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The epitome of data paucity: deep-sea habitats of the Southern Indian Ocean

Berta Ramiro-Sánchez[a], **Alexis Martin**[a], **Boris Leroy**[a]

[a] Unité 8067 Biologie des Organismes et Ecosystèmes Aquatiques (BOREA), Muséum national d'Histoire naturelle, Sorbonne Université, Université de Caen Normandie, CNRS, IRD, Université des Antilles, Paris, France.

Alexis.martin@mnhn.fr
leroy.boris@gmail.com

Corresponding author:

Berta Ramiro-Sánchez
Email address: b.ramirosanchez@gmail.com
Telephone: +33 (0) 7 51 26 86 76
Present address:
Muséum National d'Histoire Naturelle
Lab. Biologie des Organismes et des Ecosystèmes Aquatiques, Dept. Adaptation du Vivant,
43 rue Cuvier – CP 26 – 75005 Paris

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Conflict of interest

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Abstract

Vulnerable marine ecosystems (VMEs) are protected from bottom-fishing impacts in international waters by UN resolutions through Regional Fishery Management Organizations. VMEs include deep-sea benthic taxa whose life-history traits make them vulnerable to disturbance. Conservation measures for VMEs require regulatory frameworks informed by biodiversity maps. Here we evaluate biogeographic patterns of deep-sea benthic biodiversity of the Southern Indian Ocean to understand conservation avenues for the Southern Indian Ocean Fisheries Agreement (SIOFA) management organization. We synthesised knowledge on the distribution of benthic deep-sea taxa and explored the quality and quantity of available data. Next, we explored how taxa are structured into bioregions using biogeographical networks. We found astounding Wallacean and Linnaean shortfalls within SIOFA's management area, which is virtually devoid of distributional data. Across the entire area, results suggest that only 73% of the expected deep-sea taxa has been sampled, and most sampled cells appeared to be inadequately sampled. Yet, our bioregionalization analysis identified multiple bioregions, some only observed within SIOFA's area. The Wallacean and Linnean shortfalls are so important for VMEs that they severely impede to make adequate maps for conservation planning. Bioregionalization results suggest that SIOFA hosts a unique faunal composition that must be safeguarded. Predictive approaches to compensate for these shortfalls exist but will likely be insufficient and uncertain. Within SIOFA's area, there is no satisfying solution to cope with the data shortfalls. Yet, biodiversity maps are a global responsibility. This study makes a call to invest in biodiversity inventories in this world's region to promote informed policy-making decisions.

Keywords

Deep-sea habitats; Bioregionalization; Indian Ocean; Conservation; Fisheries; ABNJs

Highlights

- Bioregionalization of the Southern Indian Ocean using bipartite networks
- Major Linnean and Wallacean shortfalls
- Unknown extent of unique bioregions in offshore areas
- Southern Indian Ocean systematically data-poor for benthic studies

Introduction

The increasing appropriation of marine resources by human societies, termed "the blue acceleration", is multiplying and intensifying pressures on the ocean (Jouffray et al., 2020). This holds especially true for the deep sea where cumulative impacts from fishing, potentially deep-sea mining, and climate change (Sweetman et al., 2017), will increase and new dynamics and threats will emerge (Halpern et al., 2019; O'Hara et al., 2021). In the deep sea, we find species such as cold-water corals and sponges with life-history traits (slow-growth, late-maturing and long-lived) that make them highly vulnerable against disturbance. These species, collectively known as indicator taxa of Vulnerable Marine Ecosystems (VMEs), have ecological and functional importance by enhancing biodiversity and providing habitat to other rare, threatened, or endangered species (FAO, 2009). Such roles confer VME taxa with conservation significance, and the United Nations require management measures that can include closing areas to fishing (UNGA, 2007). As a result, there is an increasing need to enforce conservation measures for deep-sea regions on a global scale, which in turn requires understanding species distributions across temporal and spatial scales (Lourie & Vincent, 2004; Rice et al., 2011).

To support conservation and spatial management objectives for VMEs, it is fundamental to define the boundaries, extent, and connections of deep-sea regions with ecological, environmental, and biogeographic characteristics (Danovaro et al., 2009). However, this fundamental definition of deep-sea regions is compromised by the critical under-sampling of deep waters (Hughes et al., 2021; Menegotto & Rangel, 2018) that prevents resolving biogeographic patterns for deep-sea taxa, although there are efforts at regional (e.g., Summers & Watling, 2021) and global (e.g., Watling et al., 2013; Watling & Lapointe, 2022) scale for certain groups. The vastness, remoteness, and required technological complexities render deep-sea scientific exploration patchy, punctual, and rather costly. At a spatial resolution of 5 km, Hughes et al. (2021) estimate the area of ocean sampled at 0.6% for all taxonomic groups between 1,000 and 1,800 m water depth and at less than 0.02 % for deeper waters. At depths between 1,000 and 1,800 m, certain groups like Cnidaria dominate the percentage of global records. Further to this sampling imbalance across depths, sampling bias prevails in the southern hemisphere (Menegotto & Rangel, 2018), underlining the inequity in scientific technological capacity needed for this realm. Accordingly, the deep sea is an environment that suffers systematically from taxonomic and geographical knowledge biases, also known as the Linnean (Brown & Lomolino, 1998) and Wallacean (Lomolino, 2004) shortfalls, respectively.

