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Research article

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Delineating biogeographical regions can provide important insights into the processes shaping large-scale species distribution patterns. Here we aimed to 1) identify global marine benthic biogeographical regions for ophiuroids extending from shallow waters to the deep sea and 2) quantify the importance of contemporary environmental conditions and geological features in shaping the delineated biogeographical regions. We delineated marine benthic biogeographical regions using a bipartite network analysis applied to a historical dataset of brittle stars. We then examined the faunal exchanges between the regions, and applied random forest models to evaluate the relative role of contemporary environmental conditions and tectonic configuration underlying the proposed biogeographic scheme. We propose ten main large biogeographical regions across the benthos. The biogeographical regions with the highest species richness and endemicity rates were found in the Indo-Pacific region, Tropical West Atlantic and Southern Ocean, and South America. The key transition regions fall within the subarctic areas of the Pacific and the waters surrounding Southern Australia and New Zealand. Tectonic configuration, surface temperature and salinity were found to be the most important predictors of the ten delineated biogeographical regions. Our biogeographic delineation, including the deep sea, is in partial agreement with those proposed in previous studies. Our results suggest that contemporary environmental conditions (sea water temperature and salinity) strongly influence the modern distribution of ophiuroids, but that plate tectonics left a marked imprint on regional species pools. Future work based on multiple benthic taxa, and with a better understanding of the environmental conditions in the deep sea, are needed to evaluate the robustness of our proposed division.

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Keywords: deep-sea biogeography, macroecology, networks, ophiuroids, plate tectonics

Introduction

The marine realm covers two-thirds of the planet's surface area, with the deep sea (i.e. depths below 200 m) providing ~ 70% of Earth's habitable space (Costello et al. 2010). These deeper areas of our oceans remain uncharacterised, particularly in terms of their biodiversity (Ramirez-Llodra et al. 2010). This lack of knowledge is alarming at a time when global biodiversity is in decline (Sala et al. 2000, Butchart et al. 2010, Pereira et al. 2010), with many scientists suspecting that the planet is in the initial stages of the sixth mass extinction (Sala 2000, Barnosky et al. 2011, Pievani 2014, McCallum 2015, Ceballos et al. 2017, Cowie et al. 2022). Therefore, understanding biodiversity patterns and gradients in the deep sea is imperative, since we can observe rapid chemico-physical changes such as warming, acidification, deoxygenation and direct disturbances from fishing, oil drilling and the ever-approaching deep-sea mining (Levin and Le Bris 2015). Conservation from these impacts first requires mapping biodiversity, which has been recognized by the United Nations Convention on the Law of the Sea (UNCLOS) to be deficient in Areas Beyond National Jurisdiction (ABNJ), which is most of the deep ocean (Visalli et al. 2020).

The considerable lack of data for deep-sea biodiversity is caused by the costs and infrastructure associated with accessing such a large, remote ecosystem. Here, global-scale data compilations are rare and plagued by sampling and taxonomic inconsistencies (Higgs and Attrill 2015). As a result, delineating zones of endemism and understanding zoogeographic barriers (i.e. bioregionalisation), and how these have been shaped by geology and climate remains challenging in deeper environments. Consequently the majority of marine biogeography studies have focused on coastal habitats and shallow depths (Spalding et al. 2007, Kulbicki et al. 2013, Hattab et al. 2015a), and deep-sea biogeography has been inferred (Mcclain and Hardy 2010). To date, bioregionalisation schemes incorporating the deep sea have relied on 1) environmental data accompanied by expert contributions (Menzies et al. 1973, Watling et al. 2013), 2) regional delineations (Griffiths et al. 2009, Saeedi et al. 2019), 3) global efforts with the majority of data from shallow depths or the pelagic realm (Costello et al. 2017) or 4) delineations based on a single or few taxa, such as amphipods (Arfianti and Costello 2020), polychaetes (Pamungkas et al. 2021), anthozoans (Watling and Lapointe 2022) or depth strata (Vinogradova 1997), thus highlighting the difficulties associated with gathering data from the deep ocean.

The importance of ecological and historical drivers of biogeographical boundaries across both shallow marine waters and the deep sea is still debated. At great depths ecological connectivity could arise from the lack of environmental and geographical obstacles, because oceanographic and topographic features are semi-permeable barriers or even mixing zones (Monniot and Monniot 1978, Danovaro et al. 2014, Mcclain and Schlacher 2015, Guggolz et al. 2017). Areas of suitable habitat become larger with increasing depth, since oceanographic conditions vary less spatially the deeper one goes (Costello et al. 2018). Furthermore, the cold temperatures in the deep sea are suspected to enhance connectivity by prolonging the duration of the pelagic larval stage, permitting dispersal of species across vast oceanic distances (Mcclain and Hardy 2010, Hilário et al. 2015). In shallow marine waters, contemporary environmental conditions such as sea-surface temperature are found to shape modern biogeographical boundaries (Belanger et al. 2012, Kocsis et al. 2018), while the motion of tectonic plates left a marked imprint on species distribution in shallow marine tropical waters as a result of colonization, extinction or speciation processes (Keith et al. 2013, Cowman and Bellwood 2013b, Leprieur et al. 2016). Additionally, shallow processes, such as primary productivity and subsequent export productivity, are considered to drive deep-sea species richness (Woolley et al. 2016). Glacial cycles have increased deep-sea diversity by generating cold, highly oxygenated bottom water in the poles that flows into lower latitudes, but periods without polar ice cover have caused the deep ocean to be anoxic and without life (Clarke and Crame 2010).

Here, we present the first global map of marine benthic biogeographical regions and potential transition regions incorporating the deep sea based on the class Ophiuroidea. We apply bipartite networks on a historical distribution data set of ophiuroids, which have become a useful model taxon for macroecological studies owing to their widespread occurrence and abundance across marine habitats, and tractable diversity (O'Hara et al. 2011, 2019, Stöhr et al. 2012). We discuss the delineation of the major biogeographical regions in the context of species richness and endemicity, and assess the importance of contemporary environmental conditions and geological features underlying the proposed biogeographic division.

Material and methods

Description of the data and sampling units

Our database is a global compilation based on the distribution of 2201 species from the class Ophiuroidea, with historical records from the last 130 years (Stöhr et al. 2023). The data consist mostly of voucher specimens stored in museums and examined by experts; see the Supporting information for more information. There are in total 95 559 records, of which 44% are from below 200 m depth extending to 8135 m depth (Supporting information). Of the deep-sea records, 15% were collected between 1976 and 2018 on cruises

organised by the Tropical Deep Sea Benthos program, which also facilitated an international network of taxonomists to work on the specimens (de Forges et al. 2021).

