths, using the polygon search function, with the CCZ polygon coordinates.

All records from GBIF and OBIS were mapped together with the CCZ shapefile, using the following R packages: 'GADMTools'[121]; 'sp'[122]; 'spatialEco'[123]; 'maptools',[124] 'rgdal'[125] and 'rgeos'.[126] All dataset records were 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 (the World Register of Marine Species).[45] 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 datasets. This resulted in a final dataset of 2185 records for OBIS (https://github.com/howlerMoonkey/CCZ_BIODIVERSITY/blob/main/Data-fin/Data_S7_OBIS.csv) and 2405 records for GBIF (https://github.com/howlerMoonkey/CCZ_BIODIVERSITY/blob/main/Data-fin/Data_S8_GBIF.csv).

Published literature

A systematic review of the literature was undertaken; the *a priori* research question being: *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 literature review was carried out primarily from 2nd February to 20th August 2021, with the date of last search the 1st of January, 2023. Search terms included: "Clarion Clipperton (Fracture) Zone"; "Central"/"East"/" Pacific"; new"/"species"/"genera"/"genus"/"family"/description"; "biodiversity"; "megafauna"; "macrofauna"; "meiofauna";

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"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 in the review. The search was not confined to lower taxonomic ranks, with all records included regardless of the level of taxonomic resolution. Publications without any taxonomic records were excluded. Any publications solely examining pelagic taxa, microbes, or foraminifera (e.g. xenophyophores) were similarly excluded (https://github.com/ howlerMoonkey/CCZ_BIODIVERSITY/blob/main/Data-fin/Data_S9A_lit_papers.csv). Records identified from imagery, e.g. ROV or AUV (Autonomous Underwater Vehicle) seabed surveys were included, i.e. the selection was not restricted to specimen-based studies. All size classes of metazoans were included. Definition of size fractions were as follows: meiofauna: animals being retained on a 63μm sieve, macrofauna, on a 250–300μm sieve, and megafauna, as 2cm and larger. Relevant information, for example taxonomic and sampling information was captured and compiled into a table (https://github.com/howlerMoonkey/CCZ_BIODIVERSITY/ blob/main/Data-fin/Data_S9B_lit_taxa.csv). Type localities for species described from the CCZ were collated from the literature, with coordinates recorded verbatim and converted to decimal format. Datasets associated with publications were also sourced from PANGAEA, incorporated into the literature dataset. The final literature dataset with georeferenced records included 57,858 records (https://github.com/howlerMoonkey/CCZ_BIODIVERSITY/blob/main/Data-fin/Data_S9C_lit_site%2Btaxa.csv).Taxonomic information was cleaned with the 'taxon-match' tool in WoRMS. Identification qualifiers were standardized according to guidelines in the literature, e.g. n sp. recorded as sp. nov.[4,5] For records held on International Nucleotide Sequence Database Collaboration (INSDC) databases (primarily GenBank) and BOLD, accession numbers were collated from publications, either direct from publications or supplementary files, and where key information was missing, e.g. marker, the databases themselves were cross-referenced. This resulted in a data file of 4738 records from GenBank and 1674 records from BOLD (https://github.com/howlerMoonkey/ CCZ_BIODIVERSITY/blob/main/Data-fin/Data_S10_INSDC.csv).

The CCZ Checklist: Known/named species

All scientific names were collated from the different data sources to create a checklist of known benthic metazoan taxa recorded from the region, here referenced as the 'CCZ Checklist'. For unnamed/undescribed species, 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, any higher taxonomic names not present were inferred, e.g. 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 (seven in total including four species, not included in final totals). Where names were only present in one data source, the origin of the records were reviewed. A taxon match to WoRDSS,[44] the deep-sea node of WoRMS, was also performed 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 Boxshall and Pedro Martinez for Copepoda; Simone Brandao for Ostracoda; author TH for Amphipoda and authors TD, HW and AGG for Polychaeta. Other potential pelagic taxa were identified by cross-referencing 'attribute' information in WoRMS where available. After these assessments, any pelagic names identified were removed from the final total, and all records of pelagic species/taxa were removed for the diversity analysis. These names were retained in the main dataset for wider reference (tagged as pelagic). Any name with a known degree of taxonomic uncertainty was noted and removed from the CCZ Checklist sensu stricto, e.g. a name interpolated from an imagery record, from a morphospecies/temporary/informal name or with any of the following qualifiers: aff.; cf.; indet; Incerta (or incertae sedis used as proxy for Incerta); and/or sp. inc. (any records with the qualifier sp. nov were included at species level, or gen. nov at genus level). Species identified to be likely misidentifications (e.g. Eurythenes gryllus, Valettietta gracilis) were also tagged and as for pelagic taxa, removed for analysis and overall totals. In total, 656 names were tagged to be excluded, but were retained in the whole dataset (tab 2 of Data S1).