Linnean and Wallacean shortfalls for deep-sea vulnerable taxa are greatest in waters beyond national jurisdiction (hereafter, high seas), which cover 61% of ocean area and 73% of ocean volume (Costello et al., 2010). There, these taxa of groups of mainly suspension feeders, tend to occur on locations where currents are accelerated by kilometre-scale topographic features, such as the crest or rims of seamount summits and ridges (Rogers, 2018). However, although Linnean (i.e., most species remain undescribed; Cardoso et al., 2011) and Wallacean (i.e., knowledge on species' distribution is inadequate; Cardoso et al., 2011) are the most prominent knowledge gaps, in reality most deep-sea taxa endure other renowned shortfalls: Darwinian (phylogenetic relationships), Hutchinsonian (environmental tolerance), Prestonian (population in time and space), Raunkerian (species traits), and Eltonian (species interactions) (see Hortal et al., 2015 for a review on biodiversity shortfalls). For example, for deep-sea octocorals of the Order Alcyonacea (Phylum Cnidaria), which can create single or multi-species aggregations known as coral gardens (Freiwald & Roberts, 2005; Rossi et al., 2017), the phylogeny has just become resolved and well supported to proceed with taxonomic revisions (McFadden et al., 2022). In addition, few studies have assessed the interaction behind octocoral species co-occurrence (e.g., Rakka et al., 2021), and baseline studies continue to shed light on life-history traits (e.g., Baillon et al., 2016; Rakka, Godinho, et al., 2021) and environmental tolerances (e.g., Rakka, Godinho, et al., 2021; Scanes et al., 2018) for a handful of species. Whilst we are steadily advancing our understanding of deep-sea species, habitats, and more generally VMEs, knowledge shortfalls on the high seas may hinder the application of conservation measures by managerial regulatory bodies, such as regional fisheries management organizations (RFMOs).

In the Indian Ocean, the Southern Indian Ocean Fisheries Agreement (SIOFA) is the entity in charge of managing deep-sea fisheries on the high seas. As other RFMOs in other world's oceans, SIOFA must comply with international obligations towards the conservation of VMEs against potential impacts from deep-sea bottom fishing. In this regard, since its relatively recent establishment in 2012, SIOFA has initiated management efforts to protect VMEs by identifying a list of VME indicator taxa for Indian Ocean waters (CMM 2018/01). In addition, SIOFA has designated five interim benthic protected areas where bottom-fishing trawling is not permitted (CMM 2019/01) and is currently undertaking work to establish new interim protected areas. Situated over seamounts and ridges, the relevance of the existing protected areas for preserving VMEs is however unknown because it has not been studied: they were areas where only exploratory or no fishing had occurred. Considering that half of the estimated number of seamounts of the Indian Ocean fall in the high seas and about a quarter are deemed to be at fishable depths (i.e., with summit depths less than 1,500 m) (Yesson et al., 2011), further conservation measures will likely also focus on seamounts and ridges, where deep-sea fisheries develop around aggregations of resident fish (Clark et al., 2007; Kerry et al., 2022). To crown it all, the Southern Indian Ocean remains one of the least explored oceans in the world (Ingole & Koslow, 2005; Rogers & Taylor, 2012; Saraswat et al., 2022; Wafar et al., 2011).

For SIOFA to develop a conservation plan, it requires to map biogeographical regions of VMEs in order to scientifically inform decision making. Biogeographical classifications, or bioregionalizations (Woolley et al., 2020), are the building blocks for the planning and implementation process of management measures and are highly connected to the development of marine protected areas (Rice et al., 2011). This is because bioregionalizations enable the identification of units that should be represented in a network, ensuring the protection of biogeographically unique areas and the development of a network that considers representativity, connectivity and replication of sites (Rice et al., 2011). Here, we compiled all the available distribution data on VME indicator taxa to map such regions and report on how problematic Linnean and Wallacean shortfalls are for VMEs on the high seas of the Southern Indian Ocean. We develop a bioregionalization, explore these knowledge shortfalls, and speculate on what are their impact and the possible avenues for VME conservation so that SIOFA meets their international management obligations.

Materials and methods

Study area

The Southern Indian Ocean Fisheries Agreement (SIOFA) covers the high seas (i.e., waters beyond national jurisdiction) of the Indian Ocean between the parallels 10° N and 45° S, and the meridians 30° E to 80° E, with the area east of 65° E to the equator outside their jurisdiction (Figure 1A). We extended the study area to encompass latitudes 13° N – 65° S and longitudes 20° E – 147° E.

The seabed of the Indian Ocean is geomorphologically complex. The Indian Ocean includes numerous mid-ocean ridges (some not active sites of seafloor spreading such as the Ninety-East Ridge, the Mascarene Ridge and the Chagos-Laccadive Ridge), seamounts, plateaus and rises, abyssal plains and trenches. Most of the geomorphological features fall within areas beyond national jurisdiction and are therefore within SIOFA's management area. Within SIOFA, the seafloor bathymetry ranges from as shallow as 1 m at Saya de Malha Bank to approximately 8,000 m in the abyssal plains, wherein the Southwest Indian Ocean Ridge and Broken Ridge summit between 1,000 m and 2,000 m, and the Central Indian Ridge, Southeast Indian Ridge and Ninety-East Ridge have generally deeper summits. With a mean peak summit at 2,250 m, there are 1,746 estimated seamounts in SIOFA (Yesson et al., 2011).

Biological data

The VME indicators list adopted by SIOFA (CMM 2018/01) at order, class, and phylum levels, includes the following categories of deep-sea (generally > 200 m) benthic taxa: Cnidaria (Gorgonacea, Anthoathecatae, Stylasteridae, Scleractinia, Antipatharia, Zoantharia, Actiniaria, Alcyonacea, Pennatulacea), Porifera (Hexctanilleda, Demospongiae), Ascidiacea, Bryozoans, Brachiopoda, Pterobranchia, Serpulidae, Xenophyophora, Bathylasmatidae, Crinoidea (stalked species only), Euryalida, Cidaroida. We downloaded all occurrence records under these categories from the public databases the Ocean Biodiversity Information System (OBIS, https://obis.org/) (accessed on 10/11/2020 and 02/04/2021), the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/) (accessed on 09/11/2020 and 14/04/2021), NOAA's Deep-sea Corals Data Portal (https://deepseacoraldata.noaa.gov/) (accessed on 16/11/2020 and 09/04/2021), and Smithsonian Natural History Museum (https://collections.nmnh.si.edu/) (accessed on 16/11/2020). We also obtained occurrence records from SIOFA's observer programme, research campaigns led by the Muséum National d'Histoire Naturelle, and the published literature (Taylor & Rogers, 2017). We obtained records for the whole Southern Indian Ocean to account for ecological continuity, that is, SIOFA's management area and all exclusive economic zones bordering it (latitudes 13° N – 65° S and longitudes 20° E – 147° E).