We evaluated the completeness profiles of our database across several spatial resolutions to find an optimal resolution for the analysis. We produced raster grids of a global extent ranging from 1 to 5° resolution ('raster' R package, www.r-project.org, Hijmans 2019) and calculated the completeness profiles at orders $q=0$, 1 and 2 (Chao et al. 2020 for a detailed description) (Supporting information). Here, completeness profiles assess the fraction of detected diversity of a dataset at different orders $q \geq 0$ based on the framework of Hill numbers extended to incidence data (Hill 1973). Completeness at order $q=0$ is an upper bound estimate of the proportion of detected species richness but, in reality, the proportion of detected species richness is inadequately estimated in most cases. Completeness at order $q=0$ is disproportionately sensitive to infrequent species. Completeness at order $q=1$ corresponds to the sample coverage, and treats all species equally, without disproportionately favoring either infrequent or frequent species. Completeness at order $q=2$ disproportionately favors highly frequent species. As our objective was to detect biogeographical regions, completeness at orders $q=1$ and 2 was particularly important. Biogeographical regions are based on the overlapping distribution of species, and therefore it is a requirement for bioregionalisation methods to detect the majority of frequent and highly frequent species across a large number of cells throughout the study area.

To compute the completeness profiles for each cell, we divided each cell into sub-cells of resolution (0.01°) and recorded species incidence data in each sub-cell. Hence, each sub-cell is considered as a sampling unit to compute completeness profiles for each cell. We computed the completeness estimators at $q=0$, $q=1$ and $q=2$ (Supporting information) as described in Chao et al. 2020 ('iNEXT.4steps' R package, www.r-project.org). We did not compute completeness indices for insufficiently sampled cells, which include cells that had less than 10 species, only singletons, or less than three sampled sub-cells, and these were manually set to have zero completeness. Our evaluation of different resolutions revealed a well-characterised trade-off where coarser resolutions led to a lower number of undersampled cells and a higher completeness at orders $q=1$ and 2 (Supporting information) (Mora et al. 2008, Lobo et al. 2018, Menegotto and Rangel 2018). However, coarser resolutions also aggregated species from different regions within a grid cell, ultimately blurring boundaries between regions. Hence, we decided to work at a resolution of 3°, which was a compromise between completeness and the identification of boundaries and transition areas between bioregions.

Delineating biogeographical regions

We applied a bipartite network analysis (Vilhena and Antonelli 2015) on the ophiuroid distribution data. This approach keeps track of species identity throughout the bioregionalisation process, making the method robust to differences in sampling intensities (Edler et al. 2017, Bloomfield 2018, Leroy et al. 2019). The algorithm assigns each species to a specific bioregion, which facilitates describing and understanding the biological significance of clusters.We constructed an occurrence network containing both species and sites (grid cells) as 'nodes', with the R package (www.r-project.org) 'biogeonetworks' ver. 0.1.1 (www.github.com/biogeonetworks). Species are linked to the sites in which they occur, and species to species or site to site linkages are not permitted. We applied the Map Equation community-detection algorithm (Rosvall and Bergstrom 2008) with 100 repetitions to detect clusters of highly interconnected sites and species, with low inter-cluster connectivity, which correspond to distinct regions of endemic taxa, thus translating the network into the final biogeographical regions. We excluded clusters with fewer than 10 sites, which were not meaningful for our global-scale analysis. Once biogeographical regions are defined, the Map Equation algorithm assigns each node of the network (site or species) to a region to which it is the most connected. This means that sites are assigned to a region that they share the highest number of species with, while species are assigned to a region where they have the highest number of occurrences (i.e. characteristic species). For each site, we assessed transition zones between regions by measuring the extent to which a node is connected to other biogeographical regions with the participation coefficient (PC) (Bloomfield 2018). A high PC for a site indicates that it contains species from different regions, whereas a low PC indicates that the site contains only species from the region to which it belongs. In other words, transition zones based on high PC values are generated by overlapping fauna between regions. Also, sites that contain widely distributed species can obtain high PC values. The latter is most likely caused by sampling biases in our data set and will not be explored further.

For each biogeographical region, we calculated its spatial extent (km^2), species richness, the number of characteristic species, the percentage of endemic species and the average PC value. We produced an alluvial diagram illustrating how species that are characteristic of a specific region are spread across different regions, to understand the interplay and faunal links between the biogeographical regions (*ggalluvial*, Brunson and Read 2020). We compared our biogeographical regions against five other global studies comprising shallow marine benthic biogeographical regions (Kocsis et al. 2018), all marine organisms (Costello et al. 2017), deep-sea biogeographic realms of the lower bathyal (800–3000 m) (Watling et al. 2013, Watling and Lapointe 2022) and the Marine Ecoregions of the World (MEOW) for coastal and shelf areas (Spalding et al. 2007).

Modelling procedure

We applied a two-step modelling approach to identify the potential large-scale predictors and processes underlying the observed biogeographical regions. We utilised the random

forest classification algorithm based on decision trees ('caret', method ranger, Wing et al. 2019) because we had no a priori assumptions on the shape of the relationships between the biogeographical regions and the variables (Cutler et al. 2007). The first step aimed at providing a global picture of the large-scale predictors influencing the ten biogeographical regions. We used the sites categorized into biogeographical regions as the response variable and the predictors as explanatory variables. In the second step, we investigated which predictors would best explain each individual biogeographical region. Here, each region was an independent binary response variable (sites assigned to the region were 1, sites assigned to other regions were 0). The predictors included a range of oceanographic variables from MARSPEC (Sbrocco and Barber 2013) and Bio-ORACLE (Assis et al. 2018); total annual net primary productivity (NPP) and seasonal variation in NPP calculated from satellite data, which affect deep-sea species richness (Woolley et al. 2016); and the tectonic plate configuration from Bird (2003), which affects the distribution of species (Keith et al. 2013, Leprieur et al. 2016). We also included current velocity (Bio-ORACLE) and distance to nearest shoreline (MARSPEC) as proxies for the physical environment affecting nutrient input, connectivity and dispersal. The environmental data were extracted only in areas where there were species records. As the MARSPEC and Bio-ORACLE data set has a resolution of 0.08, the values of the variables were aggregated per grid cell, producing an average value per each 3° grid cell (Supporting information). We assessed collinearity using Cramér's V for categorical predictors and the Spearman's rank correlation coefficient for numerical predictors. To assess the strength of association between numerical and categorical predictors, we calculated the eta measure from an ANOVA (i.e. square root of the between-groups sum of squares/total sum of squares). For all three measures of association between variables, we used a threshold of 0.7 to filter out collinear variables. When collinearity was present between two or more variables, we chose the variable that we deemed more ecologically relevant and had the strongest correlation with the biogeographical regions. See Supporting information for the full list of variables considered for the analysis. The surface variables generally showed a better correlation with the bioregions, since most of the distribution data fell within the 0–1500 m water depth (Supporting information). The final predictors were annual mean sea-surface temperature and salinity, depth of the seafloor, productivity variables, current velocity (long-term maximum at mean depth), distance to shore and tectonic plates (a categorical variable) averaged across a 3° grid cell.