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 to gauge the 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. For the main macrofaunal groups, any species described using specimens from the CCZ but a holotype originating from elsewhere were recorded as such in the Checklist. Life-history and functional traits such as key habitat association (e.g. sediment-dwelling) and feeding type were recorded from the literature where present. The checklist was prepared for publication as a webpage in WoRDSS to allow data to be FAIR.[127] A landing page was prepared by the WoRMS Secretariat in consultation with authors TH and MER in February–April 2023, available at (https://www.marinespecies.org/deepsea/ccz_checklist.php).

Unnamed species/informal name species list

A separate list of 'open nomenclature' informal names for the unnamed species was collated for analysis (Data S2). Open nomenclature is a system of signs to describe uncertainty around identifications, or designate taxa as undescribed.[4,5] Temporary names are also termed 'morphospecies', 'informal names', 'undescribed species', 'working species', morphotypes' or 'molecular/operational taxonomic units' (M/OTUs).[4,5] 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 (also see List of Abbreviations and Terms in supplemental information). For consistency, here we use the term 'unnamed species' a term to delineate undescribed species but which allows for the inclusion of uncertainty in identification, or the possibility some of these unnamed species may be known species yet to be correctly identified. This term is equivalent to 'taxonConceptID' in Darwin Core[4] (https://dwc.tdwg.org/terms/#dwc:taxonConceptID). Names recorded specifically as 'undescribed new species/genera' were distinguished as such in the unnamed species list (Data S2). Species recorded with open nomenclature identification 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'. Any duplicates of names across data sources e.g. identical names were identified by cross referencing and removed. Also, text string analysis showed very similar names published at different times and identified to have originated from the same dataset but with slightly different formatting (e.g. underscores added or removed). These were also removed as duplicates (all retained in the full dataset). Synonyms within the unnamed species list (sensu synonyms in scientific names i.e. multiple names for the same species) were also identified through cross-referencing publications and databases. These were tagged as synonyms in the main dataset and removed from totals (Data S2).

QUANTIFICATION AND STATISTICAL ANALYSIS

Diversity estimates
Records at all taxonomic levels from all data sources, DeepData, the literature (including those harvested from PANGAEA), OBIS and GBIF that included either abundance and/or sampling information were compiled into a dataset for diversity analysis (Data S3 and S4). Any duplicates identified within and across data sources were removed, for example records from the same dataset present both in the literature and in GBIF, or duplication of datasets present within the DeepData database.[67] The species-level data included named and unnamed species. In total, 27 of the informal names were specified as higher taxa, e.g. an undescribed genus name. These names were included in the species-level dataset given that any unnamed higher taxa record would also represent a new unnamed species. All synonyms in the informal names identified as above via cross-referencing were removed for analysis to avoid inflation of estimates. This resulted in a final dataset for diversity analysis of 91,996 records at all taxonomic levels and 66,679 at species level only (Data S4).