We applied verification procedures for taxonomic consistency, error detection, as well as evaluation of records in the environmental space. Specifically, we first checked species names against the most updated authority, the World Register of Marine Species (WoRMS, 2021) for synonyms and fossil records. Secondly, we applied automatic error and outlier detection using the function clean-coordinates from the R package CoordinateCleaner version 2.0-18 (Zizka et al., 2019). We tested for equal coordinates, coordinates over land using the Natural Earth data ocean shapefile version 4.1.0 (www.naturalearthdata.com, accessed November 2020), and zero coordinates. Finally, we used the catalogue number and geographical coordinates to filter out potential duplicates across GBIF and OBIS.

Our download strategy incorporated numerous shallow water species in the dataset, particularly zooxanthellate corals (i.e., corals with photosynthetic algae) – however, only deep-sea species fall under the definition of VME indicator taxa. Although very few zooxanthellate corals occur below 50 m (Cairns, 2007), using the typical definition of deep sea as waters below 200 m would exclude deep-water species that expand into shallower depths. Consequently, we aimed to integrate the ecology of taxa and the general definition of deep sea by applying several filters to exclude zooxanthellate corals and other strictly shallow-water taxa. First, we individually assessed the depth distribution of each species, and we kept a species if 90% of its records were below 200 m water depth. To assess the depth range of records, we relied on their original recorded depth as indicated in the sample record. In the cases where this information was not available, we used the General Bathymetric Chart of the Oceans (GEBCO, 2021) to assign depths. Second, we further filtered species known to be shallow water as we worked through with peer-reviewed deep-sea taxa lists (Cairns, 2017; Kocsis et al., 2018). Our filtered dataset of deep-sea VME indicator taxa comprised 1,997 species (of which 1,312 had an observation date).

Completeness of the inventory

We investigated the accuracy and uncertainty of our consolidated occurrence dataset by calculating the completeness of our inventory based on a class of diversity measures known as Hill numbers (Hill, 1973). Hill numbers are defined as the effective number of equally abundant species and are parameterized by a diversity order "q". Hill numbers for order $q \geq 0$ include the species diversity measures species richness, Shannon diversity, and Simpson diversity as special cases of order $q = 0$, $q = 1$, and $q = 2$, respectively. For incidence-based data, as here, this class of measures quantifies the effective number of equally frequent species. For $q = 0$, this measure reduces to species richness, and the measures of $q = 1$ and $q = 2$ can be interpreted respectively as the effective number of frequent and highly frequent species in an assemblage (Chao et al., 2014). As our objective is to detect biogeographical regions, completeness at orders $q = 1$ and $q = 2$ are particularly important. Biogeographical regions are based on the overlapping distribution of species, and therefore it is a requirement for bioregionalization methods to detect the majority of frequent and highly frequent species across a large number of sites throughout the study area.

We used the estimated sample completeness profile, which depicts completeness as a function of a diversity order q in a four-step integrated approach developed by Chao et al. (2020) that links the concepts of sample completeness and diversity. In practice, a completeness profile is plotted for all values of q from q=0 to q=2, beyond which the profile generally stabilizes (Chao et al., 2020). A bootstrap method permits to obtain 95% confidence intervals. We computed the completeness estimators at $q = 0$, $q = 1$, and $q = 2$, as described in Chao et al. (2020) (iNEXT.4steps R package; Chao & Hu, 2023). We estimated the sample completeness on a per-grid cell basis at resolutions ranging from 1° to 5°, because the quality of estimates of taxonomic richness is dependent on the spatial scale (extent and resolution) of the study (Soberón et al., 2007). We did not compute completeness indices for insufficiently sampled cells, which include cells that had less than 10 species, only singletons, or less than 3 sampled sub-cells, but instead these were manually set to have zero completeness. Our evaluation of different resolutions revealed an equal completeness at orders $q = 1$, and $q = 2$. However, coarser resolutions also aggregated species from different regions within a grid cell, ultimately blurring boundaries between regions (Lobo et al., 2018; Menegotto & Rangel, 2018; Mora et al., 2008). We decided to work at a resolution of 1°, which was a compromise between completeness and the identification of boundaries between bioregions. Further details on the computation of the sample completeness profiles can be found in the Supplemental Material (section "1. Inventory completeness").

Bioregionalization

We delineated biogeographical regions for VME taxa using bipartite biogeographical networks (Vilhena & Antonelli, 2015) with the hierarchical clustering algorithm Map Equation (Rosvall & Bergstrom, 2008). Bipartite biogeographical networks have been recommended to map biogeographical regions (Bloomfield et al., 2018; Edler et al., 2017; Rojas et al., 2017) and perform better in data-poor situations than similarity-based approaches (see Leroy et al., 2019, Appendix S2). A bipartite network represents the distribution of species across sites as a network of nodes, where each node is a species or a site. A network comprises nodes that can be connected to each other by links (or edges). Here, nodes represent grid cells and, separately, the species that occur in them, while edges link grid cell and species nodes indicating whether a species is present in a grid cell. The network is bipartite because each type of node, grid cell and species, cannot connect to another node of the same type; that is, species nodes can only connect to grid cell nodes and grid cell nodes can only connect to species nodes. Thus, a species can be found in several sites and a site can host several species. In this study, we divided the Southern Indian Ocean into a 1° latitude-longitude grid, created a species/grid cell contingency table of presence-absence and transformed it into a bipartite occurrence network (Vilhena & Antonelli, 2015).