To test the performance of our models for both the multi- and individual region model, we applied a repeated fivefold cross-validation three times. For each test data set, we assessed the quality of the predictions by comparing the predicted values to the observed values to calculate the success rate in predicting the correct region (Supporting information). We evaluated the importance of each environmental variable using the standard random forest variable importance procedure. All data analysis was conducted in R (www.r-project.org); see Supporting information for the model specifications and parameters, and the data and code.

Results

Proposed biogeographical regions

Our bioregionalisation analysis revealed a total of 23 benthic biogeographical regions (Supporting information). We focused on exploring the ten most important biogeographical regions identified by the algorithm, which were both spatially extensive and geographically coherent (Fig. 1). The minor biogeographical regions mostly consisted of abyssal plains at great depths that have been poorly sampled, such as the deep Indian Ocean. The regions with some of the highest biodiversity metrics were the Indo-Pacific, Tropical West Atlantic, and the Southern Ocean and South America (Table 1). The regions characterised by low biodiversity metrics included the Arctic and Boreal, Northern Pacific, South Pacific and Tasman Sea, and Subtropical Japan (Table 1). We compare our biogeographical regions to previous biogeographic delineations in Table 2.

Transition zones between biogeographical regions

Based on faunal overlap across regions, the main transition zones occur in areas of the subarctic Pacific, particularly in Subtropical Japan and Southern Australia and the South Pacific and Tasman Sea (Table 1, Fig. 2). When exploring faunal relationships between regions, the Indo-Pacific shows many interactions with major and minor regions across the Indian and Pacific Oceans (Fig. 3), since it has the highest number of characteristic species (Table 1). Notably, it forms part of a prominent three-way faunal interaction between Southern Australia and the South Pacific and Tasman Sea (Fig. 3).

The Arctic and Boreal biogeographical region has high PC values in the area of subarctic Pacific and slightly elevated values in the Atlantic, but low values inside the Arctic Ocean. The Arctic and Boreal region has faunal links with the Northern Pacific; Subtropical Japan, which has the highest PC value (Table 2); and North Atlantic and Mediterranean Sea biogeographical regions (Fig. 3, Supporting information). Within the Northern Pacific Ocean, there is an overlap between three biogeographical regions, including the Eastern Pacific region (Fig. 1). One-third of the Eastern Pacific biogeographical region's fauna is endemic, but the rest is shared with other regions, with biotic exchanges occurring with the minor regions and the Northern Pacific, Subtropical Japan and the Tropical West Atlantic biogeographical regions (Fig. 3). We also observe other biogeographical regions that extend spatially across the globe with many links to other regions (see Supporting information for details on regions labelled 12, 13 and 22).

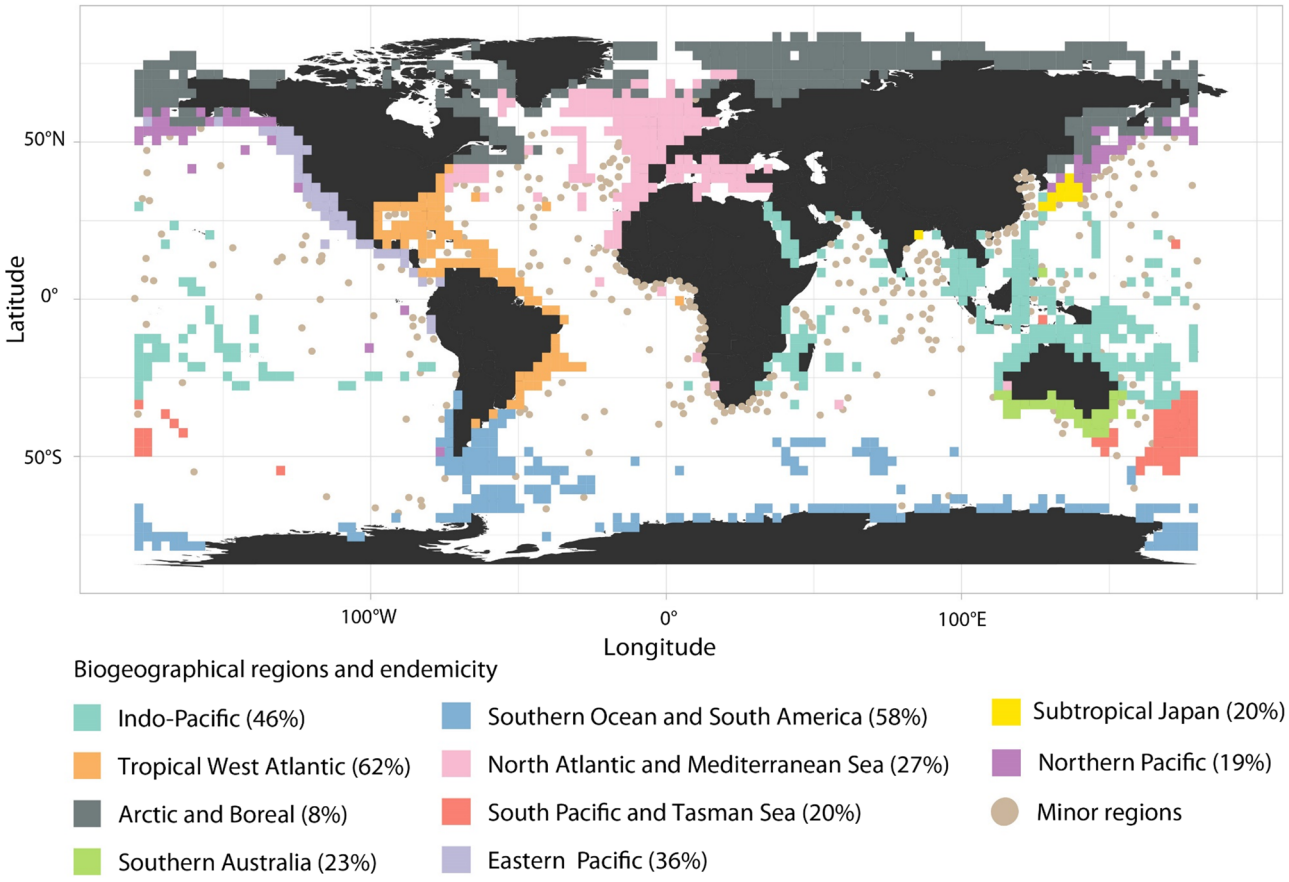

Figure 1. The top ten largest biogeographical regions identified by our bipartite network, for which we assessed the effect of macroecological predictors. The minor biogeographical regions group represents the other 13 biogeographic regions identified by the network analysis, which are not spatially extensive and/or geographically coherent.

Ecological and geological predictors

The multi-region model had a high success rate in correctly predicting biogeographical regions (Supporting information).

