i. Title

A global biogeographic regionalization of the benthic ocean

ii. Running title

Global seafloor biogeographic regions

iii. Authors

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vi. Abstract and keywords

ABSTRACT

Aim. The delineation of biophysical regions that characterize distinct biota provides key units of analysis for ecology, biogeography, and conservation. In the oceans, global regionalizations have been developed for coastal, surface, and mesopelagic systems. Yet, despite their extraordinary richness, seafloor ecosystems have so far not been given the same attention. This has limited progress for benthic research and excluded this marine habitat from conservation recommendations. To address this gap, we present an expanded biogeographic delineation, the Benthic Provinces of the World (BPOW), that integrates earlier work from Spalding et al. (2007), Watling et al. (2013), and Belyaev (1989).

Location. Global seafloor.

Taxon. None.

Methods. We divided the ocean seafloor into four main bathymetric types, following the literature on vertical and spatial regionalizations: coastal and upper bathyal (0–800m), lower bathyal (800–3,500m), abyssal (3,500–6,500m), and hadal trenches (>6,500m) using existing layers and high-resolution ocean depth data. We applied this distinction to available regionalizations of benthic ecosystems and reconciled geospatial layers to create a single regionalization of the benthic provinces of the world: BPOW. We demonstrate how this delineation supports species distribution boundaries for species across a range of taxa using spatial occurrence data and expert knowledge.

Results. The BPOW regionalization consists of 100 provinces: 62 coastal and upper bathyal, 14 lower bathyal, 14 abyssal, and 10 hadal provinces. For all selected species, spatial occurrence points falling in the correct bathymetric types or sub-ocean basins ranged from 83 to 100%, providing confidence that the layer meaningfully captures biogeographic boundaries.

Main conclusions. BPOW complements other global regionalizations of coastal, oceanic, and pelagic habitats and addresses a critical biogeographic data gap. The data product has the potential to simplify the inclusion of benthic ecosystems in research and conservation and support a more thorough understanding of this diverse but threatened system at the global scale.

KEY WORDS (6-10 keywords)

benthic provinces, seafloor, marine biodiversity, deep-sea, coastal, biogeography

vii. Main text

BACKGROUND & SUMMARY

The distribution of biodiversity is highly heterogeneous across the planet, with regions characterized by different environments. Recognizing and characterizing these regions and their geographic boundaries is at the heart of biogeography (Lomolino et al. 2006; Morrone 2009). The delineation of the Earth's geographic space into distinct environments and species assemblages provides critical units of broad relevance for biodiversity and ecosystem sciences, conservation, and resource management (Whittaker et al. 2005).

Early biogeographic regionalizations were originally developed based on observations of major geographic transitions in the distribution of species groups such as terrestrial vertebrates (Sclater 1858; Wallace 1876), and later marine taxa (Ekman 1953). These regionalizations were typically constructed from expert knowledge on environmental conditions and species composition of regional assemblages. Important boundaries have since been refined and further described (Briggs and Bowen 2012; Briggs 1995). More quantitative approaches were introduced to delineate regions based on species distributions (Kreft and Jetz 2010) and environmental data (Oliver et al. 2004), and have seen substantial development in marine biogeography (Zhao and Costello 2020; Costello et al. 2017; Woolley et al. 2020). While quantitative species-based regionalizations offer methodological transparency and utility, they also rely on globally comprehensive species information that is not readily available because the distribution information remains lacunar and geographically biased, especially at the global scale (Hughes et al. 2021; Lenoir et al. 2020; Meyer et al. 2015; Miloslavich et al. 2018; Oliver et al. 2021; Troudet et al. 2017). As a result, global regional delineations using biophysical, bioclimatic, and biochemical characteristics and recognized knowledge of major biogeographic boundaries remain broadly used in both basic and applied research (e.g., Olson et al. 2001; Spalding et al. 2007; Sherman 1991). While not truly quantitative biogeographically or environmentally, this type of regionalization is less dependent on fine-scale and taxa-specific data. It can coarsely delineate distinct assemblages or environments, often representing the distributional limits of many species (Floeter et al. 2008; Robertson and Cramer 2014). They have proven popular and valuable in part because they offer a pragmatic method to support conservation and the global science-policy interface (Rice et al. 2011; Roberts et al. 2003; Whittaker et al. 2005; Hoekstra et al. 2005; Lamoreux et al. 2006).

In marine environments, global biogeographic regionalizations have so far mostly characterized epipelagic and coastal environments (Duffy 2021; Zhao and Costello 2020). The major efforts by Longhurst (2007) and Reygondeau et al. (2013) linked oceanographic knowledge with ecology, and divided the global ocean into 57 biogeochemical provinces. Spalding et al. (2007) defined coastal oceans biogeographic regions using a combination of expert environmental and species endemism knowledge, a methodology that was applied later to the epipelagic oceanic compartment (Spalding et al. 2012). More recently, complementary global provinces for the mesopelagic ocean were proposed, using expert knowledge of the environment and faunal distributions (Sutton et al. 2017) and clustering algorithms of spatially- and vertically-resolved environmental data (Reygondeau et al. 2018). Sayre et al. (2017) proposed a three-dimensional delineation to the entire water column based solely on hydrographic data. To capture the seasonal dynamics of seascapes, more efforts on four-dimensional delineations based on physical and chemical attributes further advance pelagic biogeographic regionalizations (Kavanaugh et al. 2016).