In order to detect biogeographical regions, we applied a community-detection algorithm to the network. Community-detection algorithms aim at grouping together nodes that have high intra- group but low inter- group connectivity, which correspond to the definition of biogeographical regions as regions of assemblages with distinct endemic taxa. This is achieved based on flows of information (Rosvall & Bergstrom, 2008). As a community detection algorithm, we chose “Map Equation” (Rosvall & Bergstrom, 2008), as it has been recommended in previous biogeographical works (Bloomfield et al., 2018; Edler et al., 2017; Rojas et al., 2017; Vilhena & Antonelli, 2015) and it features hierarchical clustering. We ran Map Equation with 1,000 trials to find the optimal clustering and we ran it with hierarchical clustering to test whether larger regions showed a nested hierarchy of subregions. We explored bioregions that had strictly more than ten occurrences as our focus was to detect the main biogeographical regions in SIOFA. We explored the biological significance of each bioregion by calculating metrics to characterise the bioregions in terms of endemicity, the affinity (A_i, i.e., range in their region / total range of the region; the higher the value, the more widespread the species is in the region) and fidelity of a species to its bioregion (F_i, i.e., range in their bioregion / total range across all regions; the higher the value, the more exclusive the distribution range of the species is located in its associated region – a fidelity of 1 means that the species is endemic to its region) (Leroy, 2021). Fidelity, in particular, is useful to detect transition bioregions. Transition bioregions are located at the interface between multiple bioregions and are thus classified as distinct bioregions by Map Equation (Vilhena & Antonelli, 2015). A transition bioregion will not have high-fidelity species, as all species occurring therein will have their distribution spread over multiple bioregions. We also calculated the indicator value (*IndVal*) for each species in each region as $A_i * F_i$ – the *IndVal* will have a high value for species that occupy most of their associated cluster (high affinity) and are not present in any other cluster (high fidelity). We created and analysed the networks using the R package “*biogeonetworks*” (Leroy, 2021).

All analyses were conducted in R (R Core Team, 2021). The R code and data are available online in Zenodo (https://doi.org/10.5281/zenodo.7704934).

Results

Linnean and Wallacean shortfalls

Our compilation of VME occurrences showed that most of the Indian Ocean was unsampled and that the bulk of available records was distributed in coastal waters, i.e., outside SIOFA's management area (Figure 1A). At 1° spatial resolution, the observed richness per grid cell was very low with a median at 5 species approximately (Figure 1B) and sample completeness was nearly 0% for all diversity orders (Figure 1C). For adequately sampled cells (i.e., those that have more than two sample sub-cells of 0.01° spatial resolution, not only singletons, and strictly more than ten species), the sample completeness increased with diversity order (Figure 1D), suggesting that we had at least sampled most of the highly frequent species (q=2) in the inventory.

We highlighted this issue at all resolutions (Figure S1). The sample and diversity profiles revealed that, at all spatial resolutions, the inventory was incomplete for infrequent species (q=0), frequent species (q=1) and for highly frequent species (q=2) (Figure S1). The estimated sample completeness profiles increased with diversity order (q), implying that there was undetected diversity (Figure S1, panel (a)). Diversity as a function of sample size (Figure S1, panel (b)) and sample coverage (Figure S1, panel (d)) indicated that at increasing resolutions we would expect higher estimates and that any diversity estimates would be lower bounds given that the asymptotic estimator does not level off (Figure S1, panel (c)). Evenness among species was similar regardless of the resolution (Figure S1, panel (e)).

Bioregions in the high seas of the Southern Indian Ocean

We detected multiple bioregions structured in two hierarchical levels for VME indicator species in the Southern Indian Ocean. At the first level (i.e., largest regions with highest degree of endemism) there were four biogeographical regions (Figure 2A): an inshore and an offshore bioregion, and two bioregions representing the Southern Ocean at latitudes south of 40°S mostly. The four bioregions are present within SIOFA's management area, where the offshore bioregion has most of its distribution. The four bioregions have distinct faunas, and a very high degree of endemism with bioregion 1 having the largest endemicity (95.01%), followed by bioregion 2 (75.94%), 3 (64.60%) and 4 (64.15%) (Table 2). In addition, we found that all four bioregions had high fidelity species (Figure 3). The top indicator species for bioregion 1 were all corals from the order Scleractinia; for bioregion 2, indicators were mostly sponges; for bioregion 3, mostly tunicates; and for bioregion 4, mostly sponges (Table S1). We provide the full list of indicator species for bioregions in Supplemental File 1.

At the second level of hierarchy (i.e., subregions nested within the level 1 regions, with a lower degree of endemism), we found nine subregions with distinct geographic characteristics (Figure 2B). The large inshore bioregion differentiated into six subregions: one covering eastern South Africa; one subregion mostly north of 20°S, and four bioregions along the western coasts of Australia. The offshore bioregion revealed only one subregion and the Southern Ocean displayed two subregions. At this level, the lack of sufficient available data was reflected by sparse subregions occurrences in the SIOFA's management area. The endemicity patterns varied by subregion, wherein subregion 1.1 (29.05%), 1.3 (41.34%) and 2.1 (43.16%) have the largest endemicity, followed by subregion 1.12 (21.62%) and subregion 1.5 (17.65%) (Table 2). The fidelity of species to their subregion is less marked than at the first level, where in some cases there is a wide bimodal distribution, reflecting species with distribution spreading across multiple subregions (Figure 3). Yet, all subregions had species with a high fidelity, suggesting that none of the subregions was a transition zone. The top indicator species for subregion 1.1 were all scleractinian corals; for subregion 1.2, mostly scleractinians too; subregion 1.3 was mostly characterised by bryozoa; subregion 1.5 by tunicates; subregion 1.12 by a mix of scleractinian, alcyonacean, and antipatharian corals, and actinians; subregion 1.23 by an equal mix of corals (alcyonacean, antipatharian, scleractinian and pennatulaceans) and sponges; subregion 2.1 in its majority by sponges of several orders; subregion 2.3 by basket stars and brachiopods; and subregion 3.1 by a mix of tunicates, sponges and antipatharian corals (Table S2). We provide the full list of indicator species for subregions in Supplemental File 2.