The most important variables for the multi-region biogeographical classification were sea-surface temperature (SST), the tectonic configuration of Eurasia and North America, and sea-surface salinity (SSS) (Supporting information). The depth of the seafloor and productivity-related variables were of minor importance for classifying multiple biogeographical regions (Supporting information), since the main ten regions span large depth and productivity

Table 1. Summary of different biodiversity metrics for the ten major biogeographical regions identified by our bipartite network. The characteristic species represent species assigned to a region based on having the highest occurrence within a particular region. PC = participation coefficient value. See Supporting information for summary statistics of the environmental conditions per bioregion.

Bioregion	Size (km^2)	Species richness	Characteristic species	Endemic species	Endemicity (%)	Average PC of region	Depth range (m)
Indo-Pacific	29 342 462	975	677	445	46	0.18	4–3571
Southern Ocean and South America	10 656 261	212	158	122	58	0.08	31–5923
Tropical West Atlantic	10 279 163	358	267	223	62	0.24	3–3546
North Atlantic and Mediterranean Sea	12 499 525	194	114	53	27	0.27	10–4426
Arctic and Boreal	14 131 532	88	27	7	8	0.09	4–2375
South Pacific and Tasman Sea	4 604 412	280	137	57	20	0.47	111–2327
Southern Australia	2 809 653	277	121	63	23	0.53	11–2432
Eastern Pacific	4 188 984	147	90	53	36	0.41	11–2582
Subtropical Japan	1 028 556	295	112	60	20	0.72	125–1280
Northern Pacific	4 131 792	147	69	28	19	0.44	5–7315

Table 2 Comparisons of the proposed biogeographical regions with previous global bioregionalisation schemes. See Supporting information for a detailed spatial comparison.

Biogeographical regions	Coastal benthic biogeographical regions	Marine realms	Lower bathyal provinces	Lower bathyal provinces	Marine ecoregions
	Kocksis et al. (2018)	Costello et al. (2017)	Watling and Lapointe (2022)	Watling et al. (2013)	Spalding et al. (2007)
Indo-Pacific	Tropical Indo-Pacific; Tropical East Pacific	South-East Pacific; Indo-Pacific seas & Indian Ocean; Gulf of Aqaba; Gulf of Aden; Gulf of Suez; Red Sea; Coral Sea; Mid South Tropical Pacific; Offshore W Pacific	West Pacific; Central Pacific; Indian Ocean	SE Pacific Ridges; Indian Ocean; West Pacific; North Pacific	Western Indo-Pacific; Central Indo-Pacific; Eastern Indo-Pacific
Southern Ocean and South America	Southern Ocean and South America; South American	Rio de la Plata; Chile; Southern Ocean	Antarctic; South Atlantic; Southwest Pacific; Nazca Plate	Southern Ocean and South America; SubSouthern Ocean and South America; Nazca Plate	Temperate Southern America; Southern Ocean
Tropical West Atlantic	Western Atlantic; European	Gulf of Mexico; Offshore S Atlantic or no data	Central Northwest Atlantic; South Atlantic	North Atlantic; South Atlantic	Tropical Atlantic
North Atlantic Ocean and Mediterranean Sea	European; Arctic	NE Atlantic; Mediterranean; offshore NW North Atlantic	Northeast Atlantic; Boreal Northwest Atlantic; South Atlantic	North Atlantic; Northern Atlantic Boreal	Temperate Northern Atlantic
Arctic and Boreal	Arctic	Arctic seas; N American Boreal	Arctic; Boreal Northwest Atlantic; North Pacific	Arctic; Northern North Atlantic; Northern North Pacific	Arctic; Temperate Northern Pacific; Northern North Pacific
South Pacific and Tasman Sea	New Zealandian	Tasman Sea; New Zealand	Southwest Pacific	New Zealand Kermadec	Temperate Australasia
Southern Australia	Temperate Australian	South Australia	Southwest Pacific; Indian Ocean	Indian Ocean	Temperate Australasia
Eastern Pacific	Arctic; Tropical East Pacific	N Pacific; South-East Pacific; Gulf of California	North Pacific; Cocos Plate	Arctic; Northern North Atlantic; Northern North Pacific; Cocos Plate	Temperate Northern Pacific
Subtropical Japan	Arctic	Offshore W Pacific	West Pacific	Northern North Pacific	Temperate Northern Pacific
Northern Pacific	Arctic	Offshore mid-E Pacific	North Pacific	Northern Pacific Boreal	Temperate Northern Pacific

gradients. Distance to shore and current speed were also of minor importance. When investigating the predictors of individual regions, our models identified SST and tectonic plates to be the most important predictors for many biogeographical regions across tropical and temperate climates, such as the Indo-Pacific, Tropical West Atlantic, North Atlantic and Mediterranean Sea, and Southern Ocean and South America (Fig. 4). The other variables were consistently less influential, with the exception of productivity variables for the Eastern Pacific (Fig. 4). We found that almost all regions were strongly explained by one or two tectonic plates and that a single tectonic plate, such as the North American plate, could be important for several biogeographical regions (Supporting information). For example, the Okhotsk plate influenced the Northern Pacific and Subtropical Japan regions, while the Australian plate had a high importance for the Southern Australia and for the South Pacific and Tasman Sea biogeographical regions. The two largest biogeographical regions, the Indo-Pacific and the Southern Ocean and South America were, in contrast, explained by several plates, which highlights the complex tectonic configuration of the large area covered by these regions.