This work offers global environmental and expert-informed regionalizations for the epipelagic and mesopelagic oceanic compartments, but a similarly comprehensive data product for the benthic oceans is crucially needed. Issues of data scarcity and spatial heterogeneity in the benthic oceans are especially common because data availability drastically decreases as depth increases (Reygondeau and Dunn 2018; Webb, Berghe, and O'Dor 2010). Therefore, biogeographic regionalizations are particularly appealing to describe benthic environments and species assemblages, which are dependent on the bathymetric structure with several important transitions from the coast to the deep sea (Rex et al. 2005; Trouche et al. 2021). Directly driven by policy and conservation needs, several regionalizations help characterize benthic habitats of the oceans (UNESCO 2009). These products cover most of the global benthic compartment from the coastal and continental shelves (Spalding et al. 2007) to the deep sea from 800 to 6,500m (Watling et al. 2013), while the upper bathyal (200–800m) is not fully covered nor properly characterized. Benthic regionalizations of the lower bathyal, abyssal, and hadal zones of the ocean using both environmental data and expert knowledge were proposed by Watling et al. (2013) and recently modified based on anthozoan distributions (Watling and Lapointe 2022). A first attempt to examine the upper bathyal distributions was made in the Pacific using octocoral distributional data (Summers and Watling 2021). While these are important advances, none of the regionalizations cover entirely the ocean seafloor nor are they complementary to or interoperable with each other.

Here, we present a new data layer, the Benthic Provinces of the World (BPOW). BPOW is the result of a suite of geospatial analyses that overcomes the limitations of existing benthic regionalizations to create a coherent and standardized global layer of 100 benthic provinces distributed within four bathymetric delimitations: coastal and upper bathyal (0–800m), lower bathyal (800–3,500m), abyssal (3,500–6,500m), and hadal trenches (>6,500m). We describe the methods used to create this new geospatial layer, apply the layer to selected marine species spanning several taxonomic groups, discuss limitations, provide suggestions for future development and applications, and present guidance for users.

The aims of the BPOW layer are to support better recognition of distinct benthic regions and facilitate improved exploration and understanding of seafloor biodiversity, ecosystem processes, and conservation. The presented layer constitutes a first version intended to be updated and refined through time with better knowledge of the benthic oceans, especially in the deep-sea. We hope it will support broader marine research and stakeholder communities to account for the three dimensions of marine benthic habitats more comprehensively. For instance, it can advance the knowledge of benthic macroecological patterns, and expand on existing taxon-specific refinements (Kulbicki et al. 2013; O'Hara, Rowden, and Bax 2011; O'Hara et al. 2019; Summers and Watling 2021; Woolley et al. 2020). It can further coarsely inform the representation of important benthic regions in marine protected areas, with important implications for marine benthic conservation practice and policy (Rice et al. 2011).

MATERIALS AND METHODS

Definition of bathymetric types

The ocean seabed extends from 0m deep at the shoreline to more than 10,000m deep. While our knowledge of the ocean seabed remains incomplete, recent development of new technologies has enabled detailed mapping of its bathymetric structure (Harris et al. 2014). Several categorizations of the ocean seabed have been described in the literature from the coast to the deep (Harris et al. 2014; Jamieson and Stewart 2021; Watling et al. 2013) which typically include: (i) the continental shelf zone including the coastal plateau with little depth variation, (ii) the continental slope zone which is the transition between the shelf and the deep sea with high depth variation, (iii) the bathyal zone, or upper deep sea areas, including the lower part of the continental slope, seamounts, and mid-ocean ridges, (iv) the abyssal zone, characterized by the deep plains, covering most of the ocean seafloor, and (v) hadal zones which include the deepest seabed areas, such as ocean trenches. The exact depth delimitations of each category are not constant and depend on the geomorphology of the ocean seabed (Harris et al. 2014; Harris and Macmillan-Lawler 2016). For instance, it was shown that most continental shelves extend from 0 to 200m on average, but the deep limit of wide and narrow continental shelves can range from 130 to 360m (Harris and Macmillan-Lawler 2016). Similarly, the literature marks the transition between abyssal and hadal zones at either 6,000 or 6,500m deep (Jamieson et al. 2010; Watling et al. 2013). Here, we follow Watling et al. (2013) and consider the five following bathymetric types: continental shelf ranging from 0 to 200m, upper continental slope (or upper bathyal) ranging from 200 to 800m, lower bathyal zone ranging from 800 to 3,500m, abyssal zone ranging from 3,500 to 6,500m, and hadal zone encompassing depths >6,500m.

Identification of reference spatial units

We selected three existing biogeographic delineations from the literature (Table 1). For the continental shelves and upper slope, we used the Marine Ecoregions of the World (MEOWs) from Spalding et al. (2007). While the upper continental slope (also called upper bathyal) merits its own regionalization, recent findings indicate a biogeographic delineation close to the MEOWs designed for coastal ecosystems (Summers and Watling 2021), so we extended the continental shelf MEOW system onto the upper slope. For the deep sea bathyal and abyssal regions, we used the Deep Sea Provinces (DSP) from Watling et al. (2013). And for the hadal trenches, we selected and adapted provinces from Belyaev (1989). MEOWs include three levels of embedded regionalizations including 232 ecoregions, 62 provinces, and 12 realms, from which we used the provinces. DSP includes 14 bathyal provinces and 14 abyssal provinces.