For alpha diversity, simple metrics of diversity, total number of new species, by region, size class and contract area/APEI were estimated. Abundance species matrix tables were generated with the R package picante[128] (Data S3) and presence/absence species matrix tables with FuzzySim.[129] Singletons, or species represented by a sole specimen for a given deployment were calculated from the abundance dataset. A broad regional classification of east, central and west was added to the final datasets, with breakpoints at −128, and −140 degrees longitude for east to central and central to west respectively. Broad patterns in species diversity and distribution at regional level were visualized with UpSet plots.[130] These plots allow visualization of multiple sets in the data, such as species richness intersections with region.[133]

Non-parametric estimators were used to estimate total species diversity for all size classes at a regional scale, i.e. for the entire CCZ region. Hill numbers for rarefied taxa richness ($q = 0$)[131] were estimated in iNEXT.[132] Rarefaction/extrapolation both for Chao2[133,134] incidence-based by sample and Chao1 abundance-based was performed in iNEXT[135,136] and plotted using ggiNEXT function (Figure 5). Sample/incidence-based species richness estimates, Chao2, and first and second order jackknife[137] were also conducted using the specpool function in vegan.[138] Abundance-based richness estimates, Chao1 and the Abundance-based Coverage Estimator ACE[65,66] were also conducted in vegan, using the estimateR function. Rarefaction for all species CCZ-wide were estimated in vegan using the rarefy and rarecurve functions. Species accumulation curves were plotted (with sampling effort defined as number of sampling events), with 1000 randomizations, using the specaccum function in vegan (Figure S1). Plots of sampling completeness (type = 2) were also performed in iNEXT (Figure S3).

Since taxonomic uncertainty is lower at higher taxonomic ranks, with less likelihood of synonyms and misidentifications (and likely higher proportional sampling completeness) than at species level, richness estimates (Chao1 and Chao2) at genus and family level were performed (Figures 5, S1, and S2). This also allowed diversity estimates at higher taxonomic levels to be compared to the known totals of taxa in the CCZ Checklist (i.e. total families/genera recorded). Estimates were based on subsets of the data where abundance and/or site-sampling information was recorded, while the Checklist was based on all records deemed valid post qa/qc as above.

To account for potential synonymies and misidentifications in the unnamed species, an analysis of recent molecular and morphology-based taxonomic studies that provided estimates of the numbers of species taxa was carried out. For the analysis assessing proportion of named to unnamed/undescribed species in the literature (the 'subset' analysis), publications were selected were a taxonomic group (or groups) were assessed in totality, rather than a taxonomic description of a new species, and where all taxa were identified to species level (named and unnamed); based on morphology and/or molecular approaches (publications where identifications were based on imagery were therefore excluded, Table S1).

Assessment of regional-scale sampling effort
A broad assessment of CCZ-wide sampling effort was also conducted to visualize sampling coverage and particular data gaps. Sampling effort was visualized as a heatmap of unique sampling sites using the Density Analysis plugin in QGIS, based on the combined all-taxa dataset[139] (Figure S4). To visually assess sampling coverage and sampling gaps or under-sampling by depth, density of

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records by depth was computed in R to visualize sampling effort by depth, by subdividing data into 10 sample quantiles (Figure S5). Total sample records by contract area/APEI and depth were also plotted to visualize differences by contract area, given the known depth gradient in the CCZ (Figure S6).[84]

Comparison of CCZ Checklist with global checklists

To provide a degree of global context to CCZ biodiversity as currently recorded, the proportion of named to unnamed species was compared to published estimates of global marine species diversity versus the current recorded total of known global marine (eukaryotic) species currently in WoRMS (241,129).[44] Relevant literature was searched to identify estimates and any assessments of their accuracy. No global estimates of deep-sea species richness published to date were identified in the search, therefore global marine species richness estimates were examined. Estimates from Mora et al. [57] and Appeltans et al.[58] were primarily used on basis of analysis by Poore et al.[101] To examine taxonomic composition of the Checklist in relation to global datasets, data were requested from WoRMS and a database copy of WoRDSS[44] was provided from the 1st of January, 2023 and archived on GitHub (https://github.com/howlerMoonkey/CCZ_BIODIVERSITY/blob/main/Data-fin/Data_S11_WoRDSS.csv). Non-metazoans were removed from the dataset and relative proportions of species by phyla were calculated and plotted to compare the CCZ to all deep-sea metazoan species recorded to date.

ADDITIONAL RESOURCES

The CCZ Checklist created in this study is published as a webpage, available via the World Register of Deep-Sea Species WoRDSS,[44] subregister of the World Register of Marine Species (WoRMS)[45] at https://www.marinespecies.org/deepsea/ccz_checklist.php.