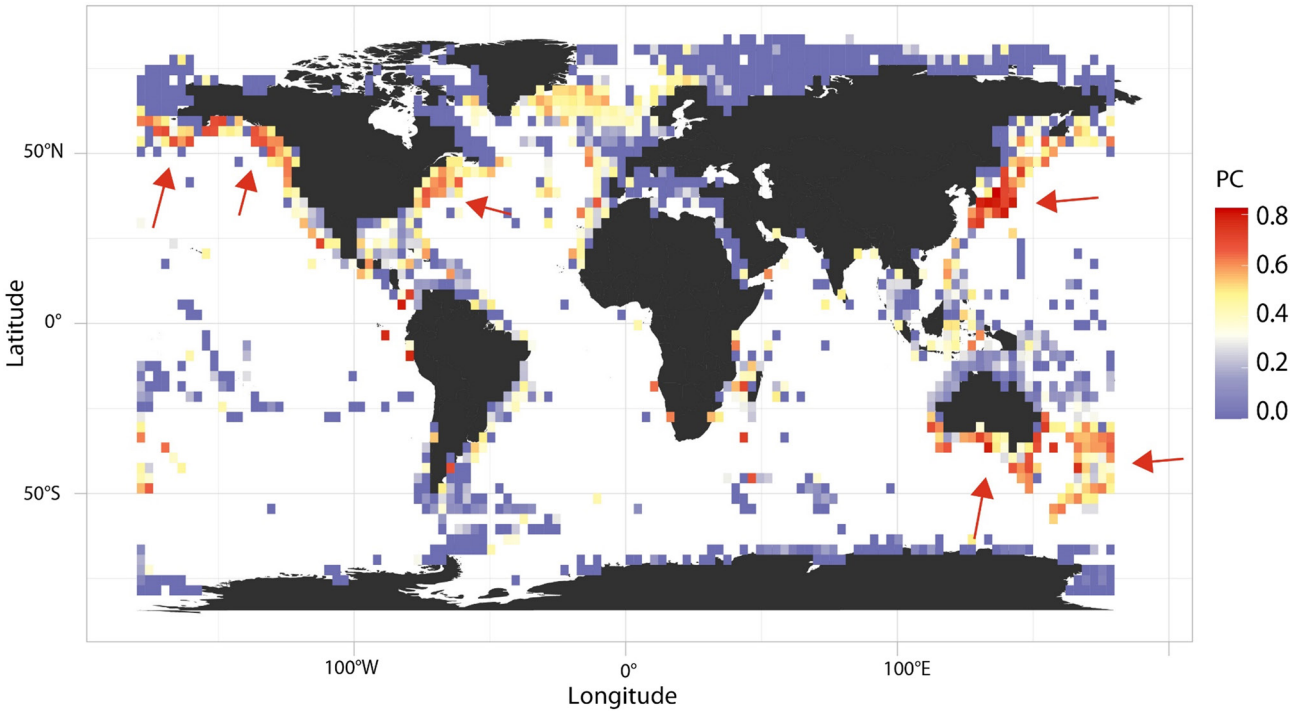

Figure 2. Participation coefficient (PC) values for the ten major biogeographical regions, illustrating potential transition zones with red arrows. Areas with high PC values contain species that are present in other regions.

Discussion

This study identified ten benthic biogeographical regions along with transitional zones based on ophiuroids, which extend to the deep sea. We also investigated how contemporary oceanographic conditions and tectonic plates have shaped the proposed biogeographical delineation at the global scale.

Biogeographical regions and faunal interactions

Our proposed biogeographical regions and their interactions through faunal links are similar to those described for the shallow benthos based on seven taxa by Kocsis et al. (2018), suggesting broad-scale patterns across the benthic habitats globally. The endemicity hotspots were the Indo-Pacific, Tropical West Atlantic, and Southern Ocean and South America biogeographical regions (Table 1), which are proposed centers of evolutionary radiation in the shallow and deep sea (Crame 2014). The tropical regions are where species are produced, exported and accumulated, making them key areas for biogeography (Jablonski et al. 2006, Bowen et al. 2013). For ophiuroids, the tropical shallow depths are considered a 'cradle' for the origination of new species, in contrast to the tropical deep sea, which acts as a 'museum', harboring ancient organisms that have gone extinct elsewhere (O'Hara et al. 2019).

The Indo-Pacific forms the epicenter of our proposed biogeographical regions with its sheer size, high number of characteristic species, high endemicity and the numerous faunal links to other regions. These patterns, together with many faunal links across several regions, show that the Indo-Pacific is characterised by widely distributed ophiuroid species, as found in fish (Briggs and Bowen 2012). We observe faunal links to other regions within adjacent seas and hypothesize that the tectonic history, the lack of barriers or the existence of semi-permeable barriers allow taxa to spread widely from the eastern coast of Africa across islands into the central Pacific, while creating provincial endemics (Cowman and Bellwood 2013b).

The diversity of the Indian Ocean and Central Pacific has been linked with high origination and dispersal rates from the Indo-Australian Archipelago over ca 30 Myr (Cowman and Bellwood 2013a), which supports the spatial extent of our Indo-Pacific biogeographical region. We identify a prominent three-way interaction between the Indo-Pacific, the South Pacific and Tasman Sea, and the Southern Australia biogeographical regions (Fig. 3), with the high PC values of the latter two suggesting they are transition zones. The Subtropical Japan biogeographical region is another transitional area located between the Indo-Pacific and Arctic, subarctic Pacific and Atlantic. This area has been described as a species richness hotspot for deep-water species (Woolley et al. 2016), suggesting it could be a transition zone particularly for deep-sea fauna. The area of the subarctic Pacific in general shows high connectivity (Fig. 2), as in this area four biogeographical regions occur in proximity with several regions having adjacent boundaries (Fig. 1). The Eastern Pacific biogeographical region displays transitional properties (Fig. 2) with clear faunal links to the neighboring Northern Pacific, Subtropical Japan and Tropical West Atlantic biogeographical regions (Fig. 3). Previous to the closure of the Isthmus of Panama 6–3 Mya ago, the