All layers and regions are based on expert knowledge of oceanographic features, species distributions and assemblages, but not directly informed by quantitative classifications using spatial data. The DSP boundaries were refined using oceanographic data including temperature, salinity, dissolved oxygen, and particulate organic carbon flux to the seafloor at a spatial resolution of 1km (Watling et al. 2013). Selected provinces were originally established within a working group on the global open oceans and deep seabed (GOODS) (UNESCO 2009; Rice et al. 2011; Watling et al. 2013), but were never reconciled into a global benthic layer. While we preserved the original regionalization schemes, we modified the province geometry to create a unified global layer for the benthic ocean following the methods described below.

Creation of the global benthic layer

We created a global benthic biogeographic layer using ArcPro v2.8.3 and R v4.0.3 (R Core Team 2021) to process and reconcile the coastal and deep-sea regions and ensure full coverage of the global seafloor by benthic provinces across the four bathymetric types (Figures 1 and 2 provide an overview of the data processing workflow; and the full methodology is available in Appendix 1):

Parts I and II—Geometry checks: We checked the geometry of the DSP layer for self-intersections in ArcPro (Part I) and corrected these geometry errors in R (Part II). This was an iterative process repeated until all self-intersections were corrected.

Part III—Fix boundary: We redefined the depth boundary of the DSP bathyal to a shallower limit than 800m (765m) at the southeast coast of the US to smooth boundaries in zones of depth transition between coastal and bathyal bathymetric types and decrease grid irregularities in this region. This was done using the General Bathymetric Chart of the Oceans (GEBCO Bathymetric Compilation Group 2020). This issue did not arise elsewhere.

Part IV—Creating complementary bathyal and abyssal layers: As the DSP layers were not fully complementary, we clipped the abyssal layer to the bathyal layer assuming the bathyal layer potentially represents more diverse habitats than the abyssal plains (Watling et al. 2013; Rex et al. 2005). From this, we created a layer including the complementary bathyal and abyssal zones.

Part V—Deep-sea clip: The boundaries of the original MEOW layer extend beyond the continental shelf and slopes areas of the world (and on land) while its regionalization nominally characterizes coastal habitats. We clipped the MEOW layer to the deep-sea layer, and then integrated the MEOW and DSP layers into a single layer.

Part VI—Identification of uncharacterized sites: The resulting benthic layer was not complete as it included many areas in the ocean that were uncategorized. We extracted these unclassified sites as polygon objects (`holes` in Figure 1).

Part VII—Isolation and classification of hadal trenches: We isolated hadal zones using the depth raster from GEBCO and assigned the selected regions using Belyaev (1989) with a few modifications (see hadal provinces in Appendix 2) as the DSP does not include hadal areas although those areas are included in the original MEOW layer.

Part VIII—Assigning biogeographic regions to unclassified polygons: We applied a 3-dimensional nearest neighbor analysis including latitude, longitude, and depth to assign the closest region to any polygon lacking a classification (Figure 2). To do this, we rasterized each unclassified polygon and the surrounding classified polygon(s) following the GEBCO raster resolution (15 arc seconds) and applied the “mcNNindex” function from the `Morpho` R package (Schlager 2017; 2022). If an unclassified polygon was surrounded by several biogeographic units and depth categories, individual raster cells were assigned to the nearest neighbor such that a single unclassified polygon could yield pixels assigned to different biogeographic units. We then aggregated the biogeographic unit associations at a coarser spatial resolution to match the DSP and assigned the dominant benthic province to smooth the boundaries of the missing raster cells and match the resolution of the deep-sea layer. Each grid cell was then assimilated within existing polygons and assigned their corresponding province code.

Part IX—Quality checks: Finally, we performed random location quality checks to ensure that layer boundaries and spatial objects of the resulting benthic biogeographic shapefile were valid, applying geometry corrections as necessary.

Part X—Clipping to global landmasses: Land areas were clipped to the 1:10m land shapefile layer from natural earth, v4.1.0. including major islands (https://www.naturalearthdata.com).

DESCRIPTION OF THE LAYER

The resulting layer includes 100 unique benthic provinces of the world (BPOW) that are divided into the four main bathymetric types: coastal and upper bathyal (0–800m, thereafter coastal, 62 provinces), bathyal (800–3,500m, 14 provinces), abyssal (3,500–6,500m, 14 provinces), and hadal (>6,500m, 10 provinces; Figure 3, Table 1). The BPOW layer incorporates the original MEOW and DSP regionalizations with their respective original names, identification numbers, and sources (Table 2). The field \`ID\` distinguishes each unique benthic province and is complemented by its corresponding bathymetric \`type\`.

While the coastal regionalization used is the same as in Spalding et al. (2007), we substantially modified the geometry of the polygon objects from that scheme to extend only to the 800m isobath (Figure 3A). The original MEOW layer included most of the hadal provinces that in BPOW have now been isolated and separately classified as recommended in the literature (Figure 3D). However, the deep-sea provinces and geometric objects in BPOW mostly follow the original product from Watling et al. (2013; Figure 3B, C).

TECHNICAL VALIDATION

We inspected the layer visually in both ArcPro and R, paying attention to the new biogeographic boundaries defined according to the methods described above and in Appendix 1, with particular focus on the boundaries between coastal and bathyal regions as well as between abyssal and hadal provinces. Multi-polygon geometries and global boundaries were checked and validated prior to finalizing the layer.