Discussion

Major Wallacean and Linnean shortfalls in the Southern Indian Ocean

We found that VME taxa of the Southern Indian Ocean and, more specifically, within SIOFA's management area, are subject to an extreme version of the Wallacean and Linnean shortfalls (Cardoso et al., 2011). First, there was very little distributional data for VME indicator taxa (Wallacean shortfall), and the bulk of records was distributed in coastal waters within national jurisdiction, where survey effort is typically concentrated (Hughes et al., 2021). This first result is particularly worrisome as it suggests that SIOFA's management area has virtually no data at species level, making it extremely challenging to resolve the biogeographic patterns of VME indicator species.

Second, considering the large spatial scale over which we calculated the completeness of our inventory, this incompleteness constitutes a major Linnean shortfall (Cardoso et al., 2011). Our analysis on a per-grid cell basis revealed that the top 20% most adequately sampled cells had a median completeness of 55% at 1° spatial resolution, but this was repeatedly observed at all resolutions (Figure S2), which is an alarming insight into the incompleteness of our data. For comparison, marine fish inventories with a level of completeness above 80% are considered as good quality (Mora et al., 2008); freshwater fish inventories with a completeness above 78% are fair quality and those with > 90% completeness are good quality (Pelayo-Villamil et al., 2018). However, Fautin et al. (2013) propose that inventories 70% complete are not well inventoried, after they examined the global distribution of the Order Actiniaria (Phylum Cnidaria) and statistically compared observed with theoretical completeness values. More recently, global marine benthic inventories have been quantified to be less than 80% complete in general, particularly in southern hemispheres and subtropical regions (Menegotto & Rangel, 2018). The fact that the percentage of undetected diversity for adequately sampled cells is 50% for all *q* diversity orders (i.e., for infrequent, frequent, and very highly frequent species) at all spatial resolutions (Figure S3) and that these cells were all in territorial waters (Figure S4) corroborate these geographic and taxonomic biases for VME taxa of the Southern Indian Ocean.

Unique yet unknown bioregions

Our bioregionalization analysis has two main implications. First, SIOFA's management area hosts several biogeographical regions both at the first and second level of the hierarchy. Such diversity suggests a decisive responsibility for this regional fisheries management organization to preserve deep-sea biodiversity. On one hand, the percentage of endemicity is high for all regions (10% is proposed as the threshold to define a biogeographic region;

Briggs & Bowen, 2012) and comparable to the endemicity of the Indian Ocean marine realms (Costello et al., 2017), which provides robustness to our findings. On the other hand, the completeness analyses suggest that, in grid cells that are not undersampled, the majority of frequent species have been recorded (Figure 1D) additionally suggesting that the biogeographical regions based on these cells are robust. Nonetheless, the bioregions will likely become better defined as new taxa are identified or existing data are added to biodiversity inventories. For now, the first-level bioregions appear to reveal differences in the species composition across different depth environments, observed in the distribution across the continental shelves and slopes and the deeper offshore areas (Figure 2A). The subregions, in contrast, have a marked geographic distribution (Figure 2B). The complex seafloor topography and oceanography of the Indian Ocean are likely to be playing a central role in structuring these subregions, such as for octocorals in the North Pacific (Summers & Watling, 2021) and anthozoans globally (Watling & Lapointe, 2022), but future research will need to adequately address the environmental drivers behind these biogeographic patterns. Deep-sea biodiversity provides a central role in provisioning services such as fisheries and biochemical compounds (Armstrong et al., 2012; Thurber et al., 2014), and biodiversity maintenance increases resilience after a disturbance (Danovaro et al., 2008); thus, maintaining such biodiversity should be a key management objective in the pursuit of sustainable use of resources by SIOFA.

Second, data shortfalls, however, make it impossible to: (1) identify comprehensively the nested biogeographical regions within their management area, and (2) map them at a higher spatial resolution relevant for conservation decisions. In other words, neither we can resolve spatially finer biogeographic clusters at a scale that matches habitat complexity and fishing operating distances, nor understand the extent of clusters, or identify new ones, because most of the area lacks distributional data, especially in the easternmost side. Presently, there are only detailed descriptions of the habitats, biological communities, and oceanography for a few seamounts in the Southwest Indian Ocean Ridge (Hestetun et al., 2017; Pollard & Read, 2017; Pratt et al., 2019; Read & Pollard, 2017; Rogers et al., 2017; Taylor & Rogers, 2017) as part of the IUCN Seamount Project (Rogers, 2012; Rogers et al., 2017) and MADRidge Project (Roberts et al., 2020). With such few information we are not able to make informative maps, nor make robust predictions that translate into fine-scale characterisation of habitats across SIOFA's management area . Therefore the only solution is to resort to using this information at a coarse spatial scale (1° spatial resolution) so that analyses can only provide a first signal (reflected in the lower endemicity of some subregions) that multiple bioregions are expected to be found in the Southern Indian Ocean, but not useful for the finer grain resolution needed for conservation measures. Future work might include the exploration of predictive modelling as a first solution to tackle the lack of data.

In light of the many unknowns, the precautionary approach will be instrumental for the designation of conservation management measures to meet UN Resolutions towards protection of deep-sea habitats in the SIOFA area. Yet, negotiations to reach an agreement in the implementation of conservation measures may result in internal divisions in RFMOs due to limited cooperation and coordination among their members. This has been previously observed for seamounts, for instance, where those falling in the areas of competence of RFMOs eventually are more heavily fished than seamounts outside areas of competence in the same ocean basin (Kerry et al., 2022).