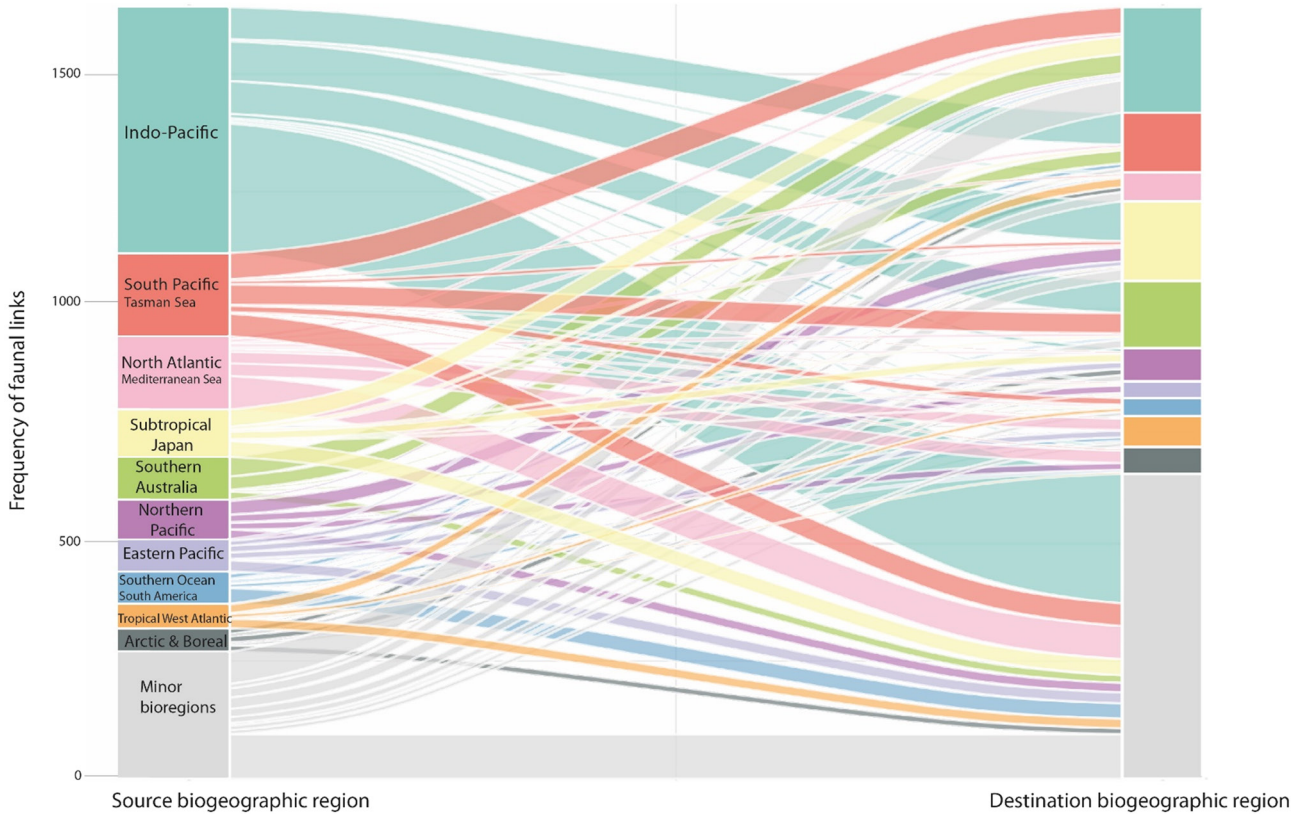

Figure 3. Alluvial diagram illustrating the frequency of faunal overlaps between biogeographical regions. Determination of the source bioregion is based on where a species occurs most frequently, and the flows show how frequently a species assigned to one region occurs in another, revealing the faunal links between different biogeographical regions. See Supporting information for the precise number of links between the biogeographical regions.

Pacific and the Tropical West Atlantic were connected by an equatorial current from the Pacific (Toonen et al. 2016).

Our results suggest that the Tropical West Atlantic biogeographical region, with high values for species richness, characteristic species and endemicity, was likely to act also as a radiation center for the North Atlantic and Mediterranean Sea biogeographical region (Fig. 3), which has areas with higher PC values along the coast of North America (Fig. 2). This observation is in agreement with previous fish studies showing that tropical fauna in the Atlantic derive from a Caribbean origin (Briggs and Bowen 2013). Another mechanism that could explain the connections we see between biogeographical regions in the Atlantic Ocean is the trans-Arctic interchange (Vermeij and Roopnarine 2008), as past biogeographical dispersal events could explain the transitional properties along the boundaries of the subarctic Pacific and slightly higher PC values in some cells in the subarctic Atlantic (Fig. 2).

We show faunal links between the Southern Ocean and South America. These have been previously alluded to at different taxonomic levels, and have been attributed to South Georgia's proximity to South America 10 Ma years ago, and the clockwise flow of the Southern Ocean and South America Circumpolar Current from South America towards the sub-Southern Ocean and South America islands (Linse et al. 2006, Griffiths et al. 2009). In ophiuroids and echinoids there is evidence of dispersal across the world's strongest current, the Antarctic Circumpolar Current, and the surrounding deep sea (Díaz et al. 2011, Sands et al. 2015). In fact, it has been hypothesized that the deep sea could be the dispersal pathway enabling faunal linkages with South America (Díaz et al. 2011, Sands et al. 2015). The Southern Ocean and South America biogeographical region also has faunal links with the South Pacific and Tasman Sea and an array of minor regions (Fig. 3), which could arise from species transitioning from the Southern Ocean and South America into the temperate deep sea, as shown by ophiuroid phylogeography (O'Hara et al. 2019). Furthermore, the dispersal of species from Antarctica has been attributed to the cold waters at shallower depths and to the Antarctic Bottom Water sending organisms to the deep sea in the 'thermohaline expressway' (Vinogradova 1997, Briggs 2003, Crame 2014). However, future studies might reveal that the faunal links highlighted in our study are not shared species, but instead reflect cryptic species complexes (Stöhr et al. 2020), which might indicate a recent dispersal limitation leading to divergence. As a consequence, the peripheral areas of the Indo-Pacific biogeographical region, such as the West Indian Ocean and mid-eastern Pacific Ocean, and Southern Ocean and South America biogeographical regions, could separate into smaller

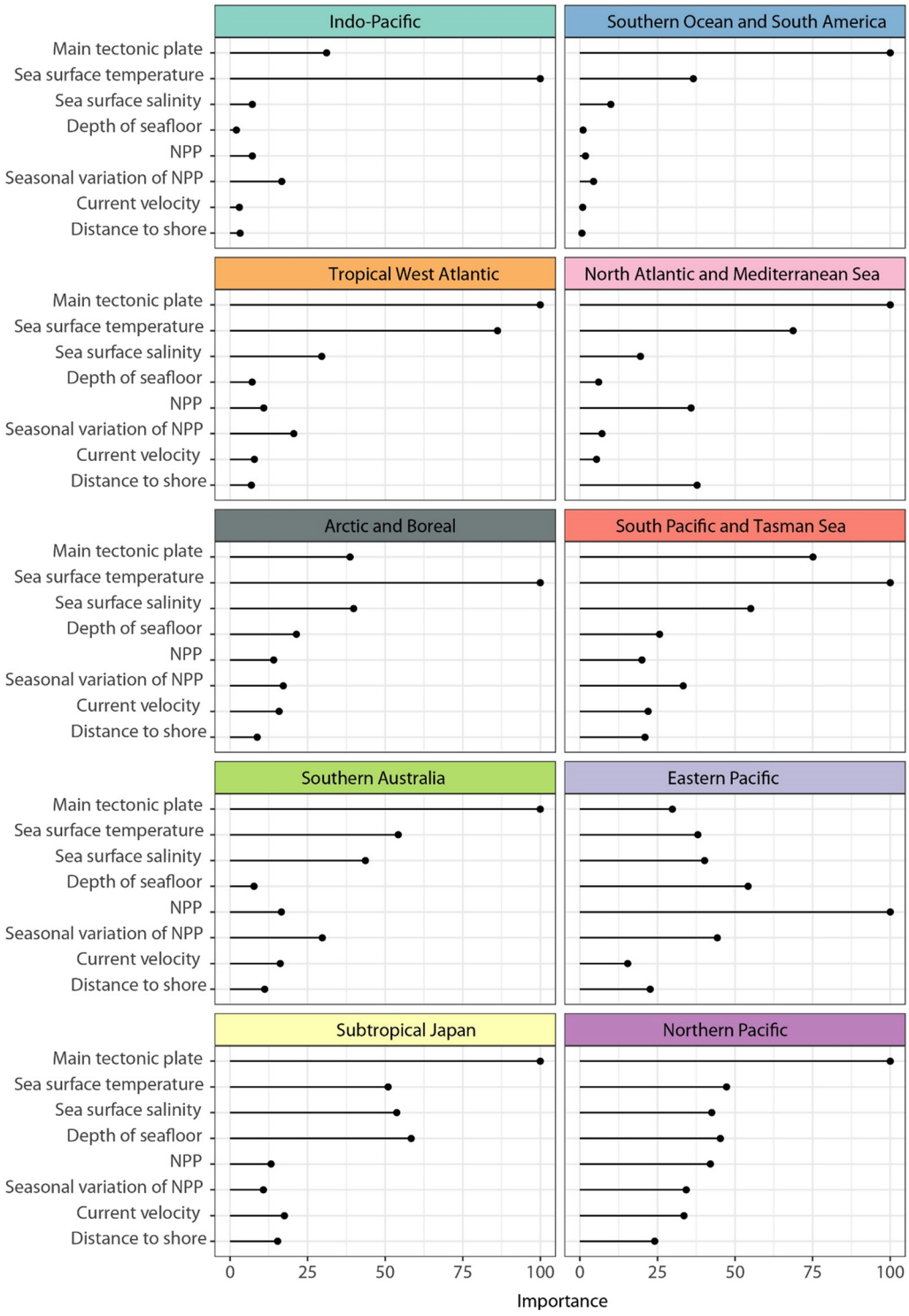

Figure 4. The importance of each environmental variable for the largest biogeographical regions based on the *varImp* function from package 'caret'. The variable 'Main tectonic plate' shows the value of the most important tectonic plate for each region. NPP = Net primary productivity. See Supporting information for a more detailed illustration of the effect of different tectonic plates per region.