EXAMPLE APPLICATION TO SPECIES DISTRIBUTIONS

Species bathymetric types

To demonstrate the potential usefulness of the BPOW layer for informing species distributions along bathymetric gradients, we conducted an analysis on eight (benthic or bathydemersal) species with habitats either restricted to one bathymetric type (3 species) or spanning several types (5 species; Table 3). Spatial occurrence records were collected from the Global

Biodiversity Information Facility (GBIF, https://www.gbif.org/) and the Ocean Biodiversity Information System (OBIS, https://obis.org/) in March 2023 (GBIF.Org 2023). We removed all records categorized as fossil and retained only presence records with existing geolocation. OBIS and GBIF occurrence data were deduplicated using the sampling date (year, month, day), species name, latitude, and longitude. The number of occurrence points per species varied from 21 to more than 25,000. To associate spatial points with the benthic provinces, we conducted an intersection with the "st_join()" function between spatial objects with the `sf` R library (Pebesma 2018). For each species we then summarized the spatial points per province.

To derive an expectation for occupied bathymetric type—whether a species is coastal, bathyal, abyssal, and/or hadal—we extracted the expert depth range from FishBase for fish species (Froese and Pauly 2022) and SeaLifeBase for invertebrate species (Palomares and Pauly 2022). We considered point-based province occurrences outside these expected regions as "false presences" and "true presences" otherwise and then summarized percent true and false presences for all occurrences across each of the eight species across benthic provinces.

We found that the benthic provinces, and specifically their bathymetric types, as identified by point occurrences are broadly in agreement with the depth range expectation (Table 3). Nearly 100% of point occurrences are in the correct zones. However, 9.2% of points for the giant clam (*Tridacna gigas*) and 15.2% for the deep-water stingray (*Plesiobatis daviesi*) are considered false presences because they fell outside coastal areas (Table 3). There are several potential causes of these apparent false positives, including: (i) the expert depth range is wider than documented, (ii) species geolocations are less precise than the data layer, (iii) the species location straddles the boundaries of the provinces, and/or (iv) ecological oceanic boundaries are not as sharp as in depicted the BPOW layer. They rather often present themselves as gradients in the natural environment (O'Hara, Rowden, and Bax 2011), so it is not surprising that less than 100% of the points are within the expected category.

The Mariana trench (deepest region of the global ocean) is very close to the Mariana islands, indicating that the depth zone transitions are geographically very proximate. Prior to the creation of this global benthic layer, the association of the Mariana hadal snailfish (*Pseudoliparis swirei*) with the previous separate biogeographic layers would have associated this very deep fish to the coastal provinces, demonstrating the importance of including the bathymetric structure of the ocean seafloor in biogeography.

Species provinces

We next related BPOW-based species ranges to a regional expectation using the main fishing FAO areas listed in FishBase and SeaLifeBase (Froese 2022; FAO 2022). While FishBase and SeaLifeBase are still expanding, FAO area lists represent a useful, global source of distribution information for many marine taxa that allows us to verify whether occurrences are associated to the large sub-divisions of ocean basins. We performed an intersection between the BPOW and the FAO fishing areas shapefile layers (https://www.marineregions.org/) in R to create an association between each overlapping benthic province and FAO fishing area. Out of the eight selected species, only six had FAO areas listed on FishBase and SeaLifeBase. The percentage of spatial points per BPOW province and considered occurrences in provinces that do not overlap the expected FAO areas as "false presences" are summarize in Table 3.

Similar to the estimated false presences by bathymetric type, most example species show a relatively small percentage of false presences. For the Portuguese dogfish (*Centroscymnus coelolepis*), 100% of occurrence points are found to follow the expectation from FAO fishing areas (Table 3), while for the Rough-skinned Sea anemone (*Actinostola callosa*), 11.69% of occurrences are found outside the expectation. This is not entirely surprising because the spatial range occupied by the Portuguese dogfish is very large (and expected in 14 FAO areas), therefore less false presences are likely to be found. For the three species that were expected in 4 to 6 FAO areas, the percentage of false presences varied from 0.03 to 12.17% (Table 3).

Species provinces within bathymetric types

Finally, we assessed false presences by (i) the bathymetric type and (ii) the main fishing FAO areas, considering occurrences in provinces that do not overlap the expected bathymetric types and/or FAO areas as "false presences".

We found interesting differences between the percentage of false presences estimated from bathymetric types or FAO areas, illustrating the importance of combining species' observations and expert information both for bathymetric and regional distributions. For instance, more false presences were found for the bathymetric types of the Deepwater Stingray, while the opposite occurred for the Rough-skinned Sea anemone (Table 3). Overall, >10% of points were considered as false presences for these two species. Combining both types of false presences can help flag and potentially exclude spatial points that are outside of the expected occurrence areas.

DISCUSSION

To our knowledge, the BPOW product closes an important gap as the first global layer completely addressing benthic biogeographic units. Several avenues may be explored to apply, improve, and validate the provinces from the BPOW. Producing the BPOW required several, necessarily imperfect decisions, especially regarding: (i) the spatial scale, (ii) the bathymetric types and associated depth ranges, and (iii) the regionalization scheme for each province type. Bathymetric types are somewhat arbitrary limits and may be improved by incorporating other data products of bathymetry (https://seabed2030.org) and geomorphology (Harris et al. 2014). More generally, a fine-scale knowledge of the seafloor in the coming years will improve our knowledge of marine geomorphology and of the seabed structure. However, current ecological divisions of the oceanic benthos and geomorphological categories are not compatible: for instance, previous work on characterization of the seafloor features did not separate the deep sea into bathyal and abyssal bathymetric types (see Fig. 3 in Harris et al. 2014). We expect that combining knowledge of depth zones with unique species assemblages and detailed geomorphology will help improved global benthic biogeographic regionalizations.