The absolute necessity of deep-sea biodiversity inventories

The shortfalls we identified here corroborate previous global data-driven biogeographic analyses (Watling & Lapointe, 2022) and global habitat suitability maps of different groups of deep-sea habitat-forming taxa (stony corals, Tittensor et al., 2009; octocorals, Yesson et al. 2012; black corals, Yesson et al. 2017; framework cold-water corals, Davies and Guinotte 2011). These knowledge shortfalls imply that global biogeographic analyses and conservation of marine biodiversity are not truly global, a fact increasingly recognized in the literature (Lenoir et al., 2020). Given the unique composition and endemicity of deep-sea ecosystems, and the increasing pressures on them due to the blue acceleration (Jouffray et al., 2020), we strongly urge the absolute necessity of investing in biodiversity inventories to start filling out these knowledge gaps. Although we advocate for this solution, we foresee that it will not change in the near future; hence, conservation decisions will have to rely on predictive modelling approaches in the short-term, which in turn will create an uncertain decision context.

Predictive approaches are useful for marine ecosystem management in data-poor situations, but are not the panacea (Reiss et al., 2015; Ross & Howell, 2013). Indeed, predictive approaches require complex models whose adequacy for the implementation of management measures needs to be well-understood by model-builders and users (Guillera-Arroita et al., 2015). More importantly, they cannot address the fundamental and underlying key issue of missing data: models cannot predict incompletely sampled biodiversity or habitats, let alone unsampled biodiversity and habitats. For example, Stephenson et al. (2021) demonstrated the shortcomings of predictive models for informing the design of spatial management measures for VME taxa in the South Pacific, and urged for the need for better quality data, such as presence-absence and abundance. In addition, the applicability of predictive approaches for the management of these taxa is further challenged by disagreements specific to the definition of VMEs (Gros et al., 2022). Thus, despite the development of state-of-the-art predictive approaches for VME taxa designed to cope with their typical presence-only nature (Ardron et al., 2014), the high seas of the Southern Indian Ocean will still necessitate of exploration efforts and release of data to overcome the alarming observed data deficiency.

Yet, detailed knowledge on the bathymetry and biodiversity of the Southern Indian Ocean exists for some areas on the high seas, through the fishing industry (e.g., Shotton, 2006; SIODFA, 2022). It will be critical that regional fisheries management organizations make information readily available just as international negotiations have agreed to a United Nations treaty on the conservation and sustainable use of biodiversity beyond national jurisdiction (the “BBNJ Treaty” or “UN High Seas Treaty"; UNGA, 2023). However, data mobilisation and digitisation of museum collections also constitute an important step in closing the gap of biodiversity synthesis to underpin conservation measures, more so in the realization of the post-2020 Global Biodiversity Framework (Orr et al., 2022). For now, conservation and management measures can be implemented in areas that benefit from existing data, building on a combination of key knowledge from RFMOs, bioregionalization schemes based on informed predictive approaches, and the precautionary approach. However, these areas are but snapshots of the deep-sea ecosystems and therefore it is unquestionable that much research exploration remains to be conducted to build comprehensive biodiversity inventories that serve to equip conservation managers with appropriate tools. In this respect, the recently proclaimed United Nations Decade of Ocean Science for Sustainable Development (2021 – 2030) might serve as a platform to catalyse opportunities and develop projects in the Southern Indian Ocean to ensure achieving sustainable management in line with international commitments (Sustainable Development Goals; UNGA, 2015).

The deep-sea community has paved the way with the development of a blueprint for a global deep-sea field programme that identifies and maps the needs and actions to achieve the objectives of the "Ocean Decade" (Howell et al., 2020). Similar as to the progress of the basin-wide Indian Ocean Observing System programme (IndOOS; Beal et al., 2020; Hermes et al., 2019), among them are identified the development of effective strategies that merge regional and basin-scale objectives, international coordination, capacity building, data sharing and, importantly, data release. These will be critical to finally put an end to the artificial empty maps that are systematically observed throughout the literature for this world's ocean region.

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Figure 1. (A) Distribution of observed richness in the study area at 1° latitude-longitude spatial resolution. The black polygon represents SIOFA’s management area. (B) Observed richness calculated over different subsets of our data at 1° spatial resolution. (C) Sample completeness profiles calculated for all cells, and (D) Sample completeness profiles calculated for adequately sampled cells only, for all *q* diversity orders at 1° spatial resolution. Undersampled cells are cells that had less than 10 species, only singletons, or less than 3 sampled sub-cells. Numbers over the boxplots indicate sample size (i.e., number of cells).