regions (Sands et al. 2015, Bribiesca-Contreras et al. 2019). Future phylogeography studies are also likely to distinguish endemics in the Red Sea, as this area is known to exhibit high endemism based on previous research (Dibattista et al. 2016, Costello et al. 2017). Our results also indicate that some biogeographical regions extend globally (Supporting information) and encompass widespread species from abyssal depths. It is possible that the abyss could form a large global

biogeographic region. However, here patterns of endemism remain undetermined and hence we believe that the delineation of these regions is partly attributed to collecting the most common organisms at great depths that remain mostly unexplored, despite their high habitat heterogeneity (Riehl et al. 2020).

Ecological and geological predictors

We identified temperature, plate tectonics and salinity as the three main large-scale predictors for the proposed biogeographical regions. Our results are in accordance with previous work for shallow marine biogeographical regions, where physicochemical barriers and gradients lead to boundaries by affecting species distribution (Spalding et al. 2007, Belanger et al. 2012, Kocsis et al. 2018).

Of these, temperature and plate tectonics remain the most important predictors for most individual biogeographical regions, though their importance varies among regions. Temperature and salinity represent water masses and drive hydrodynamic circulation. These in turn create dispersal pathways across ocean basins, shaping connectivity and contemporary patterns of biodiversity and endemicity across the global benthos. An example of this is the North Pacific current which flows along the lower boundary of the Arctic and Boreal biogeographical region, off the coast of Japan, and merges into the California Current. This flow creates a thermal boundary (Summers and Watling 2021) that is most likely separating the Arctic and Boreal from the Northern Pacific biogeographical region, while simultaneously enabling the observed transition zone by creating faunal linkages along its path (Fig. 2).

Tectonic activity is considered a key driver behind contemporary biogeographical patterns across terrestrial and marine realms (Leprieur et al. 2016, Ficetola et al. 2017). In the marine environment, the movement of tectonic plates has led to 'hard' barriers to dispersal, modulating speciation and extinction processes, but also to 'soft barriers' by altering the area of shallow and deep seafloor and by influencing ocean circulation and thus the connectivity between populations (Renema et al. 2008, Cowman and Bellwood 2013a, b, Leprieur et al. 2016). In this study, our models show the importance of the tectonic configuration in predicting the ten major regions (Fig. 4; Supporting information), with a clear biogeographic break between the Indo-Pacific and Atlantic Oceans (Fig. 1). We provide two possible hypotheses to explain these results. First, historical processes led to the isolation of biogeographical regions among plates because, for example, of long-standing barriers to dispersal. For example, the collision of the Arabian and Indian plates with the Eurasian plate (starting 50 Mya) interrupted the tropical Tethys Sea flow across the globe, leading to the modern Mediterranean Sea and consequently to a 'hard' barrier, which has prevented the dispersal of tropical fauna between the Indo-Pacific and the Atlantic Ocean (Renema et al. 2008, Leprieur et al. 2016). However, in the Pliocene the Bering Strait submerged, allowing Pacific fauna to disperse through the Arctic into the Atlantic, and for some limited dispersal of Atlantic fauna into the Pacific (Vermeij and Roopnarine 2008). Conversely, we did not find tectonics to be of major importance for the Indo-Pacific biogeographical region (Fig. 4), because this large region extends across multiple plates (Supporting information). The Indo-Pacific, and more especially the Central Indo-Pacific, results from a complex geological history, with the collision of Australia and New Guinea with Sunda and Eurasia, leading to a reconfiguration of marine habitats and the creation of the Indo-Pacific Barrier (Williams and Duda 2008, Bowen et al. 2016, Leprieur et al. 2016). For fauna that disperse in deeper water, this barrier could prevent dispersal between the Pacific and the Indian Oceans at all times, explaining why, in our biogeographical regional delineation, the deep-sea fauna of the Indian Ocean are separate from those of the Indo-Pacific biogeographical region (Supporting information). The second hypothesis on why plate tectonics is a good predictor of biogeographical regions is that plate polygons are large enough to be able to predict geographically coherent biogeographical regions. Plate boundaries do not necessarily lead to barriers, as also seen in the Southern Ocean and South America biogeographical region occurring on the Antarctic and South America plates (Supporting information).

The influence of depth in creating biogeographical regions by stratifying faunal communities is central in the context of the deep sea, and discrete biogeographical regions have been proposed for the lower bathyal, abyssal and hadal depths (Vinogradova 1997, Watling et al. 2013). Our models did not suggest depth to be a main driver of the main ten biogeographical regions, as these regions ranged from the shallow to the deep sea.

The species are likely to overlap across the depth gradient, and our analysis used a coarse grid cell size, pooling organisms together into a single cell that made it difficult to detect biogeographical boundaries across a depth gradient. However, it was not possible to separate the data into depth bins, as the majority of the data were collected using trawls and dredges sampling wide depth ranges (Supporting information). Previously, depth zonation has been linked mostly to food availability and specifically to POC flux (Smith et al. 2008). POC flux has been highlighted as a key driver of biodiversity and biogeography in the deep sea by shaping the distribution of deep-sea fauna through energy availability (Mcclain and Hardy 2010, Watling et al. 2013, Woolley et al. 2016). Conversely, we found that productivity variables are less important across multiple regions, which is in agreement with results from the shallow benthos (Belanger et al. 2012, Kocsis et al. 2018). In our results, productivity variables are important only for certain biogeographical regions, as seen in the Eastern Pacific region where high net primary productivity is the single most important variable. High productivity in this biogeographical region has been documented before (Watling et al. 2013), and can be explained by its spatial overlap with an Eastern Boundary Current System that leads to POC enrichment along the coast and offshore (Amos et al. 2019). Thus, food availability could be more reflective of

the contemporary characteristics of a region as opposed to a historical driver. Alternatively, productivity variables could operate on a finer scale within an individual region, with only certain areas of a biogeographical region having high or low productivity, without being a predictor for most biogeographical regions. Our results suggest that for the correct classification of multiple or individual biogeographical regions, predictors that operate over wider spatial and temporal scales and create dispersal limitations appear to supersede other variables. The importance of predictors varying across different regions illustrates how a biogeographical region's distinct history results in the boundaries we observe. These boundaries might have been stable since the late Cenozoic (Kocsis et al. 2018). Therefore rapid global changes such as increasing temperatures and changes in ocean circulation, like the projected re-emergence of the trans-Arctic pathway (Vermeij and Roopnarine 2008), can reshape biogeographical boundaries. Range shifts in shallow depths are better understood compared to the deep sea, where we lack fundamental data that would enable us to identify faunal range expansions and contractions. Together with perturbations in deep waters, such as the projected 1°C rise between 3000–6000 m depth by 2100 (Sweetman et al. 2017), range shifts in the deep sea could occur before we are able to understand the fundamental macroecological patterns of this system.