Creating new regionalizations for some specific bathymetric compartments will be an important area of refinement of benthic regionalizations. In particular, the upper bathyal (~200–800m) and hadal compartments (excluding trenches, also named lower abyssal, ~6,000–6,500m deep) are unique zones in terms of biodiversity and species compositions (Jamieson 2015; O'Hara et al. 2019; Summers and Watling 2021). Ecological knowledge of both compartments indicates that they should be separated from coastal and abyssal bathymetric zones, respectively, and be characterized as their own biogeographic regionalizations. Such global delineations and associated data products will be facilitated by the accumulation of global data and knowledge from the deep sea in all ocean basins.

Region- and/or taxon-specific biogeographic classifications may help validate larger-scale products and represent an opportunity for refining and reporting the accuracy of region boundaries. For instance, the Greater Caribbean shore regions have been classified into at least eight different biogeographic schemes of varying scale over the last 60 years based on distinctiveness, physical variables, and/or endemism of reef fishes (Robertson and Cramer 2014). Extended ecological knowledge from this region was used to revise the biogeographic boundaries characterizing unique marine species compositions and their relation to the regional environmental conditions. Refinements of regionalization supported by quantitative classifications on taxonomic spatial occurrence data can further inform the biogeography of the benthic oceans (Costello et al. 2017). However, biogeographical boundaries are usually defined as hard boundaries (as in the BPOW layer), rather than represented as ecological continuum. The Global Ocean Biodiversity Initiative (https://gobi.org/) has developed classifications of the Southwest Pacific and Indian Oceans supported by transparent statistical regionalization methods including specific considerations regarding the uncertainties associated with the region boundaries (Woolley et al. 2020; Dunstan et al., n.d.). Developing similar refinements and boundaries for the BPOW would more accurately characterize biogeographic boundaries.

Marine species are often widely distributed, and identifying areas of near-certain absence when predicting their geographic distribution with species distribution models can be challenging. Therefore, in one potential application, we expect the BPOW layer to inform and potentially improve modeling predictions of benthic taxa by defining the modeling domain with proposed biogeographic boundaries (Kaschner et al. 2019; Merow, Wilson, and Jetz 2017). However, this is only possible given a minimum number of spatial occurrence points, and for most species of the benthic oceans, we critically lack information on their distribution. Scarce occurrence points and the BPOW might be the only source of distribution data for some taxa. This is the case for marine crabs, for which there is no expert range maps available for many other groups existing via the Red List of Threatened Species, or other taxon-wide range initiatives (Marsh et al. 2022; Lumbierres et al. 2022). Improving and inferring species distributions is an important application of biogeographic regionalizations.

Biogeographic regions are especially useful where species occurrence data are lacking, but human impacts are increasing and conservation efforts are needed (Kuempel et al. 2019; Watson et al. 2016; Hoekstra et al. 2005). Benthic species abundance and distributions are affected by climate change and human activities at all depths (Amoroso et al. 2018; Brito-Morales et al. 2020; Kroodsma et al. 2018; Thresher et al. 2015). Biogeographic regions provide a basis for understanding the displacement of important biomes and provinces under climate change, as previously investigated in terrestrial and pelagic ecosystems (Boonman et al. 2022; Reygondeau et al. 2020). The BPOW layer could similarly inform biogeographic boundary shifts in response to climate change for the benthic compartment, where rising temperatures are creating new local environmental conditions even into deep water (Brito-Morales et al. 2020). Pressures to benthic biodiversity are further increasing with the development of more destructive activities in the deep sea, such as deep sea bottom trawling (Althaus et al. 2009; Priede et al. 2011), as well as proposed mining of the seabed for rare earth metals (Leal Filho et al. 2021). Therefore, investigating the representation of unique benthic important areas in marine reserves may spotlight needs for protection, monitoring, and decision making (Jantke et al. 2019; Lourie and Vincent 2004; Rice et al. 2011; Roberts et al. 2003). We recommend that such assessment should be at least partly informed by marine benthic biogeographic regionalizations.

New classifications improve our knowledge of biogeography, but each independently developed region- or taxon- specific product is hard to reconcile with larger schemes. Besides, no single classification would apply equally well to all taxa. For instance, Summers & Watling (2013) found that no existing biogeographic regionalization allowed to accurately characterize the species composition of deep sea octocorals. Similar conclusions were found for Mediterranean fishes (Hattab et al. 2015) where the coastal marine ecoregions from Spalding et al. (2007) integrated in the BPOW did not support the clustered coastal fish species assemblages. Therefore, many marine biogeographic regionalizations exist, and these need to be better connected to improve the transfer of methodologies and delineation of boundaries across regions. Although one single regionalization scheme applicable to many groups might be desirable (Morrone 2002), allowing for the plurality of biogeographic regions that can be compared and integrated by end-users—by creating, updating geospatial layers, and documenting them in databases (Fischer, Walentowitz, and Beierkuhnlein 2022)—will provide a stronger basis for comparative biogeographic research, biodiversity science, and conservation.