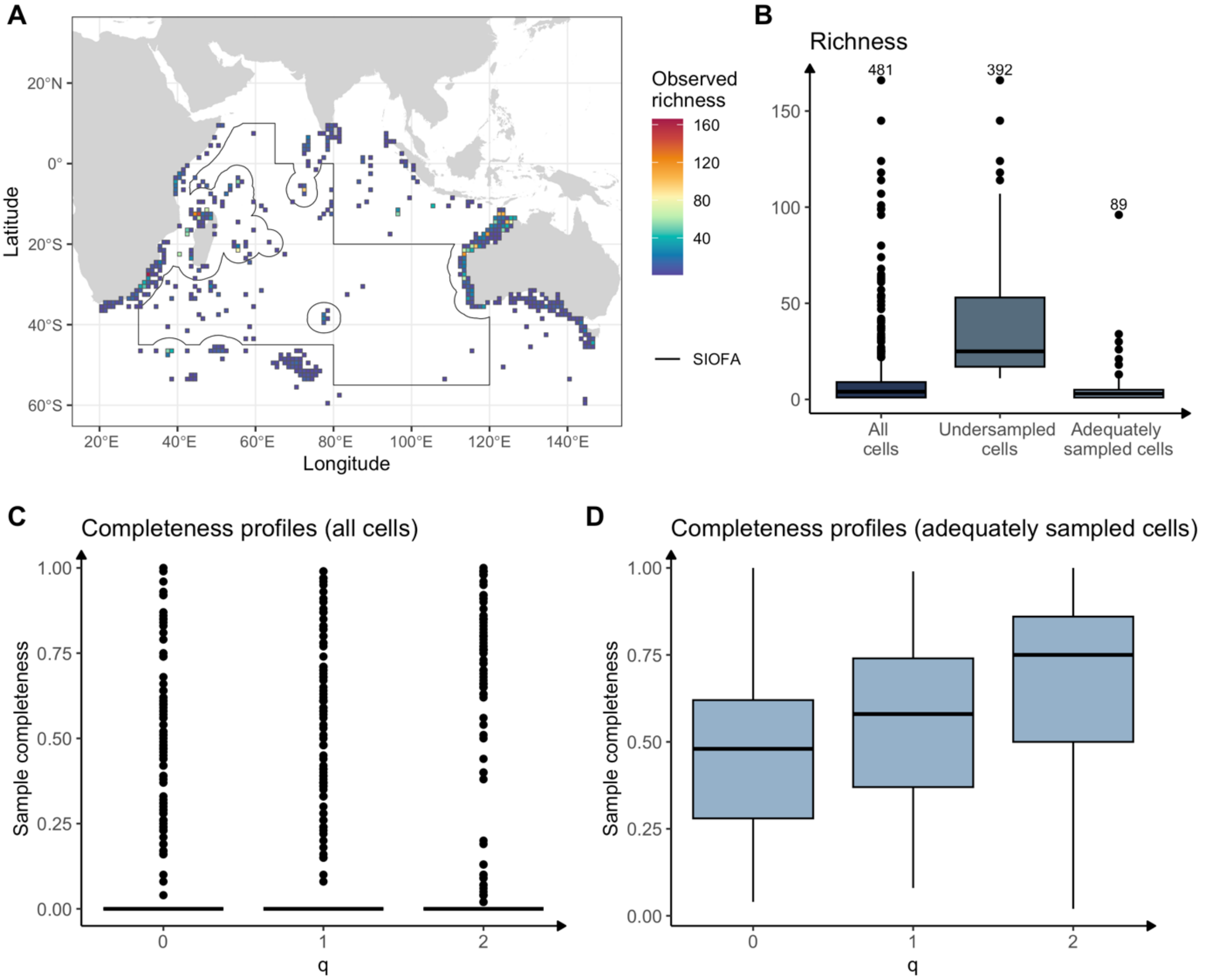

Figure 2. Distribution of bioregions (A) and subregions (B) at 1° spatial resolution. There are four bioregions at the first level: an inshore (1), an offshore (3), a Southern Ocean (2) and a sparse (4) bioregion. At the second level, there were six subregions nested within bioregion 1 (prefix 1), two subregions in the Southern Ocean bioregion (prefix 2) and one in the offshore bioregion (prefix 3). The black polygon denotes SIOFA's management area. Bathymetric contours (every 1000 m) are shown for reference.

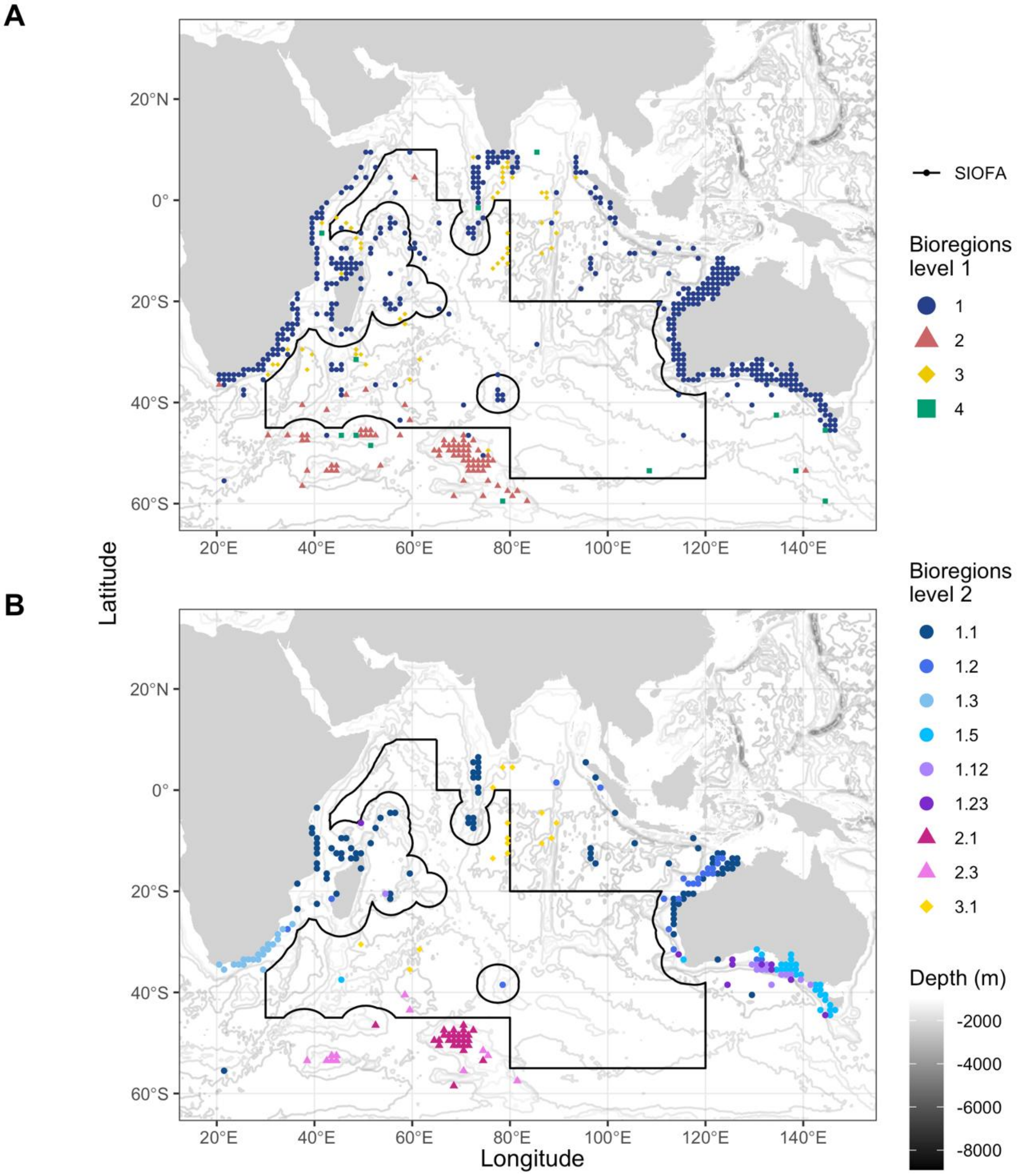

Figure 3. Distribution of fidelity values of species to their assigned first-level (A) and second-level (B) bioregions.