Comparisons to other studies

Comparisons of our major regions against a suite of other biogeographic studies are summarised in Table 2, highlighting how major biogeographical patterns in the marine realm are still being resolved. Here we focus on the main differences between studies, but a more detailed comparison across different schemes is available in the Supporting information. Differences with the bioregionalisation produced by Costello et al. (2017) occur in the sense that, in their scheme, many of our major biogeographical regions are separated into smaller areas corresponding to individual seas (Table 2). Their biogeographical regions have been suggested to represent lower hierarchy provinces (Kocsis et al. 2018). The existence of our large biogeographical regions and the faunal links presented (Fig. 1,3) ties in with the broad biogeographical distribution of deep-sea species caused by an extended pelagic larval duration, enabling dispersal across large distances (Mcclain and Hardy 2010, Hilário et al. 2015). The majority of ophiuroid species have pelagic larvae and spawn annually or continuously (O'Hara and Byrne 2017). The boundaries of our biogeographical regions are also distinct from the lower bathyal provinces (Watling et al. 2013) in both temperate and tropical regions in a latitudinal and longitudinal manner. The separation of South America and Southern Ocean in the MEOW delineation (Spalding et al. 2007) differs with the single Southern Ocean and South America biogeographical region in our study, but ophiuroids are phylogenetically quite similar across both areas (O'Hara et al. 2013). Differences between studies are likely to arise from the taxa studied and their dispersal abilities, data compilations that vary across different habitats and depth intervals, the spatial resolution of the sampling units and the statistical approach. Most importantly, the lack of data from deeper parts of the ocean forms a fundamental problem, leading to changes in major patterns as deep-sea exploration progresses. These points also affect endemicity rates, in addition to benthic macroinvertebrates influencing endemicity patterns more than pelagic fauna (Costello et al. 2017, Arfianti and Costello 2020). Overall, the boundaries of our benthic biogeographical regions generally agree better with other fauna-based biogeographic studies, rather than the deep-sea provinces which are assembled with environmental data (Watling et al. 2013). Despite the wide use of these provinces in underpinning efforts within deep-sea research, discrepancies between them and biogeographic regions delineated using species data indicate that the environmental provinces might not accurately capture macroecological and macroevolutionary relationships, which are crucial in answering fundamental questions about deep-sea biodiversity. Many of our biogeographical regions range from coastal to the deep sea as seen by their minimum, maximum and average depths (Supporting information). Traditionally, however, shallow and deep-sea biogeographical regions are considered separately. The exact boundary is ambiguous, as what can be considered deep sea varies geographically and can be dynamic (Watling et al. 2013, Costello et al. 2017). Another argument confounding this division is that spatial and depth ranges for most of the deeper organisms are still poorly known, and can be extremely large. While the origin of marine species is often unknown (Mcclain and Hardy 2010), phylogenetics and phylogeography continue to reveal evolutionary links across shallow and deep areas, as recently seen in fish (Friedman and Muñoz 2023). In particular, ophiuroids show historically multiple lineage transitions across shallow and deep habitats, leading to the contemporary diversity patterns of this class (Bribiesca-Contreras et al. 2017). Therefore, it is worth considering combining data from different benthic habitat types to avoid artefacts that are generated when species are considered as endemics or rare, but in fact occur beyond an artificially partitioned ocean depth or region.

Advances and limitations

Our proposed delineation of global benthic biogeographical regions is based on the distribution of a single taxon, and future work should focus on evaluating the robustness of this scheme based on multiple marine benthic taxa with data from the deep sea. Additionally, it is worth noting that we have an incomplete understanding of environmental processes in the deep sea, and the scarcity of direct measurements leaves us relying on modelled variables that are interpolated from shallower depths. The variables best correlating with the biogeographical regions represent water masses that can affect the dispersal of ophiuroids, reflecting that the majority of the species have pelagic larvae (O'Hara and Byrne 2017) and that most of our data are from 0 to 1500 m depth (Supporting information). The low availability of curated deep-sea data

in a global context means that ophiuroids provide a novel opportunity for us to develop global benthic biogeographical regions without a complete oversaturation of shallow water data. The completeness analyses suggest that in grid cells, which are not undersampled, the majority of frequent species have been recorded making the biogeographical regions containing these grid cells robust (Supporting information). However, most of the ocean lacks sampling, as shown by our completeness analyses with a large number of undersampled grid cells, despite using a state-of-the-art ophiuroid database (Supporting information). In the shallow benthos, seven taxonomic groups showed good agreement among them (Kocsis et al. 2018) and displayed similar patterns to our study, suggesting that our findings are potentially generalisable. Still, certainty can only be achieved through more sampling of the deeper areas, especially at abyssal depths, where the data are too scarce to form geographically coherent biogeographical regions (Supporting information). Our study allows high reproducibility with future studies. The data consist of voucher specimens examined by experts and can be re-examined, while the network approach provides a framework not affected by species richness with high robustness to sampling discrepancies (Vilhena and Antonelli 2015, Bloomfield 2018, Kocsis et al. 2018, Leroy et al. 2019).

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Author contributions

Lissette Victorero: Conceptualization (lead); Formal analysis (lead); Methodology (equal); Writing – original draft (lead); Writing – review and editing (lead). **Sarah Samadi**: Conceptualization (supporting); Data curation (equal); Funding acquisition (lead); Resources (equal); Supervision (supporting); Writing – review and editing (supporting). **Timothy D. O'Hara**: Data curation (lead); Resources (equal); Writing – review and editing (supporting). **Maud Mouchet**: Conceptualization (supporting); Funding acquisition (equal); Supervision (supporting); Writing – review and editing (supporting). **Juliette Delavenne**: Writing – review and editing (supporting). **Fabien Leprieur**: Writing – review and editing (supporting). **Boris Leroy**: Conceptualization (supporting); Formal analysis (supporting); Funding acquisition (supporting); Methodology (equal); Supervision (lead); Writing – review and editing (supporting).

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Data availability statement

The ophiuroid distribution dataset and scripts used in this study are available from the Zenodo Digital Repository: https://zenodo.org/record/7656699 (Victorero et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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