USAGE NOTES

Users should be aware that while each province and geometric object is defined by hard boundaries, these boundaries are likely neither clear nor static in the natural environment. For instance, a species might be strongly associated with a province, but still be observed slightly outside because suitable habitats would be present around, and its range could extend over more than one province (see Watling and Lapointe 2022). As such, interpretations and use of the layer should ideally account for buffered areas allowing flexibility around the province boundaries. Such limits are demonstrated in the application section of the manuscript and should provide guidance for users who wish to work on improving species distributions with biogeographic knowledge.

viii. Tables

Table 1. Description of biogeographic classifications collated to create the global benthic layer. Biogeographic delineation depth range, the corresponding number of units, and literature source for each bathymetric type. See Appendix 2 for more information on the hadal classification.

Bathymetric type	**Depth range (m)**	**Level**	**Number of units**	**Source**
Coastal and upper bathyal	0–800	Province	62	(Spalding et al. 2007)
Bathyal	800–3,500	Province	14	(Watling et al. 2013)
Abyssal	3,500–6,500	Province	14	(Watling et al. 2013)
Hadal	>6,500	Province	10	adapted from Belyaev (1989)

Table 2. Description of fields in the GIS biogeography layer file.

Field	**Description**
ID	unique identification code for each province, from 1 to 100
type	bathymetric category associated with the province: \`coastal\`, \`bathyal\`, \`abyssal\`, or \`hadal\`
depth_r	corresponding depth range from Table 1 for each category
prov_n	province name, using original names from sources described in Table 1
prov_id	province identification code, from the original sources described in Table 1
source	source of the original classification, following Table 1
geometry	\`POLYGON\` or \`MULTIPOLYGON\` geometric object

Table 3. Test of biogeographic regions with occurrence data and expert distribution information for eight benthic species. Scientific and common name, number of occurrence records (points), expert depth ranges from FishBase for fish species and SeaLifeBase for invertebrates when available, expert bathymetric types (derived from the expert depth ranges), and the list of FAO fishing areas (region IDs) similarly extracted from FishBase and SeaLifeBase. We report the percentage of false presence according to three criteria: (i) the bathymetric type (ii) the FAO areas expectation (iii) combination of (i) and (ii). False presences are described with the number of occurrences and the respective percentage.

Taxon	**Scientific name**	**Common name**	**Number of points**	**Expert depth range (m)**	**Expert bathymetric type(s)**	**FAO fishing areas list**	**Number of false presences for bathymetry**	**Number of false presences for FAO areas**	**Number of false presences for both**
Bivalvia (bivalves)	*Tridacna gigas*	Giant clam	515	0–35	coastal	51; 57; 61; 71; 77	48 (9.32%)	11 (2.14%)	48 (9.32%)
Asteroidea (sea stars)	*Patiria pectinifera*	Blue bat star	228	N/A	coastal	N/A	1 (0.44%)	N/A	N/A
Chondrichthyes (rays/sharks)	*Plesiobatis daviesi*	Deep water stingray	111	44–708	coastal	51; 57; 61; 71; 77; 81	17 (15.32%)	2 (1.80%)	19 (17.12%)
Arthropoda (arthropods)	*Chionoecetes opilio*	Snow crab	26,035	4–1400	coastal; bathyal	18; 21; 27; 61; 67	5 (0.02%)	0 (0%)	5 (0.02%)
Cnidaria (cnidarians)	*Actinostola callosa*	Rough-skinned sea anemone	248	14–2047	coastal; bathyal	18; 21; 27; 31	2 (0.81%)	29 (11.69%)	29 (11.69%)
Chondrichthyes (rays/sharks)	*Centroscymnus coelolepis*	Portuguese dogfish	1,616	138–3700	coastal; bathyal; abyssal	18; 21; 27; 31; 34; 37; 41; 47; 51; 57; 58; 61; 71; 81	0 (0%)	0 (0%)	0 (0%)
Holothuroidea (sea cucumbers)	*Psychropotes depressa*	N/A	157	957–4200	bathyal; abyssal	31	9 (5.73%)	17 (10.83%)	26 (16.56%)
Chondrichthyes (rays/sharks)	*Pseudoliparis swirei*	Mariana hadal snailfish	21	6200–8100	abyssal; hadal	N/A	0 (0%)	N/A	N/A

ix. Figures

Figure 1. Schematic of the analytical steps for developing the global biogeographic benthic layer. Gray shaded boxes denote individual stages (parts) of the data processing workflow. The colored boxes indicate whether the analyses and steps were performed in ArcPro (yellow) or R (blue). The full methodology, including input and output data, individual steps, and functions is detailed in Appendix 1.

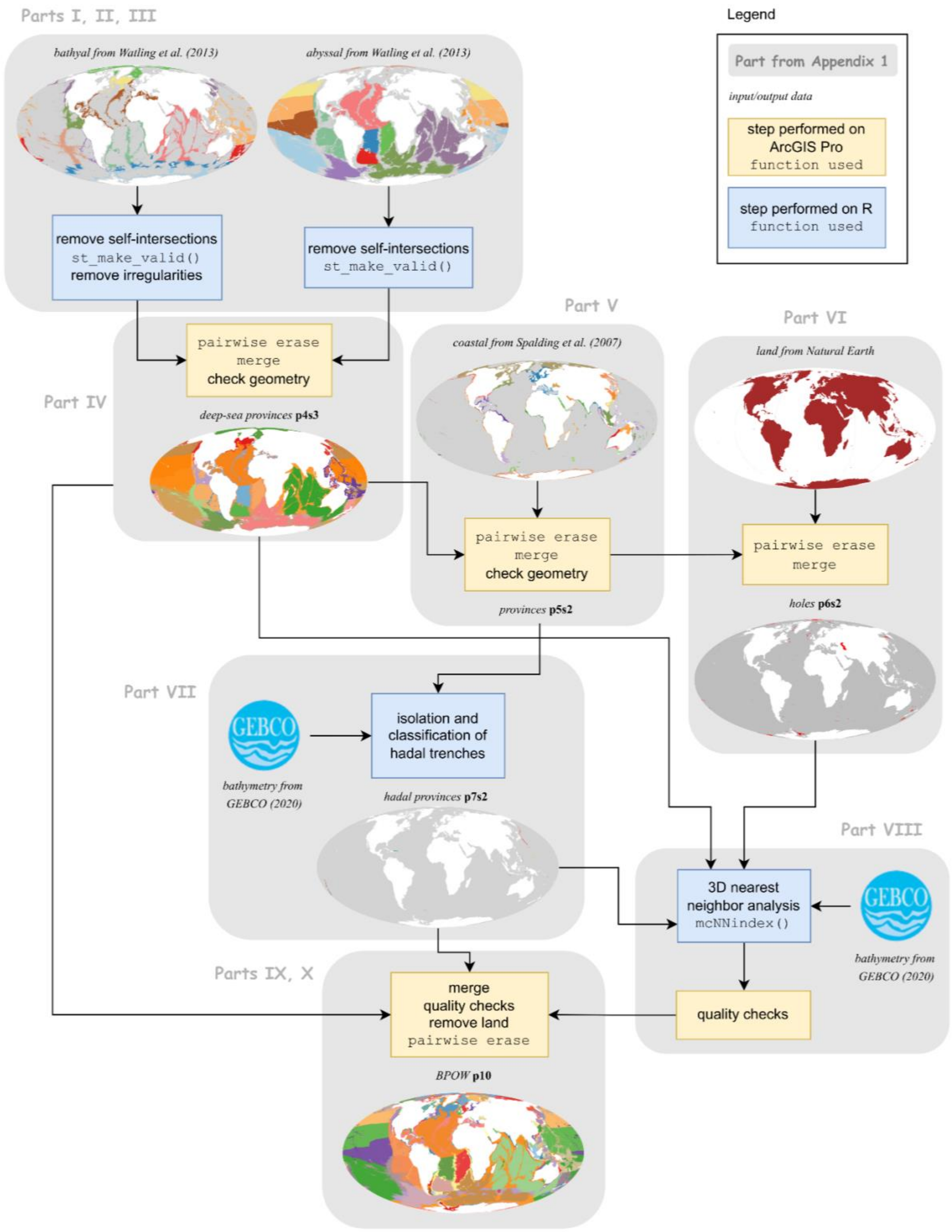


Figure 2. Illustration of the three-dimensional nearest neighbor analysis. The global map (top left) shows the holes layer generated during Part VI of Figure 1 (unclassified pixels are denoted in red) and identifies the three example unclassified sites (black boxes) on which the 3D distance is applied (Part VIII of Figure 1): (**A**) East American continental shelf between the Arctic coastal province and the Northern North Atlantic bathyal province. (**B**) Restricted uncharacterized zone around the Antarctic bathyal province. (**C**) Antarctic zone attributed to the Continental High Antarctic and the Antarctic bathyal provinces.

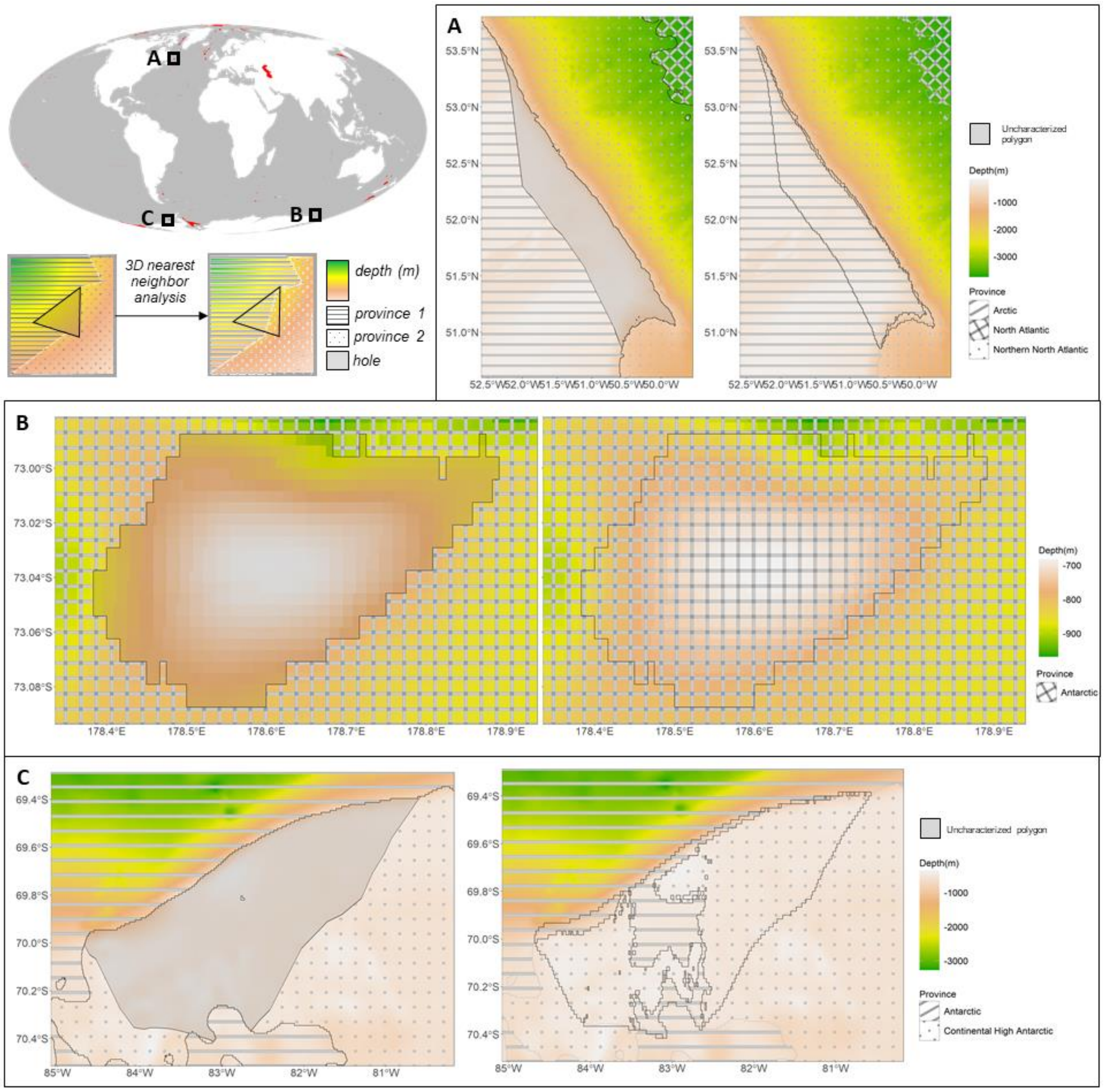
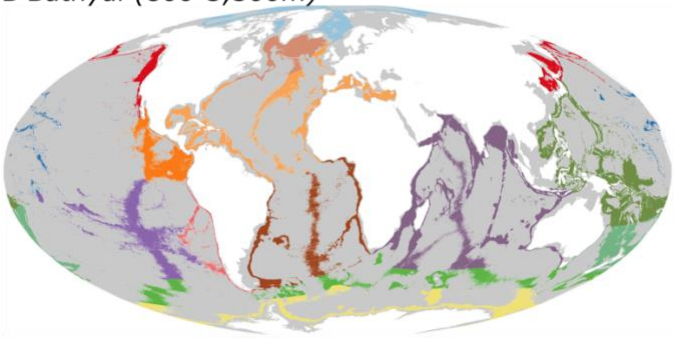


Figure 3. Map of the global biogeographic benthic layer divided by bathymetric type: (**A**) Coastal and upper bathyal provinces, (**B**) bathyal provinces, (**C**) abyssal provinces, and (**D**) hadal provinces. Each global map displays a distinct color scale according to the provinces, where land areas are white and gray areas are ocean areas belonging to one of the other three bathymetric types. Colors are reused between the four bathymetric types/panels, but there is no relation between similar colors across the four types/panels.

A *Coastal & upper bathyal (0-800m)*

B *Bathyal (800-3,500m)*



C *Abyssal (3,500-6,500m)*

D *Hadal (>6,500m)*

x. Data availability statement

The code developed to create the BPOW layer is available under an open access license. Analyses were performed on both R 4.0.3 and ArcGIS Pro 2.8.3. The R code and overall summary of the methods are available with the following GitHub repository and downloadable from Zenodo: https://github.com/AquaAuma/bpow (Maureaud et al. 2023). The ArcGIS Pro analytical steps and all calculations performed are detailed in the Appendix 1 supplementary file. Following the README.md file from the GitHub repository, users may follow steps performed on R and steps performed on ArcGIS Pro. Users may also visit the OSF project `bpow`, available at: https://osf.io/as6wn/

xi. References

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xii. Biosketch

Aurore A. Maureaud is a marine quantitative ecologist, conducting research on biogeography, biodiversity, and ecosystem functioning. Her research improves biodiversity synthesis of marine taxa by combining taxonomy, traits, spatial data, and expert knowledge. She is integrating benthic biogeography in marine conservation under global change. Her synthesis research led her to develop new open databases, international consortia, and interdisciplinary efforts.

xiii. Contributions

conceptualization: A.A.M., G.R., K.I., K.W., W.J.; data collection and treatment: A.A.M., L.W., G.R., J.G.V.; methodology: A.A.M., G.R., K.I., K.W., J.G.V.; species analysis: A.A.M., K.I., K.W.; visualization: A.A.M.; supervision: W.J.; writing - original draft: A.A.M.; writing - review & editing: all.

xiv. Appendices

Appendix 1 | Methods file describing all data processing steps to create the GIS layer.
Appendix 2 | Classification of hadal provinces isolated from coastal ecoregions.

xv. Supplementary materials

Supplementary File 1 | ESRI shapefile layer BPOW