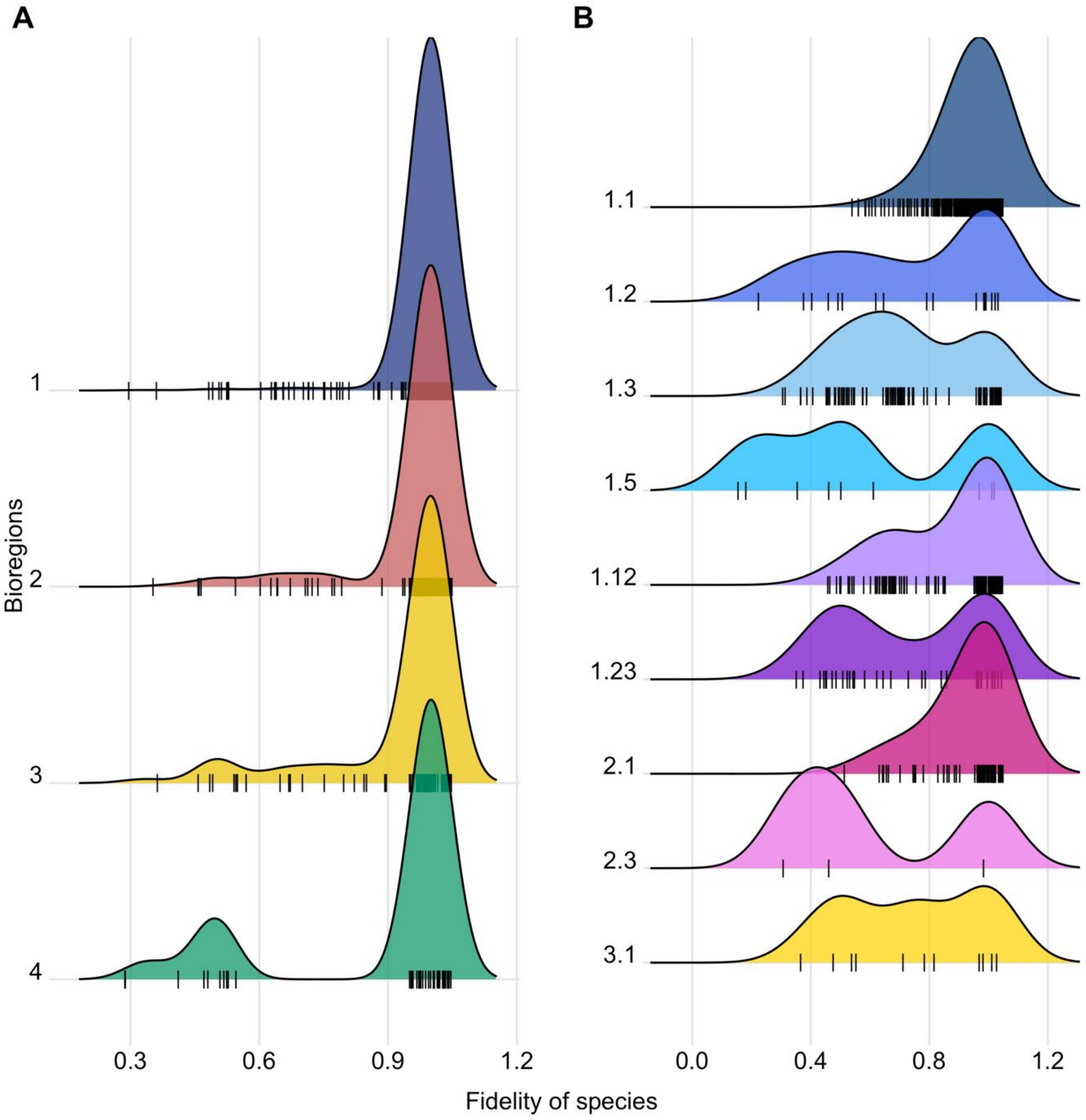

Table 1. Number of species and endemicity of each biogeographical region for the species-based bioregionalization. Total richness refers to the total number of species found in a bioregion. Assigned richness refers to taxa that the Map Equation algorithm has grouped into the same bioregion (even if a species is assigned to a bioregion, its distribution can expand into other bioregions). Endemic richness refers to taxa exclusively found in a bioregion. Percentage of endemicity refers to the endemic richness in a bioregion divided by the total number of species in that bioregion. Percentage of species in the study area refers to the number of assigned species to a bioregion divided by the total richness in the database.

Bioregion	**Total richness**	**Assigned richness**	**Endemic richness**	**Percentage of endemicity**	**Percentage of species in study area**
Level 1					
1	1664	1621	1581	95.01	83.32
2	212	183	161	75.94	10.62
3	113	93	73	64.60	5.66
4	53	44	34	64.15	2.65
Level 2					
1.1	754	416	219	29.05	37.75
1.2	206	90	27	6.89	10.32
1.3	179	119	74	41.34	8.96
1.5	95	38	15	17.65	4.76
1.12	48	18	8	21.62	3.00
1.23	22	9	3	6.00	1.10
2.1	96	60	41	43.16	4.81
2.3	8	3	1	10.00	0.40
3.1	22	11	4	9.09	